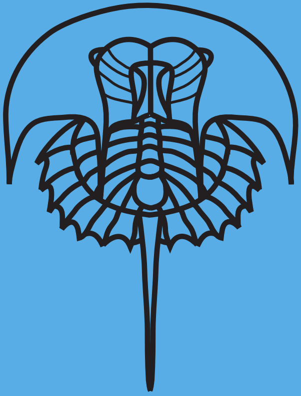

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Evolutionary Ecology of the Bivalvia

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PART N, REVISED, VOLUME 1, CHAPTER 19: EVOLUTIONARY ECOLOGY OF THE BIVALVIA

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INTRODUCTION

Modern bivalve mollusks display a wide array of life habits, as illustrated in Figure 1. The relative numbers of species representing the various modes of life illustrated here have changed dramatically during the Phanerozoic. We recognize these changes primarily by interpreting the functional morphology of bivalve shells, but paleoecological inferences based on other kinds of evidence also come into play. As bivalves diversified throughout the Phanerozoic, they occupied new habitats. For example, early in the Ordovician there appears to have been no species that attached epifaunally to a solid substratum by byssal threads, and attachment by cementation apparently did not evolve until the Permian. Even by the end of the Ordovician, no suspension-feeding species was a deep burrower (in terms of absolute depth) by modern standards. It appears that not until at least the Jurassic was any bivalve species able to burrow rapidly enough to occupy shifting sands within or close to the wave-ridden zone of a sandy beach.

The Bivalvia exemplify Cope's Rule, in the sense that they arose at a body size that was quite small in relation to the body-size distribution that subsequently emerged for the class (STANLEY, 1973). In fact, for very few Ordovician bivalve species did the geometric mean of shell height and shell width exceed 6 cm.

The life habits of the few Cambrian bivalve taxa are debatable, in part because these animals were of very small size and such forms can live in a variety of ways because of scaling problems. For example, the ratio of strength to weight (see *Treatise Online,* Part N, Revised, Volume 1, Chapter 5, p. 3) is relatively high at small sizes. Possibly, the earliest bivalves were grazers on microbial mats (FANG & SÁNCHEZ, 2012), but bare, bioturbated areas existed in proximity to microbial mats on Cambrian sea floors (BAILEY & others, 2006), so non-mat habitats were available for habitation. It is clear, however, that by mid-Ordovician time all bivalve higher taxa included burrowers or byssate forms that were descendants of burrowing taxa.

Important changes in bivalve modes of life during the Paleozoic and early Mesozoic were polyphyletic transitions from burrowing to endobyssate habits (endobyssate bivalves live infaunally or semi-infaunally in soft sediment) and from endobyssate to epibyssate (epifaunal) habits (STANLEY, 1972) and then to free-living and cemented epifaunal habits. Some of these transitions were occasionally reversed.

There were also major adaptive advances within particular modes of life, such as evolution of the ability to burrow rapidly or deeply, and the ability of epifaunal forms to swim or cement to hard substrata or employ endosymbionts for nutrition. Even the more common advances were not comprehensive, however. For example, although increases in the intensity of predation rendered many evolutionary changes highly adaptive, some bivalve taxa have persisted to the present day despite lacking the antipredator traits possessed by others. In other words, evolution has not systematically optimized adaptations, but has achieved adaptive advances sporadically and imperfectly. Relatively high rates of extinction

Stanley, Steven M. 2015. Part N, Revised, Volume 1, Chapter 19: Evolutionary ecology of the Bivalvia. Treatise Online 72:1–48, 39 fig., 1 table.

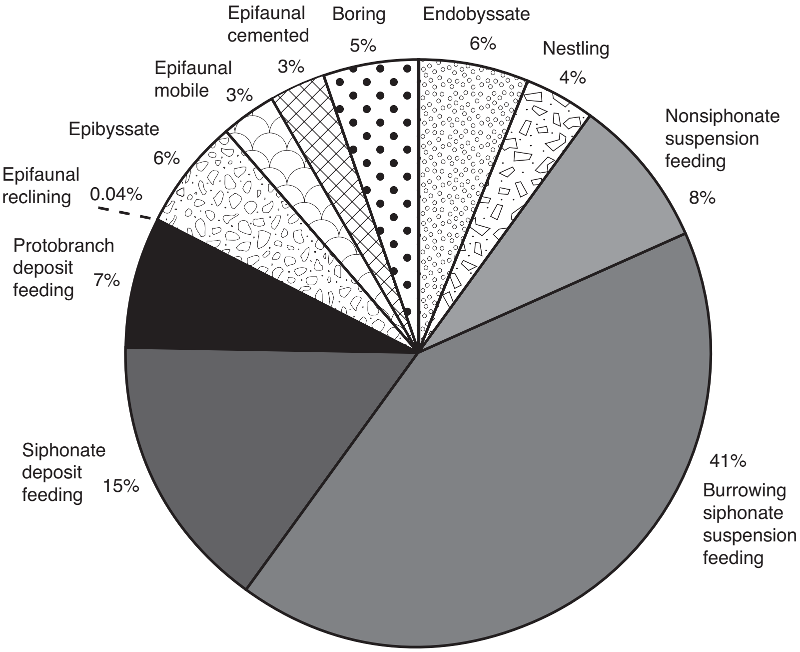

FIG. 1. Percentages of modern marine bivalve species belonging to various life habit groups (based on taxonomic compilations by Warmke & Abbott, 1961; Keen, 1971; Abbott, 1974).

have weeded out many less highly evolved taxa, but extinction has not operated with adherence to strict rules that quickly result in the demise of all such taxa.

COMMON MISUNDERSTANDINGS ABOUT BIVALVE LIFE HABITS

Several misconceptions about bivalves' modes of life are conspicuous in the literature. Before these are discussed, a few words are necessary about the life habit groups depicted in Figure 1. Some researchers have divided extinct burrowing taxa into shallow and deep burrowers, as if the two groups occupied different ecospace. This distinction is unjustified, however, because a deep burrower occupies the same volume of sediment just below the sediment-water interface as a shallow burrower: the presence of either one precludes the presence of the other. Furthermore, both also utilize the same water above the sediment-water interface for food and respiration. In addition, tallying particular species as shallow or deep burrowers is problematical because depth is a continuum. There is also an issue as to whether burrowing depth should be measured in absolute terms or assessed in relation to shell size. For these reasons, I have not divided extant burrowers into shallow and deep infauna in Figure 1, but instead have divided them into nonsiphonate and siphonate forms. This anatomical distinction is important not because of competition for ecospace, but because it relates to maintenance of a life position in the sediment: to avoidance of predation or transport to a hostile environment. Siphonate burrowers tend to have advantages with respect to both of these threats because they are, on average, both more rapid and deeper burrowers than nonsiphonate taxa (TRUEMAN, 1966; STANLEY, 1968).

Although sometimes represented as mobile infauna (e.g., SEPKOSKI, 2002), most burrowing bivalves are essentially sedentary, undertaking few lateral movements in the course of their lifetime. Exceptions are deposit-feeders, which need to acquire fresh food, and suspension-feeders that live in unstable substrata, from which they are frequently exhumed by strong water movements. The latter include inhabitants of the wave-ridden zones along sandy beaches. They also include forms that occupy unstable, but less frequently disrupted, substrata and occasionally crawl about in semi-infaunal life positions: for example, glycymerids (STANLEY, 1970; THOMAS, 1976), freshwater unionids (MCCALL, TEVESZ, & SCHWEIGEN, 1979), and some species of cardiids (SAVAZZI, 1985), and *Chione* MEGERLE VON MÜHLFELD, 1811 (STANLEY, 1970). Most suspension-feeding bivalves must occasionally make short downward movements as they increase in size, but they have little need to move laterally. For most shallow-burrowing forms, the critical function of burrowing is resumption of an infaunal position after being exhumed by waves or currents.

In pictorial reconstructions of ancient faunas, extinct epibyssate taxa are often portrayed as living on the surface of soft substrata, but this habit must always have been uncommon. Any species that attaches in this way will lack the support from surrounding sediment that stabilizes endobyssate forms against strong water movements. In addition, fully epifaunal forms are highly vulnerable to predation, unless they happen to occupy habitats with few predators, as do extant oysters adapted to brackish conditions or mussels living on intertidal rocky shores. For firm attachment and predator avoidance, most extant epibyssate bivalve species attach to solid surfaces—often to reefs or rocky substrata and sometimes to fleshy organisms, such as algae or alcyonarians. In fact, numerous extant taxa that we often refer to as epifaunal actually live well above the surrounding sea floor or are partial nestlers in crevices or shallow depressions. Today, nearly all species of *Pteria* SCOPOLI, 1777, attach preferentially to alcyonarians (see *Treatise Online,* Part N, Revised, Volume 1, Chapter 5, Fig. 37–38). *Mytilus* LINNAEUS, 1758 in 1758–1759, though sometimes carpeting broad rocky intertidal areas, occupies shallow crevices when first colonizing a surface and can thrive only because its intertidal position excludes most predators. Even *Chama* LINNAEUS, 1758 in 1758–1759, and *Spondylus* LINNAEUS, 1758 in 1758–1759, which attach by cementation, often live in the protection of cavities. The extant genus *Arca* LINNAEUS, 1758 in 1758–1759, although normally considered an epibyssate genus, might well be classified as a semi-borer, habitually grinding into its carbonate substratum with its anterior ribs so that most of its shell is protected (STANLEY, 1970). A large majority of byssally attached pectinids in the modern ocean, although often classified as epifauna, habitually nestle in cavities within, between, or beneath rocks or reef structures.

It is a misconception that a variety of byssate bivalves live as so-called free swingers, loosely attached by a byssus—that *Pteria*, for example, lives in this fashion with its byssus extending out from its point of attachment, with its hinge line horizontal, with the wing pointing in the direction of the ambient current like a weather vane (KAUFFMAN, 1969). Actually, such horizontal extension of the bivalve on a flexible byssus is impossible because bivalves are denser than seawater. Furthermore, as noted above, in the modern ocean *Pteria* usually lives tightly attached to alcyonarians (STANLEY, 1970, 1972). Nearly all byssate taxa that attach to hard substrata, including other pteriids in addition to *Pteria* as well as pectinids, are also firmly attached. Among extant bivalves, loose pendant attachment is characteristic only of some limids, which nestle in the protection of cavities.

A variety of small, thin-shelled byssate bivalves found in black shales of relatively deep water origin have been considered to have been pseudoplanktonic forms, but it appears that most were actually benthic taxa that occupied dysaerobic environments (WIGNALL & SIMMS, 1990), especially during intervals of global warming, when the ocean was highly stratified (Fischer & Bottjer, 1995). One form of evidence here is the frequent occurrence of many of the species in question as dense accumulations, a taphonomic condition unlikely to result from the death of pseudoplankton. Bivalves apparently live as epibionts on *Sargassum* in the modern ocean only rarely and facultatively (Weis, 1968; Fine, 1970), and it seems likely that obligate pseudoplanktonic life styles for bivalves have been rare throughout the Phanerozoic.

It should be understood that, although most extinct bivalves can be assigned life habits with a high degree of certainty, errors are possible. Some species with endobyssate and epibyssate morphologies, especially ones of small body size, live as habitual nestlers. Also, small byssate forms of any morphology, if relatively thin-shelled, have the potential to live pseudoplanktonically because the substratum imposes few restrictions on shell outline for species with this mode of life. In fact, as already noted, very small bivalves, regardless of shell shape, can live in a variety of ways because scaling problems decline with body size. In addition, as the foregoing discussion illustrates, life habits do not always fall into discrete categories. These codicils imply that, when we assess the history of bivalve life habits, there will inevitably be errors. Nonetheless, the major themes that emerge from an informed assessment of the history of bivalve functional morphology are solidly supported: the life habits of a great majority extinct bivalve species can be deduced with a high degree of certainty from their shell morphology.

CAMBRIAN BEGINNINGS

The evolutionary origin and early history of the Bivalvia will be treated in another chapter and are not reviewed in detail here. The five Cambrian genera considered to be possible Bivalvia are all minute (shell length <2 mm): *Fordilla* Barrande, 1881; *Pojetaia* Jell, 1980; *Tuarangia* MacKinnon, 1982; *Camya* Hinz-Schallreuter, 1995; and *Arhouriella* Geyer & Streng, 1998 (Pojeta, 2001). All have shapes compatible with an infaunal mode of life, although they would have been essentially interstitial if occupying coarse sand. Actually, they may have lived epifaunally (Tevesz & McCall, 1985), but it seems more likely that they lived as nestlers, perhaps in the protection of larger organisms, as many lasaeids do today. The combined range of imputed Cambrian bivalves is from Tommotian to early Late Cambrian; bivalves are unknown from later Cambrian time.

THE GREAT ORDOVICIAN RADIATION

All Early Ordovician Bivalvia are known only from Gondwana, so the Ordovician radiation of the group probably began there (Babin, 1993, 1995; Cope, 2002). Thus, it appears that all Cambrian bivalve taxa known from Europe and North America died without issue. The geographic pattern of the Early Ordovician radiation remains to be documented, however, as evidenced by the pattern in Argentina, which differed from those documented elsewhere (Sánchez, 2008).

It has been hypothesized that lack of a byssus delayed the post-Cambrian evolutionary expansion of the Bivalvia (Stanley, 1972). Today a byssus is present in the earliest benthic stage of every autobranch bivalve taxon (Yonge, 1962). If the minute earliest bivalves lacked this anchoring organ or a sheltered habitat, they would have been vulnerable to dislodgement and harmful transport. Juvenile byssal attachment is not a feature of the protobranchs, however (Allen & Hannah, 1986), but the protobranch habit of deposit-feeding in soupy muds, seldom exposed to strong water movements, would render a byssus not only difficult to employ effectively, but also of little value. The evolution of a juvenile byssus was a key innovation for suspension-feeders, perhaps triggering their initial radiation. Another key adaptive breakthrough, however, was the filibranch (feeding) gill (Cope, 1995).

It has been suggested that byssal attachment evolved as a juvenile feature and was advanced ontogenetically by neoteny to the adult stage of many taxa (Yonge, 1962). It is possible, however, that byssal attachment actually evolved as a juvenile *and* adult feature of very small early bivalves and was then retained only in the juvenile stages of descendant taxa that grew to larger size.

PROTOBRANCH DEPOSIT-FEEDERS

Not surprisingly, because of their conspicuously plesiomorphic anatomy (e.g., protobranch ctenidia and lack of a byssus), nuculoids are among the earliest known Ordovician bivalves (Cope, 2004). Some Middle Ordovician nuculoids resembled extant Nuculidae in being anteriorly elongate but almost equant in overall shape. Others had elongate posterior regions resembling those of extant nuculanids and, like the latter, probably employed siphons. Some cucullellids with pallial sinuses were also present. Thus, very early in their history, the nuculoids evolved a range of deposit-feeding life habits resembling those of their present-day descendants. By Late Ordovician time, nuculoids were quite diverse. Deposit-feeding nuculoids have remained successful and maintained substantial diversity up to the present, especially in fine-grained, organic-rich sediments.

SOLEMYIDS AND BACTERIAL FARMING

Solemyid nuculoids existed by the Middle Ordovician. Although able to swim by jet propulsion, present-day species of *Solemya* Lamarck, 1818 in 1818, 1819, 1822, occupy Y-shaped burrows (Stanley, 1970). This habit is probable for early solemyids but has not been demonstrated. Extant solemyids, although presumably feeding partly on suspended organic matter, also consume sulfide-oxidizing bacteria that live intracellularly within them (Felbeck, Childress, & Somero, 1981). In keeping with the solemyids' feeding and locomotory behavior, their gut is much reduced (even absent in some species), and their ctenidia, foot, and anterior shell region are greatly expanded. Waller (1998) concluded that these features evolved at the base of the Solemyoidea because they are present in all living Solemyidae and Manzanellidae (=Nucinellidae).

EARLY BURROWING SUSPENSION-FEEDERS

Figure 2 is a reconstruction of typical Late Ordovician burrowing, endobyssate, and epibyssate bivalves. Free-living Ordovician infaunal bivalves were mostly small, slow burrowers. Many had equant, somewhat inflated shells, which are inconsistent with a capacity for rapid burrowing. Probably, like similarly shaped arcoids, they were often positioned with their shell posteriors projecting slightly above the sediment-water interface. Very few extant bivalve taxa that lack siphons and extensive ventral mantle fusion are rapid burrowers because the hydraulic system used to operate their foot is inefficient (Trueman, 1966; Stanley, 1968). *Lyrodesma* Conrad, 1841, is an Ordovician genus with a pallial sinus; therefore, it has been widely considered to have been siphonate. The sinus, however, is extremely shallow, so that siphons, if present, would probably have been very short. *Lyrodesma* was also quite small (generally <3 cm in length) and has the angled, truncated posterior of a very shallow burrower (Fig. 2.11). It resembles many trigoniids in its orthogyrate morphology, and it resembles all of them in possessing large, crenulated hinge teeth that radiate far into the shell interior. *Lyrodesma* or a close relative was likely ancestral to the trigonioids. As in the trigoniids (Stanley, 1977), the complex dentition of *Lyrodesma* must have served to maintain valve alignment during extrusion of a muscular foot. Therefore *Lyrodesma*, like the trigoniids, was presumably a relatively rapid burrower for a nonsiphonate taxon.

Sánchez and Benedetto (2007, p. 531) described the pallial line of Early Ordovician *Konduria coloradoensis* Sánchez &

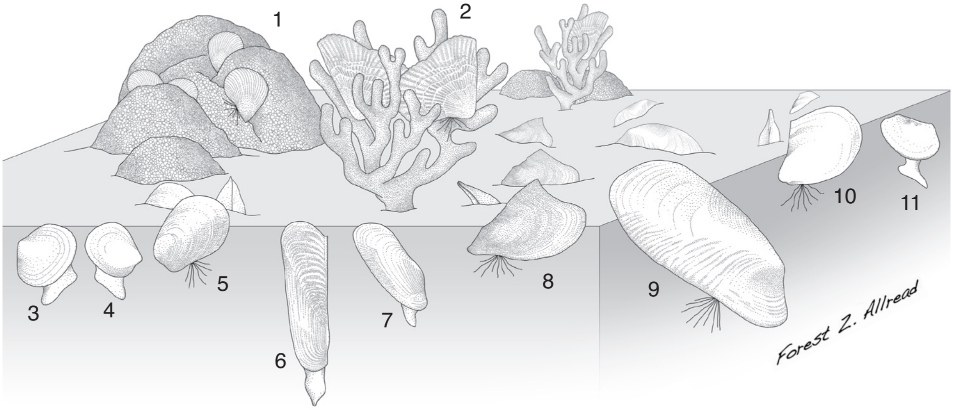

FIG. 2. Life habits of Late Ordovician bivalves; *1*, *Ambonychia ulrichi* (POJETA, 1962) (Ambonychiidae); *2*, *Ambonychia alata* MEEK, 1872 (Ambonychiidae); *3*, *Cycloconcha* MILLER, 1874b (Cycloconchidae); *4*, *Cyrtodonta* BILLINGS, 1858 (Cyrtodontidae); 5, *Thorslundia* ISBERG, 1934 (Cyrtodontidae); *6*, *Orthonota* CONRAD, 1841 (Orthonotidae); *7*, *Whiteavesia* ULRICH, 1893 (Modiolopsidae); *8*, *Pterinea* GOLDFUSS, 1832 (Pterineidae); *9*, *Pholadomorpha* FOERSTE, 1914 (Modiolopsidae); *10*, *Ambonychiopsis* ISBERG, 1934 (Ambonychiidae); *11, Lyrodesma* CONRAD, 1841 (Lyrodesmatidae); animals in the foreground are to scale (Allread, 2012).

BENEDETTO, 2007, as "entire, although a few specimens . . . show a small, shallow inflection." However, this species had a greatly reduced anterior region that was partially occupied by an adductor muscle and could not have housed a foot employed for effective burrowing; this species has the morphology of an endobyssate animal. FANG and COPE (2004, p. 1138) reported that "there seems to be a shallow pallial sinus" in Early Ordovician *Fasciculodonta impressa* FANG & COPE, 2004. The pallial sinus present in *Lyrodesma,* and possibly in other Ordovician taxa, might only have accommodated a slightly expanded, unfused region of the mantle. *Neotrigonia* COSSMANN, 1912, the only extant trigonioid genus, lacks siphons. In any event, no Ordovician bivalves were deep burrowers, and it is possible that none passed a siphonate condition on to post-Ordovician descendants.

Among the nonsiphonate, slow-burrowing Ordovician bivalves were a large number of cyrtodontid taxa: i.e., those that were relatively equant in lateral view (Fig. 2.4; Fig. 3.1). Like some of their extant arcoid descendants with similar shapes, these forms may have employed an accessory byssus that provided weak anchorage in soft sediment. The duplivincular ligament, though perhaps representing an adaptive breakthrough when it arose, imposed a severe handicap not only on cyrtodontids but also on the burrowing arcoids that descended from them. It is generally too weak to open the valves of infaunal animals; pressure from the foot is also required (THOMAS, 1976). On the other hand, the broad taxodont dentition of arcoids has the advantage of virtually eliminating shearing of the valves as they open.

Also present in the Ordovician was a small variety of slow-burrowing cardiomorphs that lacked mantle fusion and a tissue-grade incurrent siphon. Among them were *Cycloconcha* MILLER, 1874b (Fig. 2.3; Fig. 4) and *Actinodonta* PHILLIPS, 1848, which were generally more laterally compressed than the cyrtodonts. *Cycloconcha* has the equant shape of a shallow burrower.

Highly elongate anomalodesmatids, such as *Orthonota* CONRAD, 1841 (Fig. 2.6) and *Palaeosolen* HALL, 1885, both of which exhibit a narrow posterior shell gape (Fig. 5), are among the few Ordovician bivalve genera yet discovered that were moderately rapid burrowers. The posterior gape indicates that they might have employed siphons, but they are apparently not known to have had pallial sinuses and remained quite small (approximately 6 cm in length).

Babinka BARRANDE, 1881, ranging back to the late Tremadocian (POJETA, 1971), is one of the oldest Ordovician bivalve genera. It has been viewed as a deep-burrowing lucinoid ancestor (MCALESTER, 1965) but lacked an elongate anterior adductor and may not have had lucinoid affinities (TAYLOR & GLOVER, 2000). There is no evidence that it formed an elongate anterior mucus tube, as lucinids do, or that it was siphonate. It was only about 2 cm in length, and because there is no evidence that it was siphonate, there is no reason to believe that it was anything other than a shallow burrower.

THE EXPANSION OF BYSSATE TAXA

Most byssally attached ostreatans are inequivalve and display a byssal notch or sinus and sometimes a byssal gape. Most mytilidans are characterized by an elongate shell in which the anterior is often reduced in association with a diminished anterior adductor muscle. Ventral flattening and a triangular, rather than lobate, anterior suggest epibyssate habits for members of this group. Elongate endobyssate mytilidans generally exhibit less anterior reduction than epibyssate forms; they typically possess an anterior lobe (STANLEY, 1970, 1972) (see *Treatise Online,* Part N, Revised, Volume 1, Chapter 5, Fig. 28–29). Some endobyssate forms display a broad ventral sinus, and many can be described as modioliform or resembling the Devonian–Holocene mytilid *Modiolus* LAMARCK, 1799 (see *Treatise Online,* Part N, Revised, Volume 1, Chapter 5, Fig. 27). Epibyssate arcoids are elongate and somewhat rectangular, often displaying a substantial byssal gape. Nestling arcoids are elongate, tend to be laterally compressed, and are sometimes xenomorphic.

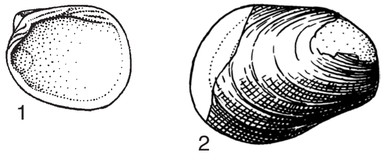

FIG. 3. Life habits of the Cyrtodontidae; *1, Cyrtodonta*, a burrower that, like some modern arcids, may have employed an accessory byssus, ×1 (Billings, 1858); *2, Thorslundia*, an endobyssate form, ×1 (Isberg, 1934).

Free Burrowing–Endobyssate Transitions

Several Early Ordovician modioliform taxa are reasonably interpreted as endobyssate: for example, *Modiolopsis* HALL, 1847 (Fig. 6.2), *Goniophorina* ISBERG, 1934 (Fig. 6.4), *Pucamya* SÁNCHEZ & BENEDETTO, 2007*, Redonia* ROUAULT, 1851, *Konduria* SÁNCHEZ & BENEDETTO, 2007*,* and *Carminodonta* COPE, 1996 (COPE, 1995; SÁNCHEZ & BENEDETTO, 2007; SÁNCHEZ, 2008). These forms retained the infaunal or semi-infaunal habits of their ancestors.

As noted above with respect to the cyrtodontids, there is not a clear demarcation between burrowers and endobyssate forms because some species that are properly viewed as burrowers also employ an auxiliary byssus for relatively weak attachment. In fact, most early (Middle Ordovician) cyrtodonts may fall into this category. During the Late Ordovician, however, a variety of clearly endobyssate cyrtodonts evolved (Fig. 2.5; Fig. 3.2). During the Ordovician, burrowing so-called modiolopsids also gave rise to endobyssate forms (Fig. 2.9; Fig. 6.2–6.5), and these soon diversified. The so-called modiolopsid grouping is actually a polyphyletic assemblage of more or less modioliform

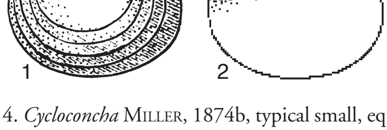

FIG. 4. *Cycloconcha* MILLER, 1874b, typical small, equant Ordovician burrower; 1, exterior of left valve, 2, interior of right valve, ×1.25 (Miller, 1874b).

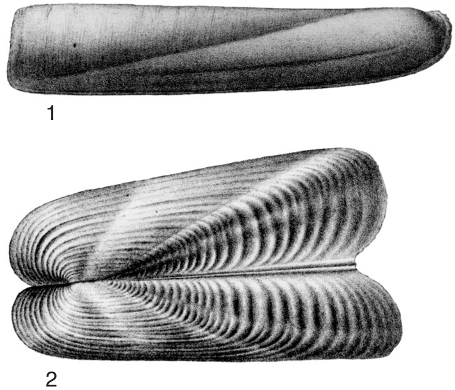

Fig. 5. Relatively rapid burrowers of Ordovician; shell posteriors of these genera gaped slightly, perhaps indicating presence of short siphons, like those of modern solenids. *1, Palaeosolen* Hall, 1885, which possessed an anterior gape for extruding the foot parallel to long axis of shell, ×1; *2, Orthonota* Conrad, 1841, ×1 (Hall, 1885).

members of Modiolopsidae, Colpomyidae, and Modiomorphidae, representing the Pteriomorphia and Heteroconchia. *Whiteavesia* Ulrich, 1893, one of the earliest (Arenigian) members of Modiolopsidae, has the shape of an elongate burrower, with a prominent anterior region and broadly convex ventral region (Fig. 2.7, 6.1).

Not all modioliform taxa have occupied soft sediment. Some have lived as nestlers in hard substrata, including carbonate skeletal material. A smaller number of such species have bored into calcareous substrata. *Corallidomus* Whitfield, 1893, was an Ordovician genus that engaged in both of these modes of life, at times boring into calcareous substrata, presumably partially by chemical means (Pojeta & Palmer, 1976). The boring habit of *Corallidomus,* however, constituted an evolutionary dead end: boring bivalves are unknown from post-Ordovician Paleozoic strata.

Endobyssate-Epibyssate Transitions

During the Late Ordovician, byssally attached pteriomorphs (cyrtodonts, ambonychiids, modiolopsids, colpomyids) diversified substantially (Cope, 2004). Ordovician taxa experienced polyphyletic evolutionary transitions from endobyssate to epibyssate modes of life—transitions for which details of many ancestor-descendent relationships remain uncertain (Stanley, 1972).

The ambonychiids arose at an endobyssate grade of evolution (Stanley, 1972). Some Middle Ordovician genera, such as *Allonychia* Ulrich, 1893 (Fig. 7.1), exhibit anterior lobes. Other ambonychiids, such as *Cleionychia* Ulrich, 1893 (Fig. 7.2), were flattened ventrally and must normally have attached to hard substrata. *Ambonychiopsis* Isberg, 1934, though lacking a distinct anterior lobe, is somewhat ovate in outline, with a convex ventral region, and was presumably endobyssate (Fig. 2.10). Epibyssate ambonychiids were moderately diverse in Late Ordovician seas (Fig. 2.1–2.2), but few if any evolved earlier.

The Pteriinae had arisen by the Dapingian (early Middle Ordovician), also at an endobyssate grade of evolution. The oldest recognized genera are Dapingian to early Darriwilian (Middle Ordovician) *Eopterinea* Fang & Cope, 2004, and Floian to lower Darriwilian (upper Lower Ordovician to middle Middle Ordovician) *Palaeopteria* Whiteaves, 1897. *Palaeopteria* displays an anterior lobe, and its right valve is slightly less convex than the left (Fig. 8.1), indicating an oblique life position with the right valve underneath. Other early pterineids, except *Eopterinea* Fang & Cope, 2004, shared these features. *Eopterinea* from the Early Ordovician (late Arenig) has the approximately equivalved shape of an endobyssate animal that lived with its plane of commissure vertical or at a high angle. It probably represents the plesiomorphic shape for the Pteriinae. *Ahtioconcha* Öpik, 1931, an early Late Ordovician genus (Fig. 8.2), has a flat or slightly concave right valve. The animal apparently lay tilted strongly to one side, with its posterior projecting out of the sediment at a low angle (Stanley, 1972). Epifaunal pterineids evolved later in the Ordovician, but remained at low diversity until Siluro–Devonian time. Pterioids have, for the most part, been inequivalve,

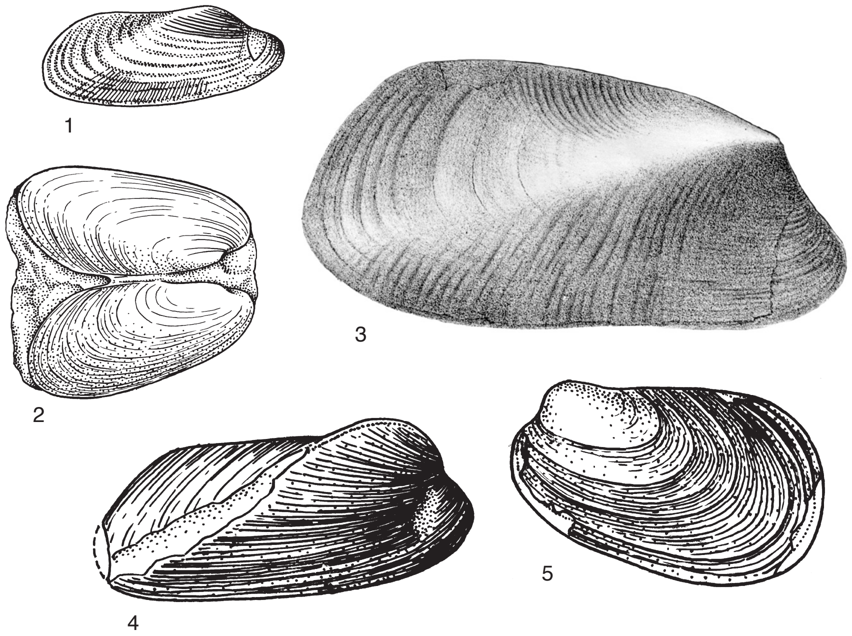

FIG. 6. Elongate Ordovician Modiolopsidae, all of which were endobyssate except *Whiteavesia,* which has morphology of a burrower; *1, Whiteavesia* ULRICH, 1893, ×1 (Ulrich, 1893); *2, Modiolopsis* HALL, 1847, ×0.8 (Ulrich, 1924); *3, Pholadomorpha* FOERSTE, 1914, ×1 (Hall & Whitfield, 1875); *4, Goniophorina* ISBERG, 1934, ×2 (Isberg, 1934); *5, Callodonta* ISBERG, 1934, ×3 (Isberg, 1934).

and it is interesting that this trait evolved very early in the history of the group.

WHY DID LIFE-HABIT TRANSITIONS OCCUR?

What were the relative diversities of bivalve taxa occupying various modes of life in Ordovician time? Obviously, free burrowers predominated at the start, but endobyssate taxa had increased markedly in diversity by the end of the period. Epibyssate taxa arose polyphyletically from endobyssate forms, for the most part late in the Ordovician, and they had not yet attained substantial diversity by the end of the period.

THE INFLUENCE OF PREDATION

To what degree did external factors influence changes in the spectrum of marine bivalve modes of life during the Paleozoic, and to what degree were changes simply the result of evolutionary opportunism—of expansion into new modes of life delayed only by the time required for the key genetic traits that underpinned them to appear and become fixed? The only environmental trends likely to have influenced life-habit transitions for bivalves on a large scale were biological in nature, the chief one being increases in the size and sophistication of predators. Predation plays a major role in the ecology of marine benthos, whereas competition plays only a minor role; heavy predation and frequent physical disturbances prevent resource limitation from occurring, except sporadically and briefly. What particular species, capable of occupying a particular habitat, are present at any given time is heavily dependent on the vagaries of larval transport (STANLEY, 2008).

Maintenance of a stable life position in a medium that is inherently unstable is a major problem faced by macrobenthos occupying soft sediment. Dislodgement creates two risks: being transported to an

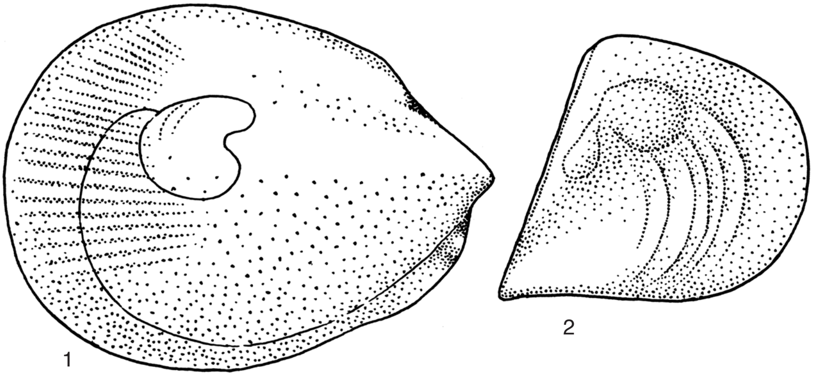

FIG. 7. Two ambonychiids, *1,* endobyssate *Allonychia* ULRICH, 1893, ×1 (Ulrich, 1893), and *2,* epibyssate *Cleionychia* ULRICH, 1893, figured in life position, ×1 (Ulrich, 1897).

unfavorable setting and being exposed to predation. Predation is the greater problem; for an infaunal bivalve that is exhumed, in most marine settings, the risk of death by predation is greater than the risk of death by transport to a hostile physical environment.

Soft-sediment dwellers can minimize the risks of exhumation in two ways: they can be adept burrowers, able to resume an infaunal position rapidly if exposed on the sea floor, or they can employ adaptations to avoid exhumation in the first place. Because early burrowing bivalves were small, shallow burrowers, they were relatively vulnerable to predation *in situ* and were also easily dislodged and transported by strong water movements. Generally lacking extensive mantle fusion as well as siphons, they were also typically sluggish burrowers. Modern nonsiphonate burrowers (such as *Noetia* GRAY, 1857; *Astarte* SOWERBY, 1816 in 1812–1846; and *Venericardia* LAMARCK, 1801) commonly require an hour or more to reburrow and sometimes cease burrowing temporarily while only partly buried (STANLEY, 1970). Endobyssate forms have the advantage of being supported by their substratum, but they also suffer the disadvantage of being relatively immobile. Many are unable to reposition themselves if dislodged. Even when not dislodged, if living semi-infaunally, they are highly vulnerable to predation.

As noted above, some burrowing Ordovician bivalves, such as the strongly ovoid cyrtodonts, probably employed weak byssal attachment. Thus, they were not only mobile, but also relatively firmly positioned in the sediment. Like modern sluggish burrowers, those of the Ordovician must often have been partly exposed above the sediment-water interface for long periods of time and, thus, were highly vulnerable to predation. It seems evident that the relatively unsophisticated nature of predation in Ordovician seas permitted the ecological success of early bivalves that were immobile or slow burrowing and that lived semi-infaunally or just below the sediment-water interface.

EXPANSION OF MODES OF LIFE WITH OCCASIONAL REVERSALS.

Although the Bivalvia experienced polyphyletic evolutionary transitions from burrowing to endobyssate habits and from endobyssate to epibyssate habits, there is no reason to believe that any form of selection pressure always favored these particular directional changes. Although epibyssate mytilids evolved in the Paleozoic, a moderate number of endobyssate mytilid species inhabit the modern ocean. Furthermore, because endobyssate morphology is, in effect, stored in the early stages of mytilid development, reversions from

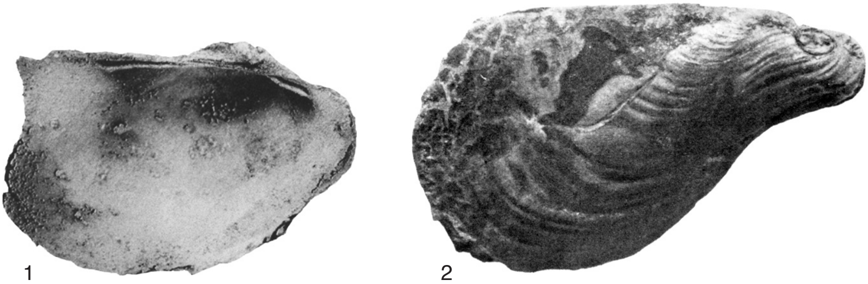

FIG. 8. Ordovician endobyssate pterioids that display conspicuous anterior lobes; *1, Palaeopteria* WHITEAVES, 1897, ×3 (Pojeta, 1971); *2, Ahtioconcha* ÖPIK, 1930, ×1 (Öpik, 1930).

the epibyssate to the endobyssate habit are easily achieved morphogenetically. Similarly, equant, burrowing morphology persists in the early stages of endobyssate carditids, permitting reversion to a free-living mode of life (STANLEY, 1972) (Fig. 9). Reversals of evolution of this sort, although largely undocumented in detail, have clearly occurred quite often in bivalve evolution.

No particular mode of life is always superior to another, and early bivalve evolution did not persistently transform any life habit into a different one. Rather, bivalves have diversified opportunistically, exploiting all modes of life that have become accessible via genetic mutation and recombination. Nonetheless, over the course of Phanerozoic time, certain modes of life have become more successful, on average, than others.

Differences in rates of speciation and extinction among established life habit groups (species selection) have reshaped the overall life-habit composition of the Bivalvia, not massive polyphyletic directional evolutionary trends within lineages (anagenesis). Endobyssate taxa have undoubtedly declined through change in these rates resulting from the appearance of increasingly advanced predators (STANLEY, 1977). Rates of extinction eventually exceeded rates of speciation for sessile, unattached epifaunal bivalve taxa that flourished in the past. Among unattached epifaunal bivalves, only pectinids, which can swim, survive at high diversity today in the face of modern predators (STANLEY, 1986).

MIDDLE PALEOZOIC DEVELOPMENTS

DECLINE OF ENDOBYSSATE TAXA

Between Ordovician and Late Devonian time, endobyssate taxa declined significantly in diversity. They were struck especially hard by the terminal Ordovician mass extinction (FREY, 1987), but they then failed to regain their former diversity during the Silurian, and in fact, declined toward the end of the period. Very few endobyssate cyrtodonts are known from the Siluro–Devonian, and only about a third as many modioliform genera are known from the Devonian as from the Ordovician. Compensating slightly for these declines was the modest diversification of endobyssate grammysioideans (Fig. 10). Predation became increasingly intense by mid-Devonian time, when durophages radiated (SIGNOR & BRETT, 1984), but the decline of modiolopsids during the Silurian likely resulted from an earlier intensification of predation. Semi-infaunal endobyssate taxa are uncommon today, being especially rare in the tropics, where predation is particularly severe (VERMEIJ, 1978). In contrast, many early endobyssate forms commonly lived semi-infaunally, as indicated by restriction of epibionts to the posterior regions of shells and by preservation in life position when killed by catastrophic burial in sediment differing from that which they inhabited.

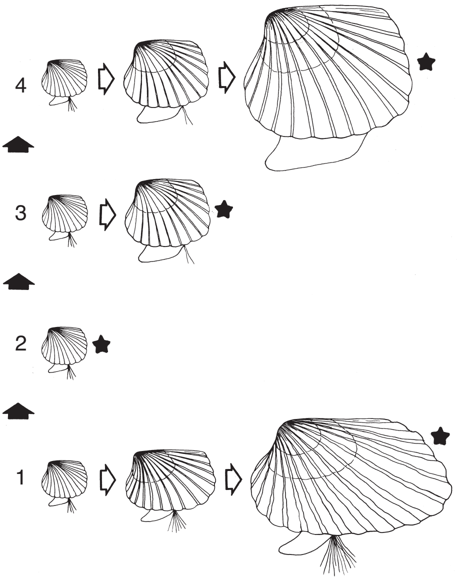

FIG. 9. Schematic view of carditid bivalves, illustrating how equant shape of an ancestral free-burrowing taxon can be retained in 1, elongate endobyssate taxon and then 2, emerge again as adult form via progenesis; 3–4,this transition is followed by evolutionary size increase; horizontal arrows connect stages of ontogeny; stars indicate adults (Stanley, 1972).

A NEW ARRAY OF BURROWERS

Members of the Infrasubcohort Arciidia (orders Cyrtodontida and Arcida) are strikingly rare in Siluro–Devonian strata. Many burrowing cyrtodont taxa appear to have died out in the terminal Ordovician mass extinction, and the group then failed to recoup its losses. New burrowing taxa arose during the Silurian and Devonian, however, and several of these were early representatives of what eventually became large clades: crassatelloideans (Fig. 11.1), myophorid trigonioideans (Fig. 1.2), pholadomyoideans (Fig. 11.3), and lucinoideans. Praecardioideans also diversified modestly in Siluro-Devonian time; initially most were shallow burrowers (although several endobyssate and epibyssate genera, as well as inequivalve recliners, evolved from them) (KŘÍŽ, 1984). The lucinoidean genera, though few in number, had long, elliptical anterior adductor muscles and, like modern lucinoideans, presumably fed via an anterior mucus-lined tube produced by a highly extensible foot. Also, like modern lucinoideans, they presumably expelled water through a single long, slender siphon. As discussed below, they apparently also farmed symbiotic bacteria. They may have been the deepest burrowers of all heteroconchian and pholadomyoidean bivalves during Siluro-Devonian time. The lucinoideans remained at quite low diversity until the Cretaceous, however. I will assess this delay subsequently.

None of the new burrowing taxa became highly diverse during Siluro-Devonian time. As a group, however, they gave shallow-burrowing Bivalvia a substantial representation on Devonian sea floors.

EXPANSION OF PTERIOMORPHS INTO EPIFAUNAL MODES OF LIFE

During the Devonian, a variety of epifaunal pterineids evolved from such endobyssate ancestors as *Leptodesma* HALL, 1883 in 1883–1884 (Fig. 12.1). An inequivalved condition was a key morphological feature of early Pteriinae and also their

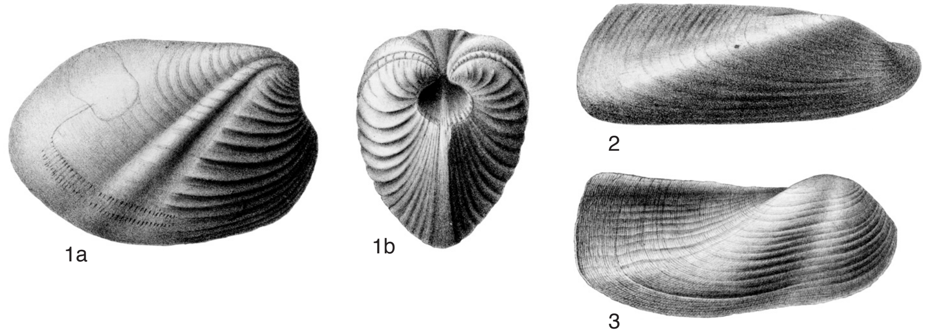

Fig. 10. Three Siluro-Devonian grammysiids that illustrate endobyssate shapes typical of family; *1a–b, Grammysia* Verneuil, 1847; *a,* right and *b,* left lateral view, ×0.7 (Hall, 1885); *2, Grammysioidea* Williams & Breger, 1916, ×0.5 (Williams & Breger, 1916); *3, Cimitaria* Hall & Whitfield, 1869 ×0.5 (Hall, 1885).

descendents within this group, with the less-convex right valve housing a byssal notch and being pressed against the object of attachment. Endobyssate members of this group presumably lived semi-infaunally, with their plane of commisure inclined and the inhalant and exhalant regions of the shell elevated above the surface of the sediment (Fig. 2.8). It is likely that many endobyssate species lived as clusters of mutually attached individuals. The orientation of the shell at a low angle would have reduced the force of strong water currents that might otherwise have torn the animal loose from the substratum.

Many Paleozoic epifaunal members of the Pteriinae possessed an anterior auricle (Fig. 12.2), which, like that of their pectinid descendants, prevented them from being easily overturned by providing two points of shell contact with the solid substratum beyond the site of byssal attachment (Stanley, 1970, 1972) (see *Treatise Online,* Part N, Revised, Volume 1, Chapter 5, Fig. 33). Many Devonian pteriinans also possessed a winglike posterior auricle (Fig. 12). This undoubtedly functioned like the homologous structure of the modern genus *Pteria,* which deflects around the exhalant current any external water currents that flow more-or-less parallel to an animal's commissure, preventing used water and waste from returning to the inhalant region (Stanley, 1972) (see *Treatise Online,* Part N, Revised, Volume 1, Chapter 5, Fig. 36). A posterior auricle was even present in some endobyssate pteriinans that must have lived semi-infaunally, and it must have functioned in the same way.

Although epifaunal pterineids are frequently portrayed as habitual soft-substratum dwellers, this is almost certainly incorrect for the reasons discussed earlier. It is far more likely that these forms attached to solid surfaces, including macroalgae and calcareous structures produced by invertebrates and algae. Presumably, they often nestled in cavities or were partly ensconced in crevices and depressions. Living well above the sea floor reduces the danger of predation. In the modern world, *Pteria,* in its habitual attachment to solid but flexible alcyonarians, is accessible only to nektonic predators. The Mississippian Bear Gulch Formation has yielded a large specimen containing about 100 individuals of the pteriinan genera *Caneyella* Girty, 1909, and *Actinopteria* Hall, 1883 in 1883–1884, attached to the ribbonlike thallus of a kelp-like alga (McRoberts & Stanley, 1989). That *Actinopteria* had only a small, lobate anterior auricle, and *Caneyella* lacked one altogether suggests that these genera were adapted to life on flexible surfaces of this kind, which would have afforded only semi-rigid attachment.

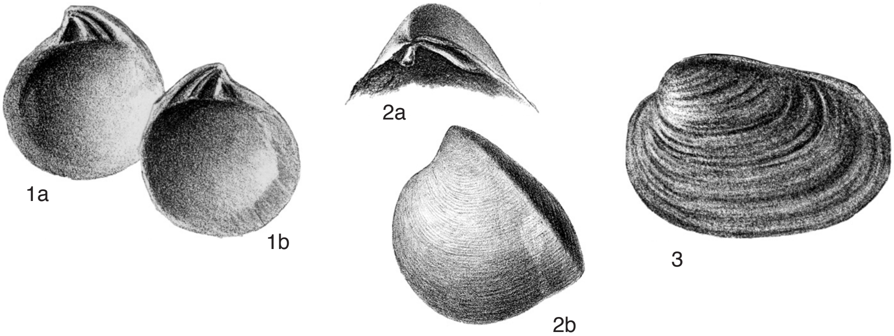

FIG. 11. Burrowing bivalve genera representing new Devonian families; *1a–b, Crassatellopsis* COX, 1951 (Crassatellopsidae), *a,* right and *b,* left valve interior, ×1 (Beushausen, 1895); *2a–b, Eoschizodus* COX, 1951 (Eoschizodidae), *a,* right valve cardinal area and *b,* left lateral view, ×1 (Beushausen, 1895); *3, Edmondia* DE KONINCK, 1841 in 1841–1844 (Edmondiidae), left valve interior, ×1 (Hind, 1899).

Less direct taphonomic evidence supports the notion that epifaunal Paleozoic pteriinans typically attached to solid objects above the sea floor. Whereas endobyssate forms, including modiolopsids, are sometimes preserved in large numbers in shell beds (e.g., LI XING & DROSER, 1999; HOLLAND & PATZKOWSKY, 2004), epifaunal pteriinans are almost always preserved as isolated specimens. Presumably, endobyssate pteriinans commonly lived in colonies and, even if not preserved in place, were sometimes transported short distances en masse before burial. On the other hand, even epifaunal pteriinans that lived in small clusters on calcareous or rocky structures would seldom have been buried together.

THE ADVENT OF UNUSUAL MODES OF LIFE

Two unusual modes of life adopted by bivalves during the Ordovician–Devonian interval have already been discussed. The first was the habit of boring into calcareous substrata by the Ordovician genus *Corallidomus.* The second was the advent of farming of chemosymbiotic bacteria by solemyids and possibly also by early lucinoideans. During the Ordovician–Devonian interval, three other novel life habits have been inferred for some bivalves. One was adaptation to dysaerobic environments, a second was farming of symbiotic algae, and a third was derivation of nutrition from chemosynthetic microbes at hydrothermal vents.

Early Dysaerobic Adaptations

A group of relatively uncommon, thin-shelled Silurian bivalves of small body size (generally <0.5–1.5 cm in maximum length) is commonly preserved in fine-grained offshore sediments with graptolites. These (belonging to the Cardiolidae, Slavidae, and Dualinidae) and the genus *Butovicella* (KŘÍŽ, 1969) (subfamily Butovicellinae, possibly belonging to the Modiomorphidae) have been interpreted as having lived pseudoplanktonically, perhaps attaching to floating algae (WATKINS & BERRY, 1977). As noted earlier, it is likely, however, that these were benthic forms adapted to dysaerobic environments, part of the evidence being their frequent occurrence in dense concentrations.

Early Employers of Endosymbionts

Megalodontids originated in the Silurian or Devonian (Fig. 13) and quickly became some of the largest bivalves that had ever lived, commonly reaching about 30 cm in length. In addition, their beaks attained shell thicknesses up to 8 cm (DE FREITAS, BRUNTON, & BERNECKER, 1993). The maximum size of a bivalve that lacks endosymbiotic nutrition is established by scaling factors. The mass of organic

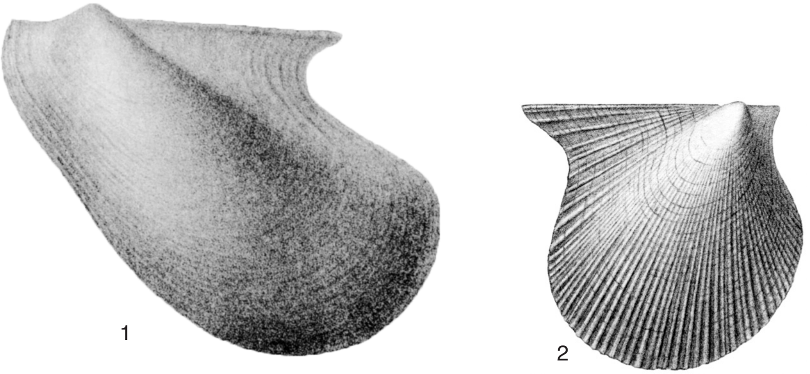

Fig. 12. Morphologies illustrating different modes of life among middle Paleozoic pterineids; *1, Leptodesma* Hall, 1883 in 1883–1884, exhibits anterior lobe and was endobyssate but must have lived semi-infaunally so that concave margin of exhalant region of shell, as well as wing shielding exhalant current, stood above sediment-water interface, ×1 (Newell & LaRocque, 1969); *2, Limoptera* Hall & Whitfield, 1869, epifaunal form with short anterior auricle that would have prevented overturning when animal was attached to a solid object, ×1 (Hall, 1884).

tissue requiring food increases with the cube of linear dimensions, as does the mass of the shell, which requires energy for growth, whereas the organ providing the food of a suspension feeder is a planar gill, the area of which increases only with the square of linear dimensions. As body size increases, the cube-square relationship at some point establishes a limit for growth. Preservation of megalodontids in life position shows that they usually lived in carbonate sediments with their anterior-posterior axes at a high angle, stabilized by their heavy beaks (De Freitas, Brunton, & Bernecker, 1993). They lived semi-infaunally with the posterior portion of their shell projecting above the substratum. The strongly prosogyrate shape of the megalodontids provided the beneficial positioning of the widest gape in the inhalant region of the shell instead of along the ventral region (Fig. 13).

Modern lucinids farm sulfide-oxidizing bacteria, and there is evidence that they began doing so in the Silurian. Nearly all extant lucinids are relatively deep burrowers. Numerous individuals of the Silurian lucinid *Ilionia prisca* (Hisinger, 1938) have been discovered in life position, about 20 cm below the inferred sediment-water interface (Liljedahl, 1992). The anterior adductor muscle was large and elongate, like that of modern lucinids, in which its ciliated surface generates the respiratory current. The form of the mantle cavity of *Ilionia* indicates reduced sizes for the ctenidia and gut, as in modern lucinids; thus, it seems evident that the Silurian genus employed bacterial symbionts (Liljedahl, 1992; Taylor & Glover, 2000).

Early Vent Dwellers

The earliest bivalve occurrence in a hydrothermal vent deposit is of the epifaunal ambonychiid *Mytilarca* Hall & Whitfield, 1869, in the Silurian of the Ural Mountains (Little & others, 1999). Devonian vent-associated bivalves have been the subject of taxonomic controversy, but they appear to include modiolopsids (Little & others, 1999), as well as anomalodesmatids and solemyids (Aitken & others, 2002). The presence of solemyids in early vent habitats is further evidence that this group farmed sulfide-oxidizing bacteria early in their history in sulfide-rich sediments not associated with vents. The fact that several additional groups employed this trophic mode to occupy vent habitats by middle Paleozoic time attests to the opportunism of bivalve evolution.

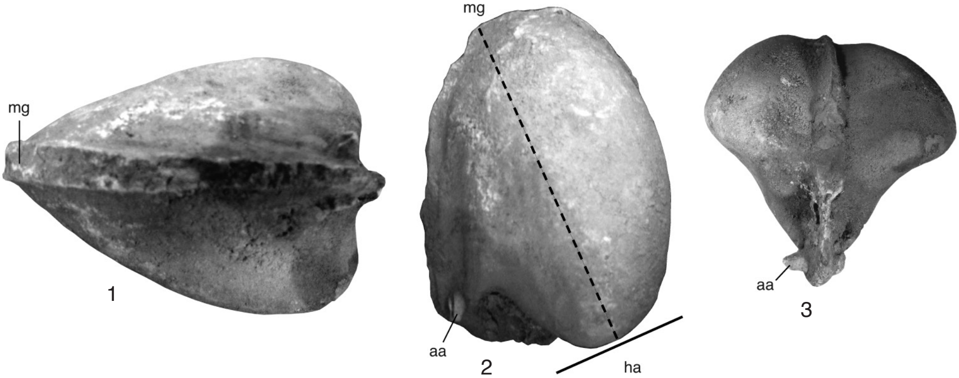

FIG. 13. Interior mold of Silurian megalodontid *Megalomoidea* COX, 1964, ×0.35; *1,* ventral view, showing gape of valves widening toward posterior; *2,* right lateral view in life orientation, showing that prosogyrate shape oriented hinge axis (*ha*) so that maximum gape (*mg*) was in inhalant region of shell margin; *3,* anterior view, with a nearly complete mold of deeply recessed pit (*aa*) that housed right-hand portion of anterior adductor muscle (Stanley, 2011).

Invasion of Freshwater Habitats

Bivalves, in the form of the Amnigenioidea (formerly Archanodontoidea), made their way into freshwater habitats in Late Devonian time, though apparently they rarely or never attained great abundance. These were elongate elliptical bivalves with laterally compressed shells. They survived into the early Permian, at which time they became overshadowed in abundance by the freshwater Anthracosiidae.

THE ISSUE OF PALEOZOIC ONSHORE-OFFSHORE GRADIENTS

A few decades ago, the generalization emerged that pre-Permian Paleozoic marine mollusks, especially bivalves, were diverse and abundant only in nearshore shelf sediments (BRETSKY, 1969; SEPKOSKI & SHEEHAN, 1983). It turns out that this generalization is invalid, however. In the Early and Middle Ordovician (Arenig), more bivalve higher taxa occupied offshore than nearshore facies (MORRIS, 1990). In the Upper Ordovician of the central Appalachians, bivalve diversities are similar for nearshore and offshore communities (BRETSKY, 1969); in the Upper Ordovician of the Cincinnati region, bivalves are much more diverse than brachiopods in clay-rich beds deposited below wave base (FREY, 1987); in the upper Silurian of the Welsh Borderland, bivalve diversity is highest in deep shelf sediments (WATKINS, 1978); and in the Upper Devonian Catskill Delta, bivalve and brachiopod diversities follow similar nearshore-offshore patterns, with both groups being most diverse in shelf, not nearshore, facies (THAYER, 1974). It is true that among brachiopods only linguloids and a few articulate taxa (mostly rhynchonellids) were able to occupy nearshore Paleozoic habitats with strongly fluctuating temperatures and salinities, while a greater variety of bivalves were tolerant of these unstable conditions. This, however, does not negate the fact that bivalves thrived at greater diversities in offshore than nearshore environments.

LATE PALEOZOIC DEVELOPMENTS

The mass extinctions of the Devonian had a greater impact than the terminal Ordovician crisis on the ecological structure of the marine ecosystem, especially with respect to the coral-stromatoporoid reef community (DROSER & others, 2000), but both crises modified the life-habit structure of the Bivalvia. The diversification of durophagous predators, which began in the Late Devonian, also altered the relative frequencies of the various bivalve modes of life (Signor & Brett, 1984). In addition, the Late Paleozoic Ice Age temporarily established a new state for the marine ecosystem (Stanley & Powell, 2003; Powell, 2005). With the onset of the ice age near the end of the Mississippian, a major extinction eliminated many marine taxa, striking stenothermal tropical forms preferentially. Until the southern ice sheets shrank in the early Permian (Sakmarian) time, taxa tended to be broadly adapted in an ecological sense, and rates of origination and extinction remained low. Throughout this great ice age, ecological changes in the global bivalve fauna were relatively minor.

FURTHER DECLINE OF ENDOBYSSATE AND EXPANSION OF EPIBISYSSATE TAXA

One of the most conspicuous consequences of the Devonian mass extinctions for the Bivalvia was that very few modioliform bivalves survived into Mississippian time. This life-habit group then failed to rebound, and, more generally, endobyssate taxa were much less diverse in the Mississippian than in the Devonian. This decline likely resulted from the diversification of durophagous predators because, as already noted, endobyssate bivalves were often semi-infaunal in habit and, therefore, highly vulnerable to attack. Even those that were infaunal were relatively immobile.

The difficulties of making a living as an endobyssate organism did not prevent new higher taxa from arising at this grade of evolution in middle and late Paleozoic time. It is striking, however, that several of the higher taxa that originated as endobyssate forms during this interval produced very few genera with this mode of life and quickly gave rise to epibyssate forms that diversified substantially. Examples (with an early endobyssate genus shown in parentheses) are the Mytilidae (*Promytilus* Newell, 1942), Isognomonidae (*Waagenoperna* Tokuyama, 1959), and Bakevelliidae (*Bakevellia* King, 1848) (Stanley, 1972) (Fig. 14). The Myalinidae (Fig. 15) also arose at an endobyssate grade of evolution, apparently having evolved from the Ambonychiidae. Their early (Late Mississippian and Early Pennsylvanian) representatives were probably all endobyssate, but by late Pennsylvanian time, nearly all myalinids were epibyssate (Stanley, 1972). Figure 15 illustrates grades of evolution in the Myalinidae, from forms like the early endobysate *Myalina (Myalina) copa* Newell, 1942, to the epibyssate subgenus *Myalina (Orthomyalina)* Newell, 1942. Juveniles of *M. (Orthomyalina)* closely resemble *M. (Myalina) copa* in form, and ontogenetic changes in its morphology closely resemble the phylogenetic trend that produced it. Clearly *M. (Orthomyalina)* underwent an ontogenetic change from endobyssate to epibyssate habits that recapitulated the evolutionary changes in form and mode of life that led to its existence. The kalenterids (formerly called permophorids) were a relatively small group of late Paleozoic heteroconchs that were unusual in being endobyssate. The Limidae were present during the Mississippian, but like modern limids, they were presumably nestlers.

The one group that arose as an endobyssate taxon and has been confined to this mode of life up to the present day is the Pinnidae, which, being large, elongate animals (Fig. 16), are deeply rooted in the sediment and, when threatened, avoid predators by withdrawing their soft tissue far down into their shell, well below the sediment interface. In addition, they can close the exposed portion of their shell by adducting their thin, flexible valves. The pinnids have avoided extinction, but, having arisen by way of evolution along a narrow, divergent adaptive path, they have never diversified appreciably or given rise to any other life habit group.

Pectinoids in the form of aviculopectinids (Fig. 17.1) radiated conspicuously from Mississippian through Permian time. With characteristically narrow umbonal angles,

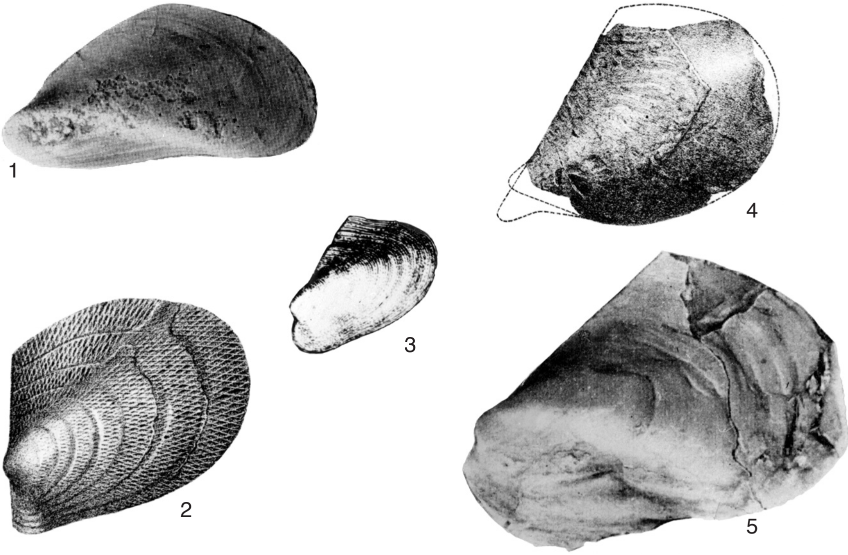

Fig. 14. Paleozoic endobyssate genera that were early representatives of four families within which many epibyssate genera subsequently arose; *1, Promytilus* Newell, 1942 (Mytilidae), ×1.2 (Newell, 1942); *2, Rhombopteria* Jackson, 1890 (Leiopectinidae), ×2 (Barrande, 1881a); 3, *Bakevellia* King, 1848 (Bakevelliidae), ×1 (King, 1850); *4, Waagenoperna* Tokuyama, 1959 (Isognomonidae), ×0.85 (Tokuyama, 1959); *5, Naiadites* Dawson, 1860 (Naiaditidae), ×5 (Newell, 1942).

nearly all were clearly byssate as adults and presumably lived as nestlers (Stanley, 1970) (see *Treatise Online,* Part N, Revised, Volume 1, Chapter 5, Fig. 34). They also possessed a long anterior auricle, which provided firm fixation by positioning two segments of the valve margin beyond the site of byssal attachment (Stanley, 1970, 1972), as it does for modern adult pectinids that are byssally attached (see *Treatise Online,* Part N, Revised, Volume 1, Chapter 5, Fig. 33). Most do not exhibit the auricular asymmetry of byssate pectinids, however, because their posterior auricle is elongate. Like their modern counterparts, they presumably possessed the ability to swim awkwardly via jet propulsion if disturbed. The first entolioid pectinoids appeared in the Mississippian and, though of small size, had relatively wide umbonal angles and nearly symmetrical valve outlines (Fig. 17.2)—features of free-living forms that are adept swimmers. Trueman (1953) showed that the absence of calcification in the large central portion of the pectinoidean ligament results in greater compression and higher efficiency than are provided by ligaments in other bivalves. This produces rapid clapping of the valves for swimming.

The curiously low diversity of arcoids persisted through the late Paleozoic, the only abundant and widespread genus being *Parallelodon* Meek & Worthen, 1866. Some species of this genus closely resemble the modern genus *Arca* Linnaeus, 1758 in 1758–1759, in shape and must have attached to hard surfaces. Like *Arca*, they may have been partial borers into carbonate substrata (see *Treatise Online,* Part N, Revised, Volume 1, Chapter 5, p. 3). Others were small forms that more closely resemble the modern species of *Barbatia* Gray, 1842, and, like it (see *Treatise Online,* Part N, Revised, Volume 1, Chapter 5, Fig. 32), were probably nestlers.

BIZARRE GIANT ALGAL FARMERS

Giant alatoconchid bivalves (Fig. 18), which attained lengths of more than 40 cm, evolved as derivatives of the myalinid Ambonychioidea during the Permian. Their shells are characterized by a flattened ventral region with flangelike lateral extensions consisting of prismatic calcite crystals

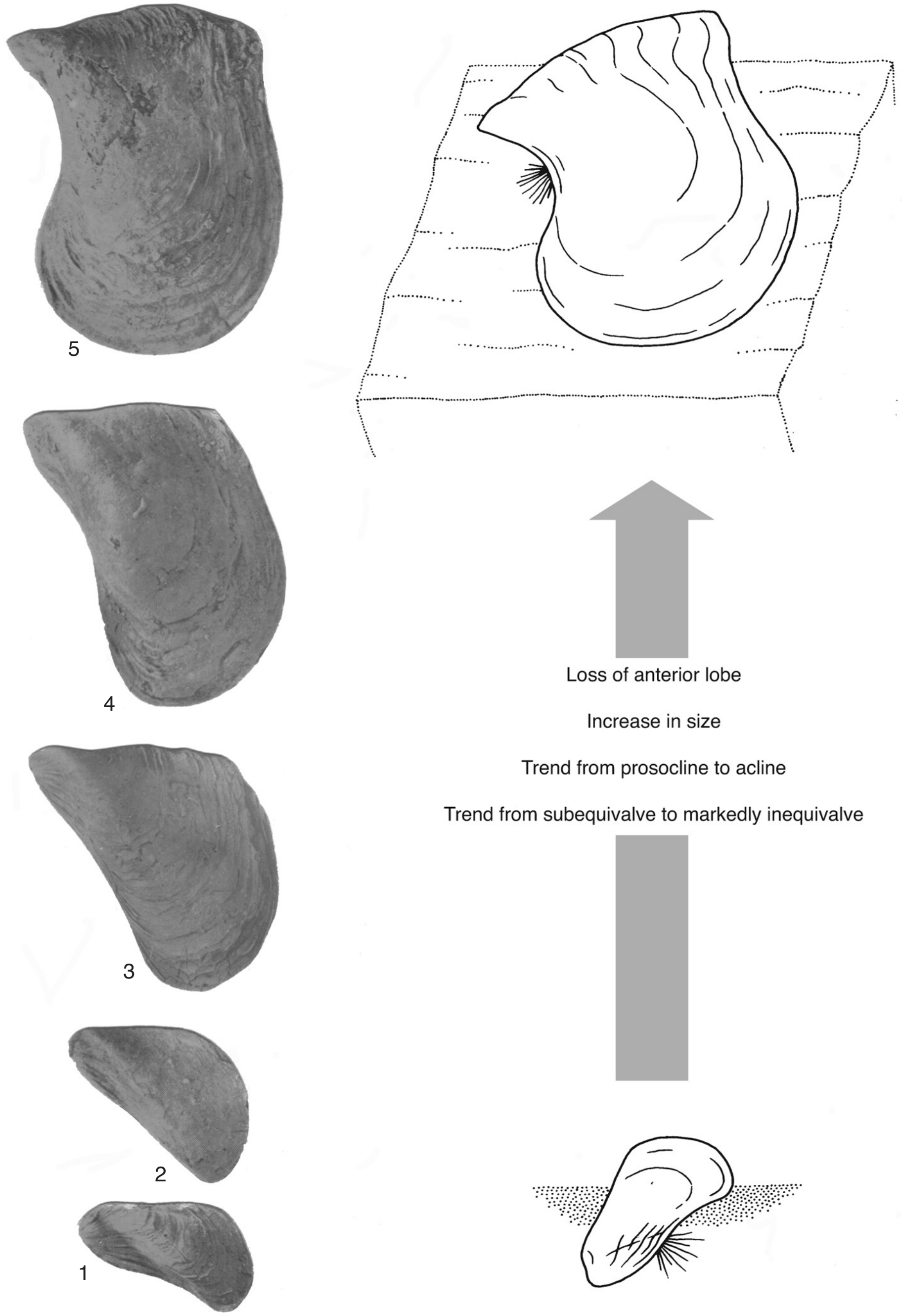

Fig. 15. Grades of evolution in North American Myalinidae between Early Pennsylvanian and early Permian time, illustrating transition from endobyssate to epibyssate habits. Juveniles of *Myalina (Orthmyalina)* Newell, 1942, were shaped like adults of its ancestral subspecies that are assigned to *M. (Myalina) copa* Newell, 1942, and presumably were endobyssate; thus, *Orthomyalina* underwent an ontogenetic shift for from endobyssate to epibyssate habits; *1, M. (Myalina) copa,* ×1.5; *2, M. (M.) lepta* Newell, 1942, ×0.8; *3, M. (M.) wyomingensis* (Lea, 1853), ×0.3; *4, M. (M.) glossoidea* Newell, 1942, ×0.55; and *5, M. (Orthomyalina) subquadrata* Newell, 1942, ×0.6 (Stanley, 1972).

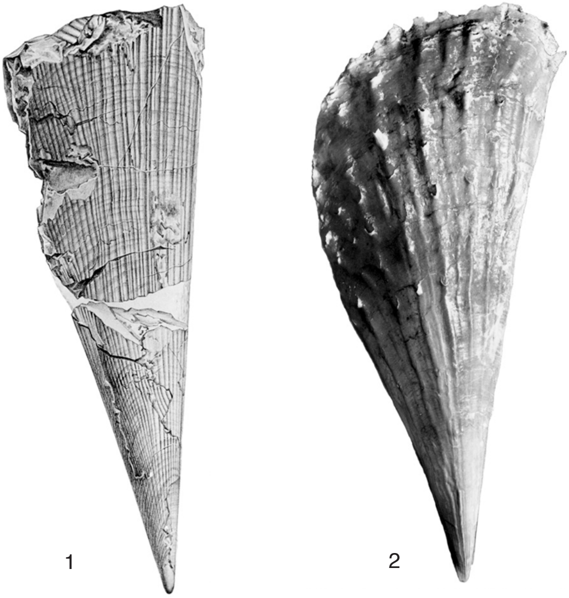

FIG. 16. *Pinna* LINNAEUS, 1758 in 1758–1759 in life position; *1,* Mississippian specimen (de Koninck, 1885); *2,* Holocene specimen (Cox, 1969).

aligned perpendicular to the surface so as to admit light effectively (ALJINOVIĆ, ISOZAKI, & SREMAC, 2008). Alatoconchids's size and morphology indicate that they farmed algae for food. They were restricted to low latitudes.

THE FIRST CEMENTERS

The first two groups of bivalves known to cement to hard substrata appeared in the Permian (NEWELL & BOYD, 1970). Of these, the pseudomonotids failed to survive into the Mesozoic, but the prospondylids (=terquemiids) did persist, to be joined by other cementing bivalve taxa in the Triassic.

EXPANSION WITHIN FRESHWATER HABITATS

The marine to brackish-water Naiaditidae and the freshwater Prokopievskiidae, both members of the superfamily Prokopievskioidea, first appeared in the Mississippian. By the Pennsylvanian, they were accompanied by the Anthracosioidea and possibly also by the Palaeanodontoidea. Although failing to attain high generic diversity, these groups became very abundant in Pennsylvanian coal swamps, where, in some cases, a thick periostracum afforded their shells with protection against acidic conditions (Fig. 14.4). The Permian saw the addition of another freshwater family, the Anadontellidae (superfamily Prokopievskioidea). Presumably, the apparent increase in abundance and diversity of freshwater bivalves in the Pennsylvanian was at least in part a result of preservational bias resulting from the widespread occurrence of coal swamps.

THE INITIAL RADIATION OF SIPHONATE DEEP BURROWERS

As can be seen from the fact that almost 60% of all extant marine bivalve species are siphonate burrowers (Fig. 1), the evolution of ventral mantle fusion, which entailed the formation of a tissue-grade incurrent siphon and permitted more rapid burrowing, was a major adaptive breakthrough in the evolution of the Bivalvia (STANLEY, 1968). Lucinoideans, which apparently had adopted monosiphonate deep-burrowing habits in the Silurian, played a minor ecologic role until the Cretaceous for reasons that will be discussed below. The advantages of ventral mantle fusion in providing for rapid and deep burrowing were extensively exploited in post-Paleozoic time by the heterodonts, but they were first exploited, though to a lesser extent, in the late Paleozoic by the pholadomyoids.

Some Mississippian pholadomyoids, including *Wilkingia* WILSON, 1959 (Fig. 19.2), display considerable anterior reduction of the shell and, like many Devonian grammysiids, were endobyssate. Other Devonian grammysioids, such as *Sanguinolites* M'COY, 1844 (Fig. 19.3), were also elongate but had the shapes of free burrowers. The Lower Mississippian *Promacrus* MEEK, 1871, now assigned to the orthonotoidean family Solenomorphidae, exhibits an elongate, pointed anterior, and its form is that of a relatively adept burrower (Fig. 19.1), but its pallial line is unknown. The first so-called pholadomyoids known to have pallial sinuses are of Pennsylvanian age; these taxa had elongate shapes inherited from endobyssate ancestors. One of them, the pholadomyid *Chaenomya* MEEK in MEEK & HAYDEN, 1865, had a huge posterior gape that, because of its flared shape, must have only partly accommodated very large siphons (Fig. 19.4). Siphonate pholadomyoids did not diversify greatly until the Permian, however. The small grammysioidean family Edmondiidae, which arose in the Early Devonian (Fig. 11.3), included taxa with more equant, venerid-like shapes (RUNNEGAR & NEWELL, 1974). During the Permian, several genera having these morphologies also evolved within the order Hiatellida, in the family Pachydomidae.

WEAK DIVERSIFICATION FOR NONSIPHONATE HETEROCONCHS

The so-called anomalodesmatans—i.e., the ancestral stock group for most post-Paleozoic heteroconchs—had a head start on the later-appearing heteroconchs in the proliferation of siphonate taxa. Heteroconchs remained largely nonsiphonate, and also at low diversity, throughout the late Paleozoic. NEWELL and CIRIACKS (1962) erected the genus *Scaphellina* (family Scaphellinidae, superfamily Trigonioidea) for a curious early Permian opisthogyrate species with a substantial pallial sinus. It has no known descendants.

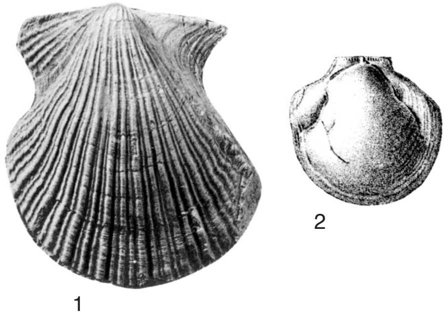

FIG. 17. Pectinoids of Mississippian age; *1, Aviculopecten* M'COY, 1851, endobyssate member of Aviculopectinidae with a narrow umbonal angle, ×2 (Newell, 1938); *2, Pernopecten* WINCHELL, 1865, early member of the Pernopectinidae (superfamily Entolioidea), with a symmetrical shell and wide umbonal angle: features of free-living pectinoideans that are adept swimmers, ×1 (Newell, 1938).

Of the non-anomalodesmatan heteroconchs, only a few schizodid and crassateloidean genera were present in the late Paleozoic and scarcely any early cardiitids. The trigonioid genera *Costatoria* WAAGEN, 1906 (Fig. 20) and *Neoschizodus* COX, 1951, possessed large hinge teeth with secondary dentition. As explained earlier, such teeth indicate that a muscular foot, resembling that of modern *Neotrigonia,* must have been present in Paleozoic taxa that were ancestral to the trigoniids. Late Paleozoic schizodids, which must have been relatively rapid burrowers, began an evolutionary radiation, only to have it interrupted by the Permian mass extinctions.

THE GREAT PERMO-TRIASSIC SEA CHANGE

The compilation of SEPKOSKI (2002) reveals that about 53% of all bivalve genera died out in the Guadalupian, or medial Permian (most in the mass extinction at the end) and 60% in the late Permian

FIG. 18. Anterior view of *Alatoconcha* TERMIER & others, 1974, a Permian genus that farmed algal symbionts within lateral extensions of its shell; this specimen, if complete, would have been about 30 cm wide (Isozaki & Aljimovič, 2009).

(most in the terminal Permian crisis). The numbers for articulate brachiopods were higher, 65% and 93%, respectively. Especially because of the large disparity in the terminal Permian extinctions, bivalves were in a much better position than brachiopods to recover rapidly in the Early Triassic. In fact, studies of silicified faunas reveal that the ecological ascendancy of the bivalves began following the first Permian extinction event, which occurred before the end of the Guadalupian (CLAPHAM & BOTTJER, 2007). This is not to say that bivalves and brachiopods were vying competitively for food or space. First of all, the fact that both groups were housed within two valves had nothing to do with their particular diets or use of ecospace; many other taxa utilized the same resources. Second, as noted earlier, predation, physical disturbance, and the vagaries of larval recruitment play such important roles in determining the distribution and abundance of benthic species in the ocean that interspecific competition is relatively insignificant (see STANLEY, 2008). In fact, the diversity of brachiopods tended to track that of the bivalves during the Phanerozoic (GOULD & CALLOWAY, 1980). Furthermore, the brachiopods made a substantial recovery during the early Mesozoic, but then declined, almost certainly because of the increase in the intensity of predation that occurred during the Mesozoic (STANLEY, 1974, 1977).

A SLOW RECOVERY

The total number of bivalve genera recognized from the Lower Triassic is only about 43% as large as the number known from the Guadalupian. It was not until the Carnian (early Late Triassic) that bivalves regained their Guadalupian level of taxonomic diversity. It is an oversimplification, however, to conclude that the bivalves experienced a single, slow evolutionary radiation throughout the Early Triassic. In fact, the group almost certainly underwent three evolutionary radiations during this interval, each terminated by a mass extinction. This pattern has been documented for both the ammonoids and conodonts, which display it strikingly because of their extremely high rates of speciation and extinction. They attained substantial diversity during each of the three radiations before being decimated (STANLEY, 2009). These crises must have struck all other marine taxa, but have not yet been detected for them because their very low rates of turnover produced much more subdued patterns of diversification and decline than those of the ammonoids and conodonts. Supporting this contention

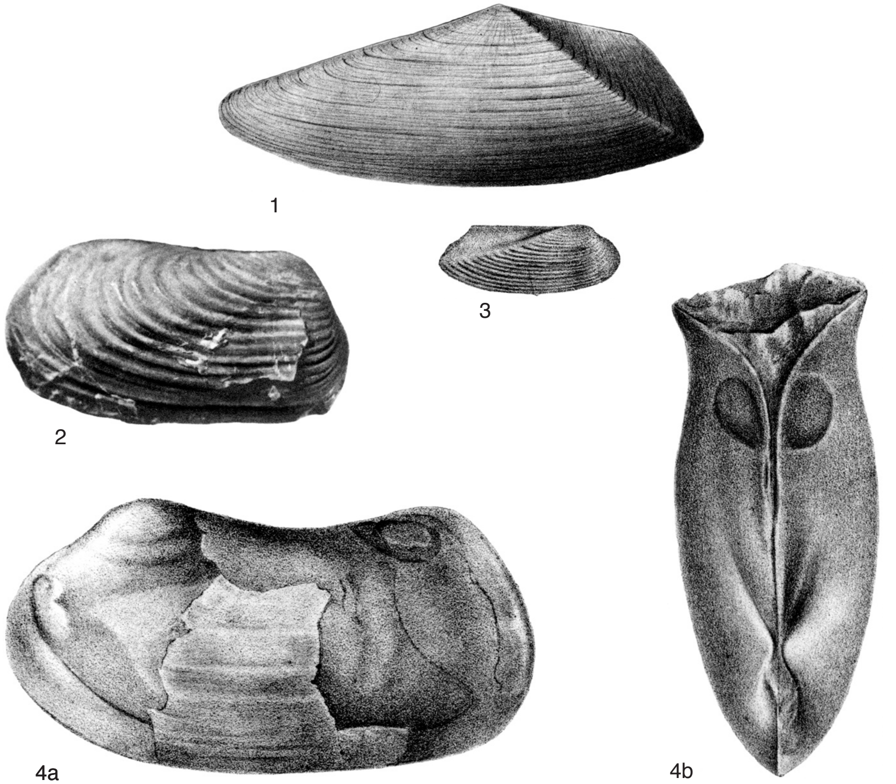

Fig. 19. Late Paleozoic bivalves representing a variety of life habit groups; *1,* solenomorphid *Promacrus* Meek, 1871, Mississippian form with triangular shape of a relatively rapid burrower, ×0.6 (Meek, 1872); *2–4,* so-called pholadomyoids; *2, Wilkingia* Wilson, 1959, endobyssate form with a reduced anterior and shallow byssal sinus, ×1 (Wilson, 1959); *3, Sanguinolites* M'Coy, 1844, shallow burrower lacking a pallial sinus, ×1 (M'Coy, 1844); *4a–b, Chaenomya* Meek in Meek & Hayden, 1865, deep burrower with very large posterior gape and pallial sinus, ×1; *a,* left lateral view; *b,* dorsal view of animal in life position (Meek & Hayden, 1865).

is the fact that the overall percentage of extinction for bivalves in the Early Triassic was nearly four times as high as that for the Anisian and about twice as high as that for the Ladinian. Such high extinction rates following a major extinction are atypical for the Bivalvia; for example, elevated rates did not follow the Late Triassic or Maastrichtian mass extinctions.

DIVERSIFICATION OF THE PTERIOMORPHIA

Of the major bivalve higher taxa, the Pteriomorphia experienced the most impressive initial Mesozoic radiation. They account for more than half of all recognized Triassic bivalve genera, although the Arcoidea continued to remain at low diversity. I estimate that about 20% of Triassic pteriomorphs were epibyssate and that a similar percentage were nestlers. Endobyssate forms comprised closer to 15%. The proliferation of the latter is one of the most striking aspects of the pteriomorphs' Triassic expansion. A second was the proliferation and ecological expansion of epifaunal forms that attached by cementation.

A polyphyletic radiation of small, thin-shelled epibyssate taxa began in the late Paleozoic and included the late Permian pterinopectinoidean *Claraia* Bittner, 1901 (Fig. 21), and a variety of pseudomonotids, posidoniids, dymiids, monotids, and entoliids. Many of these forms occur

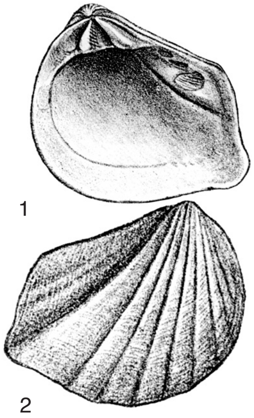

FIG. 20. Permo-Triassic trigonioid *Costatoria* WAAGEN, 1906, displaying large, ventrally directed hinge teeth bearing secondary dention, morphologic features indicating that this form had a large, muscular foot like extant *Neotrigonia* COSSMANN, 1912, *1,* interior or right valve; *2,* exterior of right valve, ×1.6 (Bittner, 1895).

FIG. 21. *Claraia* BITTNER, 1901 a pseudoplanktonic pterinopectinoidean characteristic of Early Triassic deep water sediments, ×1 (Bittner, 1901).

most commonly in deep-water black shales. Although in the past they were widely interpreted to have been pseudoplanktonic, the large majority were apparently benthic forms adapted to dysaerobic conditions (e.g., FISCHER & BOTTJER, 1995; ABERHAN & PÁLFY, 1996).

The Triassic diversification of cemented bivalves was also impressive. Employing cementation for attachment in the Triassic were not only prospondylids (=terquemiids), which had arisen in the early Permian (Fig. 22), but also ostreids, lophids, plicatulids, and dymiids. HAUTMANN (2004) identified the replacement of the lateral ligament by hinge teeth as a key feature of the latter two groups in resisting shearing pressure applied by predators. Some of the new cementing taxa, often in multispecies clusters, formed small reeflike structures (FÜRSICH & HAUTMANN, 2005). The oldest known Triassic bioherms of any kind are in the Lower Triassic of the southwestern United States. They were formed by cementing bivalves tentatively assigned to the anomioidean genus *Placunopsis* MORRIS & LYCETT, 1853 (PRUSS, PAYNE, & BOTTJER, 2007). There is no reason to assume that any global change in the physical environment drove various Triassic groups to attach by cementation. Furthermore, the impact of predaceous crabs, teleost fishes, and neogastropods came later in the Mesozoic. Cementation has inherent advantages, providing greater stability than byssal attachment and yielding spinose and thick-shelled morphologies that are less easily attacked by durophagous predators (STANLEY, 1979; HARPER, 1991). In addition, cementation permits a group of individuals to form a large carbonate buildup for stability. Another important advantage of tight clustering is that it affords protection from predation and boring for animals not exposed at the periphery. This is equivalent to the benefit that fishes gain by schooling.

HAUTMANN (2010) recognized the oldest known pectinid as a Middle Triassic species of *Pleuronectites* VON SCHLOTHEIM, 1820 (Fig. 23.1), and concluded that this form evolved from an aviculopectinoid. *Pleuronectites* had an alivincular-alate ligament and also a ctenolium, which is regarded as a defining feature of the Pectinidae. Several features indicate that *Pleuronectites* was byssally attached as an adult (though presumably possessing the ability to swim if disturbed): the ctenolium, functioning to guide byssal threads (WALLER, 1998); a large byssal notch; an inequilateral shape; and a narrow umbonal angle. It was presumably a nestler. Pectinids diversified only modestly in the Triassic, although the extant byssate nestler *Chlamys* RÖDING, 1798, made an appearance, and the equilateral Late Triassic genus *Indopecten* DOUGLAS, 1929 (Fig. 23.2), has the morphology of a free-living form and would have been a relatively adept swimmer.

MORE EXTENSIVE EXPLOITATION OF FRESHWATER HABITATS

The freshwater unionoids arose in the Triassic and have since experienced a huge evolutionary radiation. The pattern of this radiation is not well known because of the unionoids' relatively poor fossil record, but they clearly attained substantial diversity by the end of the Mesozoic. Unionoids, though suspension-feeders, often crawl about (MCCALL, TEVESZ, & SCHWEIGEN, 1979). This behavior relates to their frequent habitation of coarse, shifting substrata at the bottoms of rivers and streams, which cause frequent dislodgment. It also accounts for the lateral compression that typifies unionoid shells and facilitates their plowing through sediment. Also reducing the resistance of surrounding sediment is unionoids' frequent assumption of a semi-infaunal life position, which is made possible by the dearth of predators in freshwater ecosystems.

The freshwater superfamily Anthracosioidea diversified during the early Mesozoic, adding the family Shaanxiconchidae in the Early Triassic and the family Ferganoconchidae in the Upper Triassic or Lower Jurassic.

A NEW GROUP OF GIANT ALGAL FARMERS

Large megalodontid bivalves that undoubtedly farmed algae persisted into the Triassic, and they were joined by members of a new megalodontoid family, the Wallowaconchidae, which were convergent in form with the unrelated Permian alatoconchids (Fig. 18). The wallowaconchid shell attained nearly a meter in length, with broad, compressed lateral extensions that exposed algal symbionts to light (YANCEY & STANLEY, 1999) (Fig. 24). Vanes divided the interiors of the wings into chambers, which presumably harbored the symbionts.

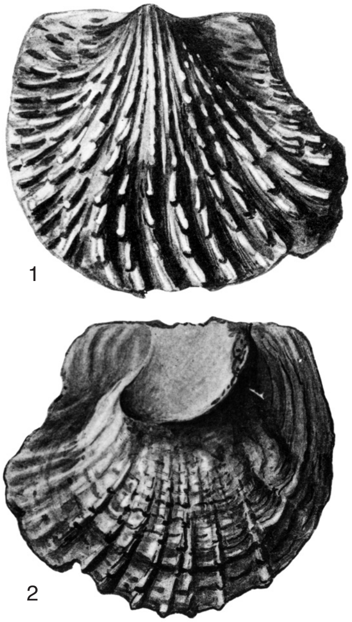

FIG. 22. *Newaagia* HERTLEIN, 1952, Triassic prospondylid that attached by cementation; *1,* right valve exterior; *2,* left valve exterior, showing attachment scar, ×1 (Frech, 1907).

MARINE BURROWERS: RECOVERY OF THE ANOMALODESMATANS AND RADIATION OF THE TRIGONIOIDS

Triassic heteroconch burrowers resemble those of the Permian in their general adaptations. Only a very small number display pallial sinuses, and these embayments are relatively shallow. The tancrediid tellinoidean *Sakawanella* ICHIKAWA, 1950, has the appearance of an adept burrower (Fig. 25.1), but it stands virtually alone in that regard among described Triassic heterodonts.

A large majority of Triassic siphonate burrowers were pholadomyoid anomalodesmatans, despite the fact that the only pholadomyoidean genus documented to have survived the terminal Permian mass extinction is *Chaenomya* MEEK in MEEK &

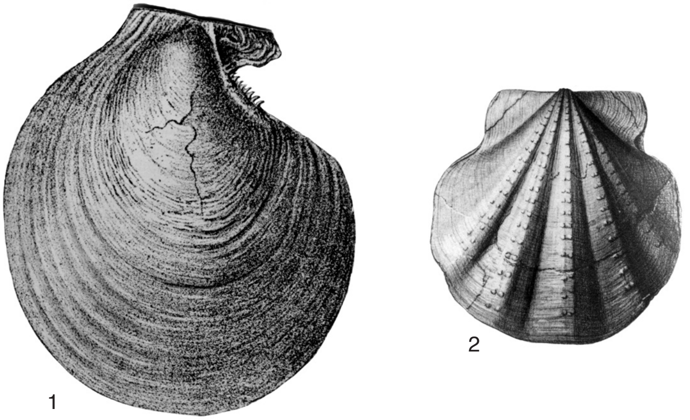

FIG. 23. Two Triassic pectinoidean genera; *1,* pleuronectitid *Pleuronectites* VON SCHLOTHEIM, 1820, oldest known pectinoidean genus, appeared in Middle Triassic and has narrow umbonal angle, large byssal notch, and ctenoleum of a byssally attached form, ×0.7 (Philippi, 1900); *2,* pectinid *Indopecten* DOUGLAS, 1929, which has shape of a free-living scallop that was an adept swimmer, ×0.7 (Krumbeck, 1913).

HAYDEN, 1865 (upper Carboniferous–Upper Jurassic: Callovian). Nonsiphonate genera outnumber pholadomyoidean genera among recognized Triassic burrowers by more than two to one, but a large percentage of the latter were trigonioids.

As previously noted, the trigoniid *Neotrigonia* is an exceptional extant nonsiphonate genus in that it is a relatively rapid burrower by virtue of its thick, muscular foot. As also noted earlier, the large teeth with secondary dentition that are associated with this foot were moderately developed in the Paleozoic taxa that were ancestral to the trigoniids and that began to diversify before being set back by the Permian mass extinctions. Adaptations for more rapid burrowing than was possible for other nonsiphonate bivalves triggered a great Mesozoic radiation of trigonioids. Because of their mobility, trigonioids were able to invade environments characterized by strong water movements, including sites of accumulation of oolitic sands, where exhumation by scour is a constant threat (STANLEY, 1977; FRANCIS & HALLAM, 2003).

CONTINUED RADIATION IN THE JURASSIC

Following the terminal Triassic mass extinction, in which about half of all marine bivalve genera died out (SEPKOSKI, 2002), the Bivalvia resumed their evolutionary radiation. Influencing the pattern of their Jurassic recovery was the impact of newly evolved crabs and boring naticid gastropods (STANLEY, 1974, 1977).

A MODEST EXPANSION OF INFAUNA

The Jurassic radiation of siphonate burrowers differed markedly from that of the Cretaceous and Cenozoic, in that it entailed fewer families. There were proliferations of small, shallow-burrowing arcticoideans (Fig. 26) and larger, deep-burrowing pholadomyoideans. Nonsiphonate trigoniids, for reasons given above, underwent a comparable radiation. Two groups of siphonate heteroconch endoliths, the mechanically boring Martesiinae and the combined chemically/mechanically boring Gastrochaeniidae, also evolved in the Jurassic, and lucinids invaded cold, methane-rich seeps, perhaps for the first time (GAILLARD & others, 1992). Several tellinoidean genera were present in the Jurassic, but none of them resembled the modern Tellinidae in form or adaptations (Fig. 27). For example, *Quenstedtia* MORRIS & LYCETT, 1853 (Fig. 27.1), possessed only a small pallial sinus.

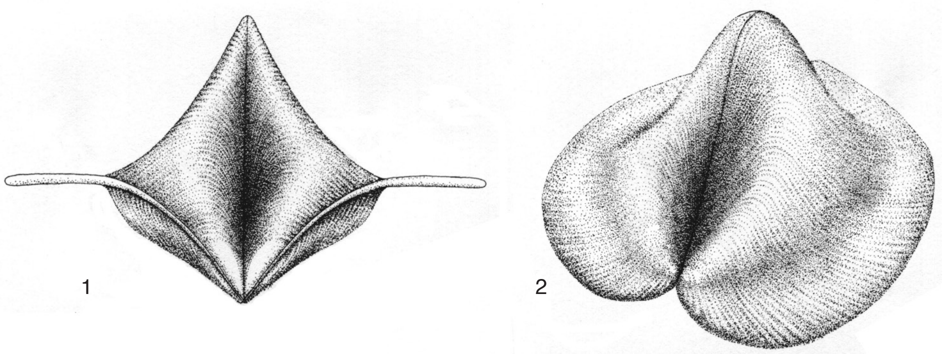

FIG. 24. *Wallawaconcha* YANCEY & STANLEY, 1999, a late Triassic megalodontid genus that farmed algal symbionts within lateral extensions of its shell; adults were typically 30 cm wide; *1,* anterior view; *2,* oblique anterodorsal view (Yancey & Stanley, 1999).

It is likely that Jurassic tellinoids included no deposit-feeders. Unlike most extant tellinids, none were inequivalved, a morphology that would indicate a life position with the commissure positioned horizontally, so that a constant depth could be maintained during the lateral movements required to reach fresh food supplies on the sediment surface (see *Treatise Online,* Part N, Revised, Volume 1, Chapter 5, Fig. 12) (STANLEY, 1970).

THE INITIAL INVASION OF SANDY BEACHES?

A few Triassic genera of the tellinoidean family Tancrediidae, including the previously mentioned *Sakawanella*, have the morphologies of relatively rapid burrowers (Fig. 25). All of these taxa, however, lacked a key feature that promotes rapid burrowing: a severely truncated posterior region of the shell, which in the modern tellinoidean Donacidae and mactroidean Mesodesmatidae positions the hinge axis at nearly right angles to the long axis of the shell, so that a large foot can emerge from the tip of the anteriorly elongate shell, where the gape is widest (see *Treatise Online,* Part N, Revised, Volume 1, Chapter 5, Fig. 1). This morphology, and a shell that tapers in width toward the site of pedal emergence (see *Treatise Online,* Part N, Revised, Volume 1, Chapter 5, Fig. 8), permits donacids and mesodesmatids to wedge rapidly into the sediment via a few downward thrusts, without any need for the rocking motion that most other bivalves employ to burrow (STANLEY, 1970). This behavior permits donacids and mesodesmatids to reburrow rapidly in the surf zone of sandy beach habitats, where they are frequently scoured out by breaking waves. Despite lacking a severely truncated posterior, some Jurassic tancrediids possessed elongate, pointed anteroventral regions, so that they possessed a large foot and, when burrowing, encountered less resistance from sediment than more typical bivalves. Possibly they were the first bivalves with the ability to occupy the surf zones of sandy beaches.

NEW EPIFAUNAL AND NESTLING TAXA

Far fewer Jurassic than Triassic bivalve taxa have been alleged to have lived as pseudoplankton, and as for many small, thin-shelled byssate Triassic taxa found in deep-water black shales, cogent arguments have been made that the similar posidonioideans *Aulacomyella* FURLANI, 1910 (Fig. 28), *Amonotis* KITTL, 1904, and *Posidonia* BRONN, 1828 (a survivor from the Paleozoic) were not pseudoplanktonic. Instead, they are now widely interpreted to have been benthic forms adapted to low-oxygen conditions (FISCHER & BOTTJER, 1995; ABERHAN & PÁLFY, 1996).

Large numbers of limid taxa arose during the Jurassic. Most of them were adapted for loose nestling in protected habitats, but a few,

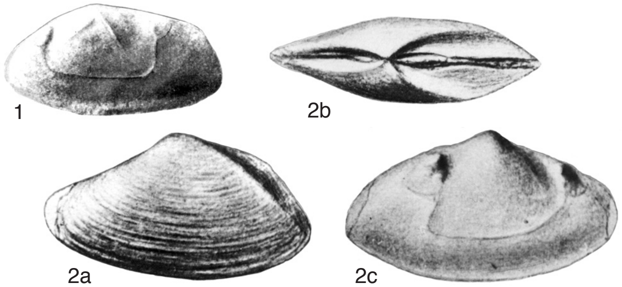

FIG. 25. Two rapid-burrowing tancrediids; *1,* left lateral view of an internal mold of Upper Triassic genus *Sakawanella* ICHIKAWA, 1950, ×1 (Ichikawa, 1950); *2a–c,* Jurassic genus *Tancredia* LYCETT, 1850, ×1; *a,* left lateral view; *b,* dorsal view; *c,* right lateral view of internal mold (Benecke, 1905).

such as *Regalilima* COX, 1943, had a broad, flat ventral region and must have attached epifaunally to hard surfaces. The pectinoids continued to diversify, but not many free-living forms that were highly evolved for swimming made an appearance—*Propeamussium* DE GREGORIO, 1884 (superfamily Entolioidea) being a notable exception. Most Jurassic pectinoids exhibit the morphology of nestlers. *Eopecten* DOUVILLÉ, 1897, was a facultative cementer (HARPER, RADLEY, & PALMER, 1996), and the extant genus *Spondylus* LINNAEUS, 1758 in 1758–1759, arose as an obligate cementer. A variety of inoceramids arose during the Jurassic, some with endobyssate and others with epibyssate morphologies (Fig. 29).

Gryphaeid ostreoideans with reclining modes of life became conspicuous benthos during the Jurassic. Some evolved broad shapes that reduced the likelihood of overturning (HALLAM, 1968).

PRODUCERS OF CARBONATE BUILDUPS

Diceratids and requieniids were inequivalve, coiled hippuritoid rudists of the Jurassic that were cemented by one valve (Fig. 30); rudists had not yet evolved the ability to grow directly upward and form bioherms. However, the pterioid lithiotid (=plicatostylid) bivalves created buildups on tropical lagoonal sea floors in Early Jurassic time, when there were few other hermatypic taxa of any kind. *Lithiotis* GÜMBEL, 1871 (Fig. 31), and *Cochlearites* REIS, 1903, were slender forms, up to half a meter in length, that grew upward in clusters with a portion of their shells stuck in the sediment (CHINZEI, 1982; FRASER, BOTTJER, & FISCHER, 2004). Presumably, these forms were initially byssally attached, but as they grew they relied on support from surrounding sediment. The umbonal regions of *Lithiotis* were cemented to each other and to other shell material to form bouquetlike clusters that often rose substantially above the sea floor. *Lithoperna* sp. BENINI, 1979, was much less elongate and probably remained byssally attached throughout life, living in clusters in which shells projected ~20 cm above the sediment-water interface (Fig. 31). It is likely that the elongate lithiotid bivalves harbored symbiotic algae, with light being transmitted through their very thin free valve (CHINZEI, 1982; FRASER, BOTTJER, & FISCHER, 2004).

THE CRETACEOUS: RADIATIONS OF SIPHONATE INFAUNA

The megaorders Cardiata and Solenata, which include the vast majority of siphonate bivalves in the modern ocean, began a spectacular evolutionary radiation during the Cretaceous. The cardiids and arcticids had an earlier evolutionary start than most other siphonate cardiatan families. By Jurassic time some members of the Cardiidae had evolved large, projecting lateral teeth (Fig. 32), which indicate the evolution of a muscular

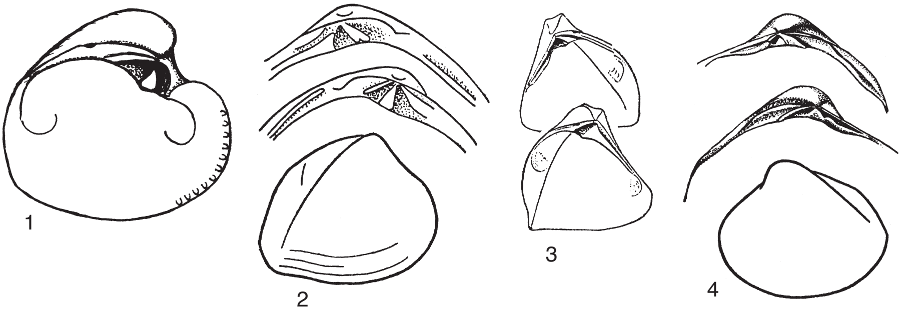

Fig. 26. Shallow-burrowing Jurassic arcticoideans; *1, Coelocyprina* Douvillé, 1921, ×0.7 (Douvillé, 1921); *2, Plesiocyprina* Fischer, 1887 in 1880–1887, ×1.7 (Fischer, 1880–1887); *3, Pronoella* Fischer, 1887 in 1880–1887, ×0.7 (Cox, 1947); *4, Antiquicyprina* Casey, 1952, ×0.7 (Casey, 1952).

foot similar to that of modern cockles (see *Treatise Online,* Part N, Revised, Volume 1, Chapter 5, Fig. 15): these lateral teeth, like the trigonoids' large cardinal teeth that bear secondary dentition, maintain valve alignment at the wide angles of gape necessitated by a muscular foot (Stanley, 1977). Cardiids diversified substantially during the Cretaceous.

The extant genus *Arctica* Schumacher, 1817, arose in the Early Cretaceous and coexisted with a substantial number of arcticid genera (Fig. 33). Of the three most species-rich cardiatan families in the modern ocean, the Mactridae arose too late to diversify greatly until the Cenozoic, but the Veneridae underwent a substantial Cretaceous radiation, and, during the Late Cretaceous, the Tellinidae expanded to a lesser degree (Fig. 27). Although a few Cretaceous tellinids possessed long siphons, none were inequivalve; thus, all apparently lived with the commissural plane vertical. It is likely that none adopted the deposit-feeding habit that characterizes most extant tellinid species, for which resting on one side facilitates lateral movement at a particular depth to obtain fresh food supplies at the surface (Stanley, 1970). Solenoideans were present in the Cretaceous, but none had the highly elongate or bladelike shapes of the rapid-burrowing Cenozoic genera *Ensis* Shumacher, 1817, *Solen* Linnaeus, 1758 in 1758–1759, and *Siliqua* Megerle von Mühlfeld, 1811.

Clearly, the cardiatan-solenatan bivalves' dramatic outstripping of nonsiphonate infaunal bivalves during the Cretaceous and Cenozoic resulted from the advantages conferred by the fully tissue-grade siphonate condition and other aspects of mantle fusion (Stanley, 1968). Fully tissue-grade siphonate taxa have, in general, been more effective than other bivalves at avoiding predators because of the abilities of some to burrow deeply and many others to reburrow rapidly when exhumed. This was an important advantage during the Mesozoic because of the advent of the more severe predation in the marine realm that resulted from the evolutionary expansion of crabs, predaceous snails, and teleost fishes, which Stanley (1974, 1977) identified and Vermeij (1977) labeled the Mesozoic marine revolution. The trigoniids were the one nonsiphonate group of burrowing bivalves that continued to radiate markedly during the Cretaceous (Guo, 1998). Undoubtedly, this success reflected the trigoniids' capacity for relatively rapid burrowing.

The intensification of predation during the Mesozoic did not induce nonsiphonate and non-fully tissue-grade siphonate infaunal bivalves to grow fully tissue-grade siphons. Rather, preexisting fully tissue-grade siphonate taxa were simply able to flourish to a greater extent than other bivalves in the face of the increasingly severe predation: they enjoyed higher rates of origination and lower

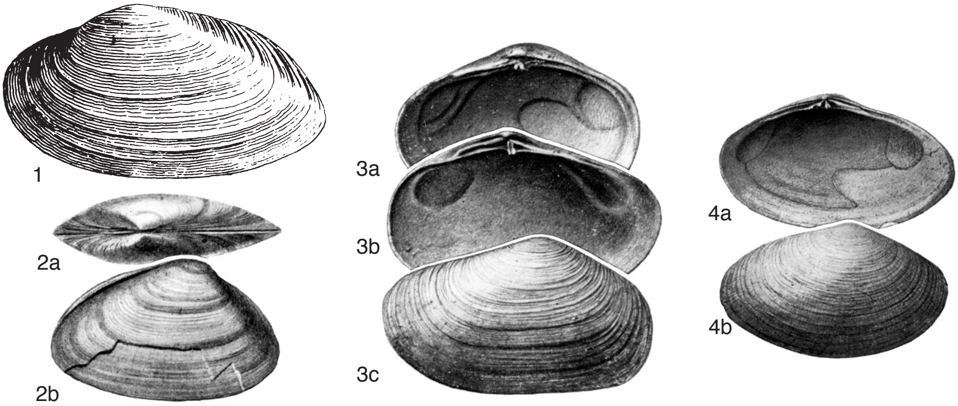

FIG. 27. Equivalbed Mesozoic tellinoideans; *1, Quenstedtia* MORRIS & LYCETT, 1853 (Quenstedtiidae), Jurassic, left lateral view, ×1 (Phillips, 1829); *2–4,* Upper Cretaceous Tellinidae; *2a–b, Tellinimera* CONRAD, 1860; dorsal and right lateral view, ×2 (Gardner, 1916); *3a–c, Liothyris* CONRAD, 1875, *a–b,* right and left valve interior, *c,* left lateral view, ×0.8 (Wade, 1926); *4, Hercodon* CONRAD, 1875, *a,* right valve interior, *b,* right lateral view, ×0.7 (Stephenson, 1927).

rates of extinction. Furthermore, although the conspicuous radiation of the cardiatan-solenatan bivalves during the Cretaceous might appear sudden, it simply followed the pattern of exponential increase that has characterized marine life throughout the Phanerozoic in the absence of mass extinction (STANLEY, 2007). We are accustomed to thinking arithmetically, but exponential increase entails increase measured arithmetically that is initially slow but in time becomes much more rapid, providing many more opportunities for evolutionary innovation. The radiation of carditan bivalves actually began in the Triassic.

In addition to burrowers, fully tissue-grade siphonate bivalves that bored into hard substrata diversified during the Cretaceous. Especially significant was the initial radiation of the Pholadidae, many of which resembled modern forms (Fig. 34). Also, the Clavagelloidea and Gastrochaenoidea, some of which occupied calcareous tubes, made an appearance.

WHAT HAPPENED TO THE MEGAORDER POROMYATA?

Why, given their evolutionary head start as a siphonate group, did the pholadomyoideans, the basal members of megorder Poromyata, fail to match the cardiatan-solenatans' post-Paleozoic radiation? It seems likely that the diversification of the pholadomyoideans was limited by morphological specialization. Only thin-shelled, elongate pholadomyoideans with long siphons were present following the Permian mass extinctions. Although not impossible, a transition from this morphology to one in which the shell is more equant in outline, thicker, and associated with shallow burrowing habits, is unlikely. The ceratomyid pholadomyoideans did originate in the Triassic with the latter morphology, but they remained at low diversity until dying out in the Late Jurassic. The remaining Mesozoic pholadomyoideans were specialized as elongate, thin-shelled deep burrowers. The taxa that arose from the Pholadomyoidea are characterized by small shells with unusual shapes and life habits (e.g., the pandorids, lyonsiids, periplomatids, and poromyoideans) or are highly aberrant (e.g., the clavagellids). Because major extinctions constricted their range of morphologies, the Poromyata failed in post-Paleozoic time to radiate on a large scale into the shallow-burrowing adaptive zone occupied so successfully by the cardiatans and solenatans.

CRETACEOUS EPIFAUNAL ADVANCES

OYSTERS AND OYSTER REEFS

The Ostreoidea diversified markedly during the Cretaceous to include about 20 recognized genera. Some, such as the large, compactly coiled *Exogyra* Say, 1820 (Fig. 35), and the elongate, curved *Agerostrea* Vialov, 1936, and *Arctostrea* Pervinquière, 1910, were cemented briefly as juveniles but then became free-living recliners. *Exogyra* benefited from the evolution of porous, chalky deposits that rendered it less dense than some muddy substrates on which it would otherwise have been unable to recline (Chinzei, 1995). Other oysters were cemented throughout life by an area of the shell that in some species was rather small but in others, quite large. For the first time, ostreoidean bioherms became common features of shallow sea floors. Often, as they do today, these buildups formed in estuarine and lagoonal settings, where fluctuating temperatures and salinities exclude many predators.

GIANT INOCERAMIDS

Inoceramids continued to diversify during the Cretaceous. For example, *Platyceramus* Seitz, 1967 (Fig. 36), became spectacularly large (occasionally greater than 2 meters in diameter) and grew at the very high rate of 5–11 centimeters per year (Kauffman & others, 2007). It could not have grown so rapidly or so large without the assistance of endosymbionts, which were presumably chemosymbionts because the inferred depth of the sea floor occupied by some populations would have precluded highly productive photosynthesis. Like many other inoceramid taxa, *Platyceramus* was adapted to dysaerobic conditions. It has been conjectured that this form was byssally attached with its plane of comissure vertical, but this posture remains to be confirmed (Kauffman & others, 2007). It seems likely that some other inoceramids also employed chemosymbionts, but this remains to be demonstrated.

Fig. 28. Jurassic posidonioidean *Aulacomyella* Furlani, 1910; this small, thin-shelled form is found in deep-water deposits and was probably a benthic form adapted to dysaerobic conditions, ×1 (Furlani, 1910).

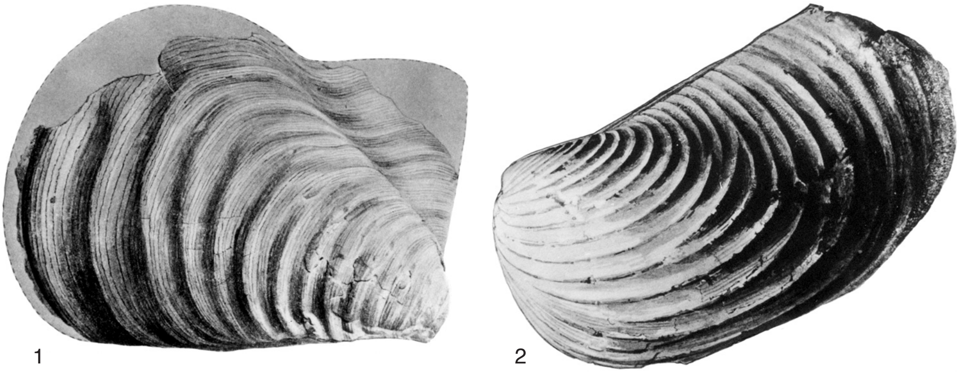

Fig. 29. Jurassic inoceramids with differing life habits, showing inferred life orientations; *1,* right lateral view of *Inoceramus* Sowerby, 1814 in 1812–1846, an epibyssate form, ×0.5 (Woods, 1912 in Woods, 1899–1913); *2,* left lateral view of *Cataceramus* Cox, 1969, endobyssate form, ×0.5 (Böhm & Heim, 1909).

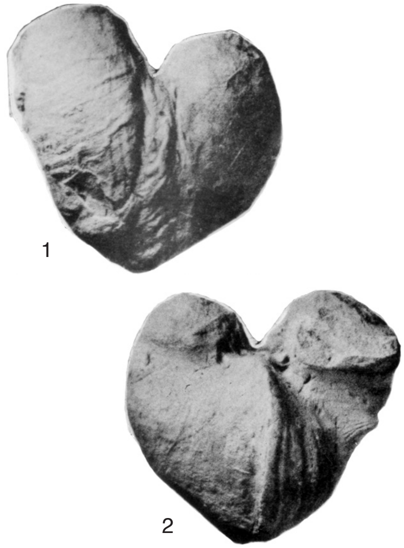

FIG. 30. Jurassic hippuritoid *Eodiceras* PCHELINTSEV, 1959, was cemented by left valve, which is slightly larger than right valve; members of this group are inferred to have farmed endosymbiotic algae; *1,* dorsal view; *2,* ventral view, ×1 (Pchelintsev, 1959).

RUDIST ELEVATORS

Rudists—primarily Caprinidae, Hippuritidae, and Radiolitidae—became major constructors of carbonate buildups during the Cretaceous. Shortening and invagination of the ligament was the key innovation that allowed rudists to uncoil and grow directly upward as so-called elevators and horn-shaped recliners (Skelton, 1978). Examples of the latter are Titanosarcolites Trechmann, 1924, and Immanitas Palmer, 1928, which grew huge, symmetrical, curved valves in which their soft parts were restricted to a very small space. Most upright rudists lived unattached and packed together, but some attached by cementation as juveniles or throughout life.

The rudists suffered heavy extinction during the episodes of global warming at the transitions between the Aptian and Albian and Cenomanian and Turonian. Following the latter episode, they (especially the radiolitids) underwent a substantial evolutionary radiation, but they declined in diversity and abundance during the Maastrichtian, before dying out in the terminal Cretaceous mass extinction.

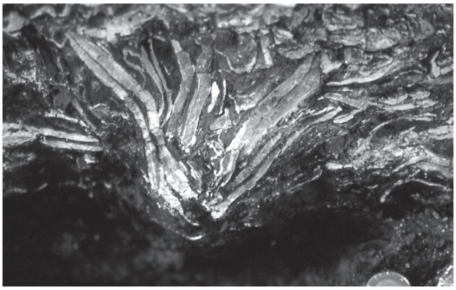

FIG. 31. A fanlike cluster of Jurassic *Lithioperna* ACCORSI BENINI, 1979, individuals cemented together near their umbos; section of coin in lower right indicates approximate size (Fraser, Bottjer, & Fischer, 2004).

It has frequently been contended that rudists replaced corals as dominant reef builders during the Cretaceous, but they most commonly formed broad, low, often monospecific banks that were by no means wave resistant (GILI, MASSE, & SKELTON, 1995) (Fig. 37).

The magnesium-calcium ratio of seawater declined to a low level during the Cretaceous, hindering the precipitation of inorganic aragonite and presumably also the growth of aragonitic coral skeletons. This change of seawater chemistry, which favored precipitation of inorganic calcite, may also have stimulated skeletal production by the predominantly calcitic radiolitid rudists (STEUBER, 2002; HAUTMANN, 2006), but this is dubious because the magnesium-calcium ratio of seawater has not had a powerful influence on molluscan shell secretion (CARTER, BARRERA, & TEVESZ, 1998; STANLEY & HARDIE, 1998).

SELECTIVITY OF THE TERMINAL CRETACEOUS CRISIS

The mass extinction that ended the Mesozoic Era eliminated about two-thirds of all bivalve genera. It changed the ecological composition of the Bivalvia by striking certain higher taxa harder than

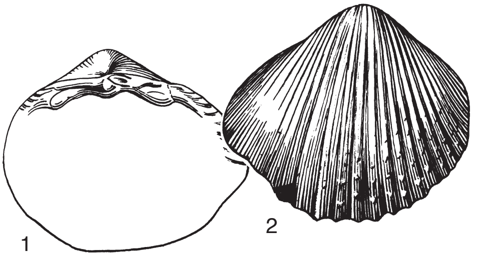

FIG. 32. The cardiid *Incacardium* OLSSON, 1944, possessed lateral teeth that projected far across the commissure, indicating that by Jurassic cardiids possessed a thick, muscular foot; *1,* right valve interior; *2,* lateral view of right valve (Olsson, 1944).

others. Among the epifauna, the rudists, inoceramids, and *Exogyrinae* disappeared, as did several major pectinoid taxa: the Oxytomidae, Entoliidae, Buchiidae, and the *Camptonectes* AGASSIZ in MEEK, 1864, group. Among the infauna, the trigoniids and arcticids, two highly successful Mesozoic groups, barely survived. Had they not suffered such heavy extinction, these two groups would undoubtedly remain relatively diverse today. As it is, each contains just one extant genus (*Neotrigonia* and *Arctica*). Deposit-feeding bivalves survived the crisis preferentially, perhaps because of the collapse of productivity by marine plankton (SHEEHAN & HANSEN, 1986; RHODES & THAYER, 1991; ABERHAN & others, 2007). Lucinids were also nearly unscathed, perhaps for the same reason, because, as will be described more fully below, they derive much of their nutrition from bacterial endosymbionts that convert sulfide in sediments to sulfate.

POOR PRESERVATION OF TROPICAL CENOZOIC FAUNAS

Many estimates of changes in the total number of marine genera through time have been based on the diversities of local faunas rather than on the Sepkoski global database (e.g., ALROY & others, 2008). These studies have ignored biases relating to poor knowledge of Cenozoic diversities in the tropics, where, in fact, the highest diversities occur. Because most modern researchers live in the temperate zone, Cenozoic tropical marine faunas are not well studied. In contrast, because most temperate regions of the modern world were situated in the tropics throughout most of the Paleozoic, most studied Paleozoic faunas are tropical (ALLISON & BRIGGS, 1993). Also, many more aragonitic fossils than calcitic fossils disappear from the fossil record through dissolution (KOCH & SOHL, 1983; WRIGHT, CHERNS, & HODGES, 2003). Because a large percentage of Cenozoic marine invertebrate taxa are bivalves and gastropods, which are predominantly (more than half of total Plio-Pleistocene genera) aragonitic (SEPKOSKI, 2002), the impact of this disparity on the entire marine fauna is much greater for the late Cenozoic than for the Paleozoic (BUSH & BAMBACH, 2004). Furthermore, most tropical marine sedimentary rocks are limestones, in which aragonitic bivalves and gastropods are often unrecognizable (STANLEY, 2007). In comparison, calcitic brachiopods, rugose corals, crinoids, and trilobites are often beautifully preserved on weathered surfaces of Paleozoic limestones. Scleractinian corals, though originally aragonitic, have a better fossil record than mollusks in Cenozoic limestones because, even when altered to calcite, they are usually identifiable at least to genus in thin section.

My yet-unpublished studies of bivalves of the Pliocene Pinecrest Formation of Sarasota, Florida, preserved in quartz sand

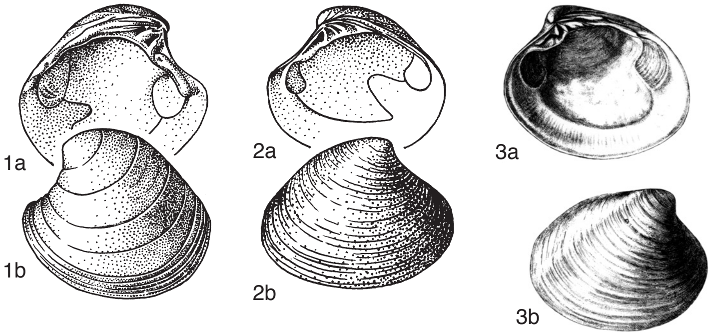

FIG. 33. Cretaceous veneroidean and arcticoidean genera; *1a–b,* meretricid veneroidean *Trigonocallista* RENNIE, 1930; interior and lateral view of left valve, ×0.5 (Woods, 1906 in Woods, 1899–1913); *2a–b,* meretricid veneroidean *Aphrodina* CONRAD, 1869; interior and lateral view of right valve, ×0.5 (Stephenson, 1923); *3a–b,* arcticid arcticoidean *Arctica* SCHUMACHER, 1817; interior and lateral view of right valve, ×0.3 (Wood, 1853 in Wood & Wood, 1848–1882).

rather than limestone, have uncovered about 200 species of bivalves that occupied a single lagoon during a very brief interval of time (even here the fossil record of bivalves, though excellent, is imperfectly known). The associated gastropod fauna, though not thoroughly studied, was even larger. According to the typical gastropod-bivalve diversity ratio of 2.5 for modern tropical regions, the two groups in the Pinecrest lagoon must have included a minimum of 700 species. Inclusion of non-molluscan taxa would expand this total considerably. Local faunal diversities for well-preserved Paleozoic faunas are vastly smaller.

EXPONENTIAL RADIATION OF CENOZOIC CARDIATANS

High Neogene molluscan diversities that are documented by the SEPKOSKI (2002) database reflect huge expansions of both bivalve and gastropod taxa (notably neogastropods) that began radiating during the Mesozoic and renewed their diversification following the terminal Cretaceous mass extinction.

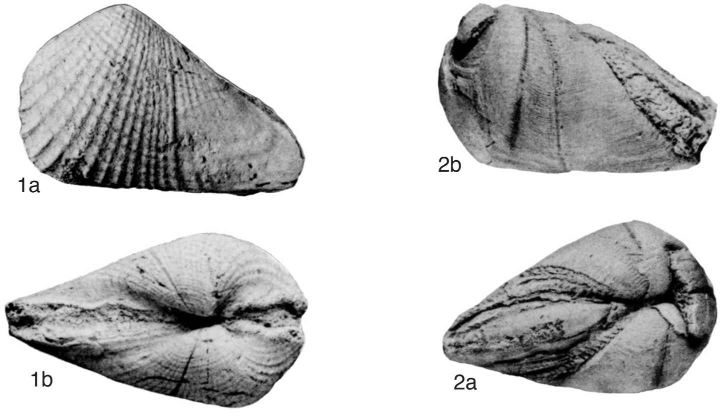

FIG. 34. Boring pholadids that appeared in Cretaceous; *1a–b, Clavipholas* CONRAD, 1868; left lateral and dorsal view, ×1.5 (Stephenson, 1941); *2a–b, Opertochasma* STEPHENSON, 1953; left and dorsal view, ×2 (Stephenson, 1953).

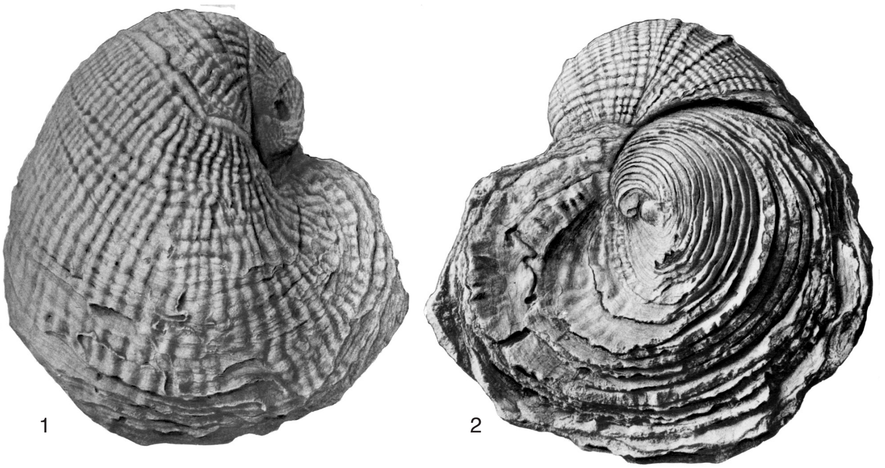

FIG. 35. The reclining coiled oyster *Exogyra costata* SAY, 1820, ×0.8; *1,* left valve; *2,* right valve (Stenzel, 1971).

The most diverse cardiatan bivalve family in the modern ocean is the Veneridae, followed by the Tellinidae and then the Mactridae. As already noted, all of these taxa began radiating in the Mesozoic, with the Mactridae getting the latest start. Like other molluscan taxa that have radiated during the past 100 million years, these groups have expanded more-or-less exponentially, except at times of crisis (Fig. 38–39). As noted above, their diversification was triggered by the evolution of mantle fusion and siphon formation (STANLEY, 1968).

The non-cardiatan family Lucinidae has also radiated since late in the Cretaceous. This is remarkable because it had persisted for about 350 m.y. (since the Silurian) at very low diversity. Only 9 genera are known from the Upper Cretaceous, but 27 are known from the Maastrichtian, 39 from the Paleocene, and 62 from the lower Eocene (STANLEY, 2014). Why did the Lucinidae suddenly begin to diversify so rapidly? Because lucinids supplement nutrition derived from suspension feeding with digestion of endosymbiotic bacteria that oxidize sulfide to sulfate (see TAYLOR & GLOVER, 2000), a large majority of extant lucinid species occupy seagrass beds, which are rich in sulfides (ALLEN, 1958; STANLEY, 1970; JACKSON, 1973; TAYLOR & GLOVER, 2000). A few species also occupy sulfide-rich sediments in the vicinity of mangroves. Molecular clock studies indicate that seagrasses arose and began to diversify in the Coniacian (JANSSEN & BREMER, 2004), and the oldest seagrass fossils are of early Campanian age (VAN DER HAM, 2007). Mangroves, which are polyphyletic, first appeared in the Maastrichtian (ELLISON, FARNSWORTH, & MERKT, 1999). It seems almost certain that the spread of these angiosperm groups, especially the seagrasses, triggered the dramatic radiation of the Lucinidae (STANLEY, 2014).

An interesting feature of the Cenozoic radiation of siphonate burrowers is that after the Paleocene it produced a variety of taxa with discordant ridges (CHECA & JIMÉNEZ-JIMÉNEZ, 2003). In most cases, this ornamentation aids burrowing (STANLEY, 1969, 1970); often the ridges are asymmetric in cross-section, with steep dorsal slopes that grip the sediment during backward shell rotation and gentle ventral slopes that reduce friction during forward rotation. If the ridges are divaricate (see *Treatise Online,* Part N, Revised, Volume 1, Chapter 5, Fig. 3), the anterior and posterior ones alternatively grip and slide; if the ridges are straight, their anterior and posterior portions operate in this way by means of a seesaw motion (STANLEY, 1969, 1970) (see

FIG. 36. Right lateral view of inoceramid *Platyceramus platinus* LOGAN, 1898 (height ~0.9 m), on display at the Sternberg Museum of Natural History; small oysters have colonized shell, especially near beak (new; courtesy of Mike Everhart, Oceans of Kansas Paleontology).

Treatise Online, Part N, Revised, Volume 1, Chapter 5, Fig. 17).

As previously noted, it seems likely that the tellinids did not adopt deposit-feeding habits until the Cenozoic. Even today, some, such as *Arcopagia* LEACH in BROWN, 1827, which have relatively thick siphons and live an essentially immobile life in seagrass (STANLEY, 1970), appear to be obligate suspension-feeders. Even deposit-feeding tellinids are facultative suspension-feeders. Through the Cenozoic diversification of the Psammobiidae and Solecurtidae, the tellinoidean adaptive zone has also expanded to include deep-burrowing suspension-feeders. In addition, as already noted, many donacids are specially adapted for life in the surf zone. Donacids arose late in the Cretaceous but did not diversify markedly until the Cenozoic.

The Mactridae are characteristically rapid burrowers, often having thin, somewhat triangular shells. The Mactroidea, however, also include deeper and somewhat slower-burrowing lutrariinid genera. They also include the Mesodesmatidae, which are convergent in form and behavior with the donacids, as noted above, and, like them, occupy the surf zone along sandy beaches.

The Myidae (megaorder Pholadata) is another Cenozoic taxon that includes deep burrowers. Though not diverse, myids have become abundant in marginal marine environments, most conspicuously in the form of *Mya arenaria* LINNAEUS, 1758 in 1758–1759, the so-called steamer clam. The related Corbulidae have diversified as small, shallow-burrowing forms, many of them occupying fine-grained sediment.

Cardiids have continued to prosper in the Cenozoic, being for the most part very shallow burrowers but also burrowing rapidly by means of their muscular foot and occasionally leaping to avoid predators. Successful new Cenozoic cardiids of this kind were the Fraginae, Laevicardiinae, and *Trachycardium* MÖRCH, 1853, group. Two aberrant genera of the cardiid subfamily Fraginae, *Fragum* RÖDING, 1798, and *Corculum* RÖDING, 1798, derive nutrition from dinoflagellate symbionts.

Cardiid diversification has entailed two spectacular episodes: the remarkable localized radiation of the Lymnocardiinae and the evolution of the Tridacninae (the latter episode will be discussed in the following section). The lymnocardiinids arose in the Pannonic Basin of eastern Europe, where more than 220 species are recognized, ranging in age from 12 to 4 Ma (GEARY, MAGYR, & MÜLLER, 2000). These forms are thought ultimately to trace back to a local population of the extant marine genus *Cerastoderma* POLI, 1795 in 1791–1795. Lake Pannon, in which the spectacular radiation took place, along with a large radiation of byssate dreissenid bivalves, formed as a weakly brackish body of water following a brief connection with the ocean between about 13.7 and 12 Ma. The lymnocardiinid radiation was remarkable in producing a wide variety of morphologies without counterpart in the marine realm.

The most important Cenozoic development for cardiatan borers in hard substrata

FIG. 37. Late Cretaceous rudist biostrome formed by species *Vaccinites vesiculosus* (WOODWARD, 1855); individual shells are typically ~20 cm long (Schumann & Steuber, 1997).

was the great radiation of the wood-boring teredinids after their appearance in the Cretaceous.

CENOZOIC EPIFAUNA

During the Cenozoic, few bivalve taxa have arisen to take the place of the extinct epifaunal rudists, inoceramids, or exogyrines: to be their equivalents in size, morphology, and mode of life. A few Cenozoic species of spondylids, such as the extant Eastern Pacific species *Spondylus calcifer* CARPENTER, 1857d, have evolved to a very large size (approximately 15 cm in width) and live as recliners. Recliners, however, are relatively vulnerable to predation. LABARBERA (1981) reported that fiberglass polyester models of large Mesozoic coiled oysters set out as artificial recliners in modern-day intertidal settings were set upon by voracious crabs, apparently stimulated by no more than the models' appearance. Presumably, early crabs did not inflict such severe attacks on coiled oysters during the Mesozoic. In fact, reclining ostreids were well represented in the Mesozoic, the most abundant being *Gryphaea* LAMARCK, 1801, and *Exogyra*. HAYAMI and HOSODA (1988) showed that when the Pliocene pectinid *Fortipecten takahashii* YOKOYAMA, 1930, reached 7–10 cm in size, it ceased to swim and became a thicker-shelled recliner, with an inflated, *Gryphaea*-like lower valve, but they also concluded that reclining bivalves have been rare in the Cenozoic because of the increased impact of predation.

Tridacnids, which attain great body size and exhibit a very high growth rate, are enabled to do these things by digesting photosynthetic dinoflagellates, which they farm in expanded siphonal mantle tissue. They attach by a thick, pluglike structure formed of bundled byssal threads. They are commonly thought of as epifaunal, but some species are actually partial borers, grinding into the carbonate rock of reef flats with ridged shells. The tridacnid fossil record extends back to the Early Miocene, and eight extant species are recognized (SCHNEIDER & O'FOIGHIL, 1999). The most conspicuous morphological trends in tridacnid evolution occurred during the Miocene; these trends include a huge increase in body size, combined with a marked expansion of the posterior (siphonal) region and

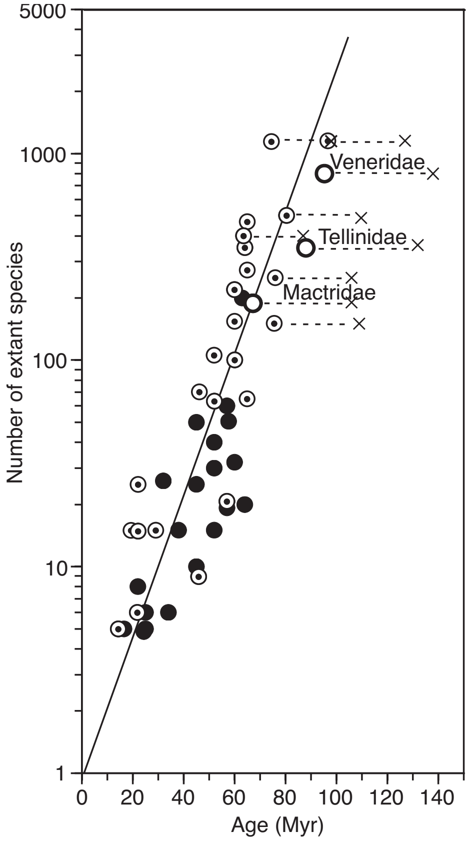

FIG. 38. Semilogarithmic plot depicting data for currently radiating clades of bivalve and gastropod mollusks; number of extant species is plotted logarithmically against time of origin; linearity indicates that radiations have proceeded approximately exponentially at a characteristic rate; large hollow circles represent three most diverse families of infaunal bivalves in modern ocean; filled circles represent other bivalve taxa; dotted hollow circles represent gastropod taxa; dashed lines illustrate shifting of points from their actual positions (X) to adjust for losses in terminal Cretaceous mass extinction (Stanley, 2007).

corresponding reduction of the anterior region, including the anterior adductor muscle (STASEK, 1961).

The most conspicuous evolutionary development for bivalve epifauna during the Cenozoic has been the diversification of pectinids of the *Chlamys* group. Although *Chlamys* itself is a byssate nestler in adulthood, many members of this group mature into free-living forms that are better swimmers than *Chlamys*. A striking change in the evolutionary history of the pectinoideans has occurred since the Mesozoic. Modal duration for Jurassic and Cretaceous pectinoidean species was approximately 20 m.y., whereas it has been only about 3 m.y. for Neogene species (STANLEY, 1986). This reduction in longevity appears to reflect the shrinkage and destabilization of populations that has resulted from increasingly intense predation by boring gastropods, crabs, and teleost fishes—groups whose Mesozoic appearance profoundly influenced the evolutionary history of many types of bivalves (STANLEY, 1974, 1977).

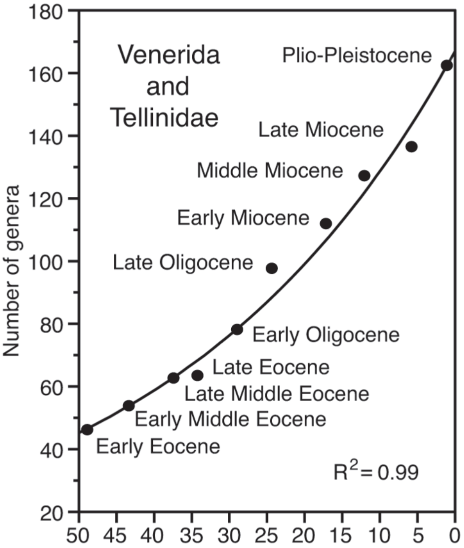

FIG. 39. Exponential increase (fitted curve) for total number of genera of Veneridae and Tellinidae recognized for ends of intervals from early Eocene to Plio-Pleistocene (adapted from Sepkoski, Jablonski, & Foote, 2002; Stanley, 2007).

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