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THE EVOLUTIONARY HISTORY OF THE BIVALVIA

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INTRODUCTION

The earliest classifications of the Bivalvia, following that of Linnaeus (1758), were produced by conchologists, e.g., Cuvier (1800) and Lamarck (1801) and depended upon shell characters. Cox (1960) has reviewed the history of bivalve taxonomy. In the early part of the 20th century, Paul Pelseneer who had worked up the material for the Siboga and Challenger expeditions began a series of studies on the Bivalvia which resulted in the production of a system of classification based on internal anatomy, notably the ctenidia (Pelseneer, 1906). C.M. Yonge was to use the Pelseneerian system with great effect to provide a firm understanding of bivalve anatomy, typically at the superfamily level, that would illustrate their diversity. In this understanding, Yonge was influenced by the meticulous researches of W.G. Ridewood (1903) and D. Atkins (1936-1938) on gill structure and J.L. Kellogg (1915), also on the mechanisms of bivalve feeding. Yonge's teaching produced a generation of malacologists, some of whom, e.g., E.R. Trueman and G. Owen, were, through early work on ligament structure (Owen *et al.*, 1953) and, in the latter case, also on ctenidium structure, to influence his perception of the adaptive radiations of the constituent orders of the class. Contributing to this understanding were the meticulous researches of C.R. Stasek on the ctenidial-labial palp junction (Stasek, 1963) and of R.D. Purchon on bivalve stomach structure (Purchon, 1987a). C.M. Yonge reviewed the Bivalvia for the *Encyclopaedia Britannica* (Yonge, 1974) but never set out a system of classification, as he saw it. This was left to N.D. Newell (Newell, 1965) who, subsequently, for the *Treatise on Invertebrate Paleontology*, provided the basis for our present understanding of bivalve classification and which relied heavily on shell characters (Newell, 1969). A palaeontologist, Newell's view of morphologists was clear: "Studies of comparative anatomy of living species are of biologic interest and of course are essential for phylogenetic conclusions. They are only supplementary, however, and cannot provide needed evidence of the historical course of evolution" (Newell, 1969; p. 210). L.R. Cox (1960, p. 68) had earlier put the opposite view just as succinctly: "The soft anatomist has always belittled the study of the shell and considered that the palaeontologist should be commiserated with for being obliged to concentrate on this part of the mollusc." The shell continued to be looked at, however, albeit in other ways, i.e., its structure and mineralogy (Taylor *et al.*, 1969, 1973), to produce another view of bivalve diversification. A significant step which helped to bridge the gulf of understanding between palaeontologists and malacologists was taken in 1977, when the Malacological Society of London, through T.E. Thompson, and the Royal Society of London, through C.M. Yonge, organized a Symposium on the Evolutionary Systematics of the Bivalvia. At that meeting, predictably, most talk was of the shell but Purchon (1978) presented a short paper on an analysis, via numerical taxonomy, of bivalve classification. Some of his views were, however, coloured by the probability in many lineages of chance duplication of structure, mosaic evolution of character complexes, convergence and parallelism. Indeed, Seilacher (1984; p. 235) believes such phenomena "set a limit to the cladistic analysis within bivalve groups". The triangular heteromyarian shell form of the polyphyletic "Anisomyaria", for example, is a case in point. Morton (1992a) has shown that some 25 families of bivalves have evolved heteromyarian representatives. Purchon did, however, refine his work and published a much more comprehensive analysis of a suite of character states to give us a biologist's view of bivalve diversity (Purchon, 1987b). A similar biologist's view of bivalve classification was presented by Boss (1982). Most recently, Waller (1990) has effectively combined the evidences from palaeontologists and malacologists to give us a better understanding of bivalve classification and, thus, diversification.

In this paper, I will draw on the studies of the above authors and others to try and present a personal view of the evolution of the Bivalvia. I shall be focusing attention on the levels of order and superfamily, in true C.M. Yonge fashion. Notwithstanding, I will not be erecting a new classification of the Bivalvia, there already being enough of these. Rather, I am going to present a broader picture. First, I will re-evaluate our concept of the primitive bivalve; second, describe the radiations of the class; third, identify important morphological adaptations that have facilitated those radiations and fourth, identify key external factors that have influenced the evolution of the Bivalvia. Such adaptations and factors have worked upon a simple theme, to produce a richness of form that sometimes seems inexplicable. It is, however, both this simplicity of original form and multiplicity of subsequent manifestation that has fascinated palaeontologists and malacologists alike, albeit from different perspectives, and led to our modern understanding of bivalve evolution.

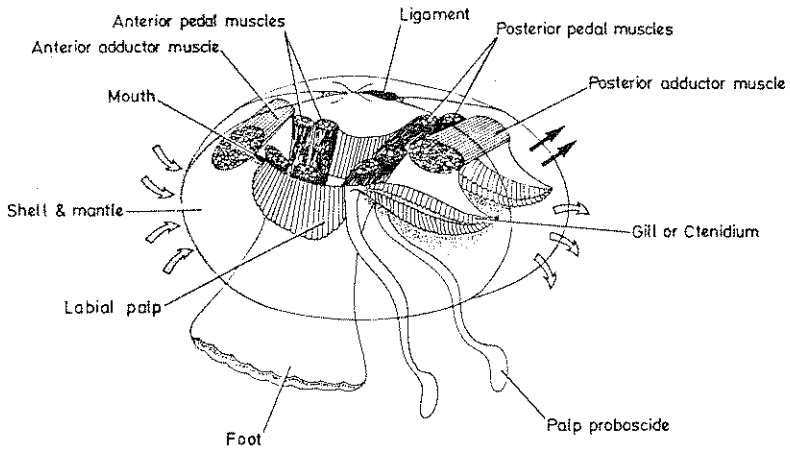

Figure 29.1. The hypothetical, primitive, bivalve as envisaged by Morton and Yonge (1964) and from which it is redrawn

THE PRIMITIVE BIVALVE

The malacologists' view of a hypothetical primitive bivalve was illustrated by Morton and Yonge (1964; fig.14) (Fig. 29.1).

This is a picture, essentially, of the protobranch *Nucula* (Yonge, 1939) and palaeontologists generally agree that such an animal is probably most akin to the primitive bivalve. It is widely accepted that the oldest known bivalve mollusc is *Fordilla troyensis* (Pojeta *et al.*, 1973; Pojeta and Runnegar, 1974) belonging to the Fordilloida. A second species is *F. sibirica* (Rozanov and Zhuravlev, 1992). Such animals arose in the early Cambrian and possessed a bi-valved shell, a simple, opisthodetic, external, ligament, bivalve-like pedal muscle insertions and well-developed adductor muscle insertions. There was no shell gape; when the adductors contracted, the valve margins closed tightly (Runnegar and Pojeta, 1974). *Fordilla* is regarded as the oldest known isofilibranch (Mytiloida) bivalve (Pojeta and Runnegar, 1985). A second Early Cambrian fossil, *Pojetaia runnegari*, from Australia, apparently possessed hinge teeth which *Fordilla* does not (Jell, 1980). The shell shape and internal morphology of *Pojetaia* indicate that it is the oldest known palaeotaxodont (Protobranchia) bivalve (Runnegar and Bentley, 1983). The Bivalvia are thus argued to have arisen from a helcionelloidan monoplacophoran via a rostroconch intermediary (Runnegar, 1978) and, by the Early Cambrian, to have already radiated into the ancestors of the Protobranchia (*Pojetaia*) and Autobranchia (*Fordilla*). While not disputing the significance of *Pojetaia* and *Fordilla*, Peel (1990) argues that the Rostroconchia and their helcionelloidean ancestors are unrelated to the ancestor of the Bivalvia which this author believes to be an exogastric tergomyan.

Pojeta and Runnegar (1976; fig. 12), provide us with four options for the arrangement of the water currents into and out of the mantle cavity of *Fordilla* (Fig. 29.2).

I have argued (Morton, 1992a) that Figure 29.2A most closely resembles what the primitive bivalve would be like in

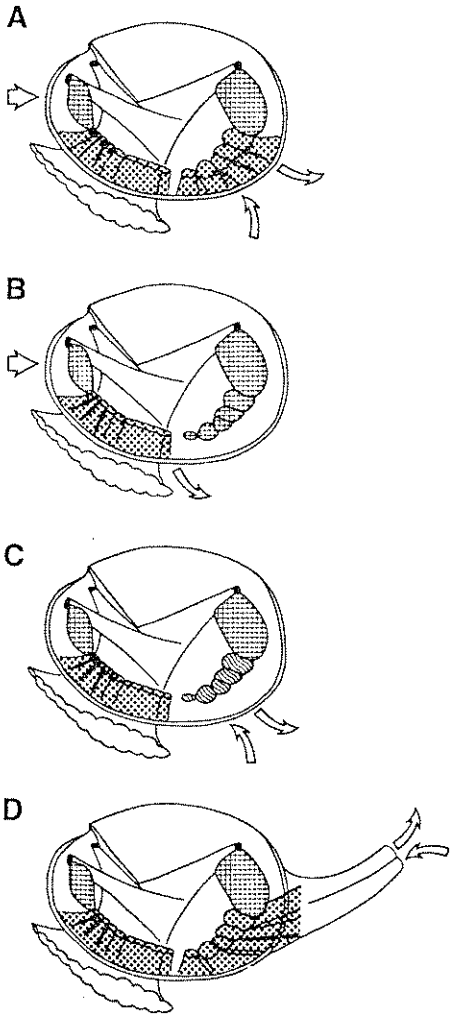

Figure 29.2. The primitive bivalve *Fordilla* with four suggested patterns of water circulation into and out of the mantle cavity. (After Pojeta & Runnegar, 1976).

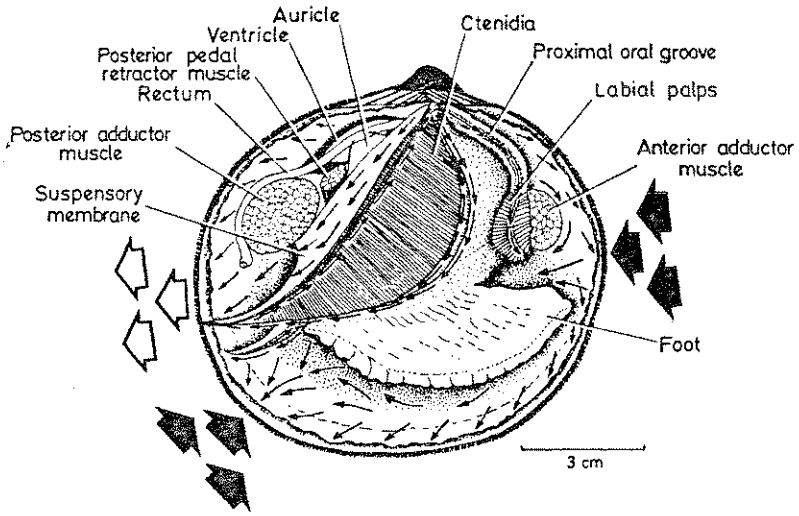

Figure 29.3. *Glycymeris glycymeris*. The ciliary currents of the mantle cavity and the areas of inhalant and exhalant flow, as seen from the right side.

terms of water circulation within the mantle cavity, i.e., entry at almost any point antero-and postero-ventrally and exit just below the posterior adductor muscle. As I will discuss, subsequent restriction of parts of this broad inhalant stream, notably by the foot, allows us to better understand how the bivalves have radiated. A second point with regard to the primitive bivalve is that it is typically portrayed as being oriented vertically, orthothetically, within the sediment, i.e., a burrowing creature, ventral margin down, again like *Nucula*. Atkins (1936-1938) thought that the life style exhibited by *Glycymeris glycymeris* represented a better picture of how the early bivalve might have behaved. Living partially buried in sublittoral deposits, *Glycymeris* is able to orient itself in a number of ways, although Atkins (1936-38) observed that it usually lies on its side, i.e., pleurothetically, with the posterior region pointed towards the sediment water interface but with an ability to bring into the mantle cavity potential food material at almost any point, although there are two major inhalant streams, anteriorly and posteriorly (Fig. 29.3).

Such a situation is fundamentally different from that of *Nucula* which, nevertheless, pumps water into the mantle cavity from a wide area, but mostly anteriorly. By confinement of the inhalant stream to the anterior, therefore, the modern *Nucula* may be a highly specialized, perpendicularly oriented and superficially burrowing, deposit-feeding bivalve. This is reflected in shell form, there being a subtle difference between that of *Glycymeris* and *Nucula* (Fig. 29.4B and C). In transverse section, the former is less, the latter more shouldered at the umbones. *Fordilla* (Fig. 29. 4A) is, in transverse shell form, more like that of *Glycymeris*.

Nucula feeds by means of palp proboscides, the posterior, protobranch, gills being respiratory. Notwithstanding, post-metamorphic *Nucula* feeds using its foot (Mortimer, 1962) and this author and Reid and Brand (1986) agree that the protobranch palps arose as primitive feeding structures and

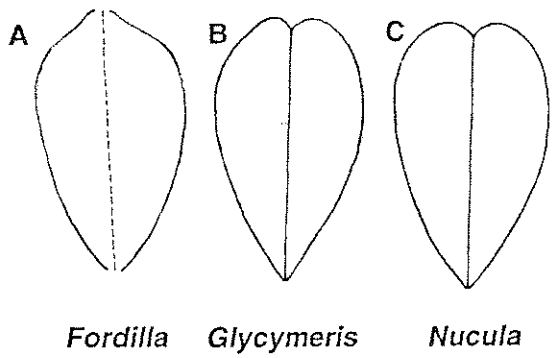

Figure 29.4. Sections through the shells of A, *Fordilla pojeteia*; B, *Nucula pusillus* and C, *Glycymeris striatularis*. (A after Runnegar and Pojeta, 1985; fig. 23).

that the elongation of the terminal pair of outer palp lamellar ridges as detritus-collecting palp proboscides was a later nuculoid specialisation. Reid *et al.* (1992) suggest that the *Nucula* juvenile, rather than the adult, should be considered as a model for the primitive bivalve. Indeed, the proto-palpal stage of *Nucula* has both anterior and posterior inhalant streams (Mortimer, 1962). I concur with the view of Reid *et al.* (1992) and it is probable, therefore, that the earliest bivalves, with inhalant streams like those of *Glycymeris*, were surface-dwelling animals which used the foot both to move and to feed, the gills functioning only in respiration (Fig. 29.5A).

The above argues that pedal feeding was the major method of obtaining nutrients in the primitive bivalve. If this is true, we should expect to see something of such a life-style in modern representatives of otherwise primitive lineages.

Representatives of the Arcoida have both anterior and posterior inhalant streams, but *Estellacar galactodes* lives deep within sediments (Oliver, 1990) and must feed by means of its foot (Fig. 29. 6 A). Cryptodonts, as representatives of an early protobranch radiation, e.g., *Solemya*, live deep within sediments, in U-shaped burrows, with two inhalant currents and a posterior exhalant one (Fig. 29.6B). Although early researchers thought they obtained nutrition from the breakdown of nutrients in the mantle cavity (Owen, 1961), it is now known that they possess symbiotic, chemoautotrophic, sulphide-oxidizing bacteria in the gills that aid in nutrient assimilation (Reid, 1990). This is especially true of gutless species (Reid, 1980). The Lucinoidea is a third ancient bivalve lineage, modern representatives of which live deep within sediments and feed using the foot. These have been reviewed by Allen (1958). In all lucinoids, there is connection

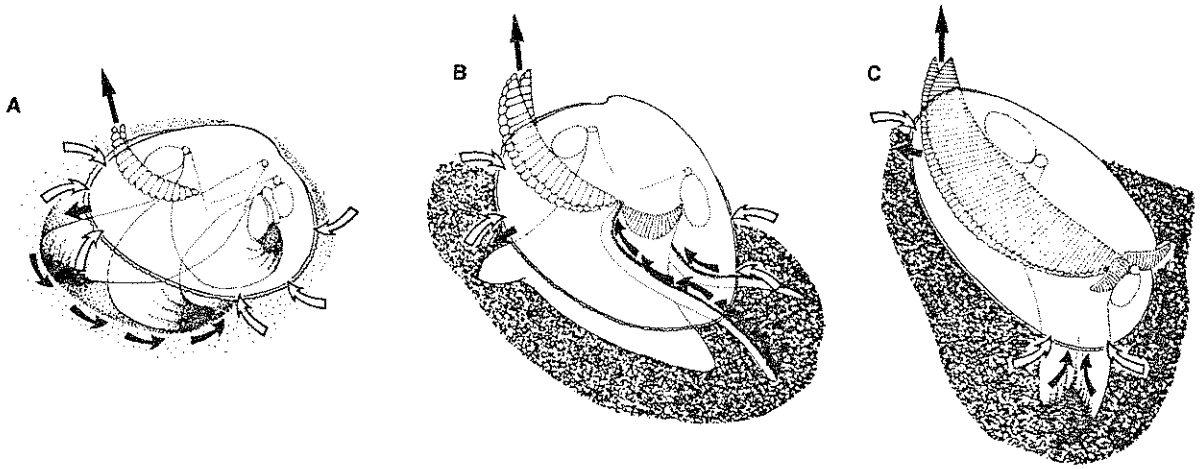

Figure 29.5. A.The hypothetical primitive bivalve, lying on its side on surface sediments, feeding using its foot; **B.**, the hypothetical primitive protobranch bivalve and **C.**, the hypothetical primitive autobranch bivalve. (Arrows indicate exhalant (solid) and inhalant (open) water currents).

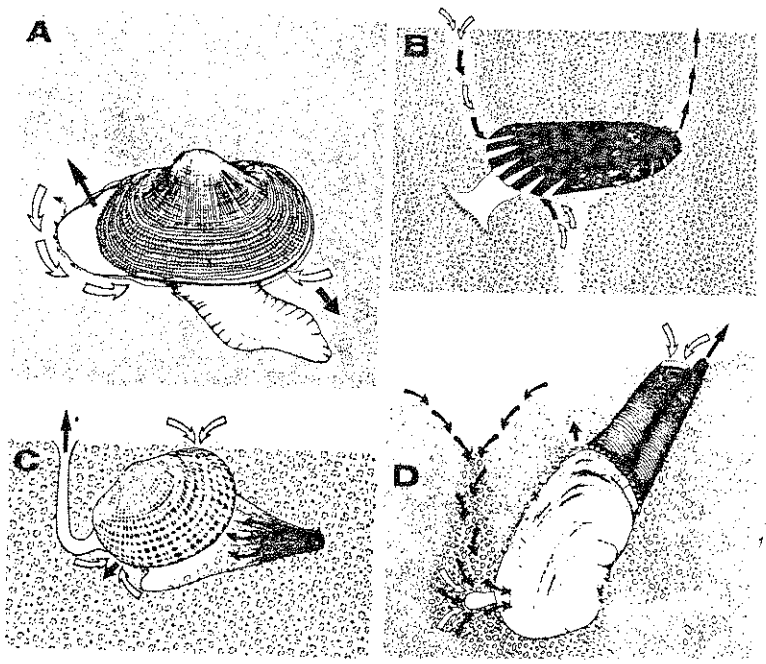

Figure 29.6. Modern representatives of ancient deep-burrowing lineages. **A.**, *Estellacar galactodes*; **B.**, *Solemya parkinsonii*; **C.**, *Fimbria fimbriata* and **D.**, *Pholadomya candida*. (A, after Oliver, 1990; B, after Owen, 1961 and Stanley, 1970; C, after Morton, 1979; D, after Morton, 1980a).

with the sediment surface via a posterior exhalant current, but there is also an anterior inhalant current and pseudofaeces are ejected from another, posterior, otherwise inhalant, aperture below the exhalant siphon. The foot can be highly modified for food collection, as in *Thyasira flexuosa* (Allen, 1958). Morton (1979) has shown how in the relatively much simpler *Fimbria fimbriata* (Fig. 29.6C), the large burrowing foot also collects particles of sand from beneath the sediment surface and which are removed from it by pallial 'palps' (there being only minute true labial palps) in the mantle cavity and passed to the mouth. It is possibly further significant, however, that many representatives of the Lucinoidea also possess sulphide-oxidizing bacteria in the ctenidia (Reid, 1990), which probably aid in nutrient assimilation as in *Solemya*. Finally, the Pholadomyoida are represented today by but a few living representatives, one of which is *Pholadomya candida* (Fig. 29.6D). In a detailed study of this bivalve, Morton (1980a) suggested that it lives obliquely within the sediment and feeds via the pedal gape using the foot as a piston, sucking in sediment. There are even special pedal gape muscles to facilitate this. Dr. P. Hodges (pers. comm.) has provided further evidence that the Jurassic fossil, *Pholadomya glabra*, fed in this way. From these examples of living representatives of what are regarded as early bivalves, it would appear that pedal feeding within sediments, utilizing an anterior inhalant stream, was the earliest autobranch life style adopted.

I thus believe that the earliest bivalve was a small, surface-dwelling animal that moved and fed on surface deposits using its foot, such material being transferred to the mouth by fleshy outgrowths of its lateral lips (Fig. 29.5A). From such a prototype, the bivalves diverged into two major lineages; the Protobranchia, where feeding is upon surface deposits using labial palps and palp proboscides (Fig. 29.5B) and the Autobranchia, which adopted deep burrowing and eventually took up suspension feeding using the ctenidia although, initially, the anterior inhalant stream and the foot were the ways in which buried deposits were collected for nutrition, the posterior inhalant stream serving mostly for respiration (Fig. 29.5C). It is worth noting that, generally, the Protobranchia are anteriorly elongate whereas, the Autobranchia are posteriorly so, in broad sympathy with the function of the gills in the mantle cavity and the entrances to that chamber.

THE PALAEOZOIC

From their modest early beginnings, the Bivalvia radiated rapidly and widely so that by the Ordovician all subclasses were extant (Pojeta, 1978),with most autecological feeding categories identifiable (Skelton *et al.*, 1990). In addition to infaunal bivalves, e.g., representatives of the Babinkidae, Cycloconchidae, Anomalodesmata, Lyrodesmatidae and Nuculoida, the class also produced epifaunal species that were either byssally attached, e.g., the Ambonychiidae and Pterineidae (Pterioida), Cyrtodontidae (Arcoida), Modiomorphidae (Mytiloida), Megalodontidae (Veneroida) and Grammysidae (Pholadomyoida), or cemented to calcareous algae (Pseudomonotidae), also in shallow water. Epifaunal lineages seem to have arisen somewhat later than the burrowing ones, but almost certainly from them. The success of such epifaunal animals hinged upon the evolution of a byssus.

It is widely believed that the byssus is a larval character retained into adult life in only some lineages (Fig. 29.7), through the process of neoteny (de Beer, 1951) whereby somatic growth is retarded so that sexual maturity is achieved earlier in ontogeny.

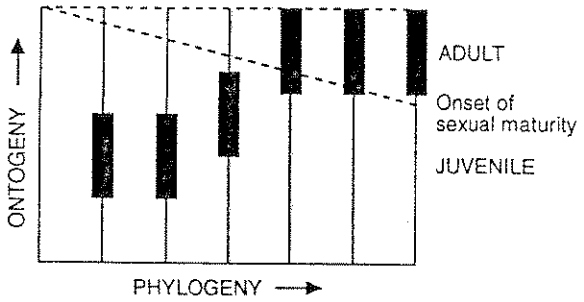

Figure 29.7. How retarded somatic growth can retain a larval character into adulthood. (After de Beer, 1951).

Representatives of the Protobranchia do not possess a byssus and its evolution has, therefore, had a profound effect upon the life style **only** of representatives of the Autobranchia where its occurrence as a larval and adult feature is widespread (Yonge, 1962). There seems to be two major types of byssus. The first, a long, unified, strip is seen in representatives of the Arcoida. It is not 'planted' as individual threads, as in other representatives of the Pteriomorphia, but is secreted into a long channel on the ventral surface of an otherwise horizontally aligned foot. The second type is a bunch of byssal threads arising from a common focus, but secreted individually from a gland in a much more mobile, plantar, foot. Such a byssus is also characteristic of representatives of other bivalve orders. The byssus seems to have evolved, as an anchoring device in the post-metamorphic juvenile, early in the history of the Autobranchia and to have been retained as an adult character on a number of separate occasions in different lineages.

In allowing exploitation of rocks and shells emergent from the surface sediment, the byssus opened up a new adaptive zone for the Bivalvia. But, importantly, it also meant that the foot could not now be used for feeding. The earliest representatives of the Pteriomorphia, gave rise to superficial burrowing forms, such as representatives of the Cyrtodontidae, with a ligament of a series of parallel longitudinal grooves and ridges. The same ligament is seen in

the Ambonychiidae, but it is in representatives of this latter family that we see the first evidence, in terms of the modioliform shell, of the presence of a byssus. Colonization of rocks, facilitated by the byssus, was adopted by a number of groups including representatives of the Arcoida, Pterioida and Mytiloida, notably the Modiomorphidae, which had a modioliform shell and were almost certainly attached to emergent stones and shells, e.g., *Modiolopsis* (Pojeta, 1971). Cemented bivalves, represented by the Pseudomonotidae, arose towards the end of the Palaeozoic (Harper, 1991). Cementation is another way of exploiting a hard surface and is facilitated by application of the periostracum of the attached valve to the substratum and secretion of a glue from the mantle.

Morton (1992a) has argued that although the byssus evolved as a larval character, its retention in the adult allowed such animals to anchor themselves into the sediment as a way of achieving stability in more dynamic sediments. An enlarged byssus and the modioliform shell must, therefore, have evolved **within** the sediments, i.e., as a structure facilitating an endobyssate life-style, prior to colonization of rocks to achieve the epibyssate life-style and mytiliform shell (Stanley, 1972). The endobyssate life-style essentially preadapts such bivalves for an epibyssate life style. Such a change in lifestyle and form has been described in general by Stanley (1972) and illustrated for the Mytiloidea and Dreissenoidea by Morton (1992a,b) but is illustrated here also for representatives of the Arcoida (Fig. 29.8).

From the primitive isomyarian ancestor, *Glycymeris*, lying on its side in sediments, species of *Anadara* evolved to burrow shallowly in soft muds. Byssally attached species of *Arca* are solitary and nestle under rocks. Species of *Barbatia* are solitary inhabitants of crevices and show a weak heteromyarian form. Species of *Philobrya* are acutely heteromyarian in shell form but have lost the anterior adductor muscle, i.e., they are monomyarian (Morton, 1978).

There is remarkable convergence in the evolution of the heteromyarian form. It is, for example, the case in all such bivalves, that only the anterior face of the shell is reduced and the posterior that is enlarged. Because of this, Purchon and Brown (1969) believed the Mesozoic Mytiloidea and the Caenozoic Dreissenoidea to be related. On anatomical grounds, this is clearly not so, but it does prove that such a heteromyarian (or, anisomyarian) form and, ultimately, the monomyarian form, arose in different lineages, independently, but always using the same blueprint. There are no anteriorly exaggerated autobranch heteromyarians, although a few protobranchs achieve this (Allen, 1985), but without reference to byssal attachment and, thus, for a different functional role. I have already noted the protobranch propensity for enlargement of the anterior face of the shell, as opposed to the posterior enlargement of the shell of the Autobranchia. The reasons for posterior enlargement, once again, relate to the inhalant ciliary currents of the mantle cavity. With water able to enter the mantle cavity at any point anteriorly, ventrally and posteriorly, the foot, initially used as an organ of feeding, created anterior and posterior streams (as discussed). With anterior shell reduction and confinement of the foot and byssus antero-ventrally, the inhalant stream became, ultimately, confined to the posterior. An understanding of the life style of modern heteromyarians thus gives us a picture of the life style of early ones. There is, however, one proviso to this. Early intermediate forms, with a modioliform shell and occupying the interface between sand and rock, could retain both inhalant streams. This is best seen in the modern Arcoida where in only a few, tiny, intertidal representatives, e.g., *Philobrya munita* (Morton, 1978), is the full heteromyarian form seen. Most, e.g., species of *Barbatia*, are modioliform with two inhalant streams, the anterior seemingly necessary for the efficient functioning of the ctenidial apparatus. Thus, modern epibyssate representatives of the Arcoida are solitary individuals and this must also have been the life style of the Cyrtodontidae in the Palaeozoic.

In contrast, representatives of the Pterioida and the Mytiloida and the lineages from which they were derived were, through extreme reduction of the anterior face of the shell and because of the evolution of a more efficient ctenidium for suspension feeding, able to enjoy the benefits of a single, posterior, inhalant stream, albeit still extensive along the postero-ventral margin. Such a simplified water-flow configuration, importantly, allowed the adoption of a gregarious life style, assisting cross-fertilization of broadcasted spawn, but also affording a greater degree of stability in the byssus-bound mass of individuals in both soft intertidal habitats and on more dynamic intertidal rocks. Pojeta (1971) illustrates Palaeozoic modiomorphids as living in clusters attached to rocks emergent from a soft sea bed. Today, byssus-bound masses of mytilids are a recurrent feature of exposed rocky shores world-wide. A similar life-style was to be seen to emerge again in Caenozoic estuaries and rivers by representatives in the Dreissenoidea (Morton, 1992b).

Other groups of Palaeozoic bivalves were cemented, for example, the Pseudomonotidae and Terquemiidae. Mesozoic oysters (Gryphaeidae and Ostreidae) and scallops (Pectinoidea) also have long, separate, histories back into the Palaeozoic (Newell and Boyd, 1978). Differences include cementation by the right valve in the scallops, but typically the left in the oysters. Gryphaeid oysters may have orginated from a scallop affiliate, the pseudomonotids during the Triassic (Newell and Boyd, 1978). Stenzel (1971) argues that the Gryphaeidae and Ostreidae have separate origins although Nicol (1984) suggests that the geologically younger Ostreidae was derived from the Gryphaeidae in the Middle Jurassic. Notwithstanding this debate, it is clear that both oysters and scallops evolved from byssate ancestors and, once again, reveal the significance of the early retention of the byssus into adult life and, thus, the importance of the foot. In the oysters, the foot is much reduced, lost in the adult, and byssal attachment is replaced by cementation. Scallops can be either byssally attached, cemented or free-living. Essentially,

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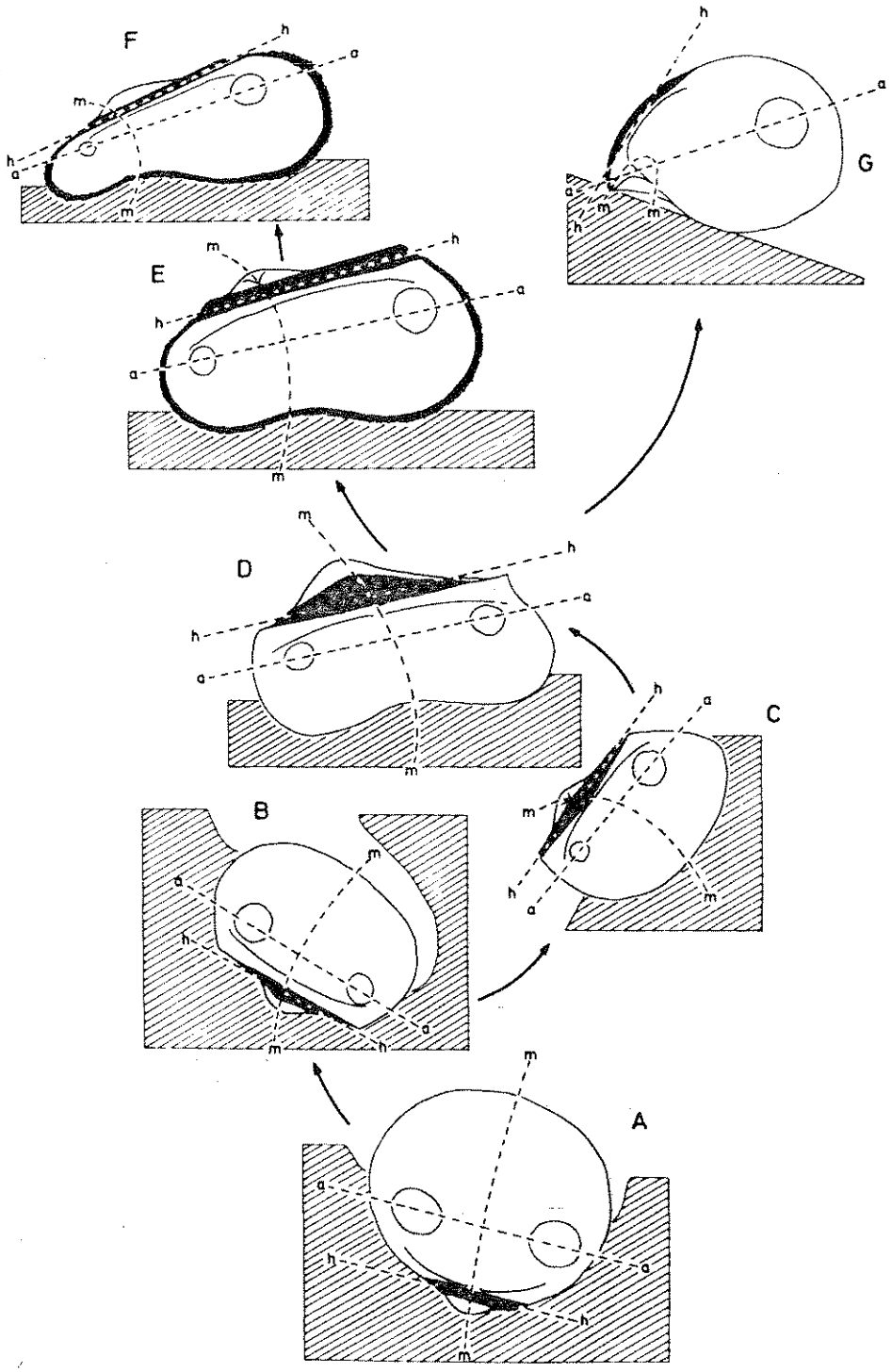

Figure 29.8. The changes in shell form necessary to obtain either a heteromyarian or a monomyarian bivalve from an isomyarian ancestor with reference to the Arcoida. A, *Glycymeris*; B, *Anadara*, C and D, *Arca*; E and F, *Barbatia* and G, *Philobrya*. (a-a, adductor muscle axis; h-h, hinge axis and m-m, mid dorso-ventral axis).

however, these two groups of bivalves have reverted to a horizontal (pleurothetic) life style reminiscent of their earliest ancestor, but suspension feeding using the ctenidium instead of deposit feeding using the foot. To achieve this, water currents enter the mantle cavity over a long valve margin, also as in the earliest bivalves, but this has been achieved secondarily by enormous enlargement of the posterior face of the shell as a result of the evolution of the monomyarian form with a centrally located posterior adductor muscle only (Yonge, 1953a).

Palaeontologists create phylogenetic links on the basis of the hinge teeth and ligament which, I agree, must be significant in that they are essential for the correct alignment and opening of the shell valves, respectively. Different morphological ways to achieve these functions have evolved independently in different lineages, for example the simple arched ligament and taxodont teeth of the Nuculoida, and the duplivincular ligament but also taxodont teeth of the Arcoida. It is also possible that internal muscle scars may tell us more about the life style of fossil bivalves, though movement of the foot for either burrowing or byssal attachment are essentially the same actions, requiring similar antagonistically-operating muscles. Byssal retractor muscles are, therefore, probably little more than pedal retractors. The posterior set of such muscles nevertheless achieve greater functional significance in pulling the animal down onto the rock surface instead of into it. Studies of such scars might, thus, be used, in the broad sense to identify life styles. Morris (1978) has, for example, suggested, on the basis of pedal muscle attachment scars of representatives of the Cycloconchidae, that the locomotory musculature was modified from a generalized to a more specialized state. We can similarly hypothesise that because of a similarity in shell form and muscle scar arrangements that heteromyarian modiomorphids and monomyarian ambonychiids probably functioned in a similar way to their modern mytiloid and pterioid counterparts.

Shell scars tell us something about the organization of the ctenidium which must have evolved from a posteriorly located respiratory gill. Originally, the bivalve gill was protobranch in configuration. When occupation of deeper, possibly anoxic, sediments was achieved, lateral enlargement of the gill towards the posterior would have improved respiratory efficiency in conjunction with the posterior inhalant stream to filter the overlying water column. There is some evidence for this. Morris (1978) has analyzed pedal and body scars in representatives of the Cycloconchidae. Such scars must occur above the top of the mantle cavity and since this is a variable feature in the Ordovician cycloconchs, later ones being larger, it is suggested that primitive protobranch gills may have been replaced by larger, more complicated ones. Oxygen-carrying blood pigments also improved respiratory efficiency. As significant occupiers of such habitats, the Arcoida are characterized by pigmented blood but, just as significantly, along with some other filibranchs, by ctenidial rejection currents, notably on the ventral margins of both demibranchs (Fig. 29.3). Enlarged ctenidia may thus have evolved, initially, for ventilating, respiratory, purposes and required ciliary currents not only to keep them clean, but also to cleanse the mantle cavity of unwanted sediment. Such material is expelled from the mantle cavity posteriorly, as pseudofaeces, through the combined action of ctenidial, visceral mass and pallial rejection tracts. Subsequently, and with further refinement of the ctenidium, the greater food potential of either inhaled suspended or deposited particles of fine organic detritus was realised and the ctenidium then assumed a more complicated role of selection, smaller particles being accepted and passed to the mouth and larger ones rejected, often by reference to different filaments on a plicated surface as, for example, in representatives of the Pectinoidea and Pinnidae.

By the end of the Palaeozoic, therefore, many of the features of modern bivalves were in place. From simple origins, 250 million years of adaptation had provided an array of form relating to function that we can recognise in today's bivalve fauna. In the Mesozoic, this array of animals was to radiate yet further and the stamp of modernity would be placed upon their descendants.

THE MESOZOIC

It is usual to think of the Mesozoic as a discrete period and one which commenced with a suite of bivalves already widely radiated, though depleted by the Permo-Triassic mass extinction. Some of these lineages, such as the shallow-burrowing Protobranchia, were in decline after their initial success, except in the deep sea (Allen, 1983), but the shallow-burrowing Arcoida were still highly evident in inshore waters. New lineages also arose and radiated, some to disappear quite quickly (Gould and Calloway, 1980).

In deeper sediments, the Lucinoidea, linked back to their primitive ancestor of the Palaeozoic, *Babinka* (McAlester, 1965, 1966), diversified, radiating into cold and warm waters, into clean tropical sands and mangrove and other vegetated muds. The colonization of the land by plants in the Silurian and their subsequent return to coastal environments provided nutrients that fertilized coastal waters creating sediments rich in organic detritus that amply suited the pedal-feeding Lucinoidea and Solemyoida. It is perhaps here also that an association between sulphide-oxidizing chemoautotrophic bacteria and representatives of these two superfamilies evolved as sediment and detritus pools enlarged to become progressively anoxic. Surface sediments also became widely occupied by representatives of the Trigonioidea, sometimes described as schizodont because of their serrated hinge dentition and thereby linked with the Palaeoheterodonta, i.e., the freshwater Unionoida. Notwithstanding their Palaeozoic origin, the Trigonioidea were and are, today, suspension feeders, burrowing shallowly in water depths no greater than 10-15m. Stanley (1978) suggests that the radiation of this

group of animals represents a post-Palaeozoic expansion of the bivalve adaptive zone. Mesozoic trigonioids were probably like representatives of the modern *Neotrigonia*, i.e., highly active animals, with a powerful leaping and reburrowing foot that is strongly reminiscent of representatives of the modern Cardiidae. Although the living remnant of this cockle-like expansion, *Neotrigonia*, is a modern animal (Stanley, 1978), in its morphology it has many "primitive" features, most notably the unfused mantle margins and a ctenidial ciliation that, if anything, recalls the situation in the Protobranchia, e.g., *Nuculana* (Atkins, 1938; Morton, 1987a). Morton (1987a) believes that the Trigonioidea share many features with the Pteriomorphia and, perhaps, thus represent a significant Mesozoic pteriomorph radiation into a burrowing mode of life. Trigonioids shared their habitats with pholadomyoids and inoceramids which were equally numerous in shallow seas. The Pholadomyoida radiated in Mesozoic seas into almost every bivalve-inhabitable zone. Unlike the Trigonioidea, which seemed to be specialized for occupation of coarse sands in shallow waters, representatives of the anomalodesmatan Pholadomyoida occupied almost every type of sediment in both shallow and deep waters. In the Cretaceous, the enigmatic, multivincular, Inoceramidae were, apparently, to be found world-wide in shallow seas (Crampton, 1988).

A peculiar feature of *Pholadomya candida*, a living remnant of the diverse Mesozoic Pholadomyoida, is the extent of pallial fusions and the formation of discrete, but fused, siphons (Morton, 1980a). We generally consider that pallial fusions are characteristic of modern bivalves — this resulting from a trend towards deeper and deeper occupation of sediments and with the commensurate need to keep sediment out of the mantle cavity. The significance of this contrasting view of the Pholadomyoida which, I believe, evolved as pedal feeders, suggests that pallial fusions, far from being a modern feature, occurred in many lineages of deeper burrowing bivalves, at various times. Notwithstanding their wide diversity in form and occupied habitats, the extant members of the Anomalodesmata are all recognisably united in the possession of an internally nacreous shell which, usually, lacks hinge teeth, suspension feeding ctenidia, extensive pallial fusions and, significantly, simultaneous hermaphroditism and short larval lives (Allen, 1961).

The Myoida (Hiatelloidea, Myoidea and Pholadoidea) are often linked to the Anomalodesmata and representatives of this order are deep burrowers in muds and shales (Myidae and Pholadidae), but have also explored the byssate nestling habit (Hiatellidae) and ultimately took up boring into rocks, corals and wood (Pholadidae; Teredinidae). In many ways, the Mesozoic adaptive radiation of the Anomalodesmata and their allies mirrors that of the Veneroida in the Caenozoic, creating much confusion. The Corbulidae have, for example, been traditionally placed in the Myoida, but Morton (1990a) believes that they may be more appropriately linked with the Veneroida.

Throughout the Mesozoic, the Pteriomorphia also radiated in shallow waters, albeit along a very different route from that of the Anomalodesmata, to produce an array of epibyssate colonisers of hard substrates. Many heteromyarian pterioids, such as the Myalinidae, Bakevelliidae and Inoceramidae became extinct by the end of the Mesozoic but the similarly anisomyarian Mytilidae survived, as did families of byssally-attached pteriomorphs (Pteriidae; Isognomonidae). Members of the Pinnidae and Malleidae are endobyssate colonizers of sediments and some mytilids also have such a life style, e.g., representatives of the Modioliinae. Hard substrata were also occupied by cemented scallops (Spondylidae and *Eopecten*), dimyids, rudists and plicatulids. Most rudists, however, attached to shell fragments as juveniles and from such foci became stabilized on soft substrata. The rudists further proliferated on carbonate platforms and shelf interiors, often forming dense associations, sometimes mistakenly referred to as 'reefs'. Ross and Skelton (1993) review the Cretaceous rudist adaptive radiations.

In the deep sea, members of the Protobranchia, Arcoida and Propeamussidae also radiated widely. Representatives of them all are small, the nuculoid protobranchs pursuing a deposit feeding life style, the Arcoida a largely suspension feeding mode of life, e.g., the Limopsidae (Oliver and Allen, 1980a,b). Both of these groups of bivalves still retain two inhalant streams into the mantle cavity, e.g., *Bathyarca pectunculoides* (Morton, 1982a), and have long pallial and ctenidial extensions beyond the posterior valve margins. Such adaptations lift the food collecting organs above the fine silt of the ocean floor.

The most bizarre adaptive radiation in the Mesozoic deep sea was, however, undertaken by the Anomalodesmata (Morton, 1981a, 1985). This involves a group of animals which are often collectively referred to as the septibranchs and which some authors, e.g., Bernard (1979), separate from the Pholadomyoida. The three families, Verticordiidae, Poromyidae and Cuspidariidae, which constitute the 'Septibranchia', all contain representatives which are carnivorous. So too, however, are members of the pholadomyoid Parilimyidae, Morton (1982b) suggesting that the subclass does better comprise one order. Adaptations to a carnivorous mode of life include a raptorial inhalant siphon that can be extended by the pumping of blood into it from blood sinuses, typically in the mantle, using pressures engendered, in the Poromyidae and Cuspidariidae, by a muscular septum that is the remnant of a highly modified ctenidium with pallial extensions. The labial palps in representatives of these families are also raptorial, extending back into the mantle cavity to grasp captured prey and stuff it into the mouth, e.g., *Poromya* (Morton, 1981c). The digestive system is highly modified for digestion of large prey items (Reid and Reid, 1974; Morton, 1981a). Colonization of the deep sea is one facet of the Mesozoic radiation of the Bivalvia. Here, the extraordinary evolution of the 'Septibranchia' as predators, is in neat counterpoint with what was happening in inshore

waters, as will be discussed.Surprisingly, however, the trend seen towards carnivory in the 'septibranchs' was matched by a similar trend in the Propeamussidae (Pectinoidea). Morton and Thurston (1989) have shown that species of *Propeamussium* suck small epibenthic plankers into their mantle cavity and consume them, the palps, mouth and alimentary canal being modified for this. Prey capture, does not, however, involve the ctenidia but, rather, a flexible upper right shell valve margin which, by closely adpressing with the left, creates a negative pressure inside the mantle cavity so that when the valves gape, prey are sucked in with the inflowing water. Waller (1971) suggests that the Propeamussidae are, in fact, more primitive than their shallow-water relatives. This is, in part, evidenced by their shell microstructure. More interesting, however, is that the non-nacreous flexible shell margin of *Propeamussium* is also a feature of many other inshore Pterioida, e.g., *Pteria* and *Isognomon* (Harper and Morton, 1994), and is probably thus a feature of the stem group, and which evolved, initially, as an anti-predation device. A further group with flexible shell margins, but of both valves, is the Pinnidae (Yonge, 1953b). Another, unique, anti-predation device seen in the Pinnidae is the pallial organ which secretes sulphuric acid (Liang and Morton, 1989). Such anti-predation devices are thought to have evolved in the Mesozoic, perhaps earlier, as defences in an arms race between bivalves and a whole suite of co-evolving predators, notably extra-orally feeding asteroids, crustaceans and proboscis-armed neogastropods (Vermeij, 1977, 1987). This author has termed this the 'Mesozoic Marine Revolution' which, essentially, laid the stamp of modernity upon the global inshore marine fauna. The Asteroidea, for example, are an ancient group with representatives recognizable in the Lower Palaeozoic. Extra-oral feeding was, however, an early Mesozoic innovation (Blake, 1981; Gale, 1987) that allowed representatives of this class to become voracious predators of, for example, bivalves. Skelton *et al.* (1990) have argued that the appearance of such a feeding method, in concert with appearance of other predatory groups, notably the Neogastropoda, was of critical importance in the evolution of the bivalves during the Mesozoic.

The effects of this predator 'revolution' were powerfully felt by the Bivalvia, Stanley (1977,1986), for example, believing that it drove infaunal species into a deeper and faster-burrowing mode of life. It was responsible for the evolution of anti-predator devices in boring bivalves and for stimulating members of the Lithophagiinae (Mytilidae) to adopt a symbiotic relationship with living corals (Morton, 1990b). It has been argued that it was also responsible for the evolution of cementation in Mesozoic bivalves (Harper, 1991) and the development of anti-predator shell devices, such as spines and projecting lamellae in a wide suite of bivalves (Morton, 1990b; Harper, 1991). One cannot help but be impressed by how important the bivalves were and are, today, a source of food for a wide range of, for example, gastropod, crab and fish predators (Vermeij, 1983). Virtually world wide, portunid crabs, in particular, crack open intertidal cockles (Sanchez-Salazar *et al.*, 1987a,b), mussels (Elner, 1978), scallops (Elner and Jamieson, 1979) and oysters (Elner and Lavoie, 1983) while the gastropod predators of bivalves include representatives of the mesogastropod Naticidae and Cymatiidae and, amongst the Neogastropoda, representatives of the Muricidae, Buccinidae and Melongenidae all of which either drill, crack or prise open their sedentary prey (Carriker, 1981). Indeed, bivalve drilling is recognized as a predation strategy which evolved specifically in the late Mesozoic (early Cretaceous) and was geared to accessing such passive and numerous bivalve prey (Taylor, 1981). Taylor *et al.*, (1983) have identified assemblages of bivalve-drilling predatory naticid and muricid gastropods from the Albian of the Mesozoic.

THE CAENOZOIC

Two hundred million years ago, the Atlantic Ocean did not exist. Present day continents were united in the single, large, supercontinent of Pangaea. The northern half of Pangaea was Laurasia, consisting of the present day North America, Europe and Asia, while the southern half was Gondwana, i.e., South America, Africa, India, Antarctica and Australasia. A major incursion into the otherwise single land mass was made by the large wedge-shaped Tethys Ocean separating the eastern half of Laurasia from the eastern half of Gondwana. The surrounding ocean, Panthalassa, was the precursor of the modern Pacific.

During the Mesozoic, Pangaea began to break up into fragments so that by 100 million years ago, the southern Atlantic Ocean was formed. The northern Atlantic took longer to form, i.e., by 65 million years ago. Notwithstanding, by the Caenozoic, therefore, the break-up of Pangaea to form our modern pattern of continents and oceans and their circulation system(s) was virtually complete (Scotese *et al.*, 1988). Newly formed, more extensive, expanses of continental margins were widely separated, facilitating speciation through geographic and climatic isolation. The Bivalvia, as with many other components of the global shallow marine biota, now occupied many realms and provincialism increased. We can see this today in representatives of ancient lineages such as the Trigonioidea restricted to southern Australia but also in comparatively modern families, such as the Tridacnidae restricted to Pacific corals reefs from their Tethyan crucible. Freshwaters too were affected. The Corbiculidae, once cosmopolitan in northern temperate streams and lakes, were restricted to Asia. Similarly, the unionoid Hyriidae is a Gondwana relict, now restricted to Australasia and South America. Crame (1993) has argued that the bipolar distributions of inoceramid, buchiid and oxytomid bivalves in the late Jurassic can be explained by the distintegration of Pangaea and the opening up of tropical seaways.

The full selective force of the Mesozoic Revolution in predation could now come into play upon the shallow marine communities that were being provoked into speciation through isolation. Taylor (1970) has identified assemblages of bivalve-drilling predatory gastropods in the Eocene of the Caenozoic. In concert, the two forces of isolation and predation have shaped the form and habits of modern bivalves. Thus, for example, a possible ancestor of modern lithophagines, *Corallidomus,* appeared in the Palaeozoic boring rugose and tabulate corals as well as poriferan stromatoporoids (Pojeta and Palmer, 1976); the Mesozoic saw its descendants boring deeply into dead corals. Caenozoic scleractinian reefs were, however, occupied by living coral borers that have a profound intimacy with their host(s) (Morton, 1990b) which is often species-specific, e.g., *Fungiacava* which bores only *Fungia* (Goreau *et al.*, 1969). Many bivalve lineages have taken up residence within living corals, including representatives of the Pholadoidea, with remarkable adaptations to shell form and internal anatomy, e.g., the spherical *Jouannetia* (Morton, 1986). Modern anomalodesmatans, such as *Clavagella,* also bore calcareous rocks and corals, as do representatives of the Gastrochaenoidea. Representatives of the Clavagelloidea also colonized soft sediments, albeit in a wholly different way from their burrowing cousins, the Heterodonta. Both the strange watering pot shell *Brechites* (Morton, 1984), and the gastrochaenoid *Eufistulana* (Morton, 1983), secrete an adventitious tube for protection, albeit in different ways and to a different design. Both of these animals can be considered specialist inhabitants of soft deposits but their close relatives are borers and *Brechites,* with its peculiar pumping at the 'watering pot' (actually the pedal gape), is reminiscent of its pholadomyoid ancestor.

Soft, nutrient-rich, sediments on continental margins are thus the seat of modern bivalve diversity and such habitats, despite representation in them from the Arcoida, Pholadomyoida and endobyssate Mytiloida are, overwhelmingly, dominated by representatives of the Heterodonta, notably the Veneroida. Either shallowly burrowing with globular shells, strongly ribbed, e.g., the Cardiidae, or burrowing deeply, with smooth, blade-like, shells, e.g., the Solenoidea and Tellinoidea, such bivalves are a unifying feature of shallow infaunal habitats, virtually world wide. Except for the razor shells (Solenoidea), however, shell form is surprisingly standardized: even the highly active Donacidae, exclusive occupiers of dynamic beach sands, are clearly recognisable as heterodonts. The same holds for the Lucinoidea. Clearly of heterodont affinity, representatives of this superfamily have radiated widely in the Caenozoic (Reid and Brand, 1986), but to occupy oxygen-deficient habitats and with a virtually common dependency upon chemoautotrophic bacteria for nutrition.

We generally only think of the Mytilidae as being dominant occupiers of exposed rocky coasts, especially species of *Mytilus* in temperate waters. They do so, also, in the tropics, albeit with different genera, e.g., *Septifer*. The reality is, however, that the Mytilidae are a highly diverse family in an equally diverse order, the Mytiloida, and show an adaptive radiation that is not often appreciated. For example, on Hong Kong shores, endobyssate mytilids, such as *Musculista senhausia* can be just as gregarious on soft flats as *Septifer virgatus* is on exposed rocky coasts and lithophagine coral borers are, by far, the most diverse group, in terms of species. Shell form is highly conservative in the Mytilidae and this is just as clearly seen in another pteriomorph group, the Pectinoidea, the ubiquitous scallops. Although some are byssally attached in crevices, e.g., *Chlamys,* and living corals, e.g., *Pedum*, many other scallops are free-living on the sea bed. Some, such as *Placopecten* and *Amusium*, have become proficient swimmers (Morton, 1980b) and it is in these animals that we see a return to the surface-dwelling, pleurothetic, mode of life on sediments which is reminiscent of their oldest ancestor; a shallowly equivalve animal with the mantle margin open from anterior to posterior. Scallops are monomyarians and the wide opening allows better water circulation for respiration on the sea bed. The scallop foot is, however, small; that of the primitive bivalve was, almost certainly, large. In all their variety, the Pteriomorphia have retained an intimacy with the substrate surface, probably because of the lack of pallial fusions and, thus, of siphons. This is in sharp contrast to the Heterodonta which have, oppositely, gone underground. These two orders thus, effectively, apportion the modern bivalve adaptive zone, whereas representatives of other, phylogenetically older, lineages occur in more specialized and, thus, narrower niches. This is best seen in the Anomalodesmata, a group with ancient origins but which has radiated in the Caenozoic into burrowing (Laternulidae), cemented (Cleidothaeridae; Myochamidae) and byssally attached (Lyonsiidae) modes of life but, significantly, always in highly specialized habitats facilitated by simultaneous hermaphroditism, self fertilization and a short larval life (Morton, 1985).

THE MODERN WORLD

Sea level has fluctuated widely over the Phanerozoic but during the Pleistocene, as polar ice sheets expanded and retreated, levels rose and fell with amplitudes of over 150 m for a period of 2 million years. Sea temperature also, therefore, oscillated. During the last interglacial period, some 125,000 years ago, sea levels were globally as much as 10 m higher than present. During the following glaciation, sea levels have fluctuated by a maximum of some –150 m at about 18,000 years ago. The sea has, however, been at its present level for between 2000 - 3000 years (Scoffin and Dixon, 1983). Although deep water assemblages of bivalves have been relatively unaffected by such changes, this is not true of their shallow water relatives which have experienced dramatic variations in habitat. The most obvious is the

emergence and submergence of the shore and continental shelf. Haq *et al.* (1987) have shown that after a sea level rise, terrigenous sediments are trapped on the inner shelf, starving the outer shelf and slope. Conversely, after a marked fall in sea level sediments are flushed from the inner to the outer slope. The implications of such changes upon infaunal, either suspension or deposit-feeding, bivalves are all too clear. Similarly, modern coral reefs have recently started anew around lands that were prominent at the time of the most recent rise in sea level. When flooded, continental shelves and inland seas, the seat of bivalve evolution, provide new areas for speciation, but, conversely, drying of the same areas would cause extinction. Our modern inshore bivalve biota must, therefore, be considered to be relatively youthful, i.e., Caenozoic.

Today, the Bivalvia comprises some forty one superfamilies, one hundred families, and approximately 8,000 species (Fig. 29.9).

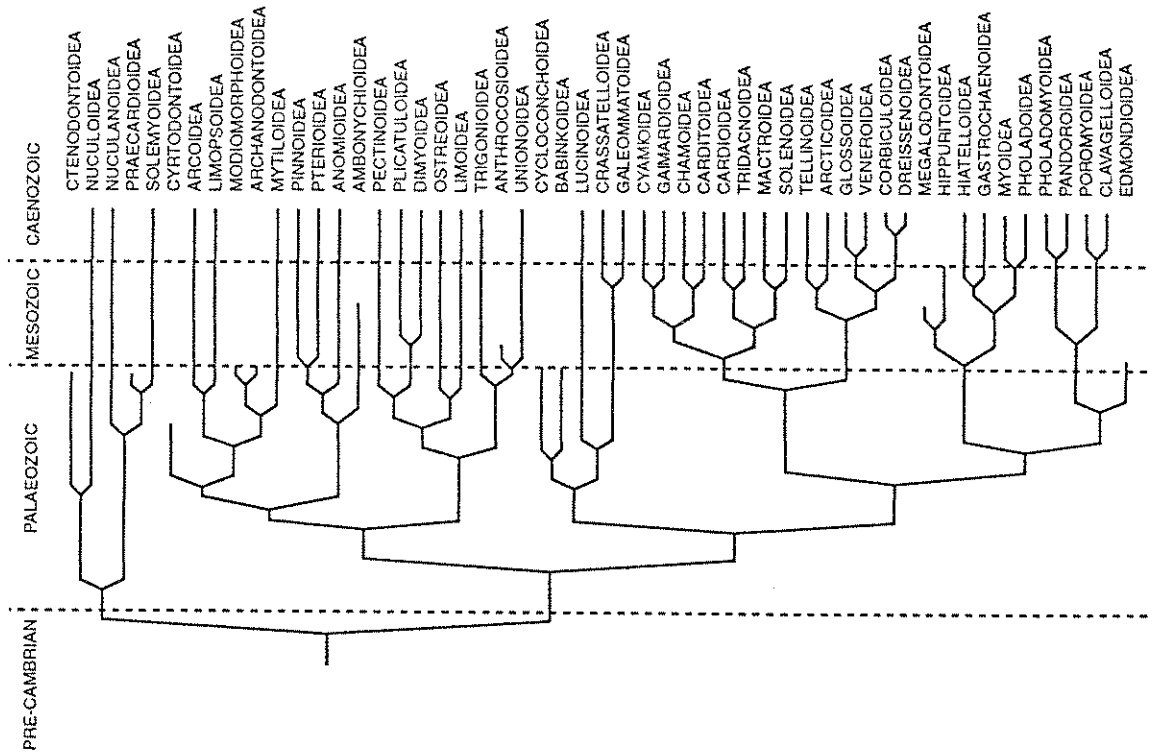

Figure 29.9. A proposed evolutionary tree for the Bivalvia

Every aquatic benthic habitat is occupied by their representatives and they possess a bewildering array of adaptations to a wide range of feeding styles — albeit based upon a simple underlying blueprint. Bivalves make poor swimmers, the most proficient being *Amusium pleuronectes* (Morton, 1980b). Nevertheless, the bivalve veliger larva has, in a sense, allowed them to, albeit temporarily, occupy the pelagic zone.

Today also, the Bivalvia are ecologically important and although I have pointed out (Morton, 1992c) that there appears to be a declining academic interest in them, they are the subject of a growing body of research in relation to their economic potential. I do not intend to review the economically important clams, mussels, cockles, oysters and scallops. There is a vast literature on these already and there can be very few people alive who are not aware of them. The bivalve, immobile and pre-packaged inside its closed valves, is an almost perfect mariculture candidate. Unfortunately, such animals are, through their feeding habits, susceptible to pollution but then, again, make ideal monitors of environmental decay.

I do, however, wish to draw attention to the expanding success of the Bivalvia. The successful introduction into and invasion of North America and now South America and Europe by *Corbicula fluminea* from Asia (Britton and Morton, 1982), the trans-Atlantic introduction of *Dreissena polymorpha* from Europe to North America (Carlton, 1992a), the introduction of *Musculista senhausia* into Australia from

Asia (Willan, 1987), that of *Mytilopsis sallei* into the Pacific from the Caribbean (Morton, 1987b), that of *Potamocorbula amurensis* into North America, similarly from Asia (Carlton *et al.*, 1990), and, most recently, in 1991, of *Limnoperna fortunei* into Argentina from Asia (Pastorino *et al.*, 1993) are facts which attest to the success of the bivalve form in the modern world.

There are two important conclusions to be reached from the above observations. First, the bivalves concerned are all members of either the Pteriomorphia or the Heterodonta. Carlton (1992b), for example, has analysed the bivalves which have been introduced into North America. Of the 24 species which have become 'established' in coastal, estuarine and freshwater systems, seven are members of the Pteriomorphia, eleven are members of the Heterodonta and five belong to the Myoida (but mostly represented by the pelagic Teredinidae) leaving *Potamocorbula amurensis* of debated affiliation (Morton, 1990a). Man's activities are assisting in the success of important representatives of these two orders. Second, it is significant that representatives of other bivalve orders are not involved and indeed there must be concern that as man impacts, most adversely, the most globally sensitive marine and freshwater habitats, so our specialist bivalves from earlier eras will disappear. The "living fossil", *Pholadomya candida* has not been found for many years (Morton, 1980a) and museum curators may never see again, in modern collections, the giant watering pot shells (Clavagellidae) of earlier ones. Conservation efforts must focus on these bivalves. The broad success of the Pteriomorphia and Heterodonta in the Caenozoic is being fuelled today by man: future diversification by the Bivalvia will be for their descendants to fulfil.

DRIVING FORCES IN BIVALVE EVOLUTION

Palaeontologists and zoologists have, from the foregoing, established a firm understanding of the diversification of the Bivalvia through time. Minor disputes with regard to such a pattern of evolution can always be found and often relate to misunderstandings that deeper researches resolve. Yonge (1967), for example, believed the rudists to be related to the Chamoidea, Purchon and Brown (1969) thought the Mytilidae and the Dreissenidae to be related. We now believe, however, that the rudists were a Jurassic radiation by megalodontids into the cemented mode of life whereas chamids evolved in the late Cretaceous, probably from a carditid ancester (Kennedy *et al.*, 1970). Similarly, the Mytilidae arose in the Mesozoic as heteromyarian colonizers of rocks in the sea, the Dreissenidae as heteromyarian colonisers of rocks in estuarine and freshwater systems in the Caenozoic. The rudists and chamids are cemented, the mytilids and dreissenids, byssally attached. Convergent evolution has driven the two into the same body form, i.e., that which is best suited for either a cemented or a byssally attached mode of life, albeit with differences reflected in shell structure (but not form) and anatomy. I thus began this paper with an agreeably appropriate quote from Newell (1969), but end up by disagreeing with him. The shell is not necessarily the only way to differentiate phylogenies and an understanding of anatomy can provide clues equally as valuable in separating lineages and is certainly more important in distinguishing between autecological categories.

I have described the Bivalvia as, mostly, sedentary occupiers of sand, mud and rock in shallow marine habitats. It is, however, also clear that predation is a significant driving force in the natural selection of new lineages through increasing levels of specialization. I have, hitherto, considered the role of predation in the Mesozoic as a significant factor influencing the evolution and adaptive radiations of the bivalves. Perhaps the same was true of the Palaeozoic. Conway Morris (1986) has analyzed the community structure of the Burgess Shale (Middle Cambrian) fossil assemblage and has shown that 10% of all individuals and 20% of all genera were carnivores and that these were mostly arthropods but with simple feeding modes, i.e., whole ingestion and crushing. The Palaeozoic had an ecological pyramid which was very much like today, with more numerous deposit and suspension feeders providing the food of predators. There probably was, thus, a good reason why a tiny, surface dwelling, deposit feeding, primitive bivalve was subject to selection pressures that quickly drove it underground.

The concept is then, throughout time, of an 'arms race' between predator and prey as each evolves, through natural selection, more specialist ways of either attacking prey or of defending itself, respectively. Such an interaction is, however, unlikely to result in the extinction of the prey, there being a natural balance, through population regulation, between the two essentially coexisting groups of species. Indeed, Stanley (1973) has traced the rates of evolution of the Bivalvia at the family and generic levels and has shown that they have diversified progressively. Such diversification has accelerated with time and, moreover, is matched by that of their significant predators, i.e., the Neogastropoda (Taylor, 1981). The significance of predation is that in its absence, speciation through hybridization would produce a world of generalist uniformity: its power, acting through natural selection, results in innovation and novelty.

Predation can be looked upon as a positive force in evolution. It has given us the wide array of highly specialised bivalves that we see today. Some attempt to 'escape' predation by either burrowing or swimming but others have evolved elaborate shell defences to 'resist' attack. There is, however, a second abiotic force acting upon the evolutionary process and which results from mass extinctions, notably in the Ordovician, Devonian, Permian, Triassic and the Cretaceous (the 'big five'), although there may have been others occurring at intervals of approximatley 26 million years (Raup and Sepkoski, 1984; Sepkoski, 1990). Biogeographers distinguish between "mass" extinctions and

"background" extinctions, the latter acting for example, through the medium of a local perturbation, upon species with either narrow distributions or specialist life styles — the two often being synonymous. Vermeij (1989) considers, for example, that small extinctions may be caused by either cooling or by reductions in primary productivity. Sea level changes may also be significant in causing "background" extinctions (Jablonski and Flessa, 1984), but not "mass" ones.

Mass extinctions are, however, much more significant and can occur on the global scale, presumably through profound climatic and geological perturbations (Stanley, 1988a). Jablonski (1986a) considers that the five major mass extinctions which occurred over the past 600 million years have each significantly perturbated the Earth's biota, perhaps as much as 96% of existing species being felled within a geological instant. The Permo-Triassic event, for example, profoundly influenced the post Palaeozoic benthos (Gould and Calloway, 1980), including reef communities (Stanley, 1988b), while, following the post Cretaceous mass extinction, the reef building Scleractinia began to dominate tropical shallow marine environments (Rosen, 1977). Jablonski (1986b) generalizes that mass extinctions remove taxa that are, for example, endemic, large bodied and tropical. Large bodied animals tend to be stenotypic (La Barbera, 1986) and would thus also tend to be selected against at the time of mass extinctions.

Jablonski and Bottjer (1990) argue that the first appearances of new orders, as indicators of innovation, coincide with periods of less global diversity such as occurred at the onset of the early Palaeozoic metazoan radiation and in the wake of mass extinctions. Such innovations reflect ecological opportunity and their cause, i.e., the preceding mass extinction, must, therefore, play a major role in evolutionary processes (Jablonski, 1986a).

If we consider that predation, as a major driving force in the evolution of the Bivalvia, is important, and this seems to be increasingly agreed upon (Skelton *et al.*, 1990), then extinctions at both mass and background levels must also be important in providing the stimulus for new innovations. Hybridization, genetic drift and founding effects would facilitate re-population of vacated habitats but predation would drive, through natural selection, the subsequent diversification and specialist occupation of niches.

Jablonski and Valentine (1981) have argued that in families which occur at less than 1m depth, i.e., intertidal and shallow subtidal depths, species tend to be geologically older than those restricted to deeper waters. Apparently, shallow water species are less vulnerable to extinction by virtue of their broad biogeographic ranges and high dispersal capabilities, the latter mediated via a planktotrophic larva. They will, thus, be less not more susceptible to environmental fluctuations and, in the event of a local extinction, able to re-occupy depopulated niches quickly. Such a view is in contrast to the older view that the deep seas are less vulnerable to perturbations and are thus time stable which would make them havens for relict species. In the deep sea, the protobranchs, as representative of an ancient lineage, have survived and radiated widely (Allen, 1985). The deep water predatory Propeamussidae, a sister group to the stem group of the Pectinoidea (Waller, 1971), are of Mesozoic origin as are the predatory Anomalodesmata (Morton 1985). Morton (1982a) thought that *Bathyarca pectunculoides* was representative of the ancient Cyrtodontidae and Allen and Sanders (1969) believe the deep water monomyarian solemyid *Nucinella serrei* to be a living actinodont. There thus seems to be the possibility of radiation into the deep seas by Palaeozoic deposit and suspension feeding bivalves and Mesozoic colonization by specialist predators. Whereas one can see that the Anomalodesmata radiated into the deep sea from shallower water ancestors, the opposite seems to be true of the Propeamussidae (Waller, 1971). The deep sea may thus be a habitat for some relict species and groups but not others. Knudsen (1970), for example, estimates that of 20 abyssal families of bivalves, eight originated in the Palaeozoic, seven in the Mesozoic and five in the Caenozoic. Another feature of deep sea bivalves, notably representatives of the Anomalodesmata and Propeamussidae, is the high incidence of hermaphroditism, ctenidial brooding and direct development of the fertilized egg, with an appropriately short larval life. Knudsen (1967) showed that of 32 species of abyssal bivalves examined by him, 20 had lecithotrophic development and a short larval life. Deep sea bivalves also have very wide distributions, sometimes encompassing different oceans (Knudsen, 1970). Knudsen (1970) believes that a great part of the abyssal bivalve fauna is Recent, descent into it from from shallower waters probably having occurred throughout geological time. Notwithstanding, I find it hard to understand how such bivalves will be more prone to mass and background extinctions: rather they would appear to be largely immune to such events and have evolved, in this habitat, extreme morphological and reproductive strategies to become specialists. No bivalves are more 'specialized' than the deep sea predatory Anomalodesmata and Propeamussidae. I do, however, agree that inshore bivalves, notably representatives of the Pteriomorphia, but more especially the Heterodonta, can have wide geographic ranges but, again more importantly, are dioecious broadcast spawners which produce large numbers of planktotrophic larvae. Such generalists in terms, broadly, of byssate pteriomorphs and burrowing heterodonts, could, I agree, more readily re-occupy perturbated inshore habitats and would thus be favoured following a background extinction event. This would be in sharp contrast to, for example, the highly specialized inshore representatives of the hermaphroditic Anomalodesmata with direct development and very short larval lives, e.g., one day in *Pandora inaequivalvis* (Allen, 1961) and two days in *Entodesma cuneata* (Campos and Ramorino, 1981), and the commensal Galeommatidae with extraordinary reproductive strategies, including dwarf males, e.g., *Chlamydoconcha* (Morton, 1981b), and ctenidial brooding to produce crawl-away juveniles.

Morton (1991) has suggested for a range of Hong Kong bivalves occupying a broad spectrum of habitats from freshwater to marine, that the life history traits and sexual strategies of each species equip them for occupation of their niche. This seems like stating the obvious. Nevertheless, putting together such information with that of Jablonski and his co-workers it is clear that larval traits which foster broader geographic ranges would further foster longer species durations and lower extinction rates. Jablonski (1986c) also considers that a planktotrophic trait would lower speciation rates.

Larval strategies are thus as important as adult morphological traits in ensuring success and whereas the adult is susceptible to both predation pressure and background extinctions, the larva facilitates species survival via an ability to repopulate either predated out or perturbated habitats. It thus seems that the planktotrophic larvae of the majority of shallow water bivalves occupying 'generalist' habitats, facilitate their survival, just as direct development and a short larval life enhances 'specialist' success in the more environmentally constant, broad, habitat of the deep sea and in highly narrow niches in shallow waters.

Scoffin and Dixon (1983) suggested that during the Caenozoic, latitudinal changes in temperature began to operate on a world-wide basis so that, for example, coral reefs became restricted in the Pliocene to between latitudes 35° North and South. During the Pleistocene, as polar ice sheets expanded and retreated, sea levels rose and fell with amplitudes of over 150 m for a period of two million years. Rosen (1984) suggests that modern corals have evolved over the last 25 million years and that, therefore, modern reefs and their associated biota are comparatively youthful. Valentine (1984) proposes a "species diversity pump" model in which during warming and cooling periods, the tropical zone has successively broadened and contracted. During such fluctuations, adaptive zones would be vacated and reoccupied consecutively (Jablonski and Bottjer 1990), providing a major stimulus to natural selection. The concept of polar stability and tropical diversification because of the former's youth and the latter's age thus has to be modified because during periods of cooling and warming, stenothermal species would be continually added to tropical systems, enriching them. Although generalist eurythermal species could survive such temperature fluctuations, niches vacated by more specialist stenothermal species would be, again, re-occupied by more generalist species, so that a recurrent addition to the potential for specialization in such environments was realised. A planktotrophic larva would, again, facilitate such re-occupations of vacated habitats.

It is, however, interesting that in each age, bivalves of similar form have evolved to occupy similar habitats. Similar habitats in different ages provoke similar adaptations, anatomies and behaviours. Thus, heteromyarian modiomorphids dominated rocks in the Palaeozoic, mytilids in the Mesozoic and mytilids and dreissenids in the Caenozoic, the two groups today apportioning the freshwater, estuarine, marine continuum. The cemented form has arisen independently on different occasions in the Palaeozoic (Pseudomonotidae, Terquemiidae), in the Mesozoic (Plicatulidae, Ostreidae and Gryphaeidae, Dimyidae, rudists, Chamidae, Spondylidae, some pectinids and, in freshwaters, the Etheriidae) and in the Caenozoic (Myochamidae, Cleidothaeridae and some pectinids, e.g., *Hinnites*).

It is convenient to look upon bivalves as autecological clades, occupying habitat via life-styles, e.g., burrowing deposit and suspension feeders, borers, cemented suspension feeders and byssally attached suspension feeders. Even predators. Skelton *et al.* (1990) have analyzed the bivalve fauna through time and separated it into such autocological categories. They recognise ten groupings and show that for nine of them there has been little overall change in relative frequency with time. The exception is a category defined as the exposed byssate, either endo or epibyssate, suspension feeders, e.g., the Mytilidae. Here there seems to have been a decline in familial diversity. This has been related, notably in the Mesozoic, to the susceptibility of such animals to predation (Harper, 1991), since such prey is both available in large numbers and can be manipulated. Cemented bivalves are, conversely, less susceptible to manipulation and, therefore, have a selective advantage. It is perhaps significant that the Mesozoic saw the greatest radiation in cemented taxa and a decline in byssally attached lineages as a result of the Mesozoic Revolution in predation. It was only in the mid-Cretaceous that the evolution of drilling notably by the Neogastropoda impacted cemented species. Harper and Skelton (1993) have, for example, demonstrated, experimentally, that cementation offers no protection against boring neogastropods although the evolution of spines by, for example, spondylids may represent a means to counter the attacks of muricids.

Throughout the evolution of the bivalves, therefore, different extant lineages have radiated into the various habitats made available by extinction and, driven by predation, have responded to such pressures to evolve similar forms. The burrowing Pholadomyoida, in their external anatomy of long siphons and fused mantle margins are highly reminiscent of modern heterodonts. Cemented oysters resemble cemented chamids and, in freshwater, etheriids; byssally-attached mytilids resemble dreissenids because invasion of such a habitat can only be accomplished by such a form. The evolutionary history of the Bivalvia is, therefore, because of functional and constructional constraints, characterized by inevitability.

DISCUSSION

The gills, (or ctenidia) and labial palps are not the first organs to be developed in the ontogeny of a bivalve. Long before the gill filaments form, the foot is already well-developed and in *Nucula* is used to collect food for the settled juvenile

(Mortimer, 1962). It is my view that bivalves first appeared with such a feeding habit. Today, some bivalves still feed in this way and, moreover, there are numerous records of modern bivalves stuffing food into the mouth using the foot, e.g., *Dreissena polymorpha* (Morton 1969), and this is the only way that the predatory *Propeamussium lucidum* can feed (Morton and Thurston, 1989). The primitive bivalve gill which, by consensus, is best represented by *Nucula*, was respiratory in function and confined to the posterior region of the mantle cavity.

Feeding using palps and palp proboscides was probably, therefore, not a feature of the early bivalve but was developed by the Protobranchia, the representatives of which radiated, notably into deeper waters, to become deposit feeders, although the cryptodont Solemyoida have evolved an intimate association with symbiotic chemoautotrophic bacteria in the gill such that the gut is either much reduced or lost (Reid, 1990).

A second bivalve lineage, the Autobranchia, evolved, however, and probably quickly from the prototype ancestor in which the posterior gill moved progressively laterally and became enlarged both antero-posteriorly and dorso-ventrally. Connection with the palps became more intimate, palp proboscoides were not developed, and a different method of collecting food particles was potentially available for future refinement into a ctenidium. Modern relicts from the early adaptive radiation of the Autobranchia, however, suggest that this option was not taken up quickly: most live in deeper sediments, and use the foot and anterior inhalant stream to feed. Probably, therefore, such gills arose as a consequence of the need for better respiratory efficiency in animals immured in sediments with no proficient connection with the surface water above, e.g., *Estellacar galactodes* (Oliver, 1990).

Such gills may, indeed, have evolved, again as in the Arcoida, to help clean the mantle cavity of unwanted sediments, i.e., they initially had a cleansing function. Such a situation is still seen in some filibranch bivalves, e.g., the anomiid *Enigmonia* (Morton, 1976a), where the dorsal food grooves transport food to the mouth but the ventral marginal grooves of the ctenidia are rejectory. Ultimately, the nutritional value of collecting fine, organic, particles of suspended or surface-deposited food using the gills, as opposed to large, inorganic particles within the sediment, albeit coated with absorbed nutrients, was realised and the modern bivalve ctenidium was selected for. At first, such a structure also had to fulfil a sorting function, in that, in such a transition, it was still necessary to cleanse the mantle cavity. Such a situation is also still seen today in many Pteriomorphia where different filaments on the plicate ctenidia fulfil different roles, e.g, the Pectinoidea. Finally, however, the modern, exclusively food-collecting, ctenidium, typical of, for example, the modern Heterodonta and the majority of the Pteriomorphia was formed. In order for such a gill to function most efficiently, however, sediment has to be kept out of the mantle cavity, i.e., the energetically expensive cost of rejecting unwanted material had to be kept to a minimum, and this was achieved by fusion of the left and right mantle margins and the creation of posterior siphons, inhalant and exhalant, of differing degrees of complexity (Yonge, 1982), both in terms of levels of fusion and elaboration of the orifices.

A number of points are worthwhile mentioning: pallial fusions are not characteristic only of Caenozoic burrowing heterodonts, but are also characteristic of, for example, the older Pholadomyoida and Lucinoida. In *Pholadomya*, moreover, water flow was not tested by inhalant tentacles on the siphon tips, but by an opisthopodium on the visceral mass (Morton, 1980a) with a unique connection to the pedal ganglia. An opisthopodium is also seen in a few other bivalves, e.g., the predatory *Halicardia* (Nakazima, 1967). Also in numerous bivalves, but notably representatives of the Pholadomyoida, and Mactridae, e.g., *Lutraria* (Heterodonta) (Yonge, 1948), there is a fourth pallial aperture from which, primitively, pseudofaeces were expelled into the sediment, as in *Fimbria fimbriata* (Morton, 1979). Modern bivalves expel pseudofaeces from out of the inhalant siphon. It is still, nevertheless, the case that some modern burrowing species have retained an ability to collect food from within the sediment, e.g., *Polymesoda erosa* (Morton, 1976b) (Fig. 29.10), in a way highly reminiscent of their oldest ancestors.

Modern researchers focus on a burrowing bivalve's relationships with the water above it; we largely continue to ignore their just as great intimacy with the substrate they live in.

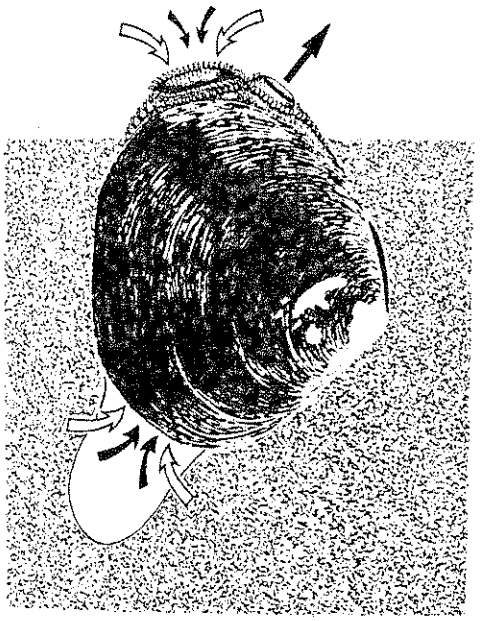

Figure 29.10. *Polymesoda erosa* buried in mangrove mud with inhalant currents (open arrows) and potential sources of food (closed arrows). The exhalant current is also shown. (After Morton, 1976b).

The fact that many modern descendants of Palaeozoic bivalves do burrow deeply is also significant in another way. If, as generally believed, Mesozoic bivalves were driven underground as a result of selection forces engendered by the evolution of new groups of predators, perhaps the same was true of Palaeozoic bivalves, as the work of Conway Morris (1986) would suggest.

If such were the case, then the course of bivalve evolution has been dominated by the selection pressure of predation in the Palaeozoic (Conway Morris, 1986), the Mesozoic (Vermeij, 1977), Caenozoic (Taylor, 1970) and still today (Vermeij, 1980; Sanchez-Salazar *et al.*, 1987a,b). Predation has driven the Bivalvia into continual refinement and increasing specialization. Many bivalves, at all times, have retained their intimate contact with the sediment on which they were born, but some have exploited the unoccupied adaptive zone of rocks emergent from the sea of, at first, inorganic sand and, later, organic mud. This has been achieved, importantly, by utilization of the byssus for attachment. The byssus, a uniquely bivalve character, evolved initially as a character that facilitated the stability of the metamorphosing larva on shifting sediments. It must, originally, have been a transitory structure useful only until such stability was achieved and pedal locomotion and feeding commenced. Yonge (1962) argued that the adult byssus was a result of neoteny, or paedomorphosis. Such juvenile arrestment creates adaptability, it opens up new niches for exploration and it simplifies the body blueprint allowing natural selection to explore new avenues of evolution.

Such a structure, the byssus, evolved initially for secure attachment, did one other thing, however: it forced such bivalves to cease pedal feeding. With one stoke, new food collecting mechanisms had to explored, giving a stimulus to the evolution of the filtering ctenidium from the respiratory gill.

Morton (1992a) has pointed out that the heteromyarian form has evolved on numerous occasions and, thus, that neoteny must have repeatedly returned lineages to the basic bivalve larval blueprint for reworking. Virtually all bivalve lineages, save the Protobranchia, have heteromyarian representatives and it is clear, therefore, that neoteny has acted upon them all, at different times, to refresh the adaptive capability of each. Neoteny, therefore, seems to be a recurrent feature of the Bivalvia. I have also always been fascinated by the concept of neoteny and how it might operate in the Bivalvia to explain their success. The ontogenetic 'depth' to which neoteny operates is probably highly variable and may not always be back to the larval level, as often visualised. Rather, evolutionary innovation probably proceeds from smaller, simpler and more 'generalized' representatives of an ancestral group, i.e., those species with the least amount of phylogenetic constraint.

In Figure 29.11, I synthesise the above ideas to suggest how the evolution of the Bivalvia has proceeded and to explain what we see today, in our modern diverse suite of families and species. I take as a basic plan a typical picture of adaptive radiations down through the ages with specialists arising from primitive, generalist, stocks — the whole process being driven by predation, possibly severe at some times, less so at others to create a complex array of species occupying a wide variety of habitats.

Mass extinctions here visualized, for simplicity of explanation, as occurring at the end of each era act upon the existing stock of bivalves, but especially the specialists (both larva and adult) to leave vacated ground open, eventually, for a new phase of adaptive radiation that, importantly, however, once again, has to arise from a more primitive, generalist, surviving stock. Thus, a few remnants from the end of the Palaeozoic mass extinction may survive to enter the Mesozoic. New Mesozoic radiations therefore arise from a simpler, generalist, blueprint. The same probably occurred in the Caenozoic at the end of the Mesozoic, following the post-Cretaceous extinction, i.e., modern bivalves are derived from a Caenozoic radiation, but with remnants of the Mesozoic radiation present, e.g., the Pholodomyoidea and Trigonioidea. There may even be remnants of a Palaeozoic radiation, for example the solemyid, *Nucinella* (Allen and Sanders, 1969). Although a mass extinction would be impartial in choosing its victims, i.e., species of all sizes, trophic clades and taxonomic groups would be vulnerable, it is clear that 'rare' specialists would be the most susceptible (Terborgh and Winter, 1980). By extinctions acting most forcefully upon the specialists, therefore, a reversion to a simpler, basic, blueprint, through neoteny, is achieved to facilitate new radiations. The significance of extinction in evolution is, thus, to reduce biodiversity so that habitat, both geographic and ecological, is made reavailable for innovative reoccupation by surviving remnants. Sepkoski (1981) analyzed the entire Phanerozoic marine fossil record and identified three great evolutionary faunas: a Cambrian trilobite-dominated fauna, a late Palaeozoic brachiopod-dominated fauna and a Mesozoic and Caenozoic mollusc-dominated, 'modern', fauna. The last fauna, in particular, arose following the Permo-Triassic mass extinction but it is interesting that Sepkoski (1981, fig. 5) suggests that surviving remnants of earlier faunas carry over to the next. Our 'modern' fauna is thus, precisely that, but it does possess survivors of its earlier radiations and extinctions.

Background levels of extinction are probably not significant in our modern concept of the evolution of the Bivalvia. I believe, for example, that throughout time 'generalist' bivalves would reoccupy quickly habitats vacated by a local extinction and, moreover, could radiate just as quickly to exploit all its niches. Patterns of predation and extinction may be different in the deep sea and in intertidal and shallow water environments. Predation levels and extinction rates are generally regarded as being lower in the deep sea, while predation and extinctions, both 'background' and 'mass', are probably more significant in shallow waters. Thus, positive (biotic) and negative (abiotic) forces driving the adaptive radiation of the Bivalvia are more powerfully felt

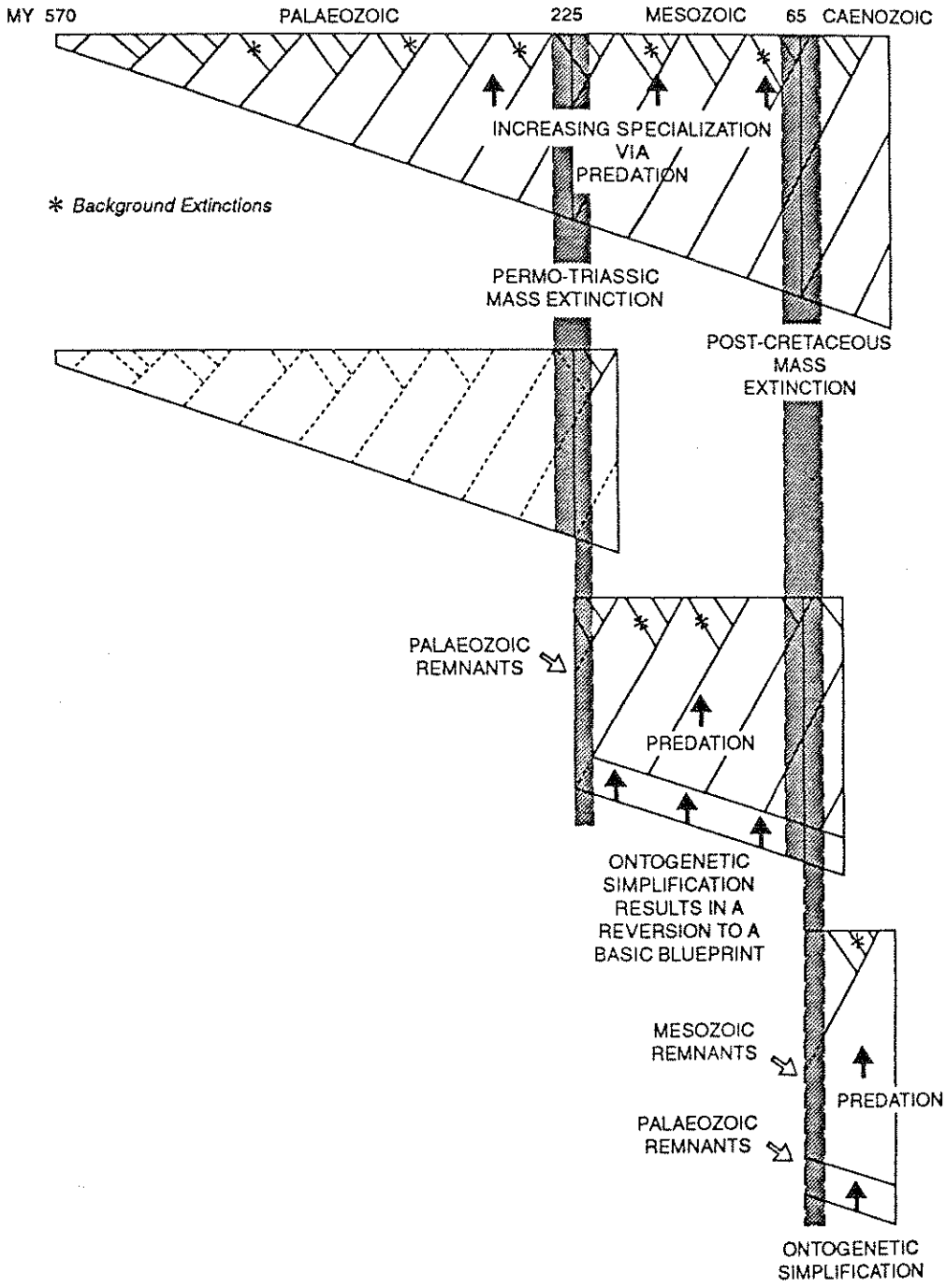

Figure 29.11. The evolutionary history of the Bivalvia showing how predation drives such readily available prey into greater degrees of specialization and how background extinctions will reduce diversity randomly over time. Mass extinctions, however, act most detrimentally upon specialists to leave vacated habitats available to the few surviving generalists which, by virtue of their simpler body plan, represent a return to a basic, blueprint, i.e., through neoteny, and have the potential for the evolution of new morphological novelties following recovery from the extinction event.

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in shallow waters and periodic radiations into the deep sea, as suggested by Knudsen (1970), perhaps fostered by more dramatic events in shallow waters, are altogether more conservative with the notable exception of the predatory 'septibranchs' and Propeamussidae.

From a relatively simple Pre-Cambrian, bivalved, pedal-feeding ancestor, the Bivalvia have emerged today as a wonderful example of multiple adaptive radiations, their multiplicity of form and life-styles attesting to the success of the basic blueprint. Throughout history, they have, either immured in sediments or attached to rocks, been highly susceptible to mass and background levels of extinction. Bursts of speciation following such events have repeatedly allowed their successful recolonization of vacated habitat, usually from a neotenous generalist blueprint. Predation has, however, been the major driving force in their adaptive radiation, particularly in shallow waters. That they have in turn become predators in the deep sea and are thus themselves agents of natural selection is a nice twist in the story that provides a remarkable counterpoint to their humble origins.

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THE EARLY EVOLUTION OF THE BIVALVIA

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INTRODUCTION

Classification of the Bivalvia has proved contentious for well over a century, and new classifications at high taxonomic level are still produced regularly. But in a group of organisms, represented today by tens of thousands of species and with an excellent fossil record, why should taxonomy at higher levels cause such problems? The answer is readily available. On the one hand, zoologists have traditionally used structures of the soft parts, in particular the gill grade (e.g. Fischer, 1880-87; Pelseneer, 1889, 1891, 1906, 1911; Ridewood, 1903), the degree of fusion of the mantle margins (Linnaeus, 1758; Cuvier, 1797), or condition of the foot (Gray, 1821; Lankester, 1883), but also stomach type (Purchon, 1958, 1959), or labial palp development (Stasek, 1963), to draw up their higher level taxa. On the other hand, palaeontologists, deprived of knowledge of these structures, save in fossil forms closely related to extant taxa, have used characters of the shell such as dentition (e.g. Dall, 1889; Neumayr, 1883; Bernard, 1898), or shell structures which can indicate soft part anatomy such as muscle scars (e.g. Phillippi, 1853; Zittel, 1881-85) or ligament type, together with phylogenetic links indicated by the fossil record (e.g. Neumayr, 1891; Douvillé, 1913).

Palaeontologists have perhaps been more ready to accept some of the zoologists' classificatory criteria than zoologists have been ready to accept some of the phylogeny demonstrated in the fossil record. The *Treatise on Invertebrate Paleontology, Volume N, Mollusca 6, Bivalvia* (Cox *et al.* 1969-71) was a real attempt towards a harmonisation of the palaeontological with the zoological classifications. Further impetus into phylogenetic studies has been provided by a series of investigations of bivalve shell microstructure, initiated by two monographs by Taylor, Kennedy and Hall (1969, 1973), which have demonstrated its phylogenetic significance and hence its relevance to higher level taxonomy in the bivalves. The most significant work on bivalve shell microstructure in recent years is contained within a large monograph on shell biomineralization (Carter (ed.), 1990).

As a result of studies on Ordovician bivalves for the past quarter of a century, notably by Pojeta (eg. 1966, 1971, 1978, 1987, 1988) it is now firmly established that most bivalve subclasses were already in existence by the mid- to late Ordovician, but little has yet been suggested as to how these forms radiated. This is principally because earlier faunas are rare and poorly known; none of the fossils provides unaltered shell material and shell structure thus remains largely conjectural. From the early Ordovician Tremadoc Series probably some five species of bivalves are known from two localities in the world (Harrington, 1938; Babin, 1982). From the lower part of the succeeding Arenig Series, the number of described species is around twelve from two localities world-wide (Hicks, 1873 — revised Carter, 1971; Babin, 1982). These faunas show that the subclasses Palaeotaxodonta, Palaeoheterodonta and Pteriomorphia were by then in existence. Another early Arenig locality, shortly to be described (Cope, MS) has yielded a further twenty species including anomalodesmatans and solemyoids. Later in the Arenig, bivalves become more common, but it is not until the late Ordovician that bivalves are frequently found fossils. The lack of earlier faunas — there are major areas of the world where no early Ordovician faunas are known, as for example in Laurentia — means that the stratigraphical (and geographical) range of many forms is unknown, and as occurrences are so infrequent, there is the certainty that major new faunas have yet to be found and many of the gaps in the evolutionary story of Ordovician bivalves to be filled. At present it is clear that the known fossil record is so imperfect that even the relative timing of the appearance of some groups can only be guessed at.

The earliest bivalves come from the early Cambrian. The genus *Pojetaia* (Jell, 1980; Pojeta and Runnegar, 1985) from the early Cambrian of Australia, is an undoubted palaeotaxodont. Although now regarded by most authorities as a bivalve, the genus *Fordilla* Barrande, 1881 (Pojeta, 1978; Runnegar and Bentley, 1983) first described from North America and now also known from Europe (Pojeta, 1974) and Siberia (Jermak, 1986), is of less certain subclass assignation. Pojeta (1978) decided on the basis of shell shape that it was an isofilibranch. But in a class of organisms where shell shape is an adaptation to mode of life, and frequently has little taxonomic significance, it appears hazardous to relate any form to a subclass purely on this basis. Further, the assignment to the Isofilibranchia necessarily means that the filibranch gill grade had already evolved by early Cambrian times, unless one is prepared to accept that the feeding gill evolved more than once. These arguments seem to present real obstacles to accepting Pojeta's (1978) placing of *Fordilla*. In a later paper, Runnegar and Pojeta (1992) describe similar replicated shell microstructures in both *Pojetaia* and *Fordilla* and on this basis reunited the two genera in the Fordillidae.

arranged in a straight line and consist of a series of taxodont-like teeth which are fused at their bases into a single long tooth (this type of dentition was referred to as pseudotaxodont by Babin, 1966). These two series overlap substantially sub-umbonally in a manner identical to that of *Cardiolaria*. Although *Glyptarca* has an elongated shape, the similarity of the dentition to that of *Cardiolaria* is quite remarkable, particularly in displaying the overlap of the anterior and posterior dentitions in the sub-umbonal region. This overlap appears to be an exceptionally rare feature of bivalve dentition and, at the moment appears restricted to *Cardiolaria* and *Glyptarca*. The fact that both these genera occur in the early to mid- Ordovician suggests that they are phylogenetically linked. I therefore conclude that, as the (admittedly poor) fossil record suggests that palaeotaxodonts were the stem group of the bivalves and gave rise to the palaeoheterodonts, *Glyptarca* was evolved from an early cardiolariid palaeotaxodont and thus provides a direct link between the Subclasses Palaeotaxodonta and Palaeoheterodonta.

Following on from this conclusion, and with the new fossils from the early Arenig, together with the recent information on shell microstructure it has been possible to derive the probable lines of descent of the principal groups of bivalves.

SUBCLASS PALAEOTAXODONTA

This subclass includes the Order Nuculoida. All extant forms are protobranch, but, for reasons stated above, it is believed that certain Ordovician members of this subclass developed the filibranch gill grade — these forms are characterized by a strongly differentiated dentition. The earliest member of the subclass is the early Cambrian *Pojetaia*, whilst the other known early Cambrian genus *Fordilla* is also likely to belong to this group (Runnegar and Pojeta, 1992). I do not subscribe to the earlier view of Pojeta (1987) that the latter genus was an isofilibranch. Shell structure in this group is essentially prismato-nacreous aragonite; the homogenous shell structure of modern Nuculanaceans was derived from a prismato-nacreous shells in post-Jurassic times (Cox, 1959). The earliest shell structure yet known is probable nacreous structure in an Ordovician Trenton Group *Deceptrix levata* (Carter, Lawrence and Sanders, *in* Carter, 1990).

SUBCLASS LIPODONTA (SUBCLASS NOV.)

The discovery of readily recognisable solemyoid bivalves in the early Arenig (early Ordovician) rocks of South Wales (Cope, MS) clearly implies that the solemyoids are a very primitive bivalve stock, which probably originated very early in bivalve history. Because extant forms are protobranch, an association with the palaeotaxodonts appears possible. Cox *et al.* (1969) included the solemyoids in the Subclass Cryptodonta; Newell (*in* Cox *et al.* 1969, p. N212) pointed out, however, that the protobranch gill was about the only feature that solemyoids shared with the palaeotaxodonts. Pojeta (1988) figured anteriorly elongated palaeotaxodonts from the mid- to late Ordovician, claiming them to be intermediates between nuculoids and solemyoids and placing them in the direct line of ancestry of the solemyoids. Following these arguments, he placed the solemyoids within the Subclass Palaeotaxodonta. The discovery of earlier, apparently fully-evolved solemyoids in the early Ordovician therefore suggests two possibilities: either Pojeta's forms were not related to the origin of the solemyoids, or that they are surviving members of intermediate stocks.

Since it now appears clear that the solemyoids and palaeotaxodonts have been totally separated since at least early Ordovician times, and because there are important differences between the two stocks, it seems best to assign the solemyoids to a separate subclass. Of the available names for this subclass, I refrain from using the Cryptodonta as that contains a collection of unrelated forms, many of which were clearly more advanced (see below). I thus use Iredale's (1939) term Lipodonta, elevated to the level of Subclass. The outer prismato-nacreous shell of the solemyoids has unique characters, but nevertheless could be readily derived from a simple aragonitic prism structure; the inner shell layer is homogenous (Taylor *at al.*, 1973). Carter, Lawrence and Sanders (*in* Carter, 1990) describe an Upper Carboniferous *Acharax* showing transition between vertical irregular simple prismatic structure and coarsely homogenous structure. Thus the Lipodonta, with their protobranch ctenidia and shell structure which could well have had a shared ancestry with the vertical outer prisms of the palaeotaxodonts, may be regarded as a very early offshoot of the palaeotaxodonts, possibly within Cambrian times.

SUBCLASS PALAEOHETERODONTA

Newell's (1965) definition of this subclass included the radially directed dentition diverging from the subumbonal region and the fact that lateral teeth, if present, were not separated by an edentulous space from the cardinal teeth. This definition immediately excludes the heterodonts and the pteriomorphians.

Most authorities (e.g. Cox *et al.*, 1969) include two extant orders within this subclass: the Trigonioida and the Unionoida. Both have prismato-nacreous shells. Extant members of the former are filibranch, of the latter they are eulamellibranch. Morton (1987) has argued, however, that hte two groups are essentially unrelated, and that they differ in grade and structure of their gills. He suggested that the ciliary pathways of the Trigonioida suggest that they are more closely related to the Pteriomorphia and that they were no more closely related to the Unionoida than sharing a remote palaeotaxodont ancestor. Taylor *et al.*, (1969, 1973) showed that the Trigonioida and Unionoida shared a similar shell

structure and calcareous gill spicules. Both groups are remarkable for the occasional fossil preservation of the gill support structures. The first example of this, mentioned by Cox (1969, p. N21), is of a *Laevitrigonia* from the Portlandian (latest Jurassic) of Wiltshire. Whyte (1991) has demonstrated that *Laevitrigonia* had filibranch gills; he has further discovered that although certain Cretaceous unoinoids were, like their extant descendants, eulamellibranch, Triassic forms were clearly filibranch (Whyte, 1992). This provides the first example of a stock in which the transition from filibranch to eulamellibranch grade can be traced — a transition which I consider has happened several times in different filibranch stocks through organic fusion of adjacent demibranchs.

It thus seems probable that all pre-Triassic palaeoheterodonts had filibranch grade gills, although there is no reason why some forms may not have become eulamellibranch . The trigonioids can be traced plausibly back to the lyrodesmatids of the mid- and late Ordovician; these in turn can be traced back into the actinodontoids of the early Ordovician. As discussed above, there are good reasons for believing that the actinodontoids arose directly from the cardiolariid palaeotaxodonts in earliest Ordovician times, as the very characteristic dentition of the cardiolariids is found in the actinodont *Glyptarca*. I regard the Order Actinodontoida as forming a very variable plexus of rapidly-evolving filibranch forms in the early and mid- Ordovician. The Order is characterized by well-developed differentiated dentition and it seems likely that although many forms had a prismatonacreous shell (as in their ancestors in the palaeotaxodonts), others may have evolved other shell microstructural types, including crossed-lamellar structure, as such structures are common to many of their descendants (see below). Many different types of dentition appear in this group including forms with radiating sheaves of cardinal teeth (e.g. *Copidens* Pojeta and Gilbert-Tomlinson, 1977 and *Ananterodonta* Babin and Guttiérez-Marco, 1985). *Glyptarca* is an example of a form with distinct anterior and posterior dentitions which overlap and appears to be directly developed from the cardiolariid palaeotaxodonts. Other forms had a reduced dentition (e.g. *Redonia* Roualt, 1851). The reduction in dentition became more noticeable in the Order Modiomorphoida where some genera are apparently totally edentulous (e.g. *Modiolopsis* Hall, 1847).

The Modiomorphoida were included by Pojeta (1978) in the Subclass Isofilibranchia and the Mytiloida were considered to be derived directly from them; Pojeta (1978) also suggested that the isofilibranchs were derived from *Fordilla* in the early Cambrian. Following Runnegar and Pojeta's (1992) revised placement of *Fordilla* within the palaeotaxodonts, the modiomorphoids must be linked back to the actinodonts, as these appear to be the stem group of the lamellibranch bivalves. Significantly, Bailey (1983, p.200), found that he was unable to effectively separate the modiomorphoids from the palaeoheterodonts, as advocated by Pojeta (1978) since some modiomorphoids, including *Modiomorpha* itself have "a heterodont arrangement with weak posterior laterals . . . other modiomorphoids . . . have strong posterior elements as part of a continuous actinodont series".

Whether the Mytiloida were derived from the Modiomorphoida remains unresolved. Carter (1990, p.273) has shown that it would need "extreme submergence" to convert a modiomorphoid external parivincular ligament to a mytiloid submarginal planivincular type; he can only quote a single species of modiomorphoid (a Devonian *Goniophora*) which displays "slight submergence", as any form of transition between the two ligamental conditions. The other possible origin of the mytiloids, considered by Cox (1960) was from a pteriomorphian group such as the ambonychiids (see below).

Modiomorphoid shell microstructure is essentially aragonitic and prismato-nacreous, with some elements of crossed-lamellar or complex crossed-lamellar structure replacing this in the ligament (Carter, Lutz and Tevesz, *in* Carter, 1990), whilst that of the mytiloids is variable. In the latter group the outer shell layer may be calcitic or aragonitic, or both; the middle layer aragonitic nacreous or crossed-lamellar, whilst the inner layer is aragonitic and may be nacreous, prismatic or homogenous (Carter *et al.*, *in* Carter, 1990). Additionally, it may be noted that some species of the mytiloid genera *Modiolus* and *Stavelia* have crossed-lamellar or complex crossed-lamellar inner shell layers (Taylor *et al.*, 1973). Thus shell microstructural studies do not contribute directly to the debate on the origin of the mytiloids.

The Palaeoheterodonta are thus a plexus of forms showing evidence of derivation from filibranch palaeotaxodonts. They are thus considered to be the stem group of all bivalves with lamellibranch gills. They evolved very rapidly in the early Ordovician producing forms with a wide variety of dentition and shell shape, and probably became adapted to many shallow marine habitats. They had also probably evolved a wide variety of shell microstructural types.

SUBCLASS PTERIOMORPHIA

The earliest fossils ascribed to the Pteriomorphia belong to the Cyrtodontoidea of the early Ordovician, which have a smooth shell and a ligamental area crossed by a series of longitudinal grooves and ridges that intersect the dorsal margin of the valves at a low angle (Pojeta and Runnegar, 1985). This latter feature develops into the duplivincular ligament, which is common to many of the other members of the subclass. The origin of the Cyrtodontoidea was clearly from the actinodontoid plexus of the palaeoheterodonts. The genus *Glyptarca*, could, by loss of the subumbonal teeth, produce dentition like that of the cyrtodontids; indeed a new genus will shortly be described from the early Ordovician showing such dentition, but still lacking the ligamental grooves (Cope, MS). In all other respects, this new genus is a cyrtodontid. Sanchez and Babin (1993) have described a new

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THE PHYLOGENETIC SIGNIFICANCE OF SOME ANATOMICAL FEATURES OF BIVALVE VELIGER LARVAE

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INTRODUCTION

Various larval types are present within the Bivalvia. The primitive protobranchs have barrel-shaped test or pericalymma larvae, some freshwater bivalves have parasitic larvae such as the glochidium or lasidium, but the most common larval development pattern involves a shelled ciliated stage, the veliger. In some cases, the veliger is lecithotrophic and may, where a free-swimming stage is short-lived or absent, be highly modified or reduced in comparison to the more characteristic planktotrophic form (Chanley, 1969).

The adults of bivalves which develop from planktotrophic veliger larvae show a considerable range of anatomical adaptations to a variety of habitats and modes of life. The anatomy of the larvae, on the other hand, is more remarkable for the close similarities between taxonomically diverse species. This perhaps reflects the fact that although the adults may occupy disparate niches, their larvae inhabit the planktonic domain and function in essentially the same way. Indeed, the common factors in the sequence of development through to metamorphosis via a veliger stage which occurs in many bivalve families (spiral determinate cleavage, blastula, gastrula, trochophore, veliger with D-shaped prodissoconch I, filter-feeding veliger with prodissoconch growing by marginal increment, pediveliger) are taken as clear evidence of the monophyletic origin of these families.

A closer examination of the anatomy of veligers has also revealed many common features of anatomy, though comparative studies, such as those by Rees (1950) and Chanley and Andrews (1971) have shown that later stage veliger larvae of different species can be distinguished. Closely related species can be distinguished by means of their prodissoconch II shell features. Unfortunately, no monographs on internal larval anatomy as detailed as the comprehensive studies of authors such as Hatschek (1880) and Meisenheimer (1901) have been produced since the advent of the electron microscope, so that the study of the comparative anatomy of veliger larvae lags a long way behind the understanding of adult morphology.

Whilst the common ancestry of bivalves with veliger larvae is rarely doubted, the relationship of the veliger to protobranch larvae, to larvae of other molluscan classes and to other spiralian phyla is the subject of widely diverging views. One school of thought, developed by Jägersten (1972) and integrated into a view of evolution of spiralian phyla by Nielsen and Nørevang (1985) views planktotrophy by means of opposed bands of cilia as a primitive larval feature, spiralian trochophore larvae as homologous forms and the veliger as the primitive larval type in the Bivalvia. Other authors view similarities between the trochophores of different phyla and between the opposed band ciliary systems as convergent features. They find the similarities between the lecithotrophic larvae of the protobranch bivalves and those of other molluscan classes which are generally believed to be relatively primitive, such as aplacophorans, to be sufficient to justify naming these forms pericalymma larvae, with the implication of homology (Salvini-Plawen, 1972). Thus, depending on which of these interpretations is correct, bivalve veligers should be viewed either as modified pericalymma larvae, the cilia of whose large ciliated cells have become organised in such a way that planktotrophy is now possible, or they are modified trochophore larvae which have retained the opposed-band pattern of prototroch and metatroch of an ancestral spiralian form.

In this paper it is proposed to review the available information on the anatomy of bivalve veligers, including all stages from D-veliger to pediveliger, with a view to: evaluating the potential for anatomical details to permit discrimination between related species; determining whether studies of larvae can supplement information regarding adult comparative anatomy in revealing higher taxonomic groupings within the Bivalvia; establishing whether current knowledge can contribute towards the debate regarding the origin of the bivalve veliger. Descriptions of bivalve veligers vary considerably in the types of information they provide. Frequently, information regarding features which this review will show to be significant is omitted. To rectify this situation, a check-list of key features to be included in larval descriptions will be proposed.

Table 31.1 Bivalve larval types and the distribution of selected anatomical characters

Taxon[1]			Type[2]	Eye[3]	Apical Cirrus[4]	Statocyst[5]	Taxodont Hinge[6]	References type	eye	cirrus	stato.	hinge
Protobranchia	Nuculoida	Nuculoidea	P	–	+/–	1		1	1	1/2	1	
	Solemyoida	Solemyoidea	P		–			3		3		
Pteriomorphia	Arcoida	Arcoidea	V	+	+		+	4	4/5	5		37
		Limopsoidea	V					6				
	Mytiloida	Mytiloidea	V	+	+	>1	+	7	7	5	8	9
		Pinnoidea	V				+	10				10
	Pterioida	Pterioidea	V				+	11				11
	Limoida	Limoidea	V	–	+	>1	+	4	4	12	4	4
	Ostreoida	Anomioidea	V	+		>1	+	13	14		13	21
		Ostreoidea	V	+	–	>1	+	15	15	16	17	15
		Pectinoidea	V	+	+	>1	+	18	18	19	20	21
Palaeoheterodonta	Unionoida	Unionoidea	G, L					22				
Heterodonta	Myoida	Hiatelloidea	V	–	+	1	–	23	23	24	4	21
		Myoidea	V	–	+	1	–	25	5	13	13	37
	Veneroida	Pholadoidea	V	–	+	1	–	5	5	14	26	21
		Arcticoidea	V				–	27				37
		Astartoidea	V				–	6				6
		Cardioidea	V	–	+	1	–	5	5	5	26	21
		Chamoidea	V					28				
		Corbiculoidea	V		+			29		29		
		Dreissenoidea	V	–	+	1		30	30	30	30	
		Galeomatoidea	V	–	+		–	31	32	31		6
		Lucinoidea	V			1	–	26			26	6
		Mactroidea	V	–	+		–	31	5	5		37
		Solenoidea	V	(–)	+		–	5	24	5		37
		Tellinoidea	V	–	+	1	–	5	5	5	4	6
		Tridacnoidea	V	–	+			33	33	33		
		Veneroidea	V	–	+	1	–	13	34	5	22	21
Anomalodesmata	Pholadomyoida	Pandoroidea	LV	–	+		–	35	5	5	6	
	Poromyoida	Poromyoidea	LV				–	36			6	

[1] Subclasses, orders and superfamilies as used by the Zoological Record, 1993.
[2] P = pericalymma, V = development including planktotrophic veliger stage, LV = only lecithotrophic veligers known, G = glochidium, L = lasidium.
[3] Pigmented eye spots reported present: + ; reported absent: –.
[4] Apical cirrus present: + ; absent: –.
[5] Single statolith within each statocyst: 1; several statoconia within each statocyst: >1.
[6] Taxodont hinge present: +; absent: –.
[7] References listed below:
1. Drew, 1899 – *Nucula, Yoldia*
2. Drew, 1901 – *Nucula*
3. Gustafson and Reid, 1986 – *Solemya*
4. Odhner, 1914 – *Arca; Lima; Anomia; Hiatella; Tellina*
5. Chanley and Andrews, 1971 – *Anadara* (Arcoidea); *Mytilus; Mya; Barnea, Cytopleura* (Pholadoidea); *Laevicardium* (Cardioidea); *Spisula, Mulinia, Rangia* (Mactroidea); *Ensis* (Solenoidea); *Donax, Tellina* (Tellinoidea); *Mercenaria, Pitar* (Veneroidea); *Lyonsia* (Pandoroidea)
6. Rees, 1950 – ?*Limopsis; Astarte*; Galeomatoidea; Lucinoidea; Tellinoidea; Pandoroidea; Poromyoidea
7. Bayne, 1971 – *Mytilus*
8. Werner, 1939 – *Mytilus*
9. Walker and Lutz, 1989 – various mytilids
10. Beets, 1979a – *Atrina*
11. Menzel-Escarbiere, 1970 – *Pinctada*
12. Ishikawa, 1936a – *Lima*
13. Boyd, 1912 – *Anomia; Mya; Mercenaria* (Veneroidea)
14. Bourne, 1946 – *Anomia; Pholas*
15. Yonge, 1961 – *Ostrea*
16. Galtsoff, 1934 – *Crassostrea*
17. Quayle, 1934 – *Ostrea*
18. Carriker and Burke, 1988 – *Argopecten*
19. Waller and Crisp, 1991 – *Pecten*
20. Mason and Nott, 1977 – *Pecten*
21. Pelseneer, 1903 – *Anomia*; various pectinids; *Cerastoderma* (Cardioidea); *Hiatella; Pholas; Venus, Venerupis, Ruditapes* (Veneroidea)
22. Lefevre, 1989 – unionids
23. Gould, 1883 – *Hiatella*

(Continued on next page)