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FORM, FUNCTION, AND EVOLUTION

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CONTENTS

INTRODUCTION

A most challenging aspect of biology is the interpretation of raw data into a meaningful picture of interrelationships between component parts of individuals, various elements of the biota, and the environment that contains them—the field of interpretive biology. The challenge is greatly magnified in paleontologic interpretation, where soft parts, natural biotic assemblages, and total representation of environments are rarely encountered, and the dimensions of time and evolution must be considered. Yet it is in the imaginative interpretation of fossils, and its application to a variety of scientific and philosophical problems, that the great potential of paleontology lies. Interpretive paleontology has gained considerable impetus from the "new systematics" with its emphasis on fossils as biological entities having a given set of soft parts, definite population characteristics, environmentally adaptive morphology, and distinct ecologic relationships. The study of adaptive functional morphology, defining relationships between the animal, its skeletal components, the environment, and the path of evolution, is basic to all paleontologic interpretation.

The Mollusca, and in particular the Bivalvia, are among the best suited of invertebrates for interpretive studies and have been the subject of many pioneer works by neontologists and paleontologists. The following factors contribute to their utility:

1) The molluscan animal shows a wide range of variation in morphology and anatomy, reflecting its successful adaptation to a great variety of habitats. The soft parts of many living mollusks, and in particular Bivalvia and Cephalopoda, are well studied.

2) The soft parts of the Bivalvia are reflected to varying degrees in the morphology of the shell, the two having evolved as an integral unit rather than separate entities. It is thus possible to reconstruct many aspects of the soft body contained within fossil shells, providing additional information for the interpretation of functional morphology, ecology, and evolutionary trends in ancient forms.

3) The shell of the Bivalvia commonly reflects, in its varying shapes and structures, the preferred habitat and mode of life of the animal (Fig. 87). Once defined for living Bivalvia, the shell-habitat relationships may be used extensively in the interpretation of evolutionary trends as a response to changing environment or habitat or both.

4) The ecology of living Mollusca has been better documented than for most phyla of invertebrates, and this information is directly applicable to the interpretation of paleoecology, environmental selectivity in evolution, and adaptive value of morphological and anatomical features. The Bivalvia are probably better known than other classes of mollusks, but in total, the ecologic information for many taxa is still insufficient for detailed interpretive studies.

5) The Mollusca have had a long and successful evolutionary history. They are among the principal invertebrates in many Paleozoic rocks, and dominate most Mesozoic and Cenozoic deposits. The Bivalvia follow this trend, having undergone several successful periods of adaptive radiation, and are now at a peak in their evolutionary history. Many lineages can be traced well back into the Cenozoic, and many modern families had their roots in Mesozoic or older rocks. Numerous genera extend back at least to the Cretaceous. It is therefore possible in many Bivalvia to make direct comparisons between Recent and fossil anatomy and morphology—the ideal situation in interpretive studies.

6) A great deal of adaptive homeomorphy has taken place in the evolutionary history of the Bivalvia, so that even in distantly related bivalves, similar (convergent) shell structures or forms are produced in response to the same environmental controls. It is thus possible to interpret the functional morphology of many extinct groups in light of its adaptive value in living homeomorphic counterparts. This is a much neglected aspect of interpretive paleontology that can greatly enhance intensive study of Paleozoic bivalves.

7) Bivalves are common and normally well-preserved fossils, especially those with calcite shell layers, and it is possible to collect populations of species showing the es-

sential morphologic features for interpretive studies in beds of all ages.

8) The majority of living Bivalvia are, wholly or in part, marine shelf dwellers, and easily available for *in situ* study. Many can be raised and observed under laboratory conditions, providing an easy method of obtaining data on the functional aspects of morphology which can be related to fossils.

CONCEPTS AND METHODOLOGY

A clear set of procedures for collecting and analyzing data in multifaceted interpretation has not yet been devised owing to its youthful stage of development in invertebrate paleontology. The current methodology, the problems set out for study, and the pitfalls encountered are all basic, and pertinent to whatever sophistication the future brings to this phase of the science. It is obvious that interpretive study of fossil Bivalvia, and particularly extinct groups, is a far more complicated process than similar analysis of the living fauna, where one can be certain at the outset of anatomical and environmental characteristics and their relationship to the shell.

DATA COLLECTING

The ability of paleontologists to interpret fossils beyond basic systematics has been hindered by a lack of basic data necessary for complete analysis, or even for the primary job of relating form, function, and habitat. Applicable field data extend far beyond a large collection of well-preserved fossils from rocks of a certain formation and age—the normal information found in collections throughout the world. Three aspects of data collecting deserve special consideration.

The first deals with the fossils themselves. The best base unit for interpretive study of a species is the population, a statistically valid sampling of the gene pool as it is reflected in the preserved fossils. The adaptive value of any structure cannot be fully evaluated for any taxon until its normal range of variation is known, or until it can be determined whether the form of the structure is predominantly a product of genetic or environmental control. It would be meaningless to analyze the functional significance of a flaring auricle on specimens of *Crassostrea* when it could be demonstrated through population analysis in a single oyster bed that this structure was only a variation of the normal shell form produced by crowding; the structure would not be functionally equivalent to the auricles of pectinoids or pterioids. An integral part of defining population characteristics is the study of the animal throughout its range in space and time.

Adaptive features of bivalves related to temperature, salinity, turbulence, or other regionally variable factors of the environment can be detected in fossils only through the study of numerous populations along time planes, throughout the geographic range of the species.

Ontogeny plays an important roll in the study of form, function and environmental relationships. Collections representing the stages of growth are as necessary as those depicting normal adult variations in a species. Changes in growth form, relative development of morphological and anatomical features, and living habit are well known in the life histories of various Bivalvia. For example, numerous Pectinidae are byssally attached during juvenile development, but become free-living forms as adults. These commonly have more inequilateral juvenile shells, with relatively enlarged auricles and a deeper byssal notch than found in the adult stage. Thus the functional significance of form and structure changes markedly with growth, necessitating study of all ontogenetic stages.

If development of a morphologic or anatomical feature can be intimately related to change in life habit during ontogeny, the adaptive value of that developing structure can be interpreted more meaningfully as structural and environmental changes are studied concurrently. Such analysis may provide a key to the functional adaptations of extinct bivalves whose characters are reflected in the ontogeny of living species.

Much is to be gained in interpretive paleontology by recording the overall com-

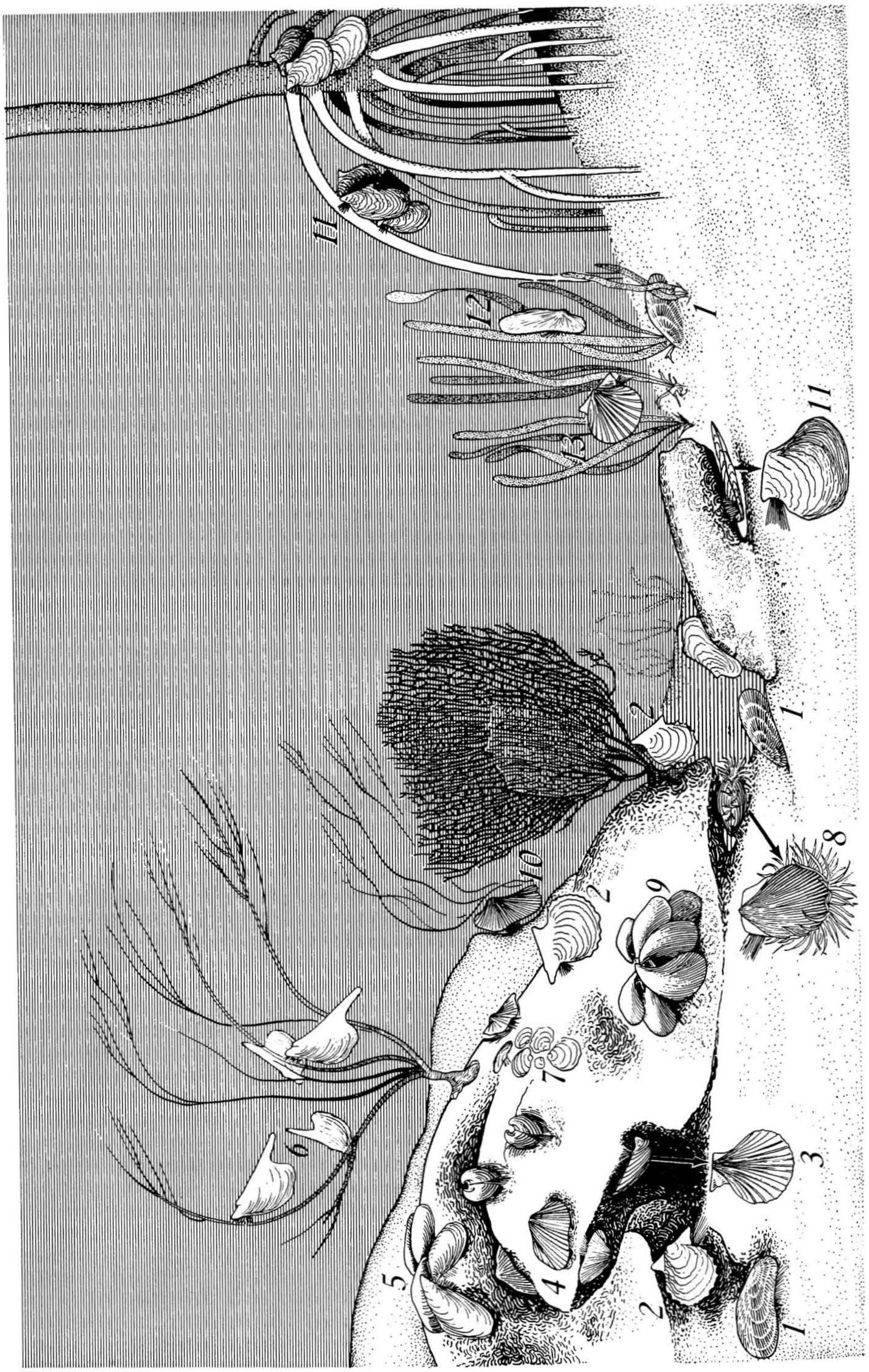

FIG. 87. Habitat and orientation of byssate epifaunal Bivalvia (Kauffman, n).

position and relative abundance of the biota associated with taxa whose functional morphology is under study. This serves two basic purposes. First, it may reflect environmental control on occurrence of particular taxa, since the entire biota better depicts the physical and chemical aspects of the depositional environment than does a single taxon or a few. Thorough knowledge of environmental influence on a taxon is critical to the functional interpretation of its morphology. Secondly, analysis of associated fossils and their relative state of preservation is useful in determining whether or not the taxa under study are natural associates of the bulk of the biota and of the sedimentary environment with which they occur, or whether they represent introduced, thanatocoenosic elements. The critical implications of this to the interpretation of form and function in fossil Bivalvia, relative to ancient environments, are obvious. Too often this factor has been ignored, and functional interpretation of fossils related to paleoenvironmental situation *not* affecting the animal in life.

The second aspect of collecting data for interpretive studies is the relationship of the fossil to the rock. This again is a frequently neglected observation.

Meaningful study of functional morphology depends upon knowledge of substrate-animal relationships during life. For extant genera and species also occurring in the fossil record this can be accomplished by direct observation of living counterparts, but for more archaic groups of bivalves the paleontologist must rely equally on broadly applicable neontologic data and evidence from fossil-rock relationships to define normal life habit, and subsequently to interpret the functional significance of morphologic features. Conjoined valves of fossil Bivalvia are commonly found preserved in or near living position, but this information is too often lost in collecting procedures. If pertinent observations on the orientation of co-attached Paleozoic Bivalvia relative to bedding had been made more frequently in the past, then the argument might be resolved as to whether forms like *Cyrtodonta* (veneriform), *Cycloconcha* (telliniform), and *Cymatonota* (soleniform) were relatively immobile, semi-infaunal, shallow infaunal, or deep infaunal elements, or vagrant forms. These genera possess many shell features characteristic of living moderate-depth to deep-infaunal bivalves which move infrequently through the sediment, but those whose interior morphology is known have an entire pallial line, probably indicating lack of siphons or short siphons not adapted to deep burrowing. Their living infaunal counterparts all possess siphons at least half as long as the shell.

Observations on the degree of fragmentation, spatial distribution, secondary orientation, and size distribution of various elements in a fossil-bearing deposit yield much data applicable to interpretation of the depositional environment, degree of faunal mixing, and ecologic relationships affecting any taxon. These data are useful in determining the probability of whether or not a particular fossil-sediment association reflects the normal habitat of the animal, and thus the environment to which its anatomy and morphology are adaptive. A highly fragmented deposit indicates considerable transport and reworking, and co-occurrence of fragmented and unfragmented species of the same general resistivity is characteristic

Fig. 87. *(Continued from facing page).*

[Explanation: Shells somewhat enlarged relative to substrate, not necessarily to scale; water depth less than 50 feet, direction of current movement from left to right (modeled mainly from author's observations in nearshore waters east of Florida keys).]

1. Semi-infaunal forms. *Arcuatula* (ribbed modiolid); also *Pinna* and *Atrina* (not shown).

1-2,5,7,9,12. Closely attached forms.——*1. Arcuatula,* also smooth-shelled *Modiolus s.s.* (on rock). ——*2.* Some *Pinctada.*——*5. Mytilus.*——*7. Anomia.*——*9. Brachidontes.*——*12. Amygdalum.*

2-4,8,10-11. Fissure-dwellers.——*2.* Some *Pinctada.* ——*3.* Some *Chlamys.*——*4.* Some *Barbatia,* usually not nestling.——*8. Lima.*——*10.* Some *Arca,* rare and usually not nestling.——*11. Isognomon* (e.g., *I. radiatus*).

2,6,11,13. Free-swinging forms.——*2.* Some *Pinctada.*——*6. Pteria.*——*11. Isognomon alatus* Gmelin.——*13. Leptopecten.*

4,10. Nestlers.——*4. Barbatia.*——*10. Arca.*

of mixed assemblages. Secondary reworking of shells, in many cases into an unnatural environment for the transported species, is commonly indicated by strong linear orientation of shells not in living position, by deposits packed with shells of species not normally crowded or gregarious in their habitat, or by deposits yielding shells of a very narrow size range.

The physical characteristics of fossil-bearing rocks provide a considerable quantity of environmental information necessary to the study of adaptive morphology; this constitutes a third type of basic field data required for interpretive paleontology. Bedding commonly reflects rate, continuity, and energy gradients of deposition. Sedimentary structures such as cross laminations, flow casts, ripple marks, and mud cracks are primary indicators of energy conditions, amount and direction of current and wave action, and water depth. Particle size and mineralogy give important clues to depth, distance from strand, circulation, and energy conditions. Sediment and skeletal chemistry reflect water chemistry and paleotemperature.

Many additional relationships are known; it should suffice to declare that sediment study provides the greatest amount of information concerning environments in which fossil organisms lived. Inasmuch as precise definition of environment is necessary to understand the adaptive value of organic structures, it follows that interpretive paleontology demands equally close field examination of the physical and biotic characteristics of rocks.

COMPARATIVE ANATOMY AND MORPHOLOGY

These are the primary tools of interpretive paleontology, and the degree to which they can be applied to the study of fossil Bivalvia is directly correlative with: 1) the amount of data available on the antomy, morphology, physiology, geographic and ecologic variation, and life habit of living counterparts; 2) the degree to which soft parts, physiologic processes, and environmental preferences are reflected in the morphology of the shell (the common fossil), and how well these relationships are understood; 3) the level of phylogenetic relationship between fossil bivalves and their living counterparts; and 4) the precision with which the paleoenvironment can be defined and compared with that supporting modern counterparts.

At present, the basic anatomy, soft-part and shell morphology, and geographic ranges of the common shelf-dwelling marine, brackish-, and fresh-water Bivalvia are reasonably well documented and these data are directly applicable to interpretive molluscan paleontology. It may be assumed that structures found in common between Recent and fossil Bivalvia probably had similar function(s), especially in phylogenetically related or homeomorphic forms. In general the soft parts and the shell of bivalves have been studied as separate entities by biologists (in particular Yonge, 1952, 1953, *47,* 1958, 1962) and paleontologists. Yet interpretive biology is based on their interrelationship, and conceives the body and mantle-shell as evolving in unity.

Little is known about the physiology, and ecologic or geographic variation of modern bivalves—a considerable gap in the Recent data required for the study of adaptive structures in fossils. Physiological adaptation may be the primary impetus for evolutionary modification to cope better with a given set of environmental conditions. Many questions concerning bivalve adaptation can be answered once molluscan physiology is better studied, such as the relationship of shell structure, mineralogy, and isotope chemistry to the containing environment. The works of Epstein & Lowenstam (1961), Lowenstam (1954, 1960, 1961, 1963), Urey, *et al.* (1951), and others have just touched on this interpretive potential.

Ecologic data of a generalized nature is scattered through the Recent bivalve literature, but is detailed for few species and generally inadequate for comparative studies. Many paleontologists find it necessary to make their own observations of living bivalves *in situ* (Fig. 87). The most neglected aspects of Recent bivalve ecology are: 1) the lack of data concerning behavior; 2) the paucity of community studies and ecologic interrelationships within communities; 3) general lack of knowledge concerning ecological control on morphologic variation; and 4) almost total absence of data on how living communities of animals are reflected in shell accumulations of the substrate (the potential fossil deposits) with which they are associated. The basic premises of paleoecology and environmental interpretation using fossils depend upon clearly establishing these relationships and testing criteria for the recognition of biocoenotic as opposed to thanatocoenotic accumulations, or for dividing mixed assemblages. Establishing natural associations of fossils and environments, picking the "in place" assemblage from the total assemblage of shells in an ancient sediment, is critical to interpreting the adaptive value of structures in fossils and matching the adaptation to the proper paleoenvironment. My own investigations along the Atlantic shelf and in the Caribbean suggest that the majority of sublittoral sediments contain shells representing a mixture of molluscan species naturally associated with the deposit, and forms introduced from other environments; the latter commonly dominate inshore (depths of 50 feet or less), the former dominate offshore.

The soft parts of most living Bivalvia are reflected to a high degree, relative to other shelled invertebrates, in the morphology of the valves: shell form and inflation, muscle insertion areas, characteristics of the pallial line, marginal gapes, dentition, ligamenture, and a variety of interior structures such as platforms, internal ribs, and shallow furrows. Exceptions are forms like *Tridacna* and *Pecten* in which torsion of the animal in evolution has taken place somewhat independent of the shell and these gross anatomical modifications are not well reflected on the valve interiors. This close relationship between soft parts and mantle-shell implies not only that the Bivalvia are well suited for studies of functional morphology, but also that the general characteristics of soft parts in fossils can be accurately deciphered and integrated with shell morphology to allow interpretation of adaptive trends in the entire animal. The intricate relationship between the body of the animal and the mantle-shell in most bivalves suggests that they constitute a single study unit in interpretive paleontology, and have evolved as an integrated whole.

It is strange therefore that the mantle-shell and the soft parts of Bivalvia commonly have been treated as separate but interacting evolutionary phenomena, independently adapting to the same set of environmental conditions (YONGE, 1953, 1958). STASEK (1953) termed this the theory of independent entities and he reviewed its prevalence in molluscan literature. The philosophy of independent entities is expressed in many ways. At least a partial split of malacologists consists of those interested in soft-part morphology, anatomy, and physiology, and those primarily concerned with shell characteristics. Further, single studies of adaptive trends in molluscan evolution commonly deal with the evolution and adaptive morphology of the mantle-shell and the soft body as distinct, unrelated entities (YONGE, 1953). STASEK demonstrated convincingly that the inability of many workers to relate evolutionary trends in the mantle-shell with those of the soft body partially reflects their failure to orient consistently the mantle-shell *relative to* the body and thus develop a uniform system of orientational terms. He described the theory of transformation, and the use of transformation diagrams as a means of relating the body and mantle-shell of Bivalvia. This theory is based on the concept that "comparable regions of the body are always adjacent to comparable regions of the mantle shell, the differences between distantly related bivalves being the result of variation in the relative proportions of body and mantle-shell as a unity" (STASEK, 1963, p. 213). I concur with this philosophy and have utilized the concept of evolutionary unity between body and mantle-shell in a recent interpretive study of Cretaceous *Thyasira* (KAUFFMAN, 1967,*11*).

FUNCTIONAL MORPHOLOGY

Relating soft parts to features of the shell is probably the most critical and basic step in interpreting functional morphology and adaptive evolution in the Bivalvia. It allows partial reconstruction of soft parts and subsequently life habit in fossil forms, and in bivalves of all ages provides a far greater spectrum of data needed for evaluation of evolutionary change. Development of a functional adaptive trait rarely involves only a single structure but rather encompasses a suite of functionally integrated features. It follows that functional interpretation of structures as separate entities is not as meaningful as interpretation based on whole systems of interrelated features—anatomical and morphological. Thus, development of a plicate commissure in evolution of various ostreids does not simply reflect an adaptation to strengthen the shell against current action and predation, but involves interrelated phenomena such as an increase in mantle area and absorption potential, increase in area devoted to sensory perception along the mantle, decrease in gape necessary for feeding without decrease in water intake area (thus providing protection against fouling by large particles), and provides better stability for the shell on its substrate in the face of high-energy environments. Interpretive paleontology must deal with the bivalve—shell and body—as a whole unit to obtain a biologically complete and objective analysis of form and function.

Rudwick (1961, 1964) added considerable impetus to detailed studies of functional morphology with his works on brachiopods and oysters and proposed an orderly process of functional analysis, the paradigmatic method. The four basic steps of this approach have been simply stated by Carter (1967) as follows:

1) *Perception:* detailed examination and comparison of a structure or set of interrelated structures with related living and fossil parallels. From this one or more plausible functions are suggested for the structure.

2) *Specification:* testing suggested functions against idealized structural specifications relevant to each, taking into account the limitations of properties for materials involved. A paradigm, the structure capable of fulfilling the postulated function with maximum efficiency attainable under limitations imposed by the materials, is conceptualized for each postulated function.

3) *Evaluation:* comparison of the observed structure with the paradigm for each postulated function, providing an evaluation of the degree of efficiency with which the structure could have fulfilled each function. This is a measure of the degree of possible functional efficiency.

4) *Interpretation:* choosing the most applicable paradigmatic analysis, that which most closely approaches the structure being analyzed.

This organized and logical approach to the study of form and function in any element of the biota has considerable merit. Its demonstrated success in treating brachiopods and bivalves is strong recommendation for its use in interpretive paleontology generally.

HOMEOMORPHY AND TAXONOMIC LEVELS OF COMPARISON

Critical comparison of structures, or structure complexes, between living and fossil bivalves furnishes the bulk of evidence used in the study of functional anatomy and morphology. The majority of works dealing with form and function in fossil bivalves utilize this principle of direct comparison, but in some cases place more emphasis on phylogenetic than on morphologic ties in interpretation. The degree of attempted interpretation in many cases seems more nearly correlative with close phylogenetic relationship, normally at the generic or genus-group level, than it does with structural similarity. Ladd (1957, p. 32) generally stated this widespread philosophy as follows: "The shape of a fossil shell may be a clue to its environment or mode of life if the shell closely resembles a living species or genus that is restricted to a certain environment. If there is no close living relative, interpretations should be made with caution." Although there is merit to this concept, it partially places emphasis on the wrong criteria as a basis for attempting interpretation, and decreases the potential scope and age span of detailed study in adaptation and functional morphology. Structural similarity, even between unrelated forms, should have priority in interpretation, whether similar whole shells are being compared, or like structures on otherwise dissimilar shells. Only through such a philosophy can the functional significance of spines on productid brachiopods be interpreted from living *Spondylus,* or the protective calcareous cup of various reef-builders—archeocyathids, solitary anthozoan corals, richthofeniid brachiopods, and rudist bivalves—be critically compared.

Comparative anatomy and morphology between closely related living and fossil bivalves can be applied widely as an interpretive concept back to the Cretaceous, and in many taxa to the Jurassic. A few Triassic and late Paleozoic comparisons are possible. Most interpretive studies accordingly deal with Jurassic or younger organisms. Paleozoic and Triassic bivalves are sorely in need of interpretive work, especially basic studies of form and function, and this can be accomplished only by following the leads of NEWELL (1937, 1942) and RUDWICK (1964) in emphasizing morphologic homology over close phylogenetic relationship. In comparative studies treating older fossil bivalves it seems necessary to utilize two working concepts: 1) high-level taxonomic comparison, in particular within the family and superfamily, and 2) recognition and use of homeomorphy in interpretation.

In adaptive radiation, principal anatomical and morphological features, and the fundamental functions they perform, become well defined early in the evolutionary history of a main phylogenetic branch (order, superfamily, or family level), and later diversification of the lineage is concerned with secondary modification of these basic structures and functions to meet small-scale environmental demands of various niches. At higher taxonomic levels, in fact, a close similarity of basic form and function exists among nearly all members of a phylogenetic branch, making it possible to compare with confidence like structures and their functional significance in only distantly related genera of the same family or superfamily. If the family or superfamily conceptually replaces the genus as the main phylogenetic level of comparison in interpretive paleontology, many extinct Paleozoic and archaic Mesozoic bivalve genera can be subjected to critical studies in form and function, adaptive value of evolutionary trends, and paleoecology. *Parallelodon* can thus be interpreted, in detail, in light of the anatomy, morphology, and function in *Arca; Pterinea* can be compared with *Pteria,* and *Aviculopecten* with living pectinoids. In such comparisons, where a considerable amount of geologic time and evolution are involved, some major morphologic differences are expected, and in fact occur, between comparable taxa. However, if functional morphology is studied not as a series of individual interpretations of isolated characters, but rather as interpretation of functionally integrated suites of characters, then a few structural differences between otherwise similar forms do not seriously detract from the sum of applicable data gained by comparative analysis of their entire shells. Determining the functional significance of independent characters is an initial step leading up to determination of interacting character suites, but is not itself a means to an end.

This concept can be expanded to allow comparison between similarly adapted forms belonging to distinct families of bivalves by changing emphasis from broad phylogenetic to homeomorphic relationships. Thus the living habit and functional morphology of Ordovician *Cymatonota* (family Modiomorphidae) can probably be interpreted from living *Solen* (family Solenidae). Although *Cymatonota* probably lacked elongate siphons characteristic of modern "jackknife clams," the sum total of its shell characters, including anterior and posterior gapes, closely resemble those of the elongate, deep infaunal *Solen.* This infers that shells of both genera were similarly adapted to rapid burrowing and an infaunal habitat with the long axis of the shell approximately perpendicular to the substrate, but that *Cymatonota* probably lived with the posterior tip of the shell exposed at the sediment-water interface. CARTER (1967,*4*) has made similar functional comparisons of the spines and concentric lamellae in *Hysteroconcha* (Veneridae) and *Hecuba* (Donacidae), remarkably convergent, unrelated bivalves from opposite sides of the Northern Hemisphere.

These examples demonstrate the broad homology of structures and functions that is common in bivalve evolution. The bivalve shell is a simple and efficient solution to the problem of protecting the soft parts that was derived early in the evolution of the class and has limited diversification potential, compared with something like an arthropod carapace. The basic adaptive radiation of the shell took place early in the Paleozoic, when most of the available marine habitats were explored and partially or wholly occupied. A variety of basic attached epifaunal groups were established in the Ordovician, as were infaunal protobranchs, ancestral lucinoids, and other ecologic groups which, except for an apparent lack of elongated siphons in most genera, had shell characteristics of various living sessile infaunal bivalves (e.g., *Cyrtodonta, Cycloconcha, Cymatonota*) and may have lived mostly buried in the substrate with the feeding margins exposed. Since the early and middle Paleozoic, no great change in these basic, adaptive shell forms has occurred, although some additional types have been added by further radiation (for example, cemented epifaunal elements—ostreids, spondylids, rudists, etc., niches of which during the Paleozoic were largely occupied by brachiopods). Instead, both related and unrelated groups of bivalves have repeatedly developed modified versions of these basic shell forms during radiation into the principal infaunal and epifaunal niches.

The second working concept in comparing the functional anatomy and morphology of fossil and Recent bivalves therefore stresses the study of structures divorced from phylogenetic relationships, within the framework of a classification based on adaptations and ecology. Such an approach takes advantage of widespread homeomorphy of shell features and its interpretive significance in bivalves of all ages. Thus the possible "rudder" function of the subtriangular posterior auricle and extended posterior shell flank in orienting free-swinging, byssally attached, epifaunal bivalves so that the inhalant margins face into the current and exhalant apertures away from it (Fig. 88) can be evaluated on a wide variety of morphologically similar but distantly related fossil and Recent genera. Among these are various Pteriacea (living *Pinctada,* Mesozoic-Cenozoic *Pteria,* Silurian-Mississippian *Leiopteria,* Devonian *Cornellites, Limoptera,* Ordovician-Pennsylvanian *Pterinea*), Mesozoic-Cenozoic Isognomonidae, Cretaceous Inoceramidae, the Pectinidae (living *Leptopecten*) and many others. The zigzag commissure occurs in an equally broad spectrum of taxa, and uniformly seems to be an adaptation to: 1) strengthening the shell during growth; 2) increasing the marginal mantle area, and number of associated sensory perceptors; 3) decreasing the minimum gape necessary for feeding and respiration, thus decreasing the size range of harmful particles able to filter between the valves and enter the mantle cavity, and other functions. Structural homeomorphy provides a successful means of comparing and interpreting form and function on a variety of bivalves without regard to age or phylogenetic relationships. It is one of the most valuable tools of interpretive paleontology, and is particularly applicable to the study of Paleozoic and early Mesozoic bivalves.

CONCEPTS OF ADAPTATION

Prior to documenting relationships between anatomy, morphology, adaptive function, and evolutionary trends in the Bivalvia, the concept of adaptation used here merits brief discussion. The whole problem of adaptation is adequately discussed elsewhere (for example, Pittendrigh, 1958).

Carter (1967) has recently reintroduced and discussed the question of whether or not all structures of an animal and its shell are, by definition, adaptive and functional. This is pertinent to the study of form and function in fossils because there is no way to observe the animal in life other than through its modern counterpart. If, in fact, features of the shell can be demonstrated as being nonadaptive or nonfunctional in living bivalves, these must be defined and avoided in the more subjective paleontologic interpretations.

Carter (1967) and before him others have pointed out that selectively neutral characters are very rare in living animals, and modern evolutionary theory incorporates this observation. Two types of nonfunctional characters are defined however, pleiotropic genetic effects and vestigial effects. Pleiotropic structures are basically formed when one gene locus gives rise to manifold morphologic consequences. Accessory structures formed during evolutionary development of a primary adaptive structure would be considered pleiotropic if they did not have a function or were not beneficial in any way to the animal. Normally, such accessory structures are not detrimental to the animal either, i.e., they are neutral, but it is conceivable that if the adaptive significance of the primary, genetically linked structure was far greater than detrimental effects of secondary structures, these features would not immediately be selected against. Conceivably a single structure will have both advantageous (adaptive) and detrimental effects, but will be retained if the former significantly outweighs the latter.

A second type of nonfunctional character is the vestigial structure, initially developed as an adaptive feature, and later in evolution losing its function due to changes in the demands of the environment or further modification of the animal so that its function is bypassed or replaced. Elongate spines on a hypothetical bivalve, adapted initially for protection against a certain predator who constantly attacked one area of the shell, would become vestigial if that predator became extinct and was not replaced in the area occupied by the bivalve, and if these spines had no other beneficial function. If they were otherwise detrimental they would probably be quickly eliminated from the lineage by natural selection or the stock would become extinct. A variation on the vestigial structure, but having an ontogenetic rather than a phylogenetic connotation, would be a spine formed at the commissure of the bivalve during growth as a support for an outgrowth of the mantle edge acting as a sensory receptor, but with continued growth deserted by the mantle sensor for a newly forming spine at the growing edge. This spine, now a permanent and unused part of the shell, might well be considered ontogenetically "vestigial" if it performed no secondary function. "Organizer" structures, necessary in early ontogeny as a base for the development of adult features, may similarly become ontogenetically vestigial.

The conclusion of most workers has been that nonfunctional structures are too rare and too hard to define, especially on fossils, to give them much consideration in interpretive biology. In fossil bivalves it is probably best to consider all structures functional, and adaptive, unless it can be demonstrated through careful evolutionary study that they are phylogenetically vestigial and on the wane. Few studies to date allow such observations. The lack of an obvious function for a bivalve structure probably reflects our lack of basic data concerning form, function, behavior, and habitat in living forms more than it suggests nonfunctionality.

Although it is conceivable that a bivalve structure may be adapted to a single function, and that this may be unrelated to other functional aspects of the individual, most commonly a structure has more than one known function and closely interacts with other structures, in various combinations (character suites) in performing these operations. It is further valid to define primary and secondary adaptation of structures whose function(s) changes with growth. In the broad sense, all structures of the bivalve shell, no matter what primary function they were selected for, are secondarily functional in providing a protective cover for the soft parts of the animal. Because functional character suites commonly include interacting parts of the shell, mantle, and soft body, total definition of these interacting characters and the intricate relationships they have to the function(s) performed, is commonly not possible in fossils. We are obligated however to utilize fully what characters are preserved for paleontologic interpretation; by critical comparison with the whole living counterpart, and imaginative thinking, reconstruction of complex form and function relationships is often possible in fossil bivalves.

In succeeding chapters dealing with specific structures and their probable function in bivalves, adaptations are listed as primary and secondary. This is basically an ontogenetic classification. Primary structural adaptations are considered as those which develop with growth to adapt the animals better at the time of their formation, to cope with the environment. Secondary adaptations are functions undertaken after the formation of a primary structure that are not necessarily related to the moment of growth but better adapt the entire animal, throughout its existence, to the immediate environment in a way distinct from that of the primary adaptation. Thus, in plicate ostreids and brachiopods, Rudwick (1964) suggested that development of a zigzag commissure has a *primary* function of producing increased sensory perception along the mantle margin, as well as decreasing the gape of the shell, and correspondingly the size range and amount of sediment that can potentially slip between the valves during periods of sensory "scanning," feeding, and respiration, while not decreasing water-intake area. Plicae produced by the continued growth of the zigzag margin are *secondarily* adaptive in strengthening the entire shell, giving it greater stability on the substrate, and possibly preventing encrustation by certain kinds of epibionts. The primary function of a structure produced at the growing edge of the shell may continue throughout life even as the growing edge proceeds beyond it. The shell itself is such a structure, providing needed protective cover at the time of formation and throughout life. Spines or shell flutes adapted to support the animal on the substrate and keep the feeding margin off the bottom are produced at the mantle edge and continue to act in this capacity throughout life of the bivalve. In many cases, primary and secondary adaptations are difficult to define; their definition depends mainly on the detail with which the ontogeny and ecology of the living bivalve is known, and the degree of similarity between fossil and living forms. It may be easier to define the secondary adaptation of a structure whose function at the growing edge of the shell is poorly known.

Primary and secondary adaptation, as used here, does not imply a ranking of the importance of a structure to the survival of the animal, nor does it necessarily suggest which of its functions was the main factor in its natural selection during evolution of the lineage. These are harder and more subjective things to define in Bivalvia than are form and function. Some workers disagree with this, stating that adaptations affecting the animal during growth are the main factors in natural selection. Conceivably however, the plicae produced by the zigzag commissure in certain bivalves (or brachiopods) could have a far greater survival value in certain environments than the mantle folding that produced them, and be the main factor favoring the selection for the crenulated mantle edge and zigzag commissure—the so-called primary adaptations.

This paper is not designed as a complete compendium of functional interpretations given to various bivalve structures. Much of this information lies hidden in otherwise wholly taxonomic studies, or in obscure articles; the job of assembling it has just begun. The man purposes of the paper are: 1) to present a fair representation of current thinking in the field of interpretive paleontology as it applies to bivalves, both in regard to concepts and absolute interpretation; 2) to discuss the principal inferences that have been made concerning the form and function of common structures, both singularly and in adaptive suites in the Bivalvia; and 3) to demonstrate through a select study the potential interpretive value of this discipline in paleontology.

FUNCTIONAL MORPHOLOGY OF BIVALVE SHELL

In paleontology, functional morphology basically involves detailed study of the shell and its component parts, soft parts insofar as they are reflected in the shell, interpretation of probable function(s) for shell structures and soft parts, and reconstruction of the environment—the selective force on morphologic adaptation. These data are then applicable to interpretation of paleoecology, evolutionary trends, sedimentary environment, biogeography, and a variety of other disciplines.

Although Rudwick's (1961) paradigmatic method of analysis suggests a procedure for analyzing the function of single structures in fossils, a broader pattern of analysis has not been defined. To discuss the total aspect of functional interpretation in Bivalvia there must be some ordering of data, a classification of topics and animals. The disadvantages of relating form and function to a system of phylogenetic relationships have been discussed and rejected as too confining on interpretative potential. Form (morphology), habitat (environment), and mode of life (ecology)—the specific adaptation, and the selective factors controlling its existence or nonexistence, are deemed the most important elements in the study of functional morphology, regardless of age and phylogeny. The following discussion is organized within this framework and oriented toward interpretation using the shell, the potential fossil. Form is classified as a series of morphologic features or suites of structures found in major areas of the shell (interior, exterior, commissure, etc.). Environments are classified in terms of their principal components: substrate, energy conditions, salinity, turbidity, etc. Bivalve living habit is divided into broad categories, each containing adaptive groups with certain unique morphologic features. In general, these categories are as follow:

1) Epifaunal Bivalvia (Fig. 87)
    a) Byssate free-swinging forms *(Pteria)*
    b) Byssate, closely attached, exposed forms; solitary *(Modiolus)* and gregarious *(Mytilus)*
    c) Byssate nestlers *(Arca, Barbatia)*
    d) Byssate fissure dwellers (some *Chlamys, Lima)*
    e) Cemented forms *(Ostrea, Chama)*
    f) Free living epifauna; swimmers *(Pecten)* and nonswimmers *(Glycymeris,* in part)
2) Semi-infaunal Bivalvia (Fig. 87)
    a) Sessile *(Pinna, Arcuatula)*
3) Infaunal Bivalvia
    a) Mobile detritus feeders *(Solemya)*
    b) Sessile detritus feeders *(Tellina, Nucula)*
    c) Filter feeders (Veneridae)
    d) Borers *(Lithophaga)*

In many of these categories, the major adaptive features of the soft parts and shell displayed by component taxa are strikingly similar, suggesting that study of the broader aspects of adaptation and functional morphology is a necessary and rewarding prerequisite for detailed studies of form and function. Some of these more generalized features will be treated first.

SHELL AS PROTECTIVE COVER

Because of their relative immobility and general lack of complex sensory receptors compared to the other main classes of Mollusca, the Bivalvia are potentially more subject to harmful influences of the environment, in particular predation, than their relatives. The swimming pectinids and limids are principal exceptions, and both have highly developed sensory areas (tentacles, eye spots) at the mantle edge. NEWELL (1965, p. 1) attributed this condition to secondary evolutionary degeneration from the condition of the hypothetical ancestral mollusk through loss of the head and its complex sensory structures, and general adoption of a passive mode of life in which feeding is accomplished either by filtering of water or sifting of sediment for particulate organic matter. This has limited the evolutionary potential of the group. In shell and body the Bivalvia have evolved along relatively simple themes, and have repeatedly, in unrelated groups, solved the problem of coping with the environment in much the same way.

With simple sensory perception, the bivalve animal probably reacts less efficiently and responds less quickly in advance of impending harm than does a gastropod or cephalopod. Further, it is generally not able to defend itself beyond closing the valve and few forms have escape mechanisms such as swimming or "jumping." Perhaps the study of bivalve physiology and biochemistry will reveal more complex sensitivity and protective chemical response than we are now aware of, but even so, the bivalve occupies one of the most precarious ecologic positions among the Mollusca. Survival of the Bivalvia as an evolutionary experiment, particularly in association with more complex and partially predatory groups of arthropods, cephalopods, and early fishes during the early and middle Paleozoic depended upon a high degree of external protection for the soft body of the animal. This was achieved prior to (in the protomollusk) or early in bivalve development by evolution or modification of the external shell and by adaptation to protective habitats, or both, in particular partial or total burial in the substrate. Most early and middle Paleozoic groups apparently lacked strong siphons but many otherwise show infaunal adaptations and were probably buried up to the feeding margin or had short siphons and were completely infaunal. The earliest known Bivalvia had two-valved, hinged, protective shells, many of them quite strong, and there is no evidence to imply that they did not completely enclose the soft parts. If the earliest history of bivalve evolution were known, we would expect to find grades between a naked or partially shelled protomollusk and completely shelled Bivalvia with soft parts totally contained between the valves, developing nearly parallel in time to the rise of potential predators.

It is obvious that the primary adaptive function of the shell in Bivalvia is protection and that any accessory structure of the containing valves, no matter how complex or for what environmental stimulus it was selected, shares in this protective function as well. Shell spines, possibly adapted primarily for supporting sensory receptors or for support on the substrate, also strengthen the shell and make it more difficult for a predator to get to the soft parts. Plicae produced by growth of zigzag mantle folds at the commissure, possibly adapted primarily for increasing the sensory area of the mantle edge, or as an aid in sediment screening, act secondarily to strengthen the shell and provide additional protection to the soft parts.

All Bivalvia during their ontogeny have a protective shell of two valves which in some groups subsequently becomes greatly modified and reduced so as not completely to enclose the mantle or body or both. In most cases these appear to be secondary modifications of the Bivalvia developed relatively late in evolution. Most forms in which the shell does not completely enclose the soft parts have compensated for this loss of protection by adapting the living habit to deep burial (*Mya:* see Cox, 1968, fig. 1, no. 2) or burial in hard substrate (*Zirfaea: ibid.*, fig. 3), by secreting secondary protective tubes around burrows (*Teredo: ibid.*, fig. 4), by inhabiting deep substrate declivities or building nests (*Lima*), or through other structural and ecologic modifications of the normal bivalve features and living habits.

FORM AND ORNAMENT OF SHELL EXTERIOR

Great diversification in form (shape and convexity), structures, and surface ornamentation of the bivalve shell is apparent from the living and fossil record. This reflects adaptive radiation of the shell and soft parts, in unity, into a considerable variety of aquatic niches. Shell form and exterior morphology are highly reflective of environmental demands and strikingly similar in even distantly related bivalves occupying the same niche. This suggests a closer correlation of form with habitat than with phylogenetic derivation and explains the great morphologic diversity among such highly adaptive groups as the Pectinidae, Ostreidae, and Mesozoic Inoceramidae. Pectinoids range from equilateral, subequally inflated swimmers (*Amusium*) and inequivalve swimmers (*Aequipecten*) and semiburrowers to prosocline, strongly auriculate byssally-attached forms (*Chlamys, Leptopecten*), to irregular oyster-like, cemented shells (*Hinnites*). The Cretaceous Inoceramidae show equivalent variety, ranging from thin nearly equal valves (*Mytiloides*), to highly inequivalve rudist-like shells (*Volviceramus*) and include byssate and nonbyssate lineages. Other families are much more conservative but are found in fewer major habitats. The degree of phylogenetic consistency in morphologic features of the shell, therefore, generally reflects the relative radiation into available aquatic niches; the greatest variety in morphology is directly correlative with the number of distinct habitats occupied. In general, epifaunal groups are more variable than those of the infauna; they are also subject to a greater variety of environmental pressures and available habitats.

Within any given ecologic niche, however, the bivalve shell form is relatively consistent among related and unrelated groups. The outstanding exceptions (e.g., *Tridacna*) do not detract from the general pattern and its application to interpretive paleontology. One and rarely two or three basic designs dominate; each is an efficient solution to a particular set of environmental demands. This tends to support NEWELL's contention that the evolutionary potential of bivalves is restricted (1965, p. 1). The bivalve shell is a simple cover with limited possibilities as to shape and convexity. One or a few basic shell forms were apparently developed early in the evolutionary history of the Bivalvia for each major habitat occupied, and subsequent evolution has only repeated and elaborated on these basic patterns. Relatively few new major specializations such as shell cementation, accessory plates, and severe modification of the shell in certain boring bivalves (e.g., *Martesia, Teredo, Bankia*) or to the bizarre Cretaceous rudists, have developed since early Paleozoic radiation. Thus the adaptive significance and function of thin, streamlined, strongly auriculate, slightly biconvex shells byssally attached to raised surfaces and swinging free to varying degrees in the current (Fig. 87), can be compared critically in such diverse groups as the living Pteriidae *(Pteria, Pinctada),* Pectinidae *(Leptopecten),* Isognomonidae *(Isognomon),* Cretaceous Inoceramidae (some *Mytiloides, "Inoceramus" fibrosus* lineage), and possibly Paleozoic Pterinopectinidae *(Pterinopectinella),* Aviculopectinidae *(Aviculopecten, Girtypecten),* and Myalinidae *(Myalina).*

Many schemes for the description of shell form in the Bivalvia have been presented. That of SHROCK & TWENHOFEL (1953) and NEWELL (1942), based on a series of linear dimensions and angles measured relative to a base horizontal, the hinge axis, has been widely utilized and supplemented by various additional axes, angles, and dimensions (for example, see YONGE, 1955; median axis, anteroposterior axis, demarcation line, etc.). However, attempts to integrate closely shell structures, based on this system of orientation, with features of the soft body have been largely unsuccessful.

STASEK (1963) has shown clearly that soft-part orientation varies independently of valve orientation in the standard system; the maximum length axis of the shell does not necessarily reflect the maximum length axis of the contained body. Thus, statements such as that by PELSENEER (1906) that development of the monomyarian condition in bivalves was accompanied by shortening of the anteroposterior axis and proportional increase in the dorsoventral (height) axis of the body are not necessarily meaningful in that they attempt to relate changes in one system (soft parts) relative to a system of orientation applied to the shell (STASEK, 1963, p. 199). The difficulty encountered in successfully relating evolutionary changes in the distribution of soft parts to modification of the shell described within the standard orientation system has led authors such as YONGE (1953, *47,* 1958, 1962) to envision the Bivalvia as consisting of two separate but interacting entities, the body and the mantle-shell (STASEK, 1963, p. 195). Such reasoning inevitably leads to the study of bivalve evolution from two, unrelated points of view. This view does not suit the concepts of interpretive paleontology, and in particular does not lend itself to the study of form and function, where the soft parts and the shell continually interact (in character suites) in adapting to and functioning in the immediate environment.

STASEK's (1963) contention that the body and mantle-shell evolve and interact in unity is well taken, and his proposed system of consistently relating evolution in shell form and structure to changes in the body—his theory of transformation—is dealt with in the preceding section (COX, 1968) and is worthy of careful consideration by students of interpretive molluscan biology and paleontology. In this system, main anatomical areas of the body can be delineated within sections of the shell by tracing consistently recognizable points of juncture between soft parts through ontogeny and evolution as marked on the shell by changes in sculpture or structure. This allows the paleontologist to reconstruct broadly the distribution of soft parts in fossil shells and to interpret more completely the function of shell structures and the evolutionary significance of their change through time. Recognition of an intricate evolutionary relationship between shell and soft parts defines a second primary function for the whole bivalve shell—a support for the enclosed soft parts. Stasek encouraged use of both the standard orientation system and transformation diagrams in studying bivalves, the latter being most useful in studies of form and function. The morphology of the Bivalvia has been thoroughly treated in the preceding section *(6)*, and the reader is referred to the detailed glossary, discussion, and extensive diagrams presented there for explanation of terms used in succeeding pages.

The observation that shell form and exterior morphology are strikingly similar among phylogenetically distantly related bivalves occupying similar niches strongly suggests that gross features of the shell are of major adaptive significance. This broad aspect of form and function has not been treated as much as many of the finer structures of the shell distinguished in published works, and so discussion here is given within the framework of the habitat groups previously described.

BYSSATE FREE-SWINGING BIVALVES

Bivalves of this type are characterized by having hydrodynamically streamlined shells (Fig. 88). They are moderately to strongly prosocline, attached anterodorsally, with a rounded anterior margin and commonly a projecting posteroventral flank. Beaks are reduced and auricles strongly developed, especially the posterior one. Prominent marginal reentrants commonly occur beneath the auricles and are generally coincident anteriorly with the byssal gape and posteriorly with the exhalant aperture or region. Shells are equivalve to moderately inequivalve and only slightly inflated, with maximum convexity umbonal or dorsocentral. Most have thin, smooth shells, although many fossil representatives are costate. Living *Pteria*, some *Pinctada* (Pteriidae), certain Isognomonidae (e.g., *Isognomon alatus* Gmelin), some Pectinidae *(Leptopecten)*, and probably extinct fossil forms such as Cretaceous Inoceramidae of the *"Inoceramus" fibrosus* or *tegulatus* lineage and *Oxytoma* (Pseudomonotidae?), Jurassic *Gervillia* (Isognomonidae), certain Triassic monotids, possibly late Paleozoic Aviculopectinidae *(Pseudaviculopecten, Aviculopecten)*, Silurian-Mississippian *Leiopteria* (Pterineidae) and Devonian *Pterinea* and *Cornellites* (Pterineidae) belong to this form group.

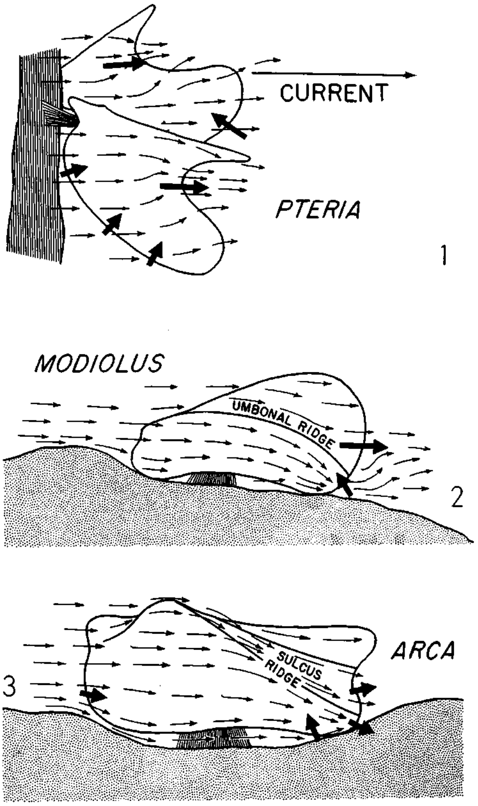

Fig. 88. Relation of inferred water-flow patterns (small arrows) to shell morphology and preferred orientation of selected byssate bivalves and to location of their inhalant and exhalant regions (heavy arrows). Shape of shell surface influences channeling of water first over incurrent areas and then over waste-bearing excurrent areas. *Pteria (1)* shown as attached to upright straight stalk (compare Fig. 87,6); *Modiolus (2)* and *Arca (3)* shown as attached to hard substrates typical of sublittoral areas (compare Fig. 87, *1,10*) (Kauffman, n).

In general the byssate, free-swinging Bivalvia are inhabitants of shallow inner sublittoral environments and all appear to be almost totally restricted to the continental shelves. Living forms are attached by a set of relatively long byssal threads to raised, firm substrates such as sea whips, algae,

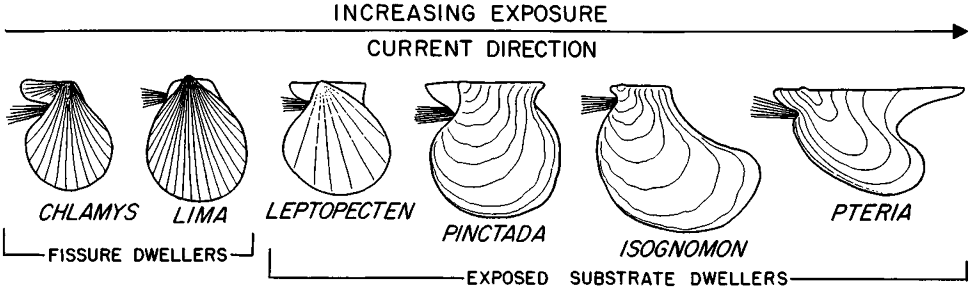

FIG. 89. Shell form of loosely attached byssate bivalves in relation to their exposure to currents (Kauffman, n).

grasses, projecting coral branches, wrecks, logs, and the like. In the shallow water preferred by most species they are subject to at least periodically strong currents and wave action; some are continually buffeted. *Pteria,* some *Pinctada,* and *Isognomon alatus* I have observed alive in the southern Atlantic and Caribbean areas, swing on the fully extended byssus to varying degrees during periods of normal feeding so that the plane of the commissure approaches or parallels the direction of the prevalent current. They are capable of retracting the byssus, thus pulling the shell up tight against the substrate when alarmed. Preferred orientation is with the plane of the commissure near vertical and the hinge axis slightly inclined to the horizontal in *Pteria* and *Isognomon alatus;* this is often modified by the nature of the available substrate and growing space. *Pinctada* is more variably oriented, with the commissure plane vertical to flat-lying. In nearly all cases these are solitary animals; *Isognomon* also grows in clusters.

The general shell form is well adapted to exposure on elevated surfaces in a set of relatively high-energy environmental conditions. In its preferred orientation, the subequivalve to moderately inequivalve, slightly inflated shell offers little resistance to currents, and with maximum convexity situated toward the leading edge of the shell, acts as a crude airfoil. The narrow shell is further adaptive in clustering *Isognomon* to more efficient packing of upright individuals into a tight aggregation. Studies on a limited number of living specimens in this morphogroup showed preferred attachment on the lee side of elevated objects, making the streamlining of the shell an even more effective adaptation for minimizing the chance of damage in severe current or wave action (Fig. 87). The enlarged posterior auricle and extended posteroventral margin of many forms functions as an effective rudder, insuring the most advantageous orientation of the shell in the face of currents (as long as the byssus is extended so as to allow a degree of play). There is a suggestion in limited studies of living free-swinging byssate forms that the highest degree of streamlining—the least convexity and greatest inclination—as well as the most pronounced posterior "rudders" (auricle and extended posteroventral margin) are found on forms occupying the most elevated and exposed habitats (Fig. 89).

The absence of projecting beaks and their strong prosogyrous inclination on many byssate bivalves is further adaptive to streamlining the shell, as may be the lack of coarse surface ornament on many members of this group. The adaptive role of surface sculpture in free-swinging byssate forms deserves considerable study and is not fully understood. Costation has been cited frequently as functioning to strengthen the shell against various energy factors and predation, providing a series of radially arranged structural ribs. This is especially critical at or near the thin shell margin. Costae and plicae would also serve to break up currents flowing over the shell surface, producing a layer of turbulent rather than lamellar flow, reducing hydraulic friction at the shell-water interface, and improving the ability of the shell to withstand currents or wave action. Yet most living members of this group are relatively thin-shelled and have smooth to finely lamellate outer shell surfaces. *Leptopecten,* a living exception, is strongly costate, with partially plicate marginal areas and commissure adapted primarily for increasing the area covered by complex mantle sensors, or acting as a sediment screen in turbulent water, as in other pectinids, or both. It thus represents a unique case. Several fossil representatives of the byssate, free-swinging epifaunal group are also costate, especially the Paleozoic pteriiform bivalves, and it would seem that general loss of radiating surface ornamentation was an evolutionary trend among inhabitants of the niche. A possible advantage of smooth shells over costate ones would be to increase the friction of water flow over the surface, and thus provide a stronger orienting force on the rudder-like shell, insuring its optimum positioning relative to current direction.

The functional significance of reentrants in marginal outline beneath the auricles has been little studied but in this group is probably of great importance. The byssal notch is primarily a product of retarded lateral shell growth around the byssal gape, keeping the gape open for extrusion of the foot and implantation of byssal threads, and for movement of the shell up and down the byssal axis. Also, depth of the byssal notch probably is related to strength of the byssal anchorage and amount of shell rotation on the byssus in the plane of the commissure. Further correlation is seen between the axis bisecting the byssal gape and the byssal axis (i.e., the line joining the center of the byssal notch and byssus with its point of origin on the foot). Thus the mean direction in which the byssus extends out from the byssal notch and implants on the substrate can be determined relative to the height-length coordinates of the shell, and a preferred angle of byssal attachment defined between shell and substrate. For an exposed byssate organism like *Pteria,* adapted in form to maintain a preferred orientation, keeping the angle of byssal attachment constant is critical not only to current orientation but also to proper feeding and waste removal, as subsequently discussed. The deep byssal notch, and small but prominent anterior auricle above it in many members of this group limit rotation of the shell on the byssus within the plane of the commissure, and thus help to maintain a consistent shell orientation. The deeper and narrower the notch and more parallel its sides, the tighter the restriction on movement.

Cox (Fig. 35) has indicated for *Pteria* and *Pinctada* that inward directed currents used in feeding and respiration enter the mantle cavity through the anteroventral and ventral portions of the shell and that outward directed currents leave the shell, bearing wastes, in the mid-posterior region, in the position of the posterior marginal reentrant below the main auricle. On a piece of coral or vegetation growing approximately vertical from the substrate, a typical *Pteria, Pinctada,* or *Isognomon* generally attaches to the lee side of the structure in a near-vertical position (*Pinctada* variable and typically more inclined, ranging to horizontal), but owing to the projecting anterior auricle, with the hinge axis inclined downward or upward (if attached in a fork) posteriorly (Fig. 87-88). In this orientation the incurrent areas face directly or diagonally into the prevailing water currents, and the excurrent area directly away from these currents so that exhaled waste material is removed quickly. For this system to act efficiently a consistent orientation must be maintained and is partially insured by restricted rotation on the byssus, as previously discussed. The posterior reentrant of the shell, at the excurrent aperture, is further functional in this system by creating a depressed posterior area on the shell into which currents are channeled as they pass over the valves (Fig. 88). Increased current flow brought about by this channeling at the position of the exhalant aperture would further insure rapid removal of waste and prevent deleterious concentration of these products in the water surrounding the shell. Current flow studies, such as those carried out by RUDWICK on brachiopods (1961), will be necessary to substantiate this function.

BYSSATE CLOSELY ATTACHED BIVALVES IN EXPOSED HABITATS

This group includes both solitary and gregarious forms which are variously adapted for relatively immobile attachment by short byssal threads close to the exposed surface of hard substrates (Fig. 87). The Bivalvia have adapted to this habitat in two principal ways, characterized by equivalve to subequivalve *Modiolus s.s.* or *Mytilus,* normally attached with the plane of the commissure nearly perpendicular to the substrate, and inequivalve forms like *Anomia,* in which the plane of the commissure parallels the substrate. *Pinctada,* partially a free-swinging byssate genus, also has representatives which approach *Anomia* in habitat and attach loosely to the substrate with the flat valve down and the plane of the commissure parallel or moderately inclined to the surface. It occupies a habitat intermediate between those of *Anomia* and *Pteria* or *Isognomon.* Both principal types of closely attached bivalves have solitary and gregarious representatives; gregarious mytiloids seem to have greater mobility in orientation (i.e., looser byssal attachment) than solitary forms like *Modiolus s.s.,* or flat-lying forms like *Anomia.* Both adaptive types solve the problems of their environment well; both are also known to a lesser extent as inhabitants of depressions and fissures on hard substrates, as is *Pinctada,* especially in intertidal or very shallow-water situations where this habitat affords extra protection.

The groups of byssate, closely attached bivalves, with few exceptions, are inhabitants of shelf environments and are concentrated in, and especially adapted to, high-energy shallow-water conditions of the littoral and shallow sublittoral benthic zones. The greatest diversity of forms is normally found in less than 50 feet of water. Strong wave and current action, periodic exposure and high turbidity, agitated well-lighted waters, and episodes of rapid scour and sedimentation are characteristic of their preferred environment. Unlike the free-swinging byssate forms (e.g., *Pteria*) which may survive intense current and wave action by moving with the flow of the current, Bivalvia of this group adapt to these conditions in having hydrodynamically streamlined shells which are normally tightly affixed to the substrate by means of a short byssus. The gregarious habit affords further protection to contained animals in that it essentially creates the effect of an individual protective depression for all but the outside members of the cluster.

The dominant bivalves in this group are solitary (many *Modiolus s.s.*) or gregarious forms (e.g., *Mytilus, Brachidontes*) oriented with the plane of the commissure approximately perpendicular to the substrate (Fig. 87,*3*). The predominantly thin shells are elongated along the anterior-posterior axis, equivalve to subequivalve, and moderately to highly inflated (except some mytiloids secondarily adapted in their low convexity to more efficient packing in gregarious clusters, as in *Isognomon*). Beaks are anterior, strongly prosogyrous and normally incurved, not projecting much above the hinge line. Maximum inflation is along the normally well-defined umbonal ridge extending from the beak area to the posteroventral margin. Auricles, if developed, are poorly defined and posterior, usually consisting of a flattened, projecting posterodorsal flank. A small anterior lobe anterior or ventral to the beaks is a common feature. Shells are characteristically subtriangular with the narrowest angle anterior. A single, shallow, concave reentrant in marginal outline is found anteroventrally to mid-ventrally in most forms and marks the site of a narrow, elongate byssal slit. Most shells are smooth, but fine to moderately strong costae occur on some genera *(Brachidontes).* Included in this ecologic group are fossil and Recent Mytilidae (e.g., *Mytilus, Brachidontes, Septifer, Modiolus s.s.*) in fresh to marine waters, Dreissenidae *(Dreissena)* from fresh (Recent) to marine (Cretaceous) environments and probably extinct forms like the early Paleozoic Ambonychiidae *(Ambonychia), Mytilarca* and probably various Mesozoic Inoceramidae *(Mytiloides),* to name a few.

The form of the shell is hydrodynamically streamlined for current flow passing from anterior to posterior and it is assumed that this is the preferred orientation during attachment to the substrate; this has not been substantiated by direct observation. Certainly clustering not only reduces the need for hydrodynamic streamlining and selective orientation to maintain stable attachment in strong currents, but also imposes a stronger orienting force on the animal—the availability of living space. Clustered individuals are therefore less likely to be oriented relative to current direction. It is postulated that in the evolution of mytiloid bivalves the primary adaptive value of the characteristic shell form was hydrodynamic streamlining. Development of the clustering habit was probably secondary and was accompanied by subsequent modifications of the basic form such as greater attenuation of the beak-umbo area and lateral flattening of the valves to allow greater efficiency in packing of shells within the cluster.

Only a posterior auricle is developed on the majority of mytiloid bivalves and this is poorly defined at best, being a flattened triangular extension of the posterodorsal flank not commonly separated from the main body of the shell by a definitive sulcus (more so in Paleozoic forms, e.g., Ambonychiidae), and angulate to broadly rounded at its extremity. This structure is the most exposed part of the shell when it is normally oriented with the recessed margin (site of byssal slit) nearly parallel to the surface of the substrate. As such it probably functions as a stabilizing rudder, helping the shell maintain a relatively constant position in the face of currents within the limited scope of free play allowed the shell by the short byssus. The limited mobility of the shell around the byssal axis in most mytiloids negates the need for a deep byssal notch and its stabilizing function. No function has been postulated for the anterior lobe in forms like *Modiolus* other than that it spatially accommodates the anterior adductor muscle internally, keeping it distant from the main area of the mantle cavity and its contained viscera (Fig. 34,*D*).

The umbonal ridge (posterior ridge, diagonal ridge of Cox, 1968) probably performs an important function in feeding and excretion within mytiliform groups. It obviously provides internally, by its inflation, needed space in the mantle cavity for proper distribution of the soft parts. If the preferred orientation of mytiliform groups is with the anterior end of the shell approximately facing into the current and closely attached to the substrate by a short byssus, with the plane of the commissure approximately perpendicular to the surface, then currents passing over the attachment surface would be partially channeled beneath the projecting umbonal ridges, especially in forms like *Modiolus s.s.* and *Dreissena* (Fig. 88), between the ridges and the attachment surface. A series of eddies would probably result. These currents, bringing in fresh food and oxygen would first pass over the inhalant aperture, lying just ventral to the termination of the umbonal ridge (Fig. 35), and in leaving the area of channeling posteriorly, secondly pass over the exhalant aperture, above or at the tip of the ridge, carrying away waste products. This remains to be tested.

A wide range of surface sculpture characterizes closely attached byssate forms, from very smooth shells *(Modiolus s.s.,* many *Mytilus),* to coarsely lamellate and costate groups *(Brachidontes,* many Ambonychiidae). Although shells lacking radiating elements dominate, there appears to be no consistent pattern of ecologic occurrence for costate as opposed to noncostate forms. Adaptive value can be attributed to both types of surfaces. The smooth-shelled forms can be packed more closely in clustered species than those with raised surface ornament. Costate shells are stronger than shells of equivalent thickness lacking costation, an important consideration in high-energy situations, and in addition are harder to extract from close quarters, in a rocky depression or in a cluster. The costae provide additional surface area and therefore increase friction against the walls of the depression or adjacent shells, as do coarse concentric lamellae.

The second adaptive morphotype included within the group of byssate, closely attached Bivalvia is less common but equally well suited for life in exposed, high-energy, shallow shelf environments, their preferred habitat. The Jurassic to Recent Anomiidae *(Anomia, Paranomia, Pododesmus)* dominate this group. Some *Pinctada* approximate the same living habit. Most living representatives of the Anomiidae cling tightly to exposed, firm substrates by means of a short, broad byssus extending from the point of origin on the foot, through a hole or notch in the dorsocentral part of the lower (right valve) to the substrate (Fig. 34,*F*). Some are depression- or fissure-dwellers, especially in shallow water. The byssus is calcified to varying degrees, and relatively inflexible. The shells are moderately to highly inequivalve, with the right (lower) valve flat, perforated for the byssus, and smaller in diameter than the inflated, irregular left (upper) valve. Valves are moderately thin, rugose to concentrically wrinkled, rarely with radiating costae, and round to ovate in outline. The lower valve commonly conforms closely to the shape of the attachment surface. Populations are highly variable. Most forms live as solitary individuals or loosely clustered, though shells may be crowded on a surface. The calcified byssus and close fit between the lower valve and substrate prevent significant movement of the shell around the byssal axis, especially when it is drawn down tightly against the substrate.

In most respects shells of this type are adaptive to the rigors of the environment in the same way as cemented bivalves, limpets, and cranioid brachiopods. Their flat lower valve and convex upper valve differentiate them from typical cemented forms and identify them with byssate bivalves, however. The large byssal notch or perforation in the lower valve functions uniquely in allowing firm attachment by a short, calcified, ventrally directed byssus. This insures that the shell will not be buffeted against the substrate or easily torn loose in strong currents. A relatively much longer and more flexible byssus results from extrusion through a byssal gape between the valves, and other means of stabilizing the shell in heavy currents must be developed, as in *Pteria*. The form of the upper valve in Anomiidae, though irregular, is most commonly round, with maximum convexity dorsocentral, the flanks being flattened and the surface irregularly wrinkled. As such, it is crudely streamlined in the face of currents and allows easy water passage over it, restricting the possibility of uprooting the shell by strong currents. No studies have demonstrated whether Anomiidae show preferred orientation in currents. If hydrodynamic stability were important, it would be expected that the dorsal margin of the valves would face approximately into the flow. The rough, irregular surface of many Anomiidae may further function to cut down the effects of strong currents on the shell by creating a layer of turbulent flow, with its relatively low hydraulic friction, close to the valve surface. Costae may serve the same function, as well as providing additional strength to the commonly thin shells.

Pinctada seems to occupy a position intermediate between free-swinging and closely attached byssate epifaunal bivalves, and incorporates characters of both morphologic groups. In shell outline it has many of the characteristics of free-swinging byssate forms, being prosocline, strongly auriculate, with relatively low convexity, and a prominent byssal notch (Fig. 89). It differs from typical free-swinging forms like *Pteria* in being more quadrate and less prosocline in outline and in being markedly inequivalve (right valve flat to slightly convex, left valve moderately convex). The byssus is directed more laterally out of a prominent notch in the right valve. YONGE (1953) considered *Pinctada* to represent an important evolutionary step between byssate and cemented Bivalvia and cited the normal living habit as being closely attached to the substrate, right valve down and the plane of the commissure parallel or at a slight angle to the surface. In this orientation it approaches the anomioid habit. My *in situ* observations of *Pinctada radiata* LEACH in the inner sublittoral zone of Florida and the Caribbean Islands contradict this to some extent. In shallowest waters (10 feet or less) continually buffeted by waves and in areas where no vertical substrate is present (e.g., sea fans, sea whips, branching coral), as on a denuded reef, *Pinctada radiata* grows as YONGE described, although as many are attached with the plane of the commissure inclined at a moderate to high angle to the substrate as are found lying flat on the surface. These are still relatively mobile on the byssus and dominantly face dorsally or anteriorly into the current. The preferred habitat in these areas, however, seems to be attachment to the lee sides or in branch junctions of sea whips and fans, predominantly the former, in much the same manner as *Pteria*. The dorsal margin is moderately to steeply inclined upward and the flat valve lies against the upright surface. This seems to be the habitat for which its streamlined shell is best adapted.

It is significant that *Pinctada* combines the shell characteristics of two distinct morphogroups, free-swinging and closely attached byssate epifaunal bivalves, and occupies both niches equally well. Contrary to YONGE's (1953) opinion, *Pinctada* seems to be among the more generalized and adaptive of the byssate epifaunal bivalves, and its form might be expected to be ancestral to more specialized groups of both niches. The predominance of this shell form in certain early Paleozoic byssate bivalves like *Pterinea* supports this.

BYSSATE EPIFAUNAL NESTLERS

Bivalves of this group are typified by many fossil and Recent Arcidae (Fig. 31,*F*, 35,*A*). Shells are subrectangular to subovate, elongated anteroposteriorly, moderately to highly inflated, prosocline, and normally have prominent, inflated moderately projecting incurved beaks and umbones, characteristically prosogyrate but ranging to opisthogyrate and situated mid-anteriorly. The hinge line is elongate, straight, and commonly projects onto small triangular auricles anteriorly and posteriorly. A shallow mid-ventral concave reentrant in the marginal outline marks the large byssal gape. Costate, thick to moderately thick shells dominate. Typical examples are living and fossil *Arca, Barbatia,* Mesozoic *Nemodon,* and Paleozoic *Parallelodon*. Not all Arcacea are included, since many of the more ovate genera are unattached, partially or wholly infaunal elements (e.g., *Noetia,* some *Anadara*).

The byssate epifaunal nestlers inhabit nearshore, shallow-water environments, predominantly at depths less than 100 feet, and prefer depressions in firm substrate for attachment to exposed surfaces. On reefs they are often found in crevices between coral heads, or within coral branches (Fig. 87). They are common in wave-cut depressions in limestone benches, on the roots of marine plants, attached to the protected sides of vegetation and hard reef blocks, and many species occupy the protected photonegative undersurfaces of rocks and growing reefs, where their range overlaps that of the byssate fissure-dwellers like *Lima* and certain *Chlamys* (Fig. 87). Inasmuch as the typical shell of the byssate nestler seems highly adapted to habitation of exposed surficial depressions in hard substrata, the habitation of the even more protected undersides of rock surfaces probably represents secondary adaptation to a new niche for additional protection.

The subrectangular arcoid shell form is structurally well adapted for nestling in crevices, and in this habitat is firmly anchored against uprooting by strong current and wave action or predator attack. The large, partially reinforced byssus extends mid-ventrally through a large gape into the base of the depression occupied and the shell is raised and lowered vertically on this structure by a powerful set of pedal-byssal muscles capable of rapid contraction (Fig. 31,*F*). In normal orientation the long axis of the shell approximately parallels the long axis of the depression, which the living forms are able to enlarge or modify in shape by rotational manipulation of the shell on the byssal axis, grinding both shell and substrate until a snug fit is insured upon contraction. When withdrawn into the depression, the shell, tapered ventrally and elongated parallel to the depression, acts like a broad wedge in a crack and cannot be moved easily either sideways or back and forth. Lamellate costae, by providing additional surface friction, aid in preventing its easy removal, wedging into smaller side depressions and strengthening the shell. The shell will break before the force of the byssus is overcome by simple prying from below. Thus, in form and direction of byssal extension, the shell functions as a virtually immovable protective shield for the soft parts in its preferred habitat. The auricles may function in this group as supporting shell structures for enlargement of the taxodont hinge and ligament area; increase in the area covered by ligamental material and in the number of interlocking teeth further strengthens the enclosing valves by prohibiting their easy disarticulation or rotation in the plane of the commissure by predators and strong wave or current action.

When feeding the shell is raised on the byssus and the valves gape ventrally near the bottom of the depression occupied. Two external features of the shell apparently have an important function in the feeding process. As in mytiliform bivalves, many arcoids possess a strong umbonal ridge and have maximum convexity located dorsocentrally. Similarly, water flowing over the attachment surface is initially channeled between the umbonal ridge or axis of maximum inflation and the base of the depression, along the inhalant areas of the mantle edge (anterior, ventral) and passes out of the trough thus created into open water as it flows past the posterior exhalant aperture (Fig. 88), continually providing clean water for feeding and respiration and flushing out waste products. Flanges or frills of periostracum around the anterior, ventral, and posterior edges of the shell and along the umbonal ridge function in many species of *Barbatia* and some *Arca* as a sediment screen over the feeding edges and in some cases may nearly seal off a narrow depression from possible infiltration of harmful material into the mantle cavity. They further enclose the main water channel. This is important in turbid, high-energy environments preferred by many arcoids.

Large triangular interareas between the hinge line and beaks of typical arcoids support the primitive ligament composed of numerous thin sheets. The broad attachment area is necessary to accommodate enough ligamental material, arranged in this inefficient manner, to open the valves. In the Bivalvia possessing more advanced, compact types of ligaments, this area is greatly reduced.

BYSSATE FISSURE-DWELLERS

Byssus-attached inhabitants of fissures mainly include partially or wholly photonegative species of bivalves belonging to two morphologic groups, one or both of which may have become adapted to the habitat secondarily during its evolution without additional significant modification in form. The primary habitats are the underside of rocks, deep, relatively dark declivities and fissures, reef tunnels, spaces inside root bundles of aquatic plants, and similar niches with good water circulation, weak light, and good protection from strong wave or current action. Some of the included species sparsely occupy other, more exposed surfaces if their preferred habitat is not available. In addition to the principal inhabitants (e.g., pectinoids, Limidae, certain Pteriidae, *Isognomon* such as *I. radiatus*), various arcoids primarily adapted for exposed depression-dwelling secondarily occupy this niche in abundance, especially in very shallow waters, thus gaining added protection from currents, waves, and exposure. Energy conditions being rarely severe in these habitats, and the number of predators being somewhat limited, arcoids occupying them are less dependent on individual depressions for firm anchorage and exist in great numbers, tightly fastened to relatively flat surfaces where depressions are not available. It appears that few arcoids bother to excavate or modify their own depressions, as they do on exposed surfaces. The same habits are shown by deep-water arcoids for many of the same reasons.

Similarly, because of the strong adaptive value of their shell morphology for habitation of exposed shallow-water depressions on hard substrates, fissure-dwelling arcoids are considered to be secondary occupants of this niche which have not developed distinct shell characters that may be considered specifically adapted to it. Oysters, mytiloids, anomioids, and a few other groups are occasional inhabitants of fissures and the undersides of rocks, especially at their edges, and in very shallow-water or littoral habitats. None are considered primarily adapted to this habitat, but they gain added protection from it under severe conditions.

The principal bivalves inhabiting these niches (besides arcoids) are byssate species of *Lima* (Limidae), *Chlamys* (Pectinidae), the more rounded or quadrate forms of Isognomonidae (e.g., *Isognomon radiatus* ANTON), and related forms. Certain of the more rounded to quadrate Pteriidae are also known from it (e.g., some *Pinctada*). Though distantly related, these bivalves share many things in common. They are all byssate and attached loosely by relatively long flexible threads protruding anterodorsally from a prominent byssal gape between the valves; the shells are capable of considerable movement about the byssus. The valves are not streamlined for ready orientation in the face of currents, however, as is *Pteria,* but are predominantly round to ovate, slightly inequilateral (prosocline except for *Lima*: opisthocline), with the height axis longest. Posterior auricles are relatively small, and posteroventral projection of the valves absent or small-scale (Fig. 87,*2-3, 8, 11*); the shells would not act as an effective rudder for orientation in currents, as does the posteriorly extended *Pteria.* Convexity ranges from low to moderate; small anterior auricles and a shallow byssal notch occur in *Isognomon* and *Lima;* a pronounced auricle and notch characterize *Pinctada, Chlamys,* and related genera.

These forms are thus not well adapted for free-swinging byssal attachment on surfaces exposed to intense current or wave action, and would be hydrodynamically unstable, easily twisted and torn loose in such a habitat. Two of the primary inhabitants, typified by *Lima* and *Chlamys,* have highly developed sensory tentacles or projected sensory regions (eye spots) at the mantle edge; in *Lima* the tentacles cannot be fully withdrawn into the shell and are easy prey for predators, especially fishes, when the shell lies exposed. Most forms are costate or coarsely lamellate, with moderately thick shells.

Shells having the form of *Lima, Chlamys,* and more ovate *Isognomon* and *Pinctada* might therefore appear to be adaptive to crevice, fissure, cave, and rock undersurface habitats primarily in a negative way—a simple round to ovate disc lacking special adaptive form or structure to deal with high-energy environments, or (in *Chlamys* and *Lima*) lacking the shell symmetry ideal for swimming, seeking protection and survival in this habitat where such modifications are unnecessary. This is not compatible with the evolutionary record of byssate bivalves, which shows these relatively equilateral forms as modifications of the more streamlined early and middle Paleozoic shells obviously belonging to exposed, byssate, epifaunal organisms or potentially free-swimming groups.

Few thoughts have been published on the adaptive advantage of rounded to ovate, nearly equilateral shell forms in epifaunal bivalves other than "freedom of organization" of the soft parts internally (Yonge, 1953), and its obvious value in the swimming habit. In swimming, the rounded shell provides a broad nearly equidimensional disc which maintains a stable horizontal attitude in the water and offers sufficient resistance to allow "gliding," once the thrust phase of the process has been completed by water currents expelled from between the valves, or by rapid clapping together of the valves. Notably, both *Chlamys* and *Lima* include swimming species, and specifically the fissure-dwelling limids are reported to be among the best swimmers in the genus group. Not only is the secretive habitat and swimming ability of forms like *Lima scabra* Born functional in protecting the nonretractile tentacles from predators or current-wave damage, but this and other species gain additional protection from their ability to build "nests" of byssal threads around the shell and tentacles, within the protected fissure habitat.

If the primary function of round shells in epifaunal organisms is, at least in Limidae and Pectinidae, the swimming habit, then the occurrence of predominantly rounded to ovate shells on byssate fissure-dwellers of these groups has little significance and suggests secondary adaptation of the animal to the habitat to seek further protection, without shell modification other than slight loss of symmetry. This is an unsatisfactory explanation for the occurrence of the more rounded to ovate *Isognomon* and *Pinctada* in the same habitat, belonging to groups which never developed the swimming habit, and may represent only part of the answer.

It is possible that round or ovate shell form has definite adaptive value because it allows optimum free spatial distribution of soft parts within it. Other shell-morphologic aspects of survival being minimized as they would be in a protected fissure habitat, the round shell form could have been selected for genetic conjunction with a decentralization of soft parts. YONGE (1953) has partially dealt with this problem.

A final possible function of rounded shell form in attached epifaunal Bivalvia is that it provides relatively greater areal distribution of sensory receptors at the mantle margin. The high degree of sensor development in Limidae and Pectinidae, among the most disclike epifaunal bivalves, suggests that this is feasible. In the design of a simple disc cut on one side by a hinge line, the percentage of marginal valve area potentially supporting mantle sensors is directly proportional to the relative length of the hinge line and the arc of the commissure it subtends. The development of auricles, depth of subauricular notches, amount of plication, size of inhalant and exhalant apertures, and relative distribution of sensors are additional individual variables. In design, an optimum coverage is attained in pectiniform shells having the hinge line, except for the part extending onto the auricles, relatively short and the commissure area potentially supporting sensory receptors (eye spots) forming an arc approximately 330° to 350°, nearly a full sensory spectrum. Of course, variations are seen in the distribution of sensors around the margins of pectinids, none or few being present dorsolaterally just beneath the auricles, but this lack of sensory coverage is compensated for by auricular sensors (WALLER, 1967). The sensory tentacles of limids cover a slightly smaller arc on the commissure, but are long and thus able to compensate for this, giving equivalent sensory coverage. The mantle edges of *Pinctada* and *Isognomon* also perform a sensory function, but are much more finely tentaculate and lack highly specialized cells or structures.

The contention may be made, therefore, that the more rounded to ovate shell form in epifaunal Bivalvia, where it is permitted to exist by the environment or specialized structures and behavior of the animal (e.g., swimming), or both, is highly adaptive and selected for in evolution, functioning to increase the area of sensory reception around the commissure and thus the ability of the animal to be forewarned of impending danger. A high degree of sensory reception may be more important in photonegative habitats, where light intensity is low, than in more exposed, well-lighted areas. I have observed frequently that many epifaunal Bivalvia, even those without specialized light-sensitive areas, as in Pectinidae, are highly sensitive to abrupt changes in light intensity and will close the valves and contract on the byssus if, for example, a diver or large fish passes between them and the light source, even at a considerable distance. The ability to detect such a change is minimized in a diffused light situation, as in fissures, caves, or rock undersides. It is possible that this is compensated for in the more rounded shell form and more highly developed sensory receptors at the mantle margin. Considerable work needs to be done to substantiate this hypothesis, and to investigate further the possibility that increased sensory perception is necessary for effective feeding in these photonegative environments. Only in these ways can the predominantly round to ovate shell form in fissure-dwelling epifaunal Bivalvia be considered a functional adaptation specifically for this habitat.

Coarse concentric lamellae (e.g., *Isognomon, Pinctada*) and strong, commonly fluted or lamellate costae (e.g., *Chlamys, Lima,* some *Pinctada*) not only strengthen the shell of byssate fissure-dwelling bivalves but also make it harder to extract from narrow crevices. In this habitat, the shell is normally attached with the ventral margin facing outward. Flutes and raised lamellar plates on costae and coarse concentric lamellae also face outward in this orientation angled like barbs against the fissure walls. They function to hold the shell in place, reinforcing the byssus, when its extraction is attempted by predators.

CEMENTED EPIFAUNAL-BIVALVES

This group includes a variety of forms and unrelated taxa which have in common cementation of the shell, normally by calcareous deposits, to hard substrate during part or all of their life cycle. The primary function of this habit is obvious; it provides continued, stable orientation of the bivalve and protects against destruction by dislodgement in the preferred habitat, commonly one of high-energy wave and current conditions. Although some cemented Bivalvia have been reported from considerable depth, the great majority are shelf-dwellers and are concentrated in the inner sublittoral benthic zone, the maximum known diversity being in marine water less than 100 feet deep. Most commonly, cemented Bivalvia prefer exposed or semiexposed substrate surfaces subject to periodically intense wave and current action, good lighting and agitation, periods of turbidity, and an abundant food supply. Representatives of this habitat group are primarily the living and fossil Ostreidae (*Ostrea, Crassostrea, Pycnodonte, Exogyra, Gryphaea, Arctostrea,* etc.), Spondylidae *(Spondylus),* Pectinidae *(Hinnites),* Plicatulidae *(Plicatula),* Chamidae *(Chama, Echinochama),* the highly diverse Mesozoic rudists, and the late Paleozoic-early Mesozoic pseudomonotids. Many parallels may be found among late Paleozoic Brachiopoda. The general evolutionary history of the Bivalvia suggests that cementation was a secondary adaptation in some cases of mobile or partially byssate epifaunal bivalves to a completely sessile habitat (e.g., Monotidae, Pectinidae) (YONGE, 1953). The origin of ostreids (NEWELL, 1960), chamids, and rudists (YONGE, 1967) has been investigated but is still not clear.

Cemented epifaunal Bivalvia include both solitary (e.g., *Spondylus*) and gregarious groups (e.g., many Ostreidae). Shell form within populations is highly variable owing to the "molding" effect of the substrate. Gregarious crowding in beds (as in *Crassostrea*) introduces a second source of variability in form, structure, and ornament, with lateral shell growth commonly impeded, auricles eliminated, and sculpture patterns disrupted. Not only is the gross character of the substrate reflected in the general form of the valves, especially the attached valve, but in some Ostreidae the fine detail of the surface is preserved on the outer surface of both valves, being imprinted on their thin growing edges in the area of attachment as they lay in conjunction against the substrate surface. STENZEL, KRAUSE & TWINING (1967) have termed this phenomenon xenomorphic growth. Many authors have also reported a great plasticity of shell form and ornament in attached bivalves in response to environment. For example, elongate *Crassostrea virginica* (GMELIN) grows in areas of strong current and more rounded forms of the same species are found in quiet-water situations.

It seems that with such variability imposed on cemented Bivalvia by environmental factors, little can be said about the adaptive value of form or specific structures beyond the stabilizing function of the cementing habit itself. Some broad patterns are worthy of comment, however. Three principal morphotypes characterize cemented bivalves: 1) uncoiled groups such as *Spondylus, Pseudomonotis, Crassostrea, Ostrea* (many Ostreidae which have slightly coiled early stages but basically are elongated to rounded, with uncoiled valves as adults); 2) bivalves with strongly coiled shells either approximating the plane of valve symmetry *(Gryphaea)* or coiled out of the plane of symmetry (*Exogyra,* some rudists like *Toucasia,* many Chamidae); and 3) cuplike bivalves with an enlarged, subconical attached valve and a caplike upper valve (many rudists, such as *Durania* and various radiolitids). Each type has specific adaptive value within the preferred nearshore habitat, but they are not clearly separated as distinct groups and intergrade with some cemented forms transitional between morphologic types.

These groups have two things in common besides cementation. They are predominantly thick-shelled and inequivalve, many grossly so (e.g., rudists), with the attached valve most inflated in the great majority. The adaptive significance of thick shells is obvious in shallow-water environments where periodically intense wave and current action, as well as potential abrasion by saltating sediment particles can be expected; the shell is considerably strengthened against the rigors of such an environment, and the animal is better protected from both high-energy conditions and predators. In fossil oysters, thick-shelled species are rarely found bored by predatory gastropods as compared to the amount of gastropod-inflicted mortality in thin-shelled bivalve species.

The prevalence of the inflated lower valve (left or right depending on the group) in cemented Bivalvia suggests that this characteristic is also highly adaptive to the shallow-shelf environment. Many authors have cited the functional significance of a deep bowl-shaped lower valve in littoral ostreids as being its ability to retain a considerable amount of water, practically enveloping the soft parts, during times of intertidal exposure. It has been cited but not clearly demonstrated that species of *Crassostrea* develop deeper lower valves in intertidal situations than in subtidial habitats. However, since most cemented forms are not intertidal at present, and apparently were not in the past, this function cannot be considered the primary factor in natural selection. The possible advantageous effects of a deep lower valve acting as a more efficient means of supporting the soft parts in bivalves oriented with the plane of the commissure approximately parallel to the substrate, as opposed to equivalve forms or those with more inflated upper valves, has not been fully investigated. It seems logical, however, to conclude that this would be a better system of support (and thus have adaptive value) than having the viscera and mantle largely supported by the upper valve (as in *Anomia*), hanging pendent from a necessarily strong set of mantle and body muscles in the mantle cavity, even though their buoyancy in water would partially offset the strain imposed on the musculature.

The inequivalve nature of most cemented bivalve shells have two additional functional aspects. First, cemented bivalves are largely exposed and wholly sessile, and thus at the mercy of the environment. Among other things, their survival depends upon keeping the feeding margin elevated above the surrounding substrate to prevent clogging and suffocation. In reef areas of sediment bypass, this is not so much a problem, but for most cemented forms attached to hard substrate in areas of active sedimentation it becomes critical. The formation of an inflated lower valve by predominantly upward growth of the valve margins from the site of cementation insures adequate elevation of the feeding margin and survival as long as the rate of marginal growth exceeds the rate of sedimentation. The tall conical Cretaceous rudists represent maximum development of this adaptation in the Bivalvia. My own observations in Chesapeake Bay and Florida support the existence of a direct relationship between the depth of lower valves, original orientation of the attached shell, and rate of sedimentation in living species of oysters at all growth stages. The upward direction of marginal growth during ontogeny is considered a primary adaptation to survival, and the resultant bowl-shaped lower valve a secondary product of this which continues to function in the adult stage for the same purpose. That this is not wholly an environmentally controlled phenomenon, but rather a genetic character selected for its adaptive value, is evidenced by the fact that cemented bivalves now almost totally restricted to areas of sediment bypass (reef-dwelling spondylids and chamids, for example) still retain the relatively more inflated character of the attached valve. A variety of "sculptural" elements also function to keep the feeding margin elevated, among them costal spines *(Spondylus)*, coarse raised lamellae *(Chama)*, and coarse costae or plicae *(Lopha)*.

Secondly, the stresses placed on the ligament or resilium in opening the shells of cemented bivalves are entirely distinct from those encountered by byssate forms like *Mytilus* or *Pteria*. The attached valve is immovable, so that the gape necessary for feeding and respiration must be created completely by raising the upper valve against the force of gravity. This feat demands overcoming the entire weight of the upper valve and a considerably greater amount of force than necessary to move the same sized valve on a pterioid sideways half the distance. Unequal stresses are placed on the ligamental material, in most cases a resilium. It is thus advantageous to the proper functioning of the ligament to have the upper valve of the cemented shell as small, flat, and thin as possible, without deleting its protective value. Reduction in convexity and thickness characterize the upper valves of many cemented taxa; in most the thickness remains sufficient for protection against predators and high-energy water movement. The most efficient system in cemented Bivalvia would be a lower valve which was deep enough to contain all soft parts except the upper mantle flap, and an upper valve acting as a light, flat cap fitting just inside the lower valve. Such a form was developed by some cemented bivalves, in particular Cretaceous rudists. The coarsely perforate nature of some rudist upper valves suggests that they acted as a permanent screen or filter analogous to that of richthofeniid brachiopods (RUDWICK, 1961) and may rarely have been raised. The shape and convexity of the upper valve must be considered in this hypothesis. Whereas a thin flat cap might be the most efficient geometric form relative to functioning of the ligament or resilium, it is advantageous only in areas of slow deposition or sediment bypass. In areas of more rapid and constant sedimentation, such a valve form (or one that was externally concave) fitted just inside the periphery of the lower valve and oriented horizontally, would act as a sediment trap, increasing the danger of deleterious sediment infiltration around the mantle edge into the mantle cavity or mantle-shell interspaces. Consequently, the upper valves of most cemented bivalves are slightly convex (outward) and are functional in that they shed material falling onto them. Flat to concave upper valves seem to predominate in groups which were either reef-dwellers (rudists) or else oriented on the substrate so that upper valves tilt toward the substrate and easily shed sediment (e.g., *Exogyra*).

The preceding remarks apply generally to adaptive form in all cemented epifaunal bivalves and specifically cover most of the points that have been made about the group of basically uncoiled forms (e.g., *Crassostrea, Ostrea, Hinnites, Spondylus*). Variation in other features of this particular group have functional significance. The size of the attachment area is highly variable among uncoiled forms and typically occupies one-third to two-thirds of the lower valve. Its size is commonly dependent on and reflective of the energy conditions of the surrounding environment, inasmuch as its primary function is anchorage. As such it has potential as a paleoecologic tool. KAUFFMAN (1965,*8*) has noted the possibility that average and maximum attainable size of the attachment surface may be in part genetically controlled in that it is related to growth form of the shell. In this study an evolutionary trend is defined in time-successive species and subspecies of *Lopha* toward relatively much larger attachment areas as the lineage adapted to shallowing of the Cretaceous seas and increased wave and current action. Some groups of extinct oysters (e.g., certain species of *Gryphaea, Exogyra*) rarely developed large attachment areas, even in high-energy environments, but apparently became detached early in adult life and lay free on the substrate, developing other stabilizing features such as broad auricles, folds, and sulci. This would tend to substantiate possible broad genetic control on size of the area.

Variously developed auricles, folds and sulci, especially posteriorly, are found on cemented, uncoiled bivalves. In many cases these serve no obvious function unless they increase the sensory mantle area, as in pectinids. In cemented forms with small attachment areas, however, and especially in those that become detached in later life, these are functionally important as supports for the shell on the substrate, providing essentially a three-point stability with the inflated valve down. They are most highly adapted to resting on soft surfaces. In the evolution of certain Cretaceous *Lopha* (KAUFFMAN, 1965, *8*), species adapted to relatively deep, quiet-water, shelf habitats and soft substrates had minute attachment areas, became detached as adults, and developed at that time prominent posterior auricles for support on the substrate. Auricles disappeared and the shell became more symmetrical as the lineage adapted to shallow water, high-energy conditions; the attachment area increased markedly in relative size, and the shell became cemented throughout life. Flattening and lateral spreading of the flanks of oyster shells in quiet water habitats with soft substrate represents a similar adaptation.

Sculpture in uncoiled cemented bivalves is highly variable, from nearly smooth surfaces to coarsely plicate or spinose shells having fine to coarse concentric lamellae. Plicae, costae, spines, flutes, and coarse lamellae function primarily to strengthen the shell, provide additional support by increasing surface area in contact with the substrate, keep the feeding margin elevated above the bottom, and possibly discourage predation (particularly by gastropods) and certain types of epibionts from encrusting the shell. In addition to these functions, the spines of *Spondylus* support sensory extensions of the mantle margin at the time of formation, elevating them well above the shell surface, and providing an effective "early warning" system.

Coiling of the lower valves in cemented epifaunal bivalves is well defined in wholly attached taxa like *Chama* and forms in which the adult probably became detached and lay free on the substrate (some *Gryphaea* and *Exogyra*). The direction and trace of coiling is relatively constant in most forms. It is thus not an environmentally produced variation possibly reflecting change in original shell orientation relative to the substrate due to increase in sedimentation rate or reorientation of the substrate itself. This is a common cause of coiled variants in normally uncoiled ostreids *(Crassostrea).* Although obviously controlled genetically in wholly cemented forms like *Chama,* the adaptive significance of coiling has yet to be clearly defined and it may be a vestigial character. The functional value of a coiled shell in free-living adults of this group is more obvious. In such bivalves, it is critical that after detachment the lower valve should remain anchored in a ventral position and that growth at its margins should proceed upward to offset the effects of sedimentation and keep the feeding margin above the sediment-water interface. The angle of marginal growth in coiled shells like *Gryphaea* accomplishes this efficiently, and in addition produces a deep, bowl-shaped, relatively heavy lower valve capable of being buried by rapid sedimentation, or sinking into soft substrate for a considerable distance before exposing the feeding margin of the valve to clogging or smothering through sediment burial. Because of the relatively tight coiling angle which approximates the plane of valve symmetry in many *Gryphaea* (e.g., *G. mucronata* GABB and *G. newberryi* MEEK & HAYDEN, in the American Mesozoic), the shell, if it had remained in a single orientation relative to the substrate surface (either attached or unattached), eventually would have coiled over so that the feeding margin would be buried in the sediment and the lower (attached) valve would become partially dorsal in position. A series of shell reorientations during the life of the animal would have been necessary, therefore. The first was probably at the time of detachment, and subsequent changes in position were probably produced by periodic tilting of the shell in or on the substrate toward the "ventral" margins. The impetus for this tilting was continued upward growth of the "ventral" shell margin (in terms of conventional orientation), shifting the center of gravity of the shell in a "ventral" direction, and creating a weight imbalance which could be compensated for only by tilting, perhaps triggered by rocking of the shell during times of exceptional bottom currents.

This theory applies mainly to gryphaeoid forms with coiling in or near the plane of valve symmetry. Forms with beaks coiled laterally, approaching the exogyroid condition, normally developed auricles, folds, and sulci posteriorly to help support the shell on the substrate after detachment and were reoriented less frequently. The type of coiling in *Exogyra,* helical and posteriorly out of the plane of symmetry, was adapted to keeping the feeding margin above the substrate without continual reorientation of the shell. Once attached, the shell grew in a low helical spiral upward and outward, with the plane of the commissure slanted at an angle, allowing the flat to concave upper valve to shed sediment. The heavy adult shell eventually titlted backward, coming to rest on the posterior auricle or flared posterior margin produced in many species, as an additional supporting surface on the substrate. A similar case probably can be made for many coiled rudists and rudist-like bivalves during the Mesozoic. Costae and strong lamellae strengthen the already thick resistant shell and provide improved anchorage in the substrate.

The tall, conical to barrel-shaped lower valve of Cretaceous rudists like *Durania* and *Barrettia* functioned both as a very thick protective cover for the soft parts and for keeping the feeding margin well elevated above the substrate when oriented vertically. These were the predominant reef-forming types of rudists during the Cretaceous. By direct observation of Caribbean rudist reefs and analogy to living and fossil corals, these forms lived predominantly upright in clusters on the reef structure, their lower parts embedded in biogenic debris, their upper parts exposed or cemented togther by mutually secreted calcareous deposits, algae, coral, and other reef-dwellers. In this environment, the rounded cross section and conical to cylindrical form of many genera may be considered adapted to tight packing of individuals on the reef, providing mutual support against vigorous wave and current action. Longitudinal costae and ridges on many forms (e.g., *Biradiolites*) potentially could interlock to furnish additional support in clustered rudists. Many of the tall cylindrical to conical forms had small attachment bases and would have been easily toppled as adults, were it not for support in the upright position furnished by these various structures, partial burial, and the clustering habit. Recumbent examples of normally upright rudists have been noted for many taxa; these individuals are characterized by abnormal flattening on one side of the lower valve and enlargement of the attachment area, providing a flat stable surface at the shell-substrate interface.

Rudists with more irregular cross-sections and regular to irregular, gentle or moderate coiling of the valves (for example, some *Caprinuloidea, Titanosarcolites*) were not well adapted for an upright posture and close packing, and lay recumbent on the substrate as adults, their flattest flanks or outside of the coil ventral in position, or both, and the feeding margin elevated above the substrate by upward curvature of the lower valve or both valves where equidimensional (e.g., *Titanosarcolites*). This living habit was effective for highly inequivalve rudists with a small cap valve (e.g., some caprinids) in areas of active sedimentation, despite the recumbent posture. The degree of spiral coiling and curvature of the coils were directly proportional to the possible elevation of the feeding margin above the substrate. In peculiar forms like *Titanosarcolites,* however, in which the valves are subequal, long, narrow, slightly coiled, slightly spiral structures, the feeding margin was not greatly elevated above the substrate as the shell lay recumbent on the surface. These could only have existed in areas of minimal sedimentation rate or bypass conditions. Most recumbent rudists not only have the flattest side in contact with the substrate, but also the most coarsely ornamented flank, costae and ridges functioning to stabilize the shell on the sediment surface and prevent skidding in the face of currents. The attachment area of many recumbent rudists is enlarged to provide firmer anchorage.

The rudists are complex, bizarre bivalves and have many unique structures which cannot be listed or interpreted in detail here. The interesting papers of ZAPFE (1937), YONGE (1967) and CHUBB (1956) interpreting rudist morphology are recommended to the reader. Two additional exterior features of the rudist shell deserve mention.

Many rudists, in particular forms like *Biradiolites,* have a basically long conical shell with subcircular cross section but are slightly flattened on one side. The site of flattening is marked by two shallow depressions separated by a low ridge and extending the length of the shell. These have been called "siphonal areas," and are variously interpreted as being supporting troughs for extruded incurrent and excurrent siphons, or merely depressions for channeling incoming and outgoing currents. Conclusive arguments have not been presented for either interpretation, or even for the existence of siphons in rudists.

The apertures of the lower valves in forms like *Durania* are surrounded by flattened, grooved to fluted areas on top of the shell wall not covered by the upper valve when in normal apposition. Similar smooth, grooved, downfolded flanges of shell material are found around the edges of the lower valve, outside of the commissure in *Thyrastylon* and related forms. The exposed surfaces of both structures are smooth and appear to have functioned as supports for lobes of fleshy material, probably extensions of the mantle, during life. Quite possibly these mantle flaps were continually exposed and could not be withdrawn into the body chamber of the lower valve. As such, they would provide an effective sensory device. Like modern Bivalvia, the sensory cells of the animal were probably concentrated at the mantle edge. It has also been suggested that the exposed mantle contained symbiotic zooxanthellae, as do living *Tridacna* in the same environment, on the exposed edges of the mantle lobes.

FREE-LIVING EPIFAUNAL BIVALVES

This group includes forms that normally lie exposed on the substrate surface without attachment by shell cementation or byssal threads (except possibly during early ontogeny). Two basic assemblages dominate this habitat among living and fossil bivalves whose ecology is well known; the contention has been made that many early Paleozoic Bivalvia occupied this habitat, but this has not been substantiated. The Pectinidae and possibly some Limidae represent the main group; the other is composed of scattered representatives of families otherwise dominated by shallow infaunal elements. Certain *Glycymeris,* Cardiidae and Veneridae (e.g., *Gemma*) have been observed living free on the substrate with the plane of the commissure horizontal, with or without a thin veneer of sediment on the upper valve.

The two main groups of free-living epifaunal bivalves are distinctly adapted to their different modes of life, but have in common a generally rounded, nearly equilateral, orthocline to slightly prosocline or opisthocline shell, a relatively short hinge line, and a dominance of strong, moderately heavy to thick valves with small auricles, or lacking auricles. The rounded shell form with a short hinge line is adaptive in that it provides a high degree of sensory perception, particularly in the pectinoids with their highly developed, light-sensitive mantle "eye spots." In shells of this design, the mantle margin containing sensory receptors of various types (light, vibration, chemical, etc.) achieves its maximum peripheral coverage (percent of total shell periphery covered) and most even distribution among the Bivalvia, with effective reception around an arc approaching 340°. Many of the Pectinidae also have sensory mantle areas around the auricles, projecting through the auricular gapes to compensate in coverage for loss of receptors in areas directly ventral of the auricles. Although mantle sensory areas are not as highly developed in forms like *Glycymeris* or *Gemma,* effective coverage is still achieved by the rounded shell design. Fully exposed, unattached bivalves are especially susceptible to predation because they may be moved, manipulated, or attacked from any side, and a high degree of sensory reception is critical to their existence.

Exposed populations of *Glycymeris* and *Gemma* which have been observed adapt similarly to the shallow-water environment they prefer. The shells are rounded in outline and moderately to highly biconvex. The valves are basically equal, thick and strong, being reinforced in *Glycymeris* by broad, heavy costae, and they can withstand considerable rolling and saltation in the face of currents or wave action. Both genera are capable of shallow burrowing (most species are dominantly infaunal), but observed free-living surface forms make little effort to do so in normal energy conditions and will gape and feed during times of relative immobility, oriented wtih the plane of the commissure parallel to the substrate. The inflated, rounded shell form permits considerable rolling of the valves across the substrate but this can be considered beneficial only in the sense that it guarantees a continually fresh food supply. Otherwise it is detrimental and restricts the periods spent in feeding to times of relative stability. In total, the adaptive morphology of these bivalves does not seem best suited for exposed surface habitats but rather for shallow infaunal living, where most Veneridae, Glycymerididae, and Cardiidae are found. They are apparently able to adapt marginally to more exposed environments, occur locally in great numbers on substrate surfaces, and grow to adult proportions in this environment. The shallow infaunal living habit, with the shell erect or lying flat on one or the other valve in *Glycymeris* (ATKINS, 1936, p. 217; YONGE, 1955) and *Gemma* (personal observation), makes them subject to frequent exposure by wave and current scour in the high-energy environments they prefer. Their ability to feed and respire on the substrate surface is adaptive to their survival.

In contrast, the Pectinidae are highly adapted to this habitat. Although some are capable of weak byssal attachment as adults, it is not commonly employed by most species lying exposed on the substrate surface; it is frequently a juvenile mode of life. Exposed, free-living pectinoids inhabit a variety of environments, ranging from shallow-water and even intertidal situations subject to strong water movement, to abyssal depths and quiet-water conditions. Most prefer relatively firm substrates of varying grain size over hard or soft sediment. They live independently, though commonly are crowded on a surface, and are typically oriented with the right valve down and the plane of the commissure nearly horizontal.

Two features of the pectinoids are considered primary adaptations to this mode of life (see WALLER, 1967). The shell form is rounded and nearly equilateral, being erect, with small unequal auricles, or slightly prosocline. Various forms are subequivalve, left convex, or right convex, and in part this is correlative with habitat and swimming ability. The left valve of some species is slightly concave. The beak projects only slightly above the hinge line, which extends laterally onto the small triangular to subquadrate auricles dorsolaterally. A byssal notch is developed beneath the anterior auricle at some time during ontogeny. Surface sculpture ranges from very fine concentric growth lines *(Amusium)* to coarse costae and partially developed plicae.

The adaptive advantage of a disc-shaped shell in sensory perception has been discussed. The pectinoid shell form is the best adapted among the Bivalvia for this purpose, allowing evenly distributed, nearly complete sensory coverage, except just below the auricles, around a peripheral arc of the shell approximating 340°. Coverage is less in forms with a long hinge line and large auricles, even though these too bear mantle sensors; it is maximum in forms like *Amusium, Placopecten,* and *Propeamusium* where the auricles are small, subequal, and slanted laterally toward the beak area. The development of "eyes" around the mantle margin of Pectinidae represents one of the most sensitive photic receptor systems among the Bivalvia. This, in conjunction with the broad sensory coverage provided by the shell form, and their swimming habit, greatly increases the ability of pectinoids to react quickly to impending danger and thus to survive in an exposed habitat. These factors offset the greater susceptibility to predation of relatively thin-shelled scallops resting loose on the substrate.

The disc-shaped shell is also well adapted to swimming in pectinoids (and some Limidae). Swimming is effected by rapid clapping of the valves (especially when alarmed) and by forceful ejection of water from within the valve out through dorsolateral shell gapes below the auricles (Fig. 35,*H*). Periods of "gliding" occur between swimming pulses. The plane of the commissure lies horizontal or gently inclined to the bottom during the main phases of swimming. To maintain an approximately horizontal position in the water, and to allow gliding of the shell between periods of propulsion, equilaterality of the valves is important, and adaptive to the swimming habit. Strongly inequilateral shells would be unbalanced and would tilt laterally during swimming and gliding. Although some of the inequilateral pectinoids like *Chlamys,* with its greatly enlarged anterior auricle, are good swimmers, the most equilateral forms, having subequal auricles *(Placopecten, Amusium,* etc.) are reported to be the best swimmers, suggesting a relationship between form and swimming ability. Shell weight, proportional to thickness and size of accessory structures (auricles) or sculpture, also affects swimming ability. The most lightweight pectinids *(Amusium, Propeamussium, Chlamys radiata)* are better adapted for swimming than thick-shelled forms. For this reason, young specimens of various genera are reported to be more active swimmers than adults. The lightweight shell and active swimming of *C. radiata* is further adaptive to the preferred soft-mud habitat of this species, preventing it from sinking into the substrate.

Relative valve convexity is an important consideration in the various habitats occupied by pectinoids. Subequal valves of low convexity characterize the best swimmers, like *Amusium,* and closely approximate good hydrodynamic streamlining necessary during swimming and gliding. But many inequivalve forms are also classified as good swimmers (e.g., *Pecten, Aequipecten*); most of these are left-convex. Apparently the left-convex shell offers less resistance than right-convex forms to being lifted off of the substrate by the initial spurts of swimming. Once water-borne, it is less liable to sink rapidly between swimming spurts than right-convex shells, the flat right valve offering greater resistance per unit area to sinking than an inflated valve of comparable size. The flatter right valve in these shells is also better adapted to resting on the substrate in a stable position. It has yet to be determined whether a correlation exists between the degree of convexity in the left valve and swimming ability, although it seems reasonable to think that such a relationship exists.

Few good swimmers are found among strongly right-convex pectinids, but shells of this form appear to be well adapted for a more sessile existence on the substrate. They are commonly found partially buried in the sediment, with the convex right valve situated in a depression up to a point just below the commissure. In some forms the upper valve is relatively flat to concave and covered with a thin veneer of sediment, which effectively conceals the bivalve from predators. The sediment depression is formed, once the shell has settled after a swimming episode, by rapid ejection of water from the right side of the disc, directed at the substrate. The scallop then lifts itself off the bottom by means of another water jet and settles into the depression thus created. Sediment stirred by this action settles as a thin film on the upper valve. This would be detrimental to cemented forms like oysters and cause fouling when the valves were gaping, but this is not a problem in scallops, which can quickly remove the veneer by rapid clapping of the valves. The deep lower valve is adaptive in that it allows firm implantation of the shell into the substrate while still keeping the commissure elevated above the bottom, retaining sufficient water to keep the animal alive in intertidal situations.

The auricles of pectinids function to extend the hinge line and ligamental area beyond the narrow beak region, providing a stronger articulation and decreasing ability of the valves to be rotated in the plane of the commissure. They also support additional mantle sensors. Reentrants beneath the auricles occur anteriorly at the site of the byssal gape and below it at the anterior water-expulsion gape. A shallower reentrant lies below the posterior auricle at the dorsal edge of the water-expulsion gape on some taxa. A relationship between the shape and depth of these notches and rate or force of water expulsion may exist but it is not presently known. The byssal notch ranges from deep *(Chlamys)* to shallow or absent *(Amusium)* and its depth is directly related to the strength and frequency of byssal attachment. The notch itself allows the byssal gape to be kept open and helps to stabilize the valve on the byssus, restricting movement in the plane of the commissure. In the ontogeny of certain pectinoids, the juvenile shell is strongly attached by the byssus, and the byssal notch is deep, whereas the adult rarely or never attaches and the byssal notch becomes weak or disappears. The gape becomes correspondingly more restricted in these adults and may actually be subsequently closed off. These trends may be traced in the ontogeny of auricular growth lines.

Finally, surface sculpture of the pectinoid bivalves shows interesting adaptive trends. Plicae and, to a lesser extent, costae strengthen the shell at its growing margin, and overall. They are functional in this respect and much needed in areas of high predation rates, strong current, and wave action. Plicae also reflect development of a crenulate commissure which is functionally important in feeding and sensory perception (see subsequent discussion). A general relationship, with many exceptions, can be seen between development of radiating ornamentation and swimming ability and between radiating sculpture and energy conditions of the habitat. Typical pectinoids of deep quiet-water habitats of the outer shelf (*Amusium, Propeamussium, Placopecten,* etc.) are predominantly smooth-shelled forms or finely costate. These are among the best swimmers, and are characterized by nearly symmetrical, subequal valves, and reduced auricles of similar size. In general, free-living epifaunal pectinoids in shallow-water, high-energy habitats have coarsely costate to plicate valves, comparably stronger and better able to cope with an active environment than shells of the deep-water groups. These aid also in anchoring the shell on the substrate surface. Many are good swimmers, others poor, but none attain the ability of *Amusium* insofar as their swimming is known. In shallow-water habitats, no work to date has demonstrated a correlation between strength of radial sculpture and swimming ability. Certain plicate forms seem to equal costate pectinoids in this respect.

If it can be demonstrated that smooth-shelled pectinids and limids are consistently better swimmers than costate or plicate forms, it would be worth investigating the possibility that greater friction created between water and shell by partial or total lamellar flow over smooth surfaces gives greater lift and gliding ability to forms like *Amusium* than the layer of turbulent water flow that would be created over the costate or plicate surface of typical *Chlamys, Aequipecten,* or *Pecten.*

The Limidae contain many excellent swimmers which are adapted in much the same way to this form of mobility as the Pectinidae. Most limids are fissure-dwellers which remain byssally attached for considerable lengths of time, however, including some of the most able swimmers. When exposed on the substrate and actively swimming, the subrounded to ovate, subequivalve, slightly biconvex shell functions as well as many pectinoids, even though it is generally more inequilateral than scallop shells. Swimming may be jerky, with short gliding periods between thrusts created by rapid clapping of the valves, or languid, with slower rhythmic clapping. Water jets are apparently emitted from only one side of the shell during swimming, and the plane of the commissure tends to be inclined to the substrate surface. The trailing tentacles of the Limidae aid in swimming and probably help to offset the posteromedian center of gravity caused by the more opisthocline shell form and the unequal thrust of the single water jet.

SEMI-INFAUNAL BIVALVES

Bivalves in this group are sessile to slightly mobile organisms with the shell normally buried one-half or more of its length in the substrate, but with the posterior portion of the shell, containing the main inhalant and exhalant apertures, permanently exposed; these do not have elongate siphons.

The principal semi-infaunal bivalves belong to the Pinnidae, long, slender, subtriangular, thin fragile shells with slight to moderate convexity (Fig. 6). Maximum inflation occurs along an angulated mid-line. Sculpture ranges from concentric growth lines and coarse lamellae or undulations without radial elements, to variously costate and weakly plicate forms. In *Atrina* the radial elements are fluted or bear spines. Pinnidae predominate in inner shelf environments, including shallow-water areas of high current and wave activity. The shells are embedded in soft sandy, silty, or clayey substrates with the narrow umbonal tip of the shell downward and the mid-shell axis vertical. Some are attached by byssal threads to particles beneath the substrate surface. The broad "posterior" margin of the shell extends above the surface of the substrate one-third to one-half the length of the shell. The animal is capable of vertical burrowing but lateral movement is restricted. The exposed shell is almost totally composed of the prismatic layer and is very fragile. Commonly, it is heavily encrusted by epibionts. YONGE (1953) and ROSEWATER (1961) have discussed the adaptive morphology and anatomy of the Pinnidae in detail.

The shell form of the Pinnidae, elongate subtriangular with low convexity and a diamond-shaped to lenticular cross section, is highly adapted to vertical penetration of the substrate. It is easily retracted into the sediment, when oriented with the narrow tip down, offering minimum frictional resistance. No projecting surfaces, other than surface sculpture, retards its downward movement. Vertical orientation and semi-burial function to anchor it against currents and predators, and greater stability can be achieved by additional downward burrowing. If the plane of the commissure is aligned into the current, the exposed shell has a streamlined profile (cross section) and does not offer much resistance to current or wave action; no studies have conclusively demonstrated that this is the preferred orientation, however. The burrowing habit may also be an adaptation for protection of the animal, which lies primarily within the buried portion of the valves. The thin shells of the Pinnidae are easily crushed or broken. If fully exposed, as rarely in reef fissures, they afford only minimal protective cover to the soft parts. Mantle receptors called "eyes" but apparently not light sensitive, are situated on the mantle edge around the exposed portion of the valve; thus necessary sensory perception is attained over nearly the entire shell margin subject to predation or damage in the semi-infaunal Pinnidae.

Radiating surface sculpture serves two obvious functions. It strengthens the shell, especially where needed at the growing edge (the main site of predator attack). Secondly, it gives increased anchorage to the shell when buried and in contact with the substrate. Spines and flutes in *Atrina* are especially effective in this respect, being inclined upward toward the sediment-water interface and concave on the upper surfaces. Once buried, they act as barbs, preventing vertical withdrawal of the shell from the substrate. In addition, they may function when first formed as supports for sensory tentacles or narrow extensions of the mantle margin, although the position of the concave troughs on their upper surfaces appears to be wrong for this function; they should face ventrally. Spines and flutes may also serve to discourage epibiont encrustation on the exposed valve surface, at least particular types.

In addition to Pinnidae, certain modioliform Mytilidae (i.e., *Arcuatula*) occupy the semi-infaunal habitat, especially in littoral or very shallow-water niches. *A. demissa* is the best known form, commonly occurring singly or in gregarious masses one-third to one-half buried, oriented nearly vertically, among root masses of vegetation or in grass mats and mud. The posterior feeding margin remains exposed. Like the Pinnidae they are byssally attached and apparently capable of downward movement by uprooting the byssus and reimplanting it at a lower level among the roots. Unlike the Pinnidae, semi-infaunal mytilids are not specifically adapted for this niche in form, being similar to closely attached exposed forms such as *Modiolus s.s.,* commonly found isolated on hard substrates and nestled into crannies or depressions near the sediment-water interface (i.e., bases of sponges, sea fans, or patch-reef coral masses). The shell of *Arcuatula,* slightly more elongate than that of normal *Modiolus,* is probably adaptive in allowing occupation of narrow spaces between roots and easier penetration of root masses. Costae, generally limited to semi-infaunal modiolids, may further aid in wedging the shell into its "burrow" by increasing surface friction. Otherwise, the semi-infaunal modiolids should probably be considered secondarily adapted to this habitat, seeking it after development of the normal exposed epifaunal habit for additional protection as the stocks radiated into shallow-water and littoral niches. The fact that *Modiolus s.s.* tends to take on a similar habitat in the shallow end of its range, even though it is primarily exposed epifaunal in habit, supports such a contention.

Individual species of characteristically infaunal groups sometimes take on the semi-infaunal habitat with the posterior edge of the shell exposed during active feeding (e.g., many protobranchs, like *Yoldia,* burrowing arcids, and venerids), or when partially exhumed by scour. This is especially true in probing detritus-feeders. These forms are basically infaunal elements; many are strongly siphonate, and do not occupy the semi-exposed niche continually. They are treated with the infaunal Bivalvia.

INFAUNAL BIVALVES

Included in this group are sessile and mobile bivalves which spend part or all of their life buried beneath the substrate. Most forms draw fresh water and food into this protected habitat through open sediment

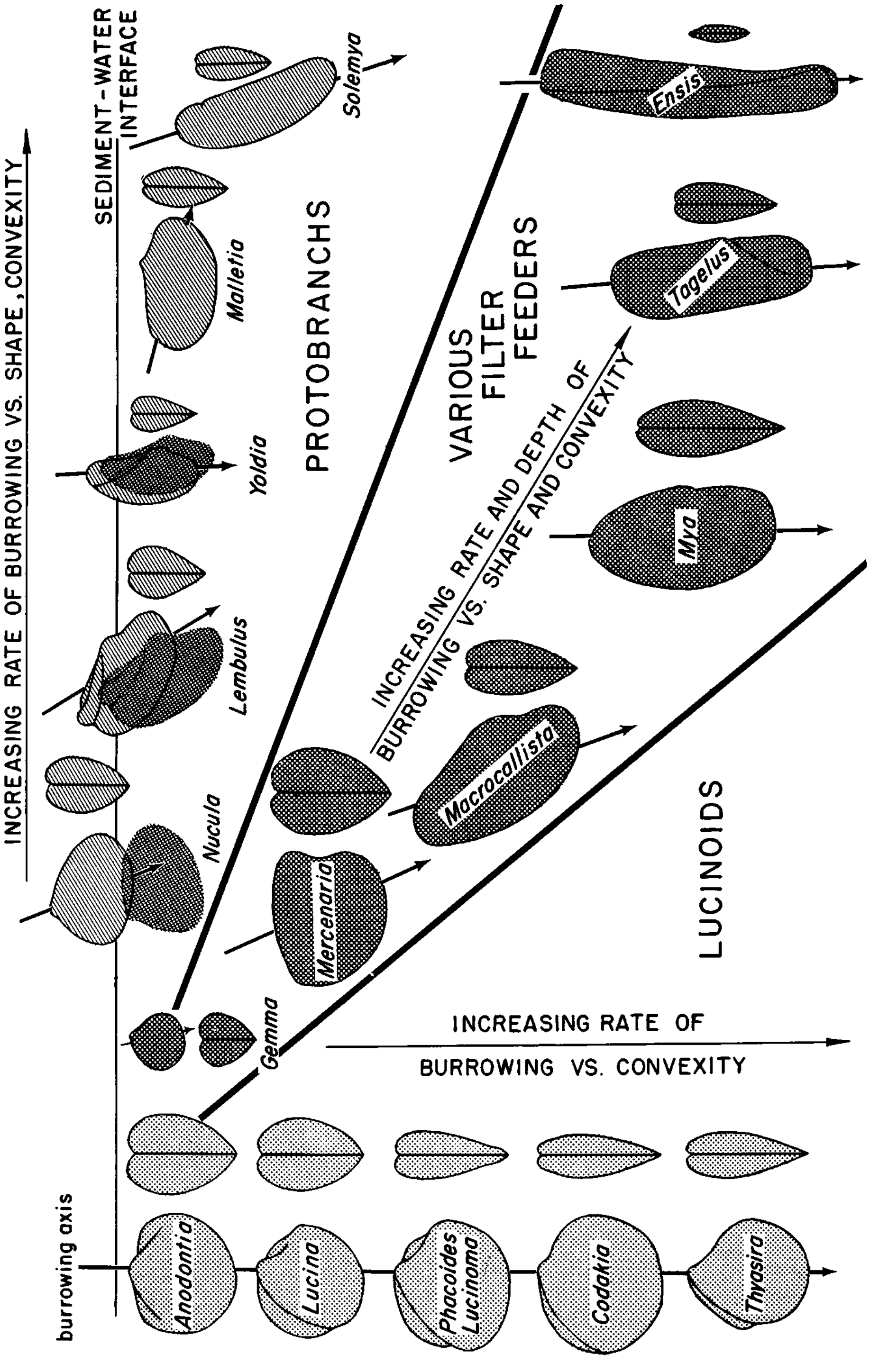

Fig. 90. General relationships in Recent Bivalvia of shell outline and convexity to depth and rate of burrowing (Kauffman, n).

tubes or fleshy siphons, or both. Many feed on organic debris within the sediment. A great variety of taxa have adapted to the infaunal habitat, which affords natural protection from many but not all molluscan predators, and from most rigorous environmental conditions. Although most infaunal elements occupy relatively soft, unconsolidated substrates and thus are still subject to scouring by waves or currents, some (e.g., *Teredo, Lithophaga,* various Pholadidae) have developed the ability to bore into partially or wholly lithified material or wood, attaining the ultimate protection afforded by the infaunal habit, a semipermanent burrow, relatively indestructible, enclosing the animal throughout life. Evolutionary simplification of the ancestral Bivalvia producing loss or retarded development of complex cephalic structures, including highly developed sensors (eyes, long tentacles, proboscis) probably left the early radiating bivalve stocks more vulnerable to elements of the environment than other main molluscan classes. Although development of an enclosing bipartite calcareous shell was the primary adaptation to protection and survival, development of the infaunal habit and structures to cope with it was an equally significant evolutionary event. Inasmuch as this would have been the most natural and available protective habitat to early Bivalvia, and would have afforded them relatively greater protective value than most others, it was one of the first invaded during early Paleozoic radiation. Invasion of the infaunal niche by several groups had occurred by Early Ordovician time, and Ordovician form equivalents to the solenoid jackknife clam *(Cymatonota),* tellinids *(Cycloconcha),* nuculids *(Ctenodonta)* and other living infaunal elements are well known. The lack of a pallial sinus in many of these groups probably indicates that they lacked siphons, or had short ones, and that most early infaunal elements were therefore buried only up to the inhalant and exhalant apertures, or completely buried just below the sediment-water interface. At least one Late Ordovician genus, *Lyrodesma,* contains species with a shallow pallial sinus [e.g., *L. poststriatum* (EMMONS)] and probably had at least short siphons (JOHN POJETA, personal communication, July, 1967).

Compared to the variety of available habitats and energy conditions encountered by epifaunal Bivalvia, the infaunal environment is relatively more uniform. This has had a profound effect on the variety of shell forms developed by infaunal bivalves. Although infaunal taxa are varied, and function in many different manners within the substrate (mobile to sessile, detritus- and filter-feeding, etc.) they are remarkably uniform in the gross adaptive characteristics of the shell (Fig. 90). Thus a similar set of environmental controls act on mobile protobranchs moving horizontally through the sediment in search of organic detritus, and on vertically boring, sessile, siphonate filter-feeders. The main factors controlling external shell form appear to be rate of movement through the substrate and depth of burial, including the anatomical modifications these demand. Maintaining stability and a preferred orientation in the substrate imposes further control on the shell form of infaunal bivalves.

Therefore, although a number of ecologic divisions may be made among the infaunal Bivalvia, as previously listed, the adaptive value and function of shell form, various structures, and ornamentation can be concurrently discussed for all of them. Thus, the adaptive streamlining of the shell for rapid movement through the substrate is

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FIG. 90. *(Continued from facing page).*

[Dark arrows indicate approximate axis of burrowing. All shells shown in normal living position, but not necessarily at uniform scale.]

For lucinoids, a consistent depth zonation is not implied; although some studies accord with depth relationships here depicted, others indicate a different ordering.

For various filter-feeders, the general depth zonation discernible in the diagram agrees with field observations, but spacing of the drawings does not indicate absolute depth differences.

For protobranchs, indicated depth distribution is approximately to scale. The dual images of *Nucula, Lembulus,* and *Yoldia* represent ultimate depth and position attained by burrowing (dark background) and progress toward these (light background) in the time it would take *Malletia* and *Solemya* to attain their normal burrowing depth, as shown.

nearly identical in the vertical burrowing, sessile filter-feeders *Solen* and *Ensis,* as it is in the horizontal burrowing, vagrant deposit-feeder *Solemya* (Fig. 90). Even more significantly, both *Solemya* and *Ensis* are capable of limited swimming when exposed on the surface, because of similar shell design and distribution of soft parts, although they are unrelated bivalves with distinct habitats.

The shape and relative convexity of infaunal bivalve shells are closely correlative with the depth and rate of burrowing, and energy expended in burrowing for all ecologic groups except the very specialized rock- and wood-borers. The following generalized observations apply to an amazingly high percentage of infaunal elements.

Obese bivalves with a rounded to broadly ovate outline are dominantly very shallow infaunal elements which burrow slowly, utilizing large quantities of energy, and once buried remain relatively stationary. Various Cardiidae (e.g., *Dinocardium, Laevicardium*) and Veneridae *(Gemma)* characterize this group. *Nucula* is the most similar detrital-feeding protobranch. Deeper-burrowing bivalves are generally less convex and more elongated, with the axis of elongation approximately coinciding with the direction of burrowing (Fig. 90). Their shells are thus more streamlined and better adapted to easy penetration of the sediment when pulled down on the implanted foot. *Mya* and *Ensis* are typical examples of deep infaunal bivalves (Fig. 90). Depth in each case is measured by the depth of burial relative to the length of the shell, not by the absolute distance below the sediment-water interface. Thus for bivalves that burrow straight down or at a moderate to high angle to the interface, low convexity and elongation of the shell along the burrowing axis are adaptive in that they decrease resistance of the shell to movement through the substrate and require less energy in burrowing. TRUEMAN, BRAND, & DAVIS (1966) have demonstrated this experimentally on four infaunal bivalves of varying shape: round, obese *Cardium;* wedge-shaped, moderately convex *Donax;* ovate moderately convex *Macoma;* and elliptical, very slightly inflated *Tellina.* Mechanical penetration tests on the shells indicated that the ease of burrowing decreased in the following order: *Tellina, Donax, Macoma,* and *Cardium,* in order of increasing shell convexity and decreasing elongation.

All other factors being equal, this information suggests that in the order given these shells would be buried with *Tellina* deepest and *Cardium* shallowest in the substrate. If convexity and elongation were the principal factors controlling depth of burrowing in infaunal bivalves, living species should be depth-zoned on the basis of their shape and this zonation would be directly applicable to the interpretation of infaunal habitat in fossils. It would be expected that forms like *Cardium* and *Gemma* would constitute the shallowest zone, followed in order by geometric forms represented by: 1) *Mercenaria,* 2) *Astarte* or *Crassatella,* 3) elongate *Macrocallista,* 4) *Mya* or *Panope,* 5) *Tagelus,* and 6) *Ensis* (Fig. 90). Observation on living species indicates that this zonation is only partially realized, and that other factors besides shell form also determine depth of burial. Among these, TRUEMAN, BRAND, & DAVIS (1966) listed: 1) ability to rock the shell during burrowing, which aids in speed of penetration; 2) size and nature of the foot, and its ability to probe and anchor in the substrate; 3) presence or absence of external ornamentation, which retards burrowing rate; 4) gape of the shell during burrowing, gaping hindering penetration; 5) ability to produce powerful water jets to clean out sediment ahead of the burrowing animal; 6) size of shell, larger ones being harder to pull into the sediment than smaller ones with the same shape; and 7) available energy used in burrowing, especially once the shell has penetrated below the substrate and burrowing becomes more difficult owing to greater drag imparted to the shell. In their test case, TRUEMAN, BRAND, & DAVIS *(41)* found that *Cardium, Macoma,* and *Tellina* burrowed to the depth of the shell in similar times (*Cardium* slightly slower), *Tellina* being aided by its streamlined shape, *Cardium* and *Macoma* by their rocking motion during burrowing. *Donax,* streamlined and with a very powerful foot, burrowed faster.

Thus streamlined shell shape, with slight convexity and elongation approximately along the burrowing axis, is primarily adapted to a rapid rate of burrowing, although even here it is not the only controlling factor. It is a useful interpretive tool in paleontology in this respect. In certain groups it also reflects depth of burial, as in the venerids, but in most cases it is related to burial depth only insofar as this depends upon rate and it is not possible to set up a reliable depth zonation of infaunal forms purely on these characters for use in interpretive paleontology. This is driven home in the protobranchiate Bivalvia *(45)*, all of which are relatively shallow burrowing detritus-feeders. Three basic geometric forms dominate this group (Fig. 90): the inflated ovate to subtriangular *Nucula;* elongate, posteriorly attenuated, moderately convex shells like *Yoldia, Nuculana,* and *Lembulus;* and very thin, slightly convex, anteroposteriorly elongated shells like *Malletia* and *Solemya.* At approximately the same burial depth *Nucula* burrows very slowly and remains relatively sessile, once buried. *Nuculana, Lembulus* and *Yoldia* are moderately fast burrowers, vertically or at an inclined angle, but remain stationary, once in place with the attenuated posterior end commonly above the substrate. *Solemya* burrows rapidly, orients horizontally in the substrate, and is sessile to moderately mobile. *Malletia* burrows very rapidly and is a vagrant detritus-feeder, moving just below the substrate surface. None are deep burrowers, even though the form of *Solemya* and *Malletia* closely approximates that of certain deep infaunal bivalves.

It is interesting to note that in bivalves which may be depth zoned on their form (Fig. 90), the angle of burrowing and eventual living position change from orientation with hinge axis approximately horizontal to one with the hinge axis nearly vertical, as in *Ensis.* Development of an elongate shell is correlative with elongation of the foot and migration of the point of pedal extrusion from the ventral to the anterior margin, causing a compensatory change in shell orientation during burrowing so that the long axis lines up with the foot and the shell offers least possible resistance to burrowing. Thus, elongation of an infaunal bivalve shell in the evolution of a lineage normally takes place along the burrowing axis and reflects not only adaptation to deeper or more more rapid burrowing, or both, but also may indicate a change in living orientation.

Not all depth zonation or differences in burrowing rate are reflected in varying outline of infaunal bivalves. Decrease in shell convexity alone is adaptive to deeper and faster burrowing (Fig. 90, left). Inflation of the valves appears to be the main factor determining resistance of the shell to penetration of the substrate; decrease in inflation in an evolving lineage commonly permits more efficient burrowing and gives rise to depth zonation among related forms of different convexity but similar outline. Thus the rounded, obese venerid *Gemma* occupies a much shallower habitat and burrows more slowly than the thin platter-like *Dosinia.* In the Lucinacea, rate of burrowing among basically round to ovate shells seems to be primarily a function of inflation and a graded series is inferred from the modern literature and *in situ* observations with tumid forms like *Anodontia,* the slowest burrowing lucinoids, followed in order of increasing rate by inflated *Lucina, Lucinoma, Codakia,* and *Thyasira* (Fig. 90). The latter is also more elongated along the burrowing axis (dorsoventral in the Lucinacea). My own observations suggest a similar depth zonation for all but *Anodontia,* a relatively deep but slow-burrowing form. STANLEY (personal communication, 1967), however, has documented different depth ordering.

Sulci and folds on infaunal Bivalvia normally reflect internal partition of the soft parts and development of interior supports for attachment of muscles, gills, or other organs. They may function externally to strengthen the shell, and in some forms deep sulci terminate near the exhalant aperture and may function secondarily to channel currents passing over the shell into the exhalant area, insuring dispersal of wastes. They aid in anchoring the shell in the substrate, but are a hindrance to burrowing, destroying the streamlining of the shell as it passes through the substrate. For this reason they are rarely present anteriorly, or along the leading edge of the shell in burrowing position. The nature of this leading edge, anterior in many infaunal filter-feeders such as the Veneridae, ventral in the Lucinacea, is closely related to the rate of burrowing, inasmuch as it is the first part of the shell to penetrate the substrate and the ability of the bivalve animal to pull the shell into the sediment depends partially upon the ease of penetration. Gently tapered, relatively flat flanks terminating in a narrowly rounded leading edge represents the most successful burrowing design, as characterized by the wedge-shaped *Donax,* deep-burrowing bivalves like *Tagelus* and *Solen,* and rapidly burrowing forms like the protobranchs *Malletia* and *Solemya.* Increase in convexity and curvature of the flanks, or decrease in curvature of the leading edge, lessen the ability to burrow rapidly.

A well-defined lunule is present in many infaunal bivalves (e.g., *Mercenaria*) and in its position anterior to the beaks, this depressed area would seem to hinder burrowing in the same way as an anterior sulcus—by increasing resistance to movement through the sediment. Notably, the lunule is best defined in shallow or slow burrowers, poorly developed or absent in deep or rapidly burrowing Bivalvia, or both. The function of the lunule has not been adequately interpreted. CARTER (1967,*3*) noted that it has been postulated to be functional in burrowing by acting as a pressure plate preventing the animal from moving upward as the foot is extended downward. These two structures are not always significantly opposed, however. He further suggested that it may function as an area of compensatory growth, maintaining the valve margins in the plane of junction (commissure plane) during rotation of the growth direction. No function has been proposed for the escutcheon, also common in infaunal bivalves.

Most infaunal Bivalvia are smooth or have fine concentric ornamentation, and this condition is adaptive to more rapid burrowing by decreasing friction between the shell surface and the sediment that is inherent in more ornate forms. Coarse lamellae (*Lucina,* some venerids), concentric ribs *(Callista, Antigona),* costae and plicae (Cardiidae) cancellations *(Chione)* and spines or raised flutes on ridges *(Pitar, Hysteroconcha, Hecuba)* occur on many infaunal bivalves. As in other Bivalvia, coarse surface ornamentation is functional in strengthening the valves, and anchoring or stabilizing the shell in the substrate. Raised areas, such as lamellae, flutes, and spines, would seem to be exceptionally useful in anchorage, as well as discouraging predation or encrustation. That these ornamental characters are functional in these respects is strongly suggested by the dominance of coarse surface sculpture in the groups of shallow-burrowing bivalves, and their general absence in deep-burrowing forms. Shallow infaunal elements are frequently subject to scouring or exposure from currents and waves and to higher predation rates, especially from gastropods. In CARTER's study of *Hysteroconcha* and *Hecuba (4)* he concluded that spines along the umbonal ridge were of minimal importance to stabilizing the animal in the substrate, inasmuch as they were not properly oriented for this function and the animal was not totally buried while feeding. He further rejected the possibility that they were supports for mantle sensors, like those of *Spondylus,* or form an effective sediment screen used in feeding (they are too far apart). He concluded that they most likely function as defensive structures against predation, inasmuch as they are long and sharp, but relatively strong, guard the most vulnerable part of the shell (being situated at the siphonal junction), and are oriented to face the direction of normal predatory approach of starfishes and gastropods.

BORING BIVALVES

Bivalves which have developed the ability to excavate permanent burrows into hard substrates are specialized, secondarily derived lineages, many of which arose relatively late in the evolution of the class. The oldest genera which possibly occupied this niche are Ordovician *Corallidomus, Endodesma,* and *Conocardium* (POJETA, personal communication, 1967). Boring bivalves are common, but like the rudists, their highly specialized nature does not warrant detailed discussion here, and only a few general aspects of form and function are dealt with.

The primary habitats are rock, wood, coral, or other calcareous shelly material, and tightly compacted mud, each providing a very high degree of protection to the contained animal. Secondary calcareous tubes are sometimes secreted within the burrows for additional protection *(Teredo)*. This permanent, built-in protective cover, and the necessity of developing boring shell structures for hard substrate, produced far greater experimentation in shell form than is found in most habitats where the shell is primarily designed for protection.

The shell form is basically similar in most boring bivalves, being elongated along the boring axis, except where secondarily reduced, as in *Teredo* (Fig. 4), in which case the animal remains elongate and the shell becomes restricted to the anterior (boring) end. In cross-section most boring bivalve shells are round to subround. This basic form, essentially a narrow cylinder, is highly adapted to the boring habitat in that it is the most efficient possible shape with respect to energy required for the penetration of hard substrates because it greatly restricts the diameter of the burrow necessary to contain the animal. Only *Tridacna,* which bores as a juvenile shell up to approximately 6 inches in length, and *Platyodon,* a *Mya*-like shell with ovate cross-section, have basically different form among the common borers. The functional morphology of *Tridacna,* among the most highly specialized bivalves, is treated by Yonge (1936, 1951) and Rosewater *(29),* and is excluded from the following discussion.

Boring is accomplished by chemical solution (e.g., *Lithophaga*) and mechanical grinding (e.g., *Botula, Pholas*) anteriorly (except *Tridacna*), aided by highly specialized structures and glands on the foot such as the sucker disc of *Pholas* and *Teredo* which grips the substrate during grinding, or the specialized siphons used to grip the walls of the excavation during boring in *Hiatella.* As expected, the grinding anterior end of the shell is highly modified in various borers. The anterior margin is usually moderately and evenly rounded, thickened in some forms, and equipped in a few with accessory toothlike projections *(Pholas)* or a bevelled cutting edge to aid in grinding. The anterior end of the shell is most commonly the widest part, and the boring diameter created by it thus is wide enough to accommodate the rest of the valves and animal. The posterior end of the shell is commonly attenuated and modified to various extents as a sheath protecting the base of the long siphons (e.g., Pholadidae). In some forms the siphons cannot be totally withdrawn into the shell, and thus a permanent posterior gape is developed. The need for withdrawal of the siphons is greatly lessened in this habitat by added protection afforded by the bore hole and, in certain forms *(Teredo)* a secondary calcareous tube secreted wtihin the boring by the animal. The shipworms (e.g., *Teredo*) represent the maximum known modification of the shell to its boring habitat. Here the valves are reduced to a series of small anterior grinding plates, leaving the soft parts mostly naked within the protective burrow and its inner calcareous tube (Fig. 4). *Teredo* and *Pholas,* among others, have a modified sucker disc on the foot that anchors the shell against the bottom of the hole during grinding, and helps the valves by changing positions of attachment. A large anterior shell gape allows this sucker disc permanent access to the substrate. All borers have greatly reduced beaks and umbones, adaptive to streamlining of the shell to fit the bore hole created at the anterior margin. A byssal gape occurs mid-ventrally in forms like *Botula;* this allows the large byssus to provide firm reinforcement of the shell in the bore hole during periods of mechanical abrasion anteriorly at the base of the excavation. In chemical borers like *Lithophaga,* which secretes an acid-bearing mucus anteriorly dissolving the carbonate rock at the base of the boring, a thick layer of periostracum functions to protect the calcareous shell of the animal from the acid.

Various types of surface sculpture aid boring bivalves in stabilizing the shell against the walls of the bore hole while downward pressure is being exerted to deepen it by mechanical erosion, i.e., grinding of the shell edge against the substrate. Costae and lamellae are the principal types of sculpture; spinose to fluted plicae occur in *Pholas* and related genera. In some forms (e.g., *Hiatella*), internal water pressure within the mantle cavity, forces the valves outward against walls of the bore hole to anchor the shell in the hole during grinding, or as means of grinding itself. The ornamentation of the shells in forms like *Teredo* is zoned into distinct regions. The anteriormost zones are characterized by short hard spines used in boring as the shells are rotated in the hole.

Accessory shell plates called pallets are developed in the Teredinidae at the ends of the siphons and act as opercula, effectively closing off the tube when the siphons are retracted.

COMMISSURE

The commissure is defined as the line of junction between valves exclusive of the hinge line—that part of the dorsal margin between the most lateral extent of the hinge teeth. In most equivalve and subequivalve taxa the commissure lies at the outer edge of both valves, but in inequivalve forms (e.g., *Corbula*) it may lie within the outer edge of the larger valve. A number of functionally important structures are associated with the commissure, among them various valve gapes, marginal crenulations, denticles, folds (plicae edges), and raised structures like spines or marginal flutings.

VALVE GAPES

In various Bivalvia the valve margins are not totally in contact around the commissural line but rather gape locally when the valves are tightly closed. In epifaunal Bivalvia, all byssate forms, and many free-living (Pectinidae) and cemented forms (e.g., *Hinnites*) have a byssal gape during their ontogeny which ranges in position from mid-ventral *(Modiolus)* to anterodorsal *(Chlamys),* and from broadly lanceolate *(Lima)* to slitlike *(Brachidontes)* in shape. The gape functions for passage of the reduced foot out of the shell to implant byssal threads on the substrate, and upon contraction of the foot, for byssal threads to pass into the shell to the byssal gland of the foot. The shape of the gape reflects the distribution of threads on the substrate, and thus the degree of anchorage and amount of expected movement about the byssal axis. It is critical in strongly byssate forms that the gape be kept open so that: 1) the byssus may be repaired by the foot if threads are broken; 2) a new byssus may be formed in taxa capable of shedding or uprooting the byssus and moving to a new location when necessary *(Lima);* 3) orientation of the shell on the byssus may be controlled; and 4) the shell may be moved along the byssal axis by pedalbyssal retractor muscles; this is protective, and allows normally free-swinging forms to draw up tight to the substrate when subjected to dangerous ecological situations. Retarded lateral shell growth around the byssal gape keeps it open as long as the byssus is functional, producing a reentrant in the shell margin—the byssal notch or sinus. The gape closes or becomes restricted if byssal attachment is lost in ontogeny, as in many Pectinidae.

In various Pectinidae and *Spondylus,* gapes occur at the lateral ends of the auricles. WALLER *(43)* noted that these function as openings for sensory eye spots on the mantle margin in pectinids and in their positioning compensate for the loss of sensory coverage in water expulsion areas just below the auricles. In swimming, the Pectinidae propel the shell through the water not only by clapping of the valves, but by forceful expulsion of water jets through lenticular dorsolateral gapes just below the auricles with abrupt closing of the valves. The narrow shape of the gapes, which remain open after the shell is closed tightly, restricts the water forced through them, producing a high-velocity jet.

Various bivalves have elongate shell gapes in the area of foot and siphonal extrusion. In deep-burrowing Bivalvia *(Ensis, Mya, Panope)* these become greatly enlarged and may actually be large enough for extrusion of the foot and siphons during burrowing without broad opening of the valves. This is adaptive to rapid burrowing, since the gaping shell in most infaunal bivalves hinders the burrowing process by destroying shell streamlining. In forms with siphonal gapes, these obviously allow active feeding and respiration, and possibly full extension of the siphons, when the valve is otherwise closed. In the extreme case of certain *Mya,* the gape is necessary to accommodate the extruded siphon, which is too large to retract into the shell when it is fully closed. In addition to the above-named gapes, many bivalves have been noted to have minute openings between the valves when fully closed, extending over a considerable area of the commissure. These are probably sensory in function, allowing direct communication between sensors at the mantle edge and the outside environment.

CRENULATIONS AND DENTICLES

Crenulations refer to regularly scalloped areas, or alternating evenly developed, raised and recessed sections of the commissural margin which interlock when the valves are closed and are expressed primarily on the valve interior. They normally occur around the ventral and ventrolateral margins of the shell (e.g., *Mercenaria, Nucula*). Denticles are small, raised, irregularly developed, circular to elongate nodes normally found just within the dorsolateral margins of forms like *Lopha, Ostrea,* and around the byssal gape of various pectinoids. Some have sockets to receive them on the opposite valve, others do not. Both structures strengthen to some extent the valve margin by providing supporting ribs or blocks to the thinnest area of the shell subject to the most frequent attacks by predators. Where they interlock or are received by sockets, both structures further function to prevent rotation of the valves in the plane of the commissure, giving additional protection from predators. Some have very specialized functions. A series of elongate denticles grouped around the byssal gape in pectinoids has been termed the ctenolium, which functions to separate and support the byssal threads at the point where they leave the shell so that they will not twist in the current. This insures a relatively constant orientation of the shell on the byssus, important in feeding and withstanding currents for some species. The presence or absence of denticles is a generic character in Ostreidae but their function other than additional support is not yet known. Denticles and crenulations may serve to anchor the free edge of the mantle in some forms; this would be especially important in females of dimorphic species which use the gills or mantle flaps as areas of egg storage and incubation before eggs are let loose into the water, or for larval implantation (Unionidae). It has been postulated that the individuals of *Astarte* and *Crassatella* with marginal crenulations within a population are females, and those without crenulations are males. Possibly the crenulations function in reproduction in these forms.

MARGINAL FOLDS

Most Bivalvia have a relatively flat commissure, but in many plicate forms the commissure margin is folded in varying degrees. The folds range from very coarse, producing a zigzag pattern at the commissure *(Arctostrea,* some *Lopha),* to broadly sinuous *(Lopha),* to small and angular or blocky (Pectinidae). Secondarily they produce strengthening plicae on the shell, which in turn perform a number of functions in various bivalves. Their primary functions, when formed at the valve margin, are far more significant. Four principal functions have been postulated for mantle folds and the folded shell margins they produce. These have been discussed by RUDWICK (1964).

Folding of the mantle and the shell around it greatly increases the area along the mantle edge relative to a given amount of distance along the marginal outline of the valve, i.e., a given arc. This functions not only for increased feeding and respiration capabilities, to the degree that the mantle margin is involved in creating currents and sorting particles, but also greatly increases the potential number of sensory receptors distributed around the mantle margin. These are primarily situated in the outer edge of the mantle lobes. Such an increase affords greater protection to exposed epifaunal bivalves.

The folded shell margin produced by the mantle also functions to reinforce the relatively thin shell material characteristic of the peripheral border. The folds provide a series of vertical to inclined lightweight struts directed against the outer shell surface. Less weight is required in reinforcing the shell in this manner than by thickening it an equivalent amount. The interlocking marginal folds further serve to prevent rotation of the valves in the plane of the commissure. Reinforcement is especially necessary in exposed epifaunal Bivalvia so commonly attacked in the region of the commissure by predators.

Schmidt (1937) and later Rudwick (1964) have discussed the possible role of the folded commissure in sediment screening on brachiopods and oysters. In bivalves with flat commissures a considerable gape is required for effective feeding and respiration; in larger forms this gape is greater than the width of most particles in the associated sediment so that during turbidity, a great number and size range of particles can potentially wash into and clog the mantle cavity if the valves are open. Folding of the mantle and shell margin greatly increases the absolute linear dimension of the commissure and the area of the mantle edge contained within it. This means that the gape between the valves can be decreased in bivalves with a folded margin without decreasing the water intake area along the commissure. Narrowing the gape not only prevents large particles from washing in but diminishes the amount of possible sediment infiltration. It further makes mantle tentacles, normally very short, more functional in sediment-screening since they are brought closer together in the process. As shown by Rudwick, the amount of protection from sediment infiltration afforded by a folded mantle depends upon the strength, relative amplitude, and angularity of the crests, as well as on how uniform the reduced slit is over the entire commissure. A completely uniform-sized gape is the ideal situation, but rarely developed. In angular folds, the maximum opening along the slit is at the crest of each fold; the opening is most restricted on zigzag commissures with angular crests on the fold. Small, triangular, secondary calcareous deposits inside the crests of the folds are formed by some species to help partially seal off the more open crestal areas.

Rudwick *(31)* has suggested that although the restricted uniform gape, made possible by angular folding of the mantle and commissure, may function in all of the preceding ways, the primary function of this arrangement is sensory. He proposed that slight, even gaping of the shell is only the first step in opening the valves more fully for feeding, and that this initial gape is basically an early warning system exposing the sensory mantle edge completely to the surrounding environment without much danger of fouling. If the water were found free of harmful elements (predators, turbidity), the valves would then gape even further for feeding, possibly to a point where marginal folds were no longer functional as sediment screens.

DENTITION AND ASSOCIATED STRUCTURES

The dentition of the Bivalvia has received a considerable amount of study and has an important role in classification at all taxonomic levels. Its evolution in the class has been speculated on many times. It is unusual that so few authors have attempted to interpret in detail the function of the dental apparatus, especially in view of its considerable diversity. The bivalve dentition is composed of interlocking teeth and sockets which in many groups are differentiated into cardinal and lateral structures, of different size, or have become greatly modified, or even lost. Structures associated with the dentition are various pits and plates for muscle attachment or ligamental material.

The teeth and sockets of the Bivalvia perform three obvious functions. They provide a means of partially or wholly locking the valves together so that they cannot be easily separated by predators (e.g., starfishes, echinoids, gastropods), high-energy water movement, buffeting, or transportation. They secondly prohibit to varying degrees independent rotation of the valves in the plane of the commissure. Again this constitutes a basic form of protection against predators and physical environmental factors. Starfishes, or large gastropods like *Busycon* with a broad muscular foot capable of independent pressure in various regions, certainly are able to put torquelike stresses on the valves when they envelop their prey. Thirdly, the teeth and sockets provide an interlocking joint mechanism partially involved in the rotation of the valves (gaping) along the hinge axis. NEWELL *(18)* has correctly pointed out that in many bivalves the ligament and not the teeth constitute the fulcrum around which the valves gape. No additional major functions have been proposed, to my knowledge, for dentition in the majority of bivalves. A few, such as the boring Teredinidae and *Pholas,* have specialized hinge structures which do not function as normal teeth but rather create a ball joint around which the valves are independently rotated by muscles, functioning as individual cutting tools at the base of the bore hole.

For each of the three main functions of the dentition, general adaptive trends can be cited in the Bivalvia. A detailed functional analysis of dentition cannot be attempted until careful interpetive studies define the precise function of individual dental units, to date much neglected. As a locking device, the taxodont, schizodont, cyclodont, heterodont, heavy isodont (e.g., *Spondylus*), and diagenodont dentition patterns provide strong juncture between the valves and in addition effectively oppose rotation in the plane of the commissure. The great majority of bivalves characterized by these dental types are shallow infaunal or epifaunal elements exposed to rigorous environmental conditions and frequent predation where strong hingement is necessary. The Arcidae, Veneridae, Trigoniidae, Astartidae, Nuculidae, Nuculanidae, Crassatellidae, and Spondylidae are among these. Weaker hingement is found in reduced isodont (Pectinidae), dysodont, asthenodont, anomalodont and edentulous hinge areas, but the relationship to habitat is not as clearly defined. Many of these are deep-burrowing and deep-boring bivalves such as *Mya, Pholas,* and *Ensis* (Fig. 90), which are protected from severe wave and current action, and have a lower predation rate; a strong hingement is not selected for by the environment. Others, however, have preferred habitats directly affected by the conditions selecting for strong hingement, including the shallow infaunal *Anodonta* (fresh water), the various Mytilidae (byssate epifaunal), various Ostreidae (attached epifaunal), and the Pectinidae (free-living epifaunal). Many of these outstanding exceptions can be accounted for because other adaptations to the environment counteract the need for strong hingement—swimming habit in *Pecten,* strong byssal attachment and long efficient ligament in mytilids, cementation in ostreids, etc. However, this does not detract from the caution with which nature of the hinge must be used as a key to habitat in living and fossil bivalves.

The distribution of teeth on the hinge line appears to be directly related to the symmetry of many bivalve shells. Teeth and sockets are subequally distributed around the beak of symmetrical shells, and stretched out on the hinge line in the direction of symmetry imbalance. Thus, long posterior lateral teeth and short anterior laterals would be expected on shells which are truncated anteriorly and projected posteriorly, as in *Crassatella.* This correlation between skewness of the hinge structures and asymmetry of the shell is an adaptation which distributes, as evenly as possible, the protective locking mechanism and the stresses imposed on the hinge area by opening and closing of inequilateral valves.

The length of the hinge line relative to the circumference of the shell margins is correlative to the degree of valve rotation permitted in the plane of the commissure. Elongate hinge lines, like those of the Arcidae or various heterodonts (e.g., *Crassatella*) are better adapted to prevent individual rotation of the valves than short hinge lines (with exception of those with deeply interlocking teeth, as in *Spondylus*) found in various dysodont mytilids, all other factors being equal. In both hingement and protection against rotation, the ligamental structures give added support to the dentition. The efficiency of the dentition in permitting free lateral movement of the valves (gaping) around the ligamental fulcrum, while still maintaining juncture, seems to be correlative with the size of the teeth, their orientation, their penetration, their anchorage in the sockets, and their curvature.

Various structures associated with the hinge complex do not function in the above manner but have specialized roles. Broad spoon-shaped depressions (chondrophores) between cardinal teeth in forms such as *Mya* and triangular pits (resilifers) in the center of the hinge of *Pecten* and various Ostreidae contain a pad of fibrous, calcified ligamental material (the resilium) which is compressed when the valves are closed and expands upon relaxation of the adductor muscles to open the valves.

In Ostreidae, which have no teeth and sockets in the strict sense, the entire hinge plate, consisting of a central resilifer and lateral cardinal plates, is covered with ligamental material which not only functions to open the valves but also to hold them together. Marginal denticles may have a minor role in articulation. Hingement is aided in many Ostreidae (e.g., *Crassostrea*) by the concave nature of the resilifer on one valve and the convex nature of its counterpart on the other, so that they form a crude locking apparatus when in apposition. In *Isognomon* and related genera, several resilifer pits are spread across the hinge line, separated by flat plates. These are opposed and do not function as crude teeth and sockets, as in *Crassostrea.* The locking effect of a number of fibrous ligament pads filling these pits along the hinge line, however, is essentially that of true dentition, though not as stable by far.

A hinge plate usually supports some or all of the dentition but on some forms is extended centrally as a shelf, beyond the dentition and over the umbonal cavity, forming a platform for muscle attachment. In *Septifer* this receives the short anterior adductor, keeping it out of the way of the main byssal muscles which pass through a notch in the platform and attach in the umbonal cavity. Highly specialized muscle attachment surfaces, analogous to the cardinal process on brachiopods, are developed on some bivalves, such as the coral-boring *Diplothyra* and wood-boring Teredinidae. These are recessed plates or surfaces situated on various-length shafts originating on the hinge plate, and are termed apophyses. They appear to be a special and bizarre adaptation placing an attachment platform in the mantle cavity, adjacent to the viscera, for the implantation of muscles with a specialized function.

LIGAMENTURE

Ligamental material is variously distributed internally and externally on the bivalve shell and functions primarily to open the valves upon relaxation of the adductor muscles, either by expansion of a compressed internal band or pad of fibrous, calcified conchiolin (resilifer) or by contraction of stretched external sheets (lamellar and fusion layers of the ligament). Only duplivincular ligamenture constitutes an exception; it has little role in opening the valves and merely acts as a flexible attachment. As previously mentioned, the ligament secondarily, and in some bivalves primarily (e.g., *Anodonta, Ostrea*) functions to articulate the valves and prevent their individual rotation in the plane of the commissure, especially when dentition is weak or absent. The structure of the ligament in Bivalvia and its function have been fully described by Newell (1937, 1938), Cox (1968) and Owen (1958) and particularly in the experimental work of Trueman (1949, 1950, 1951). As Cox pointed out, the ligament is a highly variable and adaptive structure in the Bivalvia, showing considerable diversification even within single lines of evolution. The type of ligament (duplivincular, alivincular, parivincular, etc.), because of its characteristic trace where implanted on the shell, or the specialized structures adapted to receive it (e.g., resilium), can be reconstructed in most fossil Bivalvia, as can the placement of different layers. Fibrous ligament lies below the hinge axis, usually in a resilifer or chondrophore; lamellar and fusion layers lie externally. The distribution of various layers is to some extent also reflected in the trace of the pallial line (Owen, 1958, and others). The gap between the ends of the pallial line and the ends of the primary ligament (reflected in fossils by the structures that contain it) is the area of anterior and posterior extension of the fusion layer.

The positioning of the ligament on the dorsal margin of the valves, like the dentition, is correlative in many bivalves with the symmetry of the shell so that stresses placed on the ligamental material in opening the valves will be as equally distributed as possible. Posterior elongation of the ligament in Mytilidae (alivincular) and Veneridae (parivincular) and addition of multivincular resilia behind the anterior beaks of *Isognomon* as the shell elongates posteriorly is a reflection of this relationship. The distribution of different types of ligamental material (e.g., fibrous, lamellar, or fusion layers; ligament sheets or pads; duplivincular, alivincular, or parivincular), and their density or reinforcement due to calcification is similarly adaptive. It is postulated but not conclusively demonstrated that the depth and size of ligament insertion areas on the valves (grooves, resilifers, nymphae) and the amount of ligament that is "internal" (concealed beneath the dorsal valve margins), is correlative with the ability or force of the ligament to open the valves, though not to the same extent as the nature of the ligament itself.

Cox *(6)* has pointed out the relative mechanical efficiency of various ligament types which, in order of increasing effectiveness are: duplivincular, alivincular, and parivincular (multivincular is still differentiated by some workers and probably fits between the last two types). It seems that a correlation exists between ligament type, its strength and efficiency, and the habitat of the bivalve, although no thorough study has been done to verify this. Many infaunal bivalves must not only overcome the weight of the valves in gaping but also partially or wholly the containing force of the sediment. Correspondingly, parivincular ligaments are common among the infaunal bivalves. Byssate epifaunal bivalves attached to exposed surfaces, where they are extremely vulnerable to harmful effects of the environment, and lacking strong dentition depend on the ligament for valve attachment as well as gaping. Most of these have strong, efficient multivincular *(Isognomon)*, parivincular, or advanced alivincular ligaments *(Mytilus)*. Some *(Pteria)* have weaker alivincular types. Many strongly cemented bivalves (e.g., *Ostrea*), fissure-dwellers *(Chlamys, Lima)*, and swimming forms *(Pecten, Lima)* are probably less dependent on strong ligamenture because of their unusual living habits, and have weaker alivincular ligamenture. There are many exceptions to this generalized pattern; nevertheless, such an approach may be a useful interpretive tool in evaluating evolution of the bivalve ligament. Thus, the apparent development of a mytilid-like advanced alivincular or parivincular ligament from an isognomonid multivincular type in the evolution of Cretaceous Inoceramidae (KAUFFMAN, 1965,9) can be interpreted as development of a more efficient and powerful ligamenture adaptive to a change of ecology from a prone, weakly byssate (or unattached) living habit on the substrate to strongly byssate, erect, free-swinging attachment to elevated objects. NEWELL *(18, 19)* has shown similar evolutionary trends in Late Paleozoic pectinids and mytilids. It is apparent that the functional significance of various types and arrangements of ligamenture deserves considerable study so that it is more applicable to the interpretation of similar, well-documented evolutionary changes.

INTERIOR SHELL STRUCTURES AND SOFT-PART MORPHOLOGY

The interior morphology of the bivalve shell is as complex, if not more so, than that of the exterior and in many cases closely reflects the soft-part morphology of the animal. The relationship between the two has not been adequately studied by either neontologists or paleontologists, possibly reflecting the common practice of zoologists to treat the mantle-shell and animal as distinct evolving entities (YONGE, 1953), and of the paleontologists to rely heavily on external features and dentition in systematics. Study of the probable nature and distribution of soft parts in fossils, a highly rewarding aspect of interpretive paleontology, is a much neglected field, although it has a long history. It demands a thorough understanding of the relationships between shell and soft parts so that one may be constructed from the other. The adductor-muscle scars and pallial line are commonly documented interior features on fossil bivalve shells. Other internal structures, however, equally reflective of the soft parts, have largely been ignored. These include smaller muscle attachment areas, interior buttresses, and muscle platforms, blood-vessel impressions, mantle-fluid channels, and other features. Thorough study of these, and an understanding of their function, allows relatively detailed reconstruction of the soft parts in ancient bivalves.

Stasek (1963) has pointed out additional difficulties in relating shell morphology with soft parts—the employment of two different systems of orientation and a lack of understanding of how one varies relative to another. His stated theory of transformations for relating both soft parts and shell in distinct taxa is based on the concept that comparable regions of the body are always adjacent to comparable regions of the mantle-shell, allowing a series of basic points to be identified on the shell of the bivalve which mark the position of various organs or regions of soft-part morphology. If these points are reflected by structures on the inner or outer shell surface that can be traced through ontogeny, they can be connected (Fig. 65), dividing the shell into distinct zones reflecting major anatomical areas or the position of particular structures, or both. Their history of development can thus be studied within a taxon, or they can be compared between diverse bivalves, indicating adaptive differences and evolutionary change in both soft and hard parts, in unity, and providing additional data for the interpretation of functional morphology in fossils. For more detailed comparison between taxa, a basic grid can be constructed on these points (Stasek, 1963, fig. 6). No matter what variation in form is developed on even distantly related Bivalvia, many of these points are identifiable through ontogeny or on the adult shell on the great majority of bivalves, or both. Thus, in comparing two distinct bivalves, if a basic grid is constructed on one and the critical points noted within it, a deformed grid using the same points can be constructed on the second (Stasek, 1963, fig. 7), allowing identification of comparable soft part areas and structures, and demonstrating evolutionary differentiation between them.

This is a potent paleontologic tool which has two primary applications to the study of form and function. First, in defining points of reference where shell and soft parts can be related, it makes possible a system of orientation common to both, and introduces a reliable means of identifying, from shell morphology alone, the probable distribution and development of soft-part morphology in considerable detail. Structures of the shell are brought to light as markers for some internal structure which rarely have been noted and interpreted by paleontologists. The work to date only introduces the possibilities; it is primarily up to the paleontologist to seek additional reflections of soft parts in the shell morphology.

Secondly, the transformation diagram is a major tool of comparative morphology in which most extinct bivalves, of all ages, may be critically compared with a living counterpart, either related to the fossil, or homeomorphic and similarly adapted to the environment. Such an approach would be a considerable boon to the study of Paleozoic Bivalvia, in particular for the interpretation of their evolution and degree of morphologic sophistication. Eventually we may be able to reconstruct soft-part morphology in such detail through this method that it will be possible to discuss the functional advantage of an enlarged foot, gill reorientation, an expanded mantle cavity, or ventrally migrating palps in the evolution of Paleozoic bivalve lineages with no related living counterparts. Features of the shell interior discussed below are all natural reference points for the construction of transformation grids because they reflect direct contact between the shell and particular structure(s) of the soft-part morphology.

MUSCULATURE AND PALLIAL LINE

The study of musculature in Bivalvia is one of the most successful means of delineating the general aspects of soft-part morphology and is a primary tool in the study of form and function. The musculature of the principal groups of living bivalves is well documented except for relationship of minor muscles of the gills and visceral mass to the shell, where they utilize it for insertion. At least the principal areas of muscle insertion, the adductors, pedal and byssal retractors, and the main pallial muscles are commonly preserved on fossil bivalves of all ages. Although these were generally ignored in earlier paleontologic works or described only in a cursory manner, a great deal of attention has been focused on musculature in recent years, and it has an important role in systematics and evolutionary studies. Their study is especially critical in Paleozoic forms. The most important aspect of musculature still to be investigated in paleontology is the spatial interrelationship between all muscle-insertion areas on the shell and other features of the animal morphology, so that the evolutionary significance and functional meaning of changes in muscle systems can be interpreted in detail, and the fossil soft-part morphology more completely reconstructed. Transformation diagrams and multivariate analyses will probably be the primary tools of such an undertaking.

Adductor muscles.—The principal muscle-insertion areas recognizable on fossil and Recent Bivalvia are those of the adductor muscles. These were defined early in the history of bivalve research and have been significant bases for classification. The terms dimyarian (equal or subequal adductors), anisomyarian or heteromyarian (unequal adductors, anterior one smallest), and monomyarian (single posterior adductor) are familiar to all students of paleontology. The adductors function primarily to close the valves, and through prolonged contraction to keep them closed against the tensional and compressive forces of the ligament. YONGE (1953, *47*) and OWEN (1958) pointed out that the adductors probably originated as hypertrophied pallial muscles at the ends of the mantle embayments on the hypothetical ancestral bivalve. They are well developed on all fossils definitely identified as Bivalvia where the musculature can be distinguished in well-preserved material. Although primitive adductor muscles may have been dominantly of a single type of tissue, the muscles of most living bivalves are divided into two parts, in some cases *(Pecten, Ostrea)* strikingly so. These are termed the catch and quick portions and are composed of nonstriated and striated muscle components, respectively. The quick portion is adapted for rapid contraction and closing of the valves and is especially functional as a defense mechanism, for cleaning the mantle cavity and valve surface, and in swimming (Pectinidae, Limidae). The catch portion is designed to keep the valves closed against the force of the ligament and is capable of sustained contraction. A comparative study of the size and distribution of these parts relative to the overall morphology and habit of various bivalves would be a rewarding and much needed endeavor.

YONGE *(47)* has discussed in considerable detail the basic differences between dimyarian, anisomyarian, and monomyarian musculature, their origin and evolution, and generally their functional significance relative to bivalve morphology and the mantle-shell of various kinds of bivalves. Many important details concerning the effects of anterior-adductor-muscle reduction and loss on the distribution and operation of associated soft parts are contained in this work and applicable to the study of form and function. The functional advantages of the anisomyarian and monomyarian conditions are treated only generally, probably because YONGE envisions these conditions as being secondarily produced by evolution in the following sequence of events, and therefore not in themselves a selected primary adaptation: 1) development of byssal attachment in dimyarian bivalves, producing a permanent fixed point for the foot and therefore restricting its ability to reorient, relative to other animal morphology, during evolutionary change in the form of the animal and its shell; 2) progressive reduction of the anterior one-half of the body without compensating shift of the foot and byssus, so that they become relatively more anterior in position and disproportional to other morphologic features; 3) secondary adaptation of the mantle-shell to the trend in 2), and reduction of the anterior adductor, as part of the mantle-shell complex.

Yonge envisioned the equilateral dimyarian byssate shell as being less adaptive to the epifaunal environment than one which is posteriorly elongated. Reduction of the anterior portion of the shell allows clustering of individuals while still keeping the inhalant and exhalant apertures, posterior in position and projecting above the substrate, free from restriction of circulation. Given the alternative of reducing either the anterior or posterior end of the animal following byssal attachment, posterior restriction would have been detrimental in that it would have restricted the ability of the inhalant and especially exhalant apertures to function properly, assuming they could not compensate in their placement relative to other soft parts.

The monomyarian condition arose by eventual loss of the anterior adductor and was accompanied by a trend toward horizontal orientation of the shell and eventual attachment (Yonge, 1953, *47*). Many monomyarians, however, retained an erect living posture (some *Pinctada,* Ambonychiidae). The tendency toward horizontal orientation, as in the pectinoids, created selective pressures for a more rounded, inequivalve shell, reflecting reorientation of the soft-part morphology, and creating the most stable geometric form for this living orientation. Centralization of the posterior adductor was a secondary result of this trend. Yonge *(47)* discussed this in detail and considered the adaptive significance of this change to be primarily increased freedom of internal orientation of animal morphology, the soft parts being distributed around the centralized posterior adductor. Development of the rounded, horizontally oriented shell and body morphology is envisioned as a return to the basic shell form—the fundamental symmetry of bivalve shell growth—by Yonge. It is made possible in development of the monomyarian condition by destruction of the influence of the anteroposterior axis of the body on the symmetry of the mantle-shell. This basic molluscan symmetry is already greatly affected in Bivalvia by evolutionary simplification of the head region so dominant in cephalopods and gastropods.

The placement of the adductor muscles on the bivalve shell is critical in that they function most efficiently when situated so as directly to oppose forces placed on the shell by the ligamental material. Dimyarian muscles shift laterally, becoming more distant from the beak, as the shell lengthens in an evolving lineage. Anisomyarian musculature reflects uneven pressures exerted on the anterior and posterior adductors in closing the valves and keeping them closed, by marked reduction of the anterior half of the shell and soft parts. In monomyarians the relationship between shell symmetry and placement of the ligament and adductor muscle is best expressed, and centralization of the muscle in an evolving lineage can be correlated with increasing valve symmetry and centralization of the ligament (Pectinidae). The size of the adductor muscles, and the relative distribution of striate and nonstriate tissue, are general indications of their strength and can be interpreted to varying degrees from the nature of the muscle insertion area. In general (many exceptions exist), the depth of the insertion area, the roughness of its surface, and the presence or absence of buttresses are thought to correlate with the strength of the muscle or the amount of pressure exerted on it when contracted, or both.

The shape of the adductors may also be diagnostic of function, but this is not fully understood. For example, what is the functional significance of a subcentrally situated ovate adductor impression on *Pycnodonte* as opposed to a comma-shaped impression on *Lopha* in the same position? In some cases these merely reflect the morphologic structures adjacent to them as they pass through the visceral mass and mantle cavity (Lucinacea); but also the detail of their shape may reflect not only the distribution of stresses on the muscle but the various types of muscle tissue. In some bivalves the catch and quick portions of the adductor are clearly marked by different surface features of the muscle impression, by a distinct line separating them, or by marked constrictions in the outline of the attachment surface. A considerable amount of functional interpretation can result from definition of the relative size of adductor muscle components. For example, the large striated muscle portion of the adductor in ostreids reflects the ability of the animal to clean the mantle cavity and shells of sediment by rapid and forceful closure of the valves.

The unusual irregular, dorsoventrally elongate shape of the lucinoid anterior adductor impression is an excellent example of how impression form may be interrelated with other aspects of the morphology and therefore have considerable interpretive potential. Lateral constriction of the muscle provides anteriorly space for the upward passage of the vermiform foot between the adductor and mantle attachment area to form and occupy the anterior sediment tube used in feeding and respiration (Fig. 91). Posteriorly compression of this muscle provides additional space in the mantle cavity necessary for the retraction and coiling of the enlarged foot. A constriction in the center of the scar denotes the contact between catch and quick muscle portions. Finally, the vertical elongation of the scar reflects its ability to satisfy the preceding spatial requirements and still maintain a size necessary to perform its main function of closing the valves. Vertical elongation also brings the ventral tip of the muscle, with its ciliated surface used in sorting, in contact with the main currents flowing into the mantle cavity for feeding and respiration.

Pallial line.—The pallial line is a band or series of pits made by the insertion of muscles attaching the mantle to the shell. Peripheral to this the mantle hangs free. The line extends subperipherally between the adductors of dimyarian bivalves, and between the posterior adductor and the hinge area of monomyarians. In some dimyarians the line extends subperipherally beyond the adductors along the dorsal and dorsolateral margins. Here it essentially acts as a secondary dorsal adductor in addition to its role of mantle attachment. The extent to which the pallial line continues dorsally is controlled by the extent of fusion of the outer layers on the outer mantle lobe adjacent to the mantle isthmus, and associated extension of the ligamental fusion layer laterally beyond the region of the primary ligament (Owen, 1958). The pallial line dorsally connects the point where the fusion layer terminates, with the adductor muscle. The dorsal extent of the pallial line may therefore be used to determine the layers involved in mantle fusion adjacent to the isthmus and the extent of the ligamental fusion layer in fossil bivalves. That fusion of the inner two mantle layers, and the inner surface of the outer layer do not produce loss of dorsal pallial attachment, whereas outer mantle fusion and development of a fusion layer does restrict it, suggests strongly a functional replacement of one for the other in evolution. The distance between the ends of the primary ligament and the inner edges of the adductor muscles in dimyarians has been thought by Owen (1958) to correspond to compensatory lateral shift of the adductors, with elongation of the animal and shell through evolution, to the position on the shell where they are most efficiently placed to perform their function of closing the valves.

The pallial line reflects the insertion of more than one band of pallial muscles, usually distinct bands of radially arranged longitudinal muscle strands. These may be differentiated in some fossils by slight differences in the texture of the insertion areas. The degree of manipulation of the free mantle flap made possible by these muscles may be reflected in the strength of their insertion and the distinctness of separate bands. Two basic types of pallial muscle attachment are developed in the Bivalvia, and most forms have one or the other: 1) continuous pallial muscle insertion along a track (e.g., *Mercenaria*), the pallial line as strictly defined, and 2) discontinuous insertion reflected in a linear series of discrete pits along the line of pallial attachment (e.g., *Isognomon*) or by local clusters of muscles (e.g., *Pinna*). In many cases the second type of pallial line is much farther within the shell than the first. Although the functional advantages of one over the other system have not been well defined, it is postulated that continuous pallial attachment provides greater control in manipulation of the free mantle edge, but that discontinuous attachment, which involves bundles of longer fibers than developed in continuous musculature, is better adapted to rapid contraction of the mantle over longer distances. The pitted system occurs in many

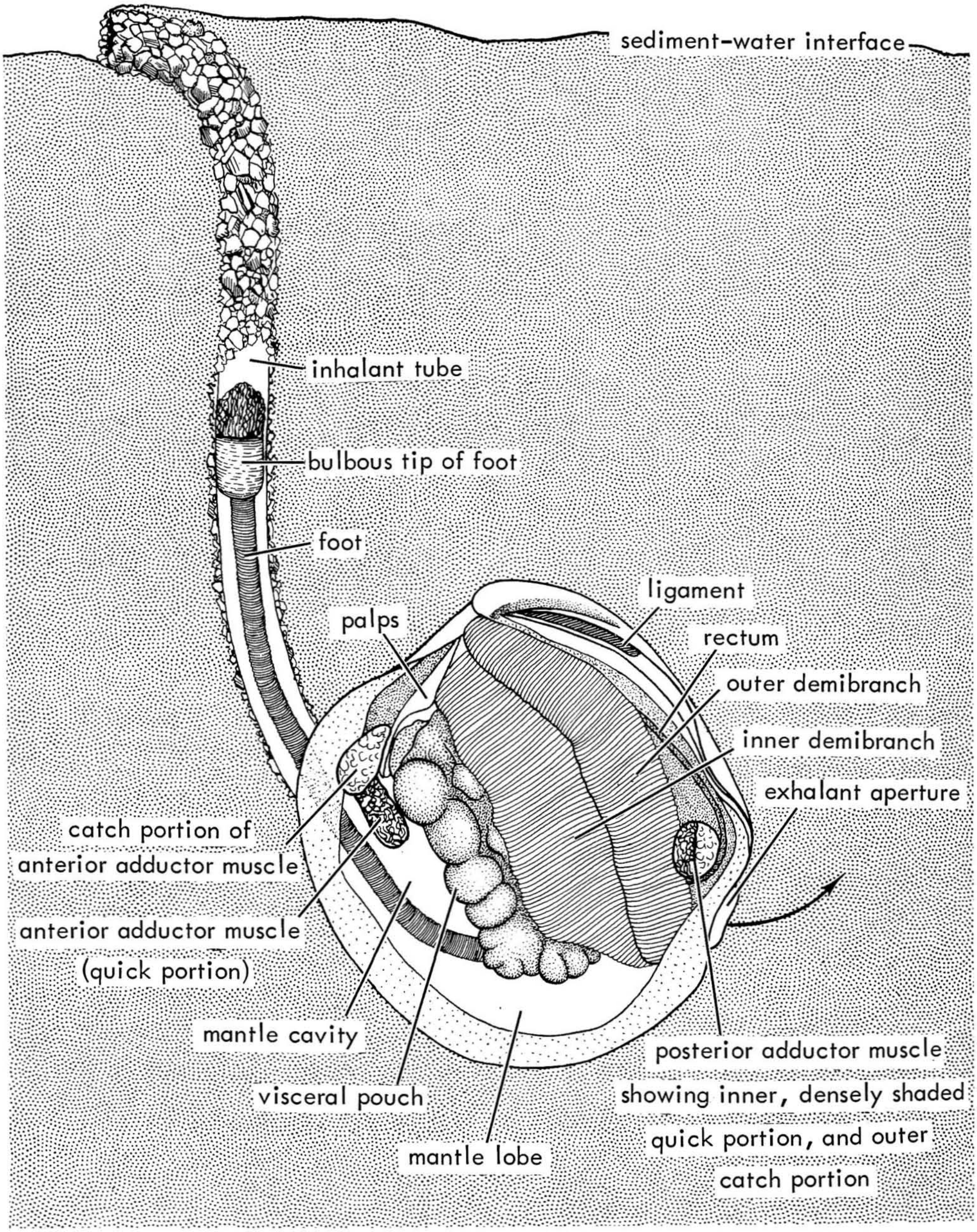


FIG. 91. General anatomy and living habit of *Thyasira flexuosa* (MONTAGU) (Kauffman, *11*, mod. after Allen, 1958).

Animal shown in living position at shallower depth than normal, anterior inhalant tube broken away in center to show elongate vermiform foot with bulbous tip. Sediment grains encasing tube enlarged to accentuate structure, no sediment-size selection being implied. Backward-directed arrow (lower right) indicates direction of current flow from exhalant nonsiphonate aperture, here somewhat extruded to show its position.

epifaunal bivalves which have a large expanse of thin delicate shell beyond the line of pallial attachment composed mainly of prismatic calcite (or other outer ostracum) and periostracum. The shell is easily broken by predators and in high-energy current situations, and it is highly advantageous for the animal in this situation to have the ability to withdraw the free edge of the mantle rapidly far into the shell when threatened. The more central position of the pitted pallial line would therefore be as adaptive as the bundled musculature itself. Such flexibility of free mantle extension and contraction may also be adaptive to rapid repair of the shell over a larger area once broken.

An obvious feature of the pallial line in infaunal Bivalvia is a distinct reentrant posteroventrally, the pallial sinus. This marks the position of the siphons where developed (although very short siphons do not necessarily produce a sinus) and embayment of the mantle attachment to allow them free movement. The bifurcating axis of the sinus generally reflects the direction of siphon extrusion. The size of the sinus is only grossly related to the size of the siphons, and more closely reflects their degree of fusion, strength, and degree of extrusibility. In Lucinacea, a reentrant of the inner shell layers, contained within the pallial line, between the pallial line and the anteroventral edge of the anterior adductor muscle insertion area delineates the position of an incurrent channel between the anterior sediment tube (Fig. 91), and the mantle cavity. This channel allows extension of the foot out through the tube and entrance of inflowing currents used in feeding and respiration.

Pedal and pedal-byssal musculature.—The foot is one of the most complex and adaptive structures of the bivalve, and it would be expected to have a complex system of operational musculature. This is certainly the case. YONGE *(47)* has reviewed the development of the principal pedal and pedal-byssal musculature on a variety of bivalves and the subject has been treated in detail and illustrated in this volume by COX *(6)*. Some general adaptive trends are evident from these data. The primitive pedal musculature is envisioned by many authors as consisting of numerous subequal dorsocentrally inserting muscles between the anterior and posterior adductors (MCALESTER, 1964) for the operation of a ventrally extending foot. Decentralization and functional differentiation in the muscle system, inequality of musculature, and general decrease in numbers of muscles in younger forms reflect evolutionary trends producing a great diversification in the types and functions of the foot, and in living habits among the Bivalvia. Numerical decrease in numbers of pedal muscles to perform a particular function is considered an evolutionary advance producing greater efficiency of operation and simplifying the musculature transgressing the mantle cavity. This trend does not apply to all bivalves, however. For example, Ordovician nuculoids do not have multiple pedal scars, whereas younger ones do (J. POJETA, personal communication, 1967). Reference to the pedal musculature developed on many different groups of Bivalvia (Fig. 31, 34) obviates functional relationships between size and distribution of muscles and the size and function of the foot. Strong musculature necessary to operate the digging foot of *Mercenaria, Anodonta, Cardium,* and *Yoldia* is reflected by large or numerous pedal muscle scars (developed as solutions to the same problem) or both; loss or degeneration of the foot accompanying byssal attachment and cementation produces a marked decrease in the development of pedal muscles.

The rate of burrowing and relative energy required in penetrating the substrate are strongly reflected in the pedal musculature of infaunal bivalves. For example, rapid burrowing requires forceful penetration of the substrate by the foot so as to obtain a deep anchorage. In some rapid burrowers (e.g., *Tellina*) a large pedal protractor is placed in near opposition to the retracted foot for this purpose. Infaunal bivalves not well adapted in form for rapid burrowing and which require a considerable amount of energy in the process (e.g., the moderately inflated *Anodonta*) have proportionately larger protractor muscles, or more of them *(Yoldia)*. Manipulation of the foot in the burrowing process requires additional strong muscle control, reflected by the great development of pedal elevators and retractors on most actively burrowing infaunal bivalves. The complicated relationships between the direction a foot extends from the shell and operates, its necessary force and scope of activity, and the placement of pedal retractors, elevators, and protractors on various Bivalvia would be an excellent line of investigation and would be wholly applicable to the interpretation of form and function. It is obvious from known examples that the placement of muscles relative to the direction of extension of the foot is critical and that a delicate balance must be maintained between the vector forces of protractors, elevators (where developed), and retractors. Shift in one during evolution might be expected to bring about compensatory shift in the others or else be accompanied by significant alteration of shell form, or soft-part morphology, or all three. For example, if *Cardium* is taken as a model of a simple ventral to ventroanterior projecting foot system in a rounded shell (Fig. 31), the equal placement of the pedal elevator, anterior retractor, and posterior retractor, and subequal development of the latter two might be expected as the most efficient and balanced system of operation, the foot being drawn straight up by equal force from the three muscles. Posterior elongation of the shell and a shift from mid-ventral to anteroventral projection of the foot during evolution, as in a form like *Anodonta* (Fig. 31) drastically imbalances this system. The pedal elevator remains below the umbo but due to anterior placement of the beak on such a form comes to lie close to the anterior retractor, adjacent to the adductor muscle. To compensate for this, the posterior retractor enlarges and shifts backward with the posterior adductor, coming into apposition with the projection of the foot and taking over as the principal retractor force. When such interrelationships are fully understood it should be possible to reconstruct relative vector forces from the muscle-insertion areas of fossils and interpret the size, projection, and operation of the foot.

The foot is reduced or lost in many attached Bivalvia and the pedal musculature greatly simplified (Fig. 34) to a dominant pedal or pedal-byssal retractor with or without small accessory protractor and anterior retractor muscles. This reflects the dominant motion in byssate bivalves of extension or contraction of the shell on the byssus, with rapid contraction especially adapted to survival by pulling the shell tight against the substrate or byssal attachment area. Correspondingly, the pedal-byssal retractor normally lies directly opposed to the direction of byssal extension, the optimum position for efficient operation. Once the position of the pedal-byssal insertion area and the byssal gape are known on fossil shells, the direction of extension of the byssus can be determined and the position of the shell relative to the attachment surface reconstructed. This in turn allows numerous functional interpretations based on other aspects of the shell morphology. Thus in *Modiolus, s.s.* (Fig. 34,*D*) the large pedal-byssal retractor and main (posterior) pedal retractor are side by side in the posterodorsal corner of the shell and projection of the byssus is anteroventral. In *Isognomon* (Fig. 34,*A*) projection of the byssus is dorsoanterior and the main retractor muscle is centrally situated, directly opposed to the byssus in a posteroventral direction.

Other muscles.—Numerous small muscles attached to the shell within the pallial line serve the mantle and other soft parts and are sometimes preserved in fossil shells. Besides the pallial line the mantle is attached by numerous small radial pallial muscles scattered over the surface. These produce small pits on the shell in some cases and function also to retract the mantle when agitated. In taxa where the mantle is not attached over a large area posteriorly *(Pteria)* special bundles of mantle retractor muscles attach centrally in the shell. Clusters of muscles around the pallial sinus in siphonate bivalves serve to withdraw the siphons by contraction; in some cases these are easily distinguished on fossils and usually larger than the mantle muscles. Gill-muscle scars have been pointed out in the Early Ordovician prelucinoid *Babinka* (McAlester, 1964) but are not commonly visible on the interior surface of bivalve shells. Newell (1937, 1938, 1942) has tentatively identified them on a variety of taxa. They form an arc which probably defines the orientation of the gills, its long axis parallel to a line connecting the ends of the arc. This could be a useful tool for determining the position and orientation of gills in other fossils if the insertion areas are preserved. Cox *(6)* has reviewed minor musculature in detail.

Muscle platforms and buttresses.—Raised areas around and below muscle insertion surfaces reinforce the adductor muscle attachment and buttress it against the predominant direction of force during operation. *Glycymeris* and various Arcidae, and especially forms like *Cucullaea* display these well. Internal ribs accomplish the same function. These may be the result of flexure of the entire shell, as posteroventral sulci (externally) or internal supporting folds (e.g., many Ostreidae), or solid internal ribs *(Leptosolen),* or hollow internal ribs (Cretaceous *Endocostea*). In the Lucinacea and possibly other bivalves the internal fold formed by the primary exterior sulcus marks the line of gill attachment and may be a platform for the gill muscles, or a buttress for gill support as well as attachment of the posterior adductor muscle.

Other features.—Various grooves and lines have been documented on the interior of bivalve shells and related in various ways to soft-part morphology. Fine, radiating sinuous grooves and raised lines have been interpreted as traces of radiating mantle attachment muscles (retractors), as impressions of mantle tentacles, and as traces of pallial fluid canals or blood vessels within the mantle. The arcuate track of one major blood vessel has been identified by its imprint on the central part of the shell in various Lucinaea and Ostreidae.

Space.—In the study of functional morphology of bivalves it has often been overlooked that the size of the mantle cavity and the distribution of soft-part morphology within it represent spatial relationships critical to the survival and efficient operation of the animal, and can be defined in fossils. Utilizing inflation of the valves internally, the trace of the pallial line, and various lines of evidence such as musculature which reflect the size and distribution of soft parts, the size and available space in the mantle cavity can be generally reconstructed. In forms like the Lucinacea, where the vermiform foot must be totally withdrawn and coiled in the mantle cavity to allow currents to enter anteriorly, or the Unionidae which retain the larval young on the gills of the female, an enlarged mantle cavity is necessary and is variously reflected in the shell morphology. In unionids this is shown by the greater inflation of the female shell, especially along the umbonal ridge. In lucinaceans it may be represented by lateral compression and submarginal position of the anterior adductor muscle, and posterior repositioning and size reduction of the gills.

EVOLUTION AND INTERPRETATION

The documentation of form and function is a necessary first step of interpretive paleontology and considerably broadens the scope with which paleontology can be applied to the solution of geologic and biologic problems. For the sake of simplicity, functions have been defined for major features of the bivalve shell, the potential fossil, and for interacting structures of the shell and its contained soft parts, as discrete entities. This step must precede integrated analysis and does not deny the existence of complex functionally interacting systems or suites of soft-part and shell morphology. These are too variable and complex to attempt description here for all Bivalvia; their characteristics depend largely on the lineage in question.

Therefore, in order to document the concept of functionally integrated character suites, the ability to define them in paleontology, and the application of this and associated paleontologic, biologic, and geologic data to broad problems of science, a selected example is presented. Although this does not incorporate all possible lines of interpretive research, it serves to point out its potential. The interpretation of evolutionary trends is basic to nearly all ventures into this field.

CRETACEOUS THYASIRA OF NORTH AMERICAN INTERIOR

The unique lucinacean *Thyasira* LEACH has worldwide distribution in cold to warm temperate, Recent marine waters, and the anatomy, morphology and living habit of modern representatives have been thoroughly studied (ALLEN, 1958). Structurally, the animal is unusually adapted to life in restricted cool water, infaunal habitats, including oxygen-poor, hydrogen sulfide-rich environments with a limited food supply, supporting an otherwise impoverished molluscan assemblage. Soft-part morphology is well defined in features of the containing shell. The earliest known fossil representatives occur in Cretaceous rocks of North America. KAUFFMAN *(11)* recently described those of the Western Interior for the first time, defining two main evolving species complexes containing five definable lineages, with seven species and ten subspecies distributed through 11 Campanian ammonite zones (see Fig. 97). Populations and ontogenetic series of well-preserved specimens showing interior shell morphology were available for study from 20 stratigraphic levels spanning about 4.75 million years. Radiometric dating indicates individual subspecies have an average time range of 0.86 million years; the more restricted subspecies range through 0.63 million years of time. This is slightly longer than comparable ammonite zones in the same rock sequence. Evolution within Cretaceous lineages was relatively conservative, and has been since the Cretaceous, the fossil forms being closely comparable in shell morphology, and soft parts indicated by it, to living species of the Atlantic Realm. These factors made the study of Cretaceous *Thyasira* an ideal test case for multifaceted inter-

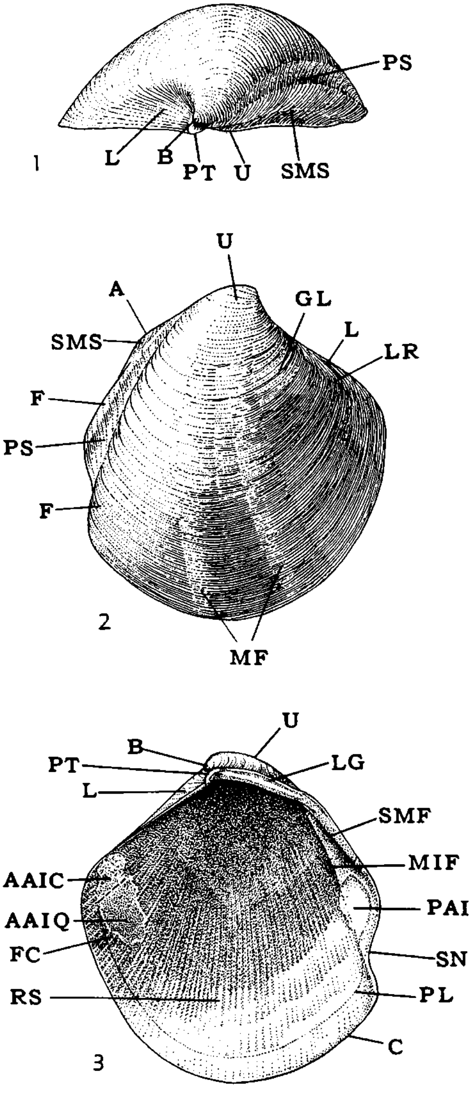


FIG. 92. Morphology of *Thyasira flexuosa* (MONTAGU) right valve, *(1)* dorsal, *(2)* exterior, and *(3)* interior views (Kauffman, *11*). [EXPLANATION: *A*, posterior auricle; *AAIC*, anterior adductor insertion area for catch portion of muscle; *AAIQ*, anterior adductor insertion area for quick portion of muscle; *B*, beak; *C*, commissure; *F*, fold on valve exterior; *FC*, foot canal or incurrent channel, reentrant between antero-ventral edge of adductor muscle scar and inner edge of pallial line, marking position of channel or opening in mantle margin leading from proximal end of anterior inhalant tube to mantle cavity (foot projects outward and feeding currents flow inward through this channel); *GL*, growth line; *L*, lunule; *LG*, ligament groove; *LR*, marginal ridge of lunule; *MF*, medial flattened areas on shell exterior; *MIF*, main or primary interior fold; *PAI*, posterior adductor muscle insertion area; *PL*, pallial line; *PS*, primary sulcus of valve exterior; *PT*, pseudocardinal tooth; *RS*, radiating interior striae; *SMF*, submarginal fold of valve interior; *SMS*, submarginal sulcus of valve exterior; *SN*, notch in marginal outline formed by its intersection with primary sulcus; *U*, umbo.]

pretive analysis utilizing comparative morphology and ecology between closely related fossil and living taxa.

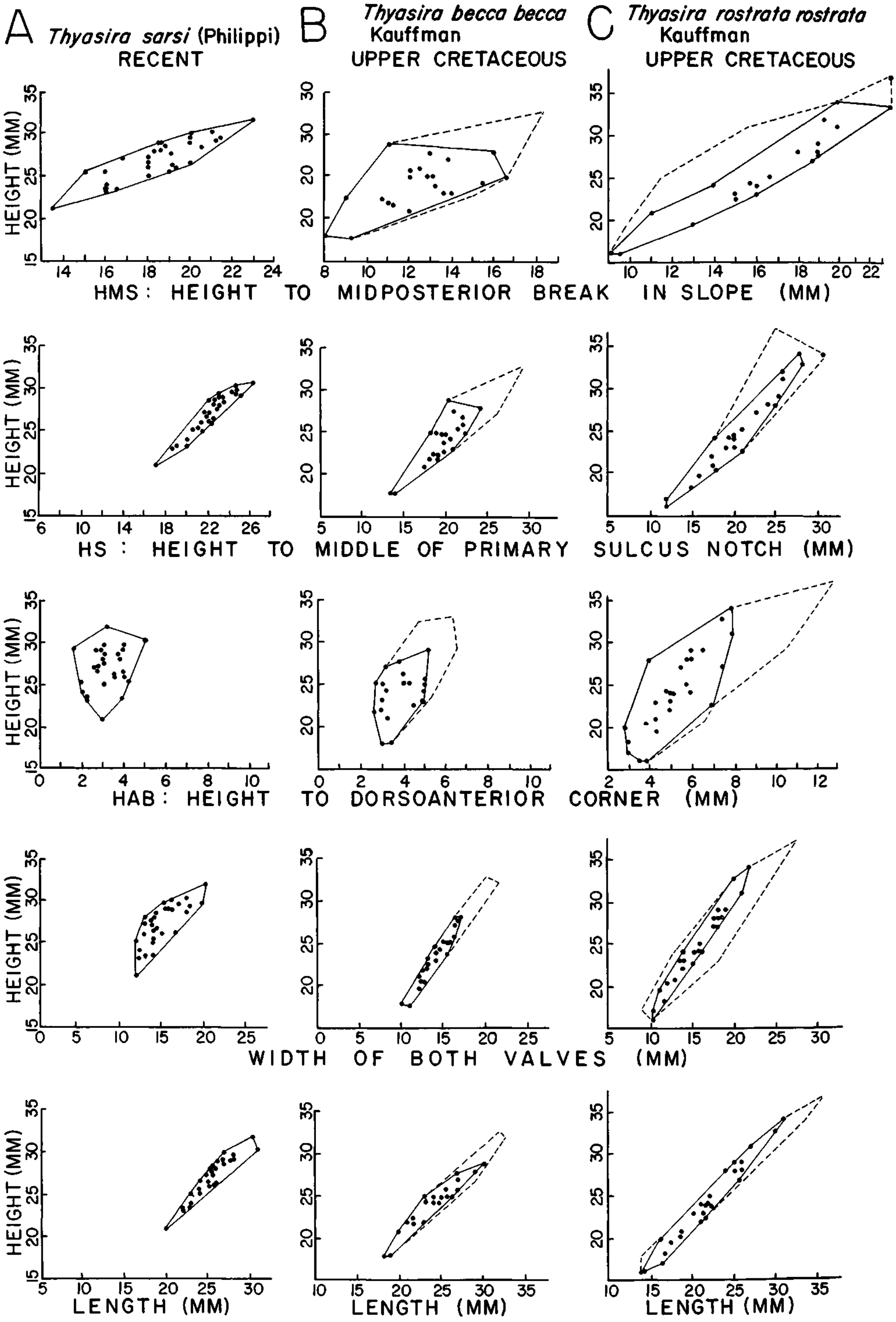
Shell.—Comparative studies demonstrated that the interior and exterior shell morphology of Cretaceous and Recent *Thyasira* were similar in all aspects but size and shell thickness. Cretaceous species are consistently larger and have thicker shells than most Recent Atlantic species to which they are related, with the exception of forms like *Thyasira sarsi* (PHILIPPI). Fossil and Recent shells are equivalve, moderately biconvex, slightly to moderately prosocline and round, subround or subtriangular in outline. They are characterized externally by prosogyrous beaks, a shallow lunule, narrow escutcheon, fine concentric ornamentation, and a prominent posteroventrally directed sulcus, posterior to which is a strong asymmetrical fold and a smaller submarginal sulcus below the dorsoposterior border. Internally the hinge is edentulous or pseudodentate, very slightly thickened, and the posterior ligamental groove long and narrow. The external sulci are expressed internally as folds. A round posterior adductor insertion area of moderate size is located astride the main fold; the anterior adductor is irregular, elongate in a dorsoanterior-ventroposterior direction, well implanted, separated ventrally from the entire pallial line, and constricted centrally. Radial grooves and low ridges cover the shell interior. Figure 92 shows additional detail.

Biometric analysis of shell characters on Cretaceous populations compared to similar variation plots in the closely allied living species *Thyasira sarsi* provided a means of depicting expected limits of population variation in fossil species and thus a basis for separating phenotypic variation from evolutionary change in time successive Cretaceous populations of each lineage. It further demonstrated the conservative nature of Cretaceous to Recent evolution in *Thyasira* and confirmed the close comparability of fossil and Recent forms. The same variable and conservative characters are found on both (Fig. 93 is a sample of this analysis) and the degree of variation shown by any character or character-pair is closely comparable on living and fossil species of the same evolving complex. Equally as significant is the close similarity in character plots of the entire sample—all collections of the species from all geographic areas and throughout its time span (Fig. 93). This marks the degree of phenotypic conservatism within the species, and further aids in separating taxa in an evolving lineage.

Functional morphology of the shell.—*Thyasira* lives erect, deeply burrowed in the substrate (Fig. 91). The shell is similarly oriented during burrowing once erected on top of the substrate; the foot extends midventrally, penetrating deep into the sediment and anchoring by expansion of the bulbous tip. The shell is then pulled straight down, ventral edge leading, by contraction of pedal muscles aided by a rocking motion of the shell. Most *Thyasira* have an externally simple shell which is well adapted for burrowing and this mode of life.

Low to moderate shell convexity, the nearly smooth outer surface, and the gradually tapering ventral and ventrolateral flanks are features streamlining the shell for vertical burrowing, creating a tapered smooth wedge adapted for easy penetration of the substrate. Elongation of the shell along the height axis occurs in many species (Fig. 92) and further streamlines the shell by reducing the length dimension relative to height, and diminishing the size of the penetration track and the frictional drag imparted to the shell by the substrate during penetration. The smoothly rounded to ovate marginal outline, lacking projecting auricles, is similarly adaptive.

Both the lunule and escutcheon face away from the burrowing direction and could act as buttresses against the overlying sediment to counteract the force of the foot against the substrate when extended ventrally. Folds and sulci are considered disadvantageous to rapid burrowing in bivalves, creating an irregular surface to be pulled through the sediment, and probably increasing the amount of frictional drag to be overcome as well as the necessary energy output. These lie dorsal to the main incising part of the shell in *Thyasira,* which


A *Thyasira sarsi* (Philippi)
RECENT
B *Thyasira becca becca* Kauffman
UPPER CRETACEOUS
C *Thyasira rostrata rostrata* Kauffman
UPPER CRETACEOUS
HEIGHT (MM)
HMS: HEIGHT TO MIDPOSTERIOR BREAK IN SLOPE (MM)
HS: HEIGHT TO MIDDLE OF PRIMARY SULCUS NOTCH (MM)
HAB: HEIGHT TO DORSOANTERIOR CORNER (MM)
WIDTH OF BOTH VALVES (MM)
LENGTH (MM)
15
20
25
30
35
14
16
18
20
22
24
8
10
12
14
16
18
6
10
14
18
22
26
5
10
15
20
25
30
0
2
4
6
8
10
12
35

minimizes their effect on burrowing, and the functional significance of their internal counterparts, the primary and submarginal folds in *Thyasira,* far surpasses any deleterious effect they may have on burrowing. The primary sulcus internally provides a strong buttress for the attachment of the gills and posterior adductor muscle, and the submarginal sulcus becomes the lower edge of the ligamental groove. Median flattened areas along the burrowing axis of many species (Fig. 92) may be advantageous in that they slightly diminish the outside convexity of the shell and further cut down on its resistance to burrowing.

In living species there seems to be a general but poorly documented correlation between convexity, outline of the valves, burrowing speed, and burrowing depth. The broadest, roundest shells belong to shallower infaunal species with a slower rate of burrowing than the less convex shells elongated along the height (burrowing) axis (e.g., *Thyasira flexuosa,* Fig. 92). A similar interpretation is applied to the variable Cretaceous *Thyasira* (see Fig. 95).

Soft-part morphology.—Allen (1958) studied in detail the anatomy and morphology of living *Thyasira,* characterized in Figure 91 by the common Atlantic species *T. flexuosa* (Montagu), shown here in living position. Like other Lucinacea, the internal morphology of *Thyasira* deviates strikingly from the usual infaunal plan and mode of adaptation to habitat, typified by the Veneridae. These deviations are primarily concerned with the foot, mantle cavity, gills, inhalant and exhalant apertures, mantle fusion, and sorting and feeding mechanisms. These are reflected in the internal morphology of the shell on both fossil and living species. The animal is adapted to a deep infaunal existence in fine substrate, oriented vertically (Fig. 91), in areas of poor productivity and potential oxygen deficiency or high hydrogen-sulphide content, or both.

The foot is highly modified, long and slender with a bulbous, expandable tip bearing mucous-secreting glands. It reaches ten times the length of the shell in some Lucinacea and when retracted lies coiled in the mantle cavity, considerably enlarged to receive it. The foot has three functions, burrowing, locomotion (not common), and formation of an anterior agglutinated sediment tube leading from the water-substrate interface to the anterior margin of the shell and carrying the principal inhalant currents used in feeding and respiration. It may also have a role in detritus-feeding but this has not been documented. It is well adapted for both burrowing and tube formation. In burrowing its form and length allows deep penetration and firm anchorage in the substrate with each thrust, and thus rapid penetration. The tube is formed by the joining of successive agglutinated sediment collars formed around the mucous-secreting tip of the foot. Periodically the foot is extruded through the tube to clean or repair it, and possibly also for feeding, creating in-

Fig. 93. (Facing page) Comparative population variations in Recent and Cretaceous species and subspecies of *Thyasira* (Kauffman, *11*).

[Explanation: Graphs show close similarity in range of variation of each character pair for single populations of living and Cretaceous species, providing comparative basis for species and subspecies concepts. Slightly greater variation shown by fossil species in some character-pairs is attributed to preservation factors. Range of variation for all specimens of fossil subspecies, regardless of locality and relative position within their known stratigraphic range, is closely comparable to that of single populations with exception of size range.]

A. Thyasira sarsi (Philippi), Rec., from Grand Banks, north Atlantic, at depth of 130 fathoms. Population of 30 valves (USNM 52733, Division of Mollusks).

B. Thyasira becca becca Kauffman, U.Cret., from single layer of concretions in middle part of *Baculites scotti* Zone of Pierre Shale, Fall River County, South Dakota. Solid line and plotted points represent population of 23 specimens, broken line showing boundary of scattergram based on measurements of all known specimens of subspecies from all different localities.

C. Thyasira rostrata rostrata Kauffman, U.Cret., from zone of limestone concretions (zone of *Baculites* sp. with weak flank ribs) in Steele Shale, Lost Soldier-Ferris district, Wyoming. Solid line and plotted points represent population of 26 specimens, broken line showing boundary of scattergram for measurements of all known specimens from all known localities.

ward directed currents, or as a plug during times of turbidity.

Expansion of the mantle cavity to accommodate the foot when retracted and coiled is produced by: 1) reduction of the size of the gills and their reorientation (compared to simple dorsal pendants) dorsoposteriorly, buttressed against the main interior fold and facing anteroventrally; 2) development of lateral body pouches on either side of the mantle cavity, possibly reflected in some species by the point of maximum valve convexity; and 3) lateral compression of the anterior adductor muscle.

The anterior adductor muscle and its insertion area are larger than the posterior adductor, elongate dorsoventrally or along a dorsoanterior-ventroposterior axis, irregular and generally constricted centrally at the junction between the striate and nonstriate part of the muscle (Fig. 91). The lower half of the insertion area is separated anteriorly from the pallial line. This separation, the incurrent channel, allows free passage of the foot in front of the muscle and out the mid-anterior portion of the commissure to form the sediment tube used in feeding and respiration. Incoming currents pass between the tube and the mantle cavity through this channel. Thus, lateral compression of the muscle is functional both anteriorly and posteriorly.

The apertures of *Thyasira* are highly modified as a result of the anterior inhalant tube. Unlike other Lucinacea with a long posterior exhalant siphon, *Thyasira* is nonsiphonate and no sinus is developed in the pallial line, even though many species prefer a deep infaunal habitat. The posterior inhalant aperture is poorly defined and formed only by partial cuticular fusion of the inner mantle lobe. It no longer functions in feeding and respiration; currents entering through it are weak and function to create vortices in the main rejection track current for the sorting and cementing of pseudofeces. The posterior exhalant aperture is well developed and retains an excretory function.

The formation of a long inhalant tube in *Thyasira* permits individuals to burrow deeply into soft sediment, some of which is chemically deleterious to many other infaunal elements, while still drawing adequate food and oxygen from waters above the interface. Many environments inhabited by Thyasiridae are characterized by a limited food supply. To adapt to these conditions the sorting mechanisms are greatly reduced, concentrated anteriorly and the food-selectivity of the animal considerably diminished compared to more normal infaunal groups like the venerids. The gills are reduced in size and lose their particle-sorting structures. Palps are similarly restricted in size, and all ciliary sorting surfaces except those of the anterior adductor muscle and anterior mantle lobes are lost or greatly reduced. These modifications make possible acceptance of a wide range of particulate organic matter, decidedly adaptive in a food-poor habitat. Further modifications of the mantle are treated in ALLEN (1958) and KAUFFMAN (1967, *11*).

In the initial evolution of the Lucinacea, including the poorly known pre-Cretaceous history of *Thyasira,* and subsequently in the development of Cretaceous to Recent lineages of Thyasiridae, evolutionary changes in shell and animal morphology had to be integrated with normal feeding and respiration. Critical to the feeding-oxygenation process are the spatial relationships of the soft parts and fluid flow within the mantle cavity. The three basic spatial relationships that had to be maintained during evolution, and therefore integrated as a selective force in the evolutionary process, were as follows: 1) Efficient operation of gills in feeding and respiration depends upon even bathing by most incurrent waters. Thus, to allow initial sorting of material by cilia at the mouth of the anterior channel, and elimination of harmful or unusable particles by countercurrents before the incoming water is distributed across the gills, the gills themselves must maintain a critical distance from the point at which incurrent waters enter the mantle cavity. 2) The most even bathing of the gills would be expected if: a) this distance was sufficient to allow the water to spread out within the cavity, and b) the gills faced perpendicular to the incoming currents. 3) The mantle cavity must be large enough to accommodate the coiled vermiform foot when completely withdrawn from the sediment tube, and still allow normal respiration and filter feeding to take place within it. Retention of these critical spatial relationships plays an important role in the evolution of Cretaceous *Thyasira.*

REFLECTION OF SOFT-PART MORPHOLOGY ON SHELL: FORM AND FUNCTION

Much of the unique soft-part morphology of *Thyasira* is reflected in detail on the shell interior, providing a firm basis for reconstruction of the basic soft parts in fossils, and considerably broadening the scope of possible interpretation of form, function, ecology, and evolution in Cretaceous species closely resembling living forms. The size of the mantle cavity is defined by the pallial line, inner edge of the adductor muscle insertion areas, and the interior inflation of the shell; the presence or absence of lateral mantle pouches is not documented in shell morphology, except possibly the point of maximum shell inflation dorsocentrally. The function of an enlarged mantle cavity has been discussed.

The adductor and pallial musculature is well defined by moderately impressed insertion areas on the shell interior. These are more coarsely striated than the surrounding shell at the adductor insertions. Their shape accurately records the shape of the muscle at insertion. The elongated shape of the anteroir-adductor-insertion area reflects lateral compression of this muscle to provide additional space medially in the mantle cavity for the coiled foot, and ventroanteriorly for the incurrent channel between the mantle cavity and sediment tube. The ventroanterior separation of the anterior adductor insertion from the pallial line marks the position of the incurrent channel and defines, by the angle of this narrow reentrant, the steep angle at which the foot projected outward in tube formation, the probable inclination of the sediment tube extending from the shell to the surface, and the point and direction at which incoming currents entered the mantle cavity. A prominent medial constriction in the anterior adductor insertion area on some species defines the juncture of the ventral striated and dorsal nonstriated muscle fibers (Fig. 91). The relatively large area of striated muscle, and the coarsely ornate surfaces of the adductors indicating firm muscle implantation, probably reflect the ability of the animal to close the valves forcefully and quickly. This creates a powerful downward jet of water which clears sediment along the ventral margin of the shell during burrowing. The large size of the anterior adductor is partly due to its lateral compression and compensating ventral elongation in order to maintain an area of musculature anteriorly adequate in size for closing the valves. Ventral elongation is also probably related to food sorting, extending one of the main ciliated areas of the mantle cavity (the ventral part of the muscle) to a position adjacent to the anterior inhalant channel. This further increases the area of ciliated surface available to create inhalant currents and sort particles at the mouth of the incurrent channel. The smaller, more rounded posterior adductor muscle is defined by an insertion area midposteriorly astride the main interior fold, which functions as a buttress for the implantation and bracing of the muscle.

Both posterior sulci on the shell exterior produce interior folds. The small submarginal fold forms the base of the ligamental groove. In addition to muscle support, the main posteroventrally directed fold internally marks the line of gill attachment in *Thyasira,* functions as a supporting buttress for the gills, and may actually represent the surface on which the gill muscles insert, although no trace of these has been found. The orientation of the gills in the mantle cavity can be determined from this structure and their approximate size reconstructed using modern representatives. From such data the critical spatial relationships between the gills and incurrent channel, and their orientation relative to the point and direction of current entry into the mantle cavity can be defined on fossils. Similarly, the distribution of the visceral pouch, foot, and other structures generally can be reconstructed in Cretaceous *Thyasira.*

The entire pallial line is well defined and marks the point of insertion of a continuous arc of mantle muscles used in retracting and manipulating the free mantle edge.

Radial grooves and ridges within the pallial line are probably the tracks of these and additional, functionally similar mantle muscles scattered over the valve interior. The lack of siphons in *Thyasira* is reflected in the lack of a pallial sinus.

It is apparent from the preceding discussion that the soft-part morphology can be reconstructed in considerable detail on fossil *Thyasira* by direct comparison with similar living species. The interpretation of form and function is coincidently greatly enlarged in scope, and the interrelationship of characters, that is the recognition of functional character suites, is made possible. Thus, the compression of the anterior adductor muscle is related to formation of an incurrent channel anteriorly and enlargement of the mantle cavity centrally, and therefore to the nature of the foot, the anterior sediment tube, the position of the incurrent channel on the commissure and the orientation of the gills to face it. It further reflects distribution and nature of ciliary sorting mechanisms, and its size, bipartite nature, and implantation are related to the force with which the valves can be closed in burrowing and cleaning of the mantle cavity. Obviously, many aspects of the soft-part morphology and many different inter-related functions can be depicted by thorough examination of a single structure.

Conversely, many structures may be modified by evolution and interact to perform a single function, and this too is better defined on fossils when the details of the soft parts are known through comparative morphology. For example, the creation of a functional inhalant current anteriorly in *Thyasira* is dependent on and evidenced by 1) the vermiform foot and the inhalant sediment tube it creates; 2) the ability of the mantle cavity to receive the large foot; 3) the alteration of the anterior adductor muscle insertion area so that an incurrent channel is formed between the pallial line and the muscle; 4) the ventral elongation and expansion of the muscle and its contained cilia to help create currents down the tube and act as a principal particle sorting mechanism; 5) the ability of the gills to be oriented through evolution so that they face the incoming current at this point; and 6) the degeneration and secondary development of the posterior inhalant aperture with its reduced role in taking small quantities of water into the mantle cavity to aid in particle sorting.

Having defined these basic form and function relationships, the next obvious step in an interpretive study would be to document their adaptive value in the behavior and preferred habitat of the animal—their ecologic inferences—and how closely this might be defined in the fossil. The close morphologic comparison between living and fossil *Thyasira* alone would imply but not demonstrate that their habitats and ecologic implications were very similar.

COMPARATIVE ECOLOGY

The ecology of living *Thyasira* is as unique as its morphology, which is specifically adapted to an infaunal habitat excluding many other burrowing mollusks. The similarity of shell and inferred soft parts of fossil *Thyasira* to living forms suggests a similar ecology. This can be demonstrated by analysis of the physical aspects of the rock, geographic distribution, shell orientation, and faunal associates of Cretaceous *Thyasira* from the Western Interior of North America. Temperature, depth, substrate type, sediment and water chemistry, the amount of available food, and competitor mollusks are the principal environmental controls on the distribution of living forms.

HABITAT OF LIVING THYASIRA

The living posture of *Thyasira* is shown in Figure 91; the animal is capable of burial up to 10 times the length of its shell, although normally it is found shallower. Upon reaching the preferred depth of burrowing the foot projects upward from the mid-anterior margin, forming the agglutinated inhalant tube by cementing together collars of mucous-cemented sediment formed around the tip of the foot. The top of the tube is bent over and probably faces into the current, providing additional force to drive inhalant waters down the tube. The reclining top of the tube further protects against quantities of sediment washing into the aperture.

Living *Thyasira* demonstrate a strong preference for dark clay mud substrates, with or without silt- to cobble-size detritus. They prefer substrates without associated coarse clastic debris (Fig. 94). Some species live in fine- to medium-grained sand; none have been reported from coarser clastics except when mixed with mud or fine sand. Soft clay mud is preferred to compact material. Many living species have the ability to inhabit, and actually prefer, oxygen-poor or hydrogen sulphide-rich substrate in areas of low productivity which ecologically exclude many other infaunal bivalves or both. *Thyasira* flourishes best in areas of low competition and is frequently abundant only with a restricted assemblage of associated mollusks. The greatest diversity of living species of *Thyasira,* in both hemispheres and all major ocean basins, is in the mid-temperate latitudes, between 30° and 55° north or south latitude. Though distributed throughout the world, *Thyasira* is rare in Arctic, Antarctic, and Tropical seas (Fig. 95). Many species, or species groups have their maximum abundance in progressively deeper, cooler waters going from north to south in their geographic range (Fig. 96). Temperature and not depth is therefore the main controlling factor in distribution. The greatest diversity and abundance of living *Thyasira* is in the outer part of the inner sublittoral zone and the outer sublittoral zone of continental shelves (200 to 600 feet), but they are known from shallow waters of the inner shelf out to 7,500 feet or more in depth.

Living *Thyasira* are well adapted to their preferred environment. The foot and streamlined shell insure rapid deep burrowing in the substrate, as previously described. Formation of the anterior inhalant tube is a striking adaptation, permitting *Thyasira* to be a deep-burrower without development of massive siphons. The tube

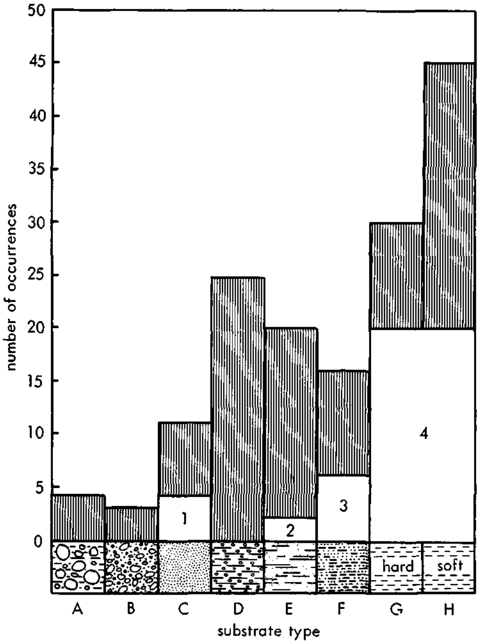


Fig. 94. Distribution of living and Cretaceous species of *Thyasira* (fossil forms from Western Interior only) relative to substrate type (Kauffman, *11*).

The diagram demonstrates a primary preference of *Thyasira* for clayey substrates without associated coarser sediment (especially where soft) and a strong secondary selection of clay containing sand, silt, or pebbles. The genus is poorly represented on substrates consisting of coarse clastics. Agreement between distribution of Cretaceous (white areas numbered 1 to 4) and Recent (vertically ruled areas) *Thyasira* with respect to substrate types is noteworthy, attention being called to the fact that plotted occurrence of Cretaceous forms is superposed on the plot for Recent and the latter not stacked on the former.

A. Coarse cobbles in a pebble-clay-sand matrix.
B. Pebbly sand.
C. Coarse to fine sand, silty sand, and sandy silt.
D. Pebbly clay.
E. Sandy clay.
F. Silty clay.
G. Firm clay, usually dark, without associated coarser clastic material.
H. Soft clay without coarser clastic material.
1. Sandstone, usually with calcareous cement and little admixed clay.
2. Sandy shale, usually cemented secondarily into concretionary masses by calcium carbonate.
3. Silty shale, usually cemented secondarily into concretionary masses by calcium carbonate.
4. Clay shale cemented secondarily into concretionary masses by calcium carbonate.

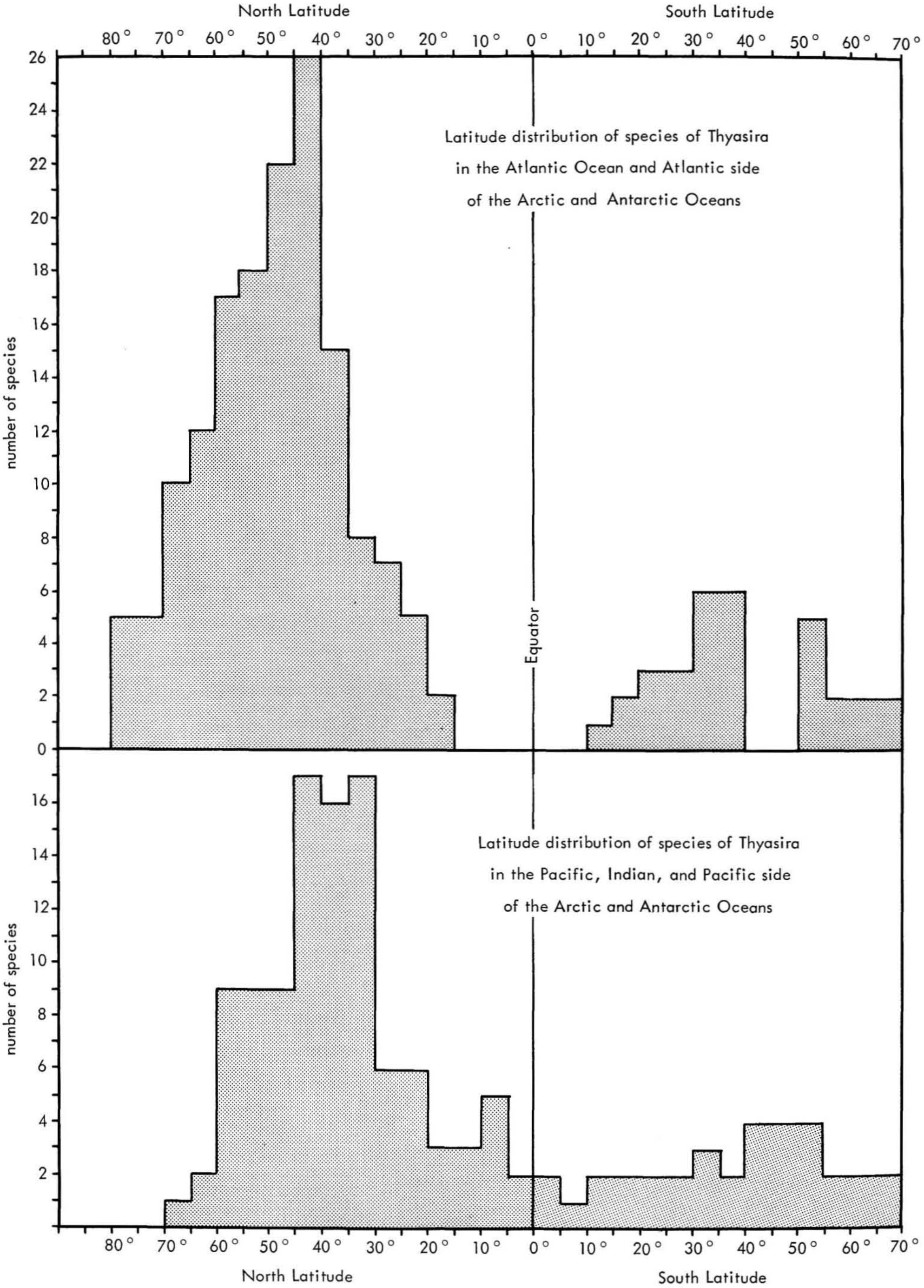


FIG. 95. Species diversity of living *Thyasira* relative to degrees of latitude, generally reflecting water temperatures (Kauffman, *11*).

is a relatively stable, lasting, incurrent structure which does not require continual energy output by the animal to operate, and is easily repaired by the foot. It provides a closed incurrent system between surface waters and the mantle cavity. This isolation of soft parts within the mantle cavity and tube, as well as an apparently broad tolerance of deleterious sediment chemistry, allows the animal to flourish in chemically unfavorable substrates which exclude many infaunal bivalves with exposed soft parts (siphons, foot, etc.). The reduction of palps and sorting mechanisms, and the ability to accept a broad size range of particulate food, adapts *Thyasira* to life in waters of low productivity where it can outcompete other infaunal mollusks.

HABITAT OF CRETACEOUS THYASIRA

Many lines of evidence support the assumption that Cretaceous *Thyasira* had the same habitat requirements, and adaptations to them, as living forms. Being a deep-burrower, the shells remain in close apposition after death as long as they are not exhumed and worked by currents. They gape and separate easily once exposed, being edentulous and having a small thin ligament incapable of keeping them together in the face of currents. It would be assumed that bivalved fossil shells which are not gaping might be contained in living posture. Ninety-five percent of the Cretaceous *Thyasira* studied from the Western Interior are bivalved specimens with valves in normal apposition. When bedding can be defined in rock containing them, the shells are invariably oriented nearly perpendicular to the laminae with the beak dorsal. Single valves, on the other hand, lie in the plane of the bedding, predominantly convex upward. The orientation of fossil bivalve shells parallels the living position of Recent species (Fig. 91). It can be concluded from this that they lived similarly in the substrate. The trace of a sediment tube found with one fossil specimen confirmed this as the living orientation.

An analysis of the rock associated with Cretaceous *Thyasira* from the North American Interior showed a strong dominance of dark clay shale, silty in some cases but without coarse clastics, and a secondary association with fine- to medium-grained sandstone (Fig. 94). Fossils occur mainly in concretions associated with the shales. These are secondary structures formed during early diagenesis and do not represent the original sediment type. Comparison of these data with the substrate distribution of living species (Fig. 94) shows a close correlation. Pyrite scattered through the shale and concretions containing *Thyasira* may reflect reducing conditions in Cretaceous sediments similar to those associated with some living species. The evidence conclusively points to highly similar substrate preferences for fossil and living species.

The geographic distribution and diversity gradients of Cretaceous *Thyasira* from the North American Western Interior, exclusive of two localities in Alberta and one questionable Cretaceous specimen from Greenland, are shown in Figure 97, superimposed on a lithology distribution map of the interior basin during the time span of known Cretaceous species (Campanian). This clearly demonstrates a geographic range in the northern hemisphere during the Cretaceous compatible with living distribution (Fig. 95). More significantly, species and subspecies diversity gradients increase south-

FIG. 95. *(Continued from facing page).*

Maximum diversity of forms is observed between latitudes of 30° and 55° in both hemispheres and both major ocean basins, especially between latitudes 30° and 45°. The smaller numbers of species in southern latitudes than in northern probably reflects difference in collecting and research in the two areas, rather than environmental differences. A southern shift of maximum diversity in the Indo-Pacific area as compared to the Atlantic may be due to the influence of cold marginal currents and upwellings along the steep eastern Pacific margin with very narrow shelf, the broad and shallow Atlantic shelf being affected by the warm Gulf Stream. [Comparison of this diagram with Figure 97 indicates close correlation of species-diversity gradients for Recent and Cretaceous species of *Thyasira* in relation to latitudes.]

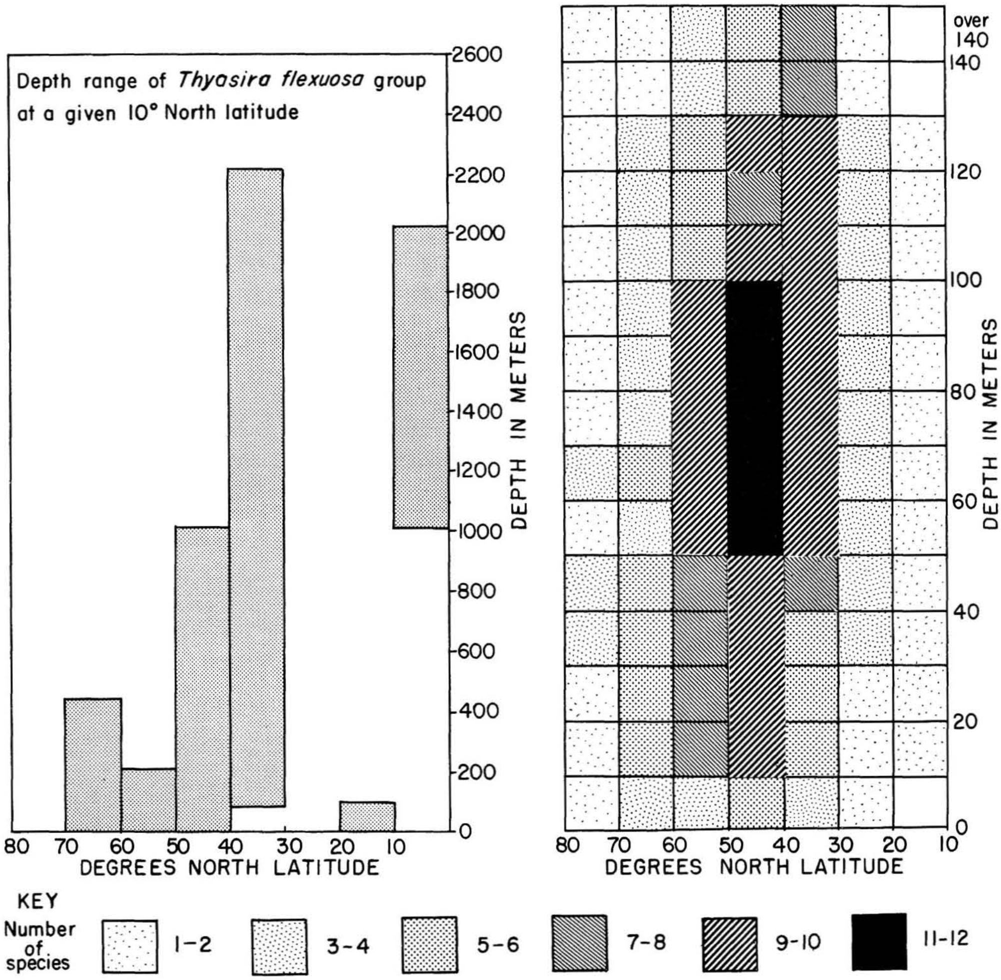


FIG. 96. Depth distribution of living *Thyasira* species in northern latitudes (Kauffman, *11*).

A general shift of bathymetric range from shallow water in most northerly latitudes to progressively deeper waters toward the south indicates temperature control of species distribution. The graph on the left is based entirely on forms belonging to the *Thyasira flexuosa* complex, for which data are sparse and ranges not significant between latitudes 10° and 30°. The graph on the right represents all species for which records of depth distribution are available, pattern density indicating number of species in 10° latitude bands. Although the total bathymetric range of the genus is nearly equivalent in all areas between 10°N and 80°N, maximum diversity in any 10° band shifts toward deeper and cooler waters in the south. Overall maximum species diversity occurs between 40°N and 50°N at depths of 50 to 100 m., defining optimum environmental conditions for *Thyasira.*

ward, reaching a maximum in Wyoming and Colorado during various parts of the Campanian, between 38° and 44° North Latitude. Although this may be in part a product of more concentrated work in these areas, it is not wholly subject to sampling error; scattered large Campanian collections from Canada and Greenland have not yielded abundant *Thyasira* in equivalent facies. The data strongly suggest that similar geographic distributions were shown by Cretaceous and Recent species and that environmental gradients affecting diversity, mainly temperature, were likewise similar during the Campanian in the Western Interior.

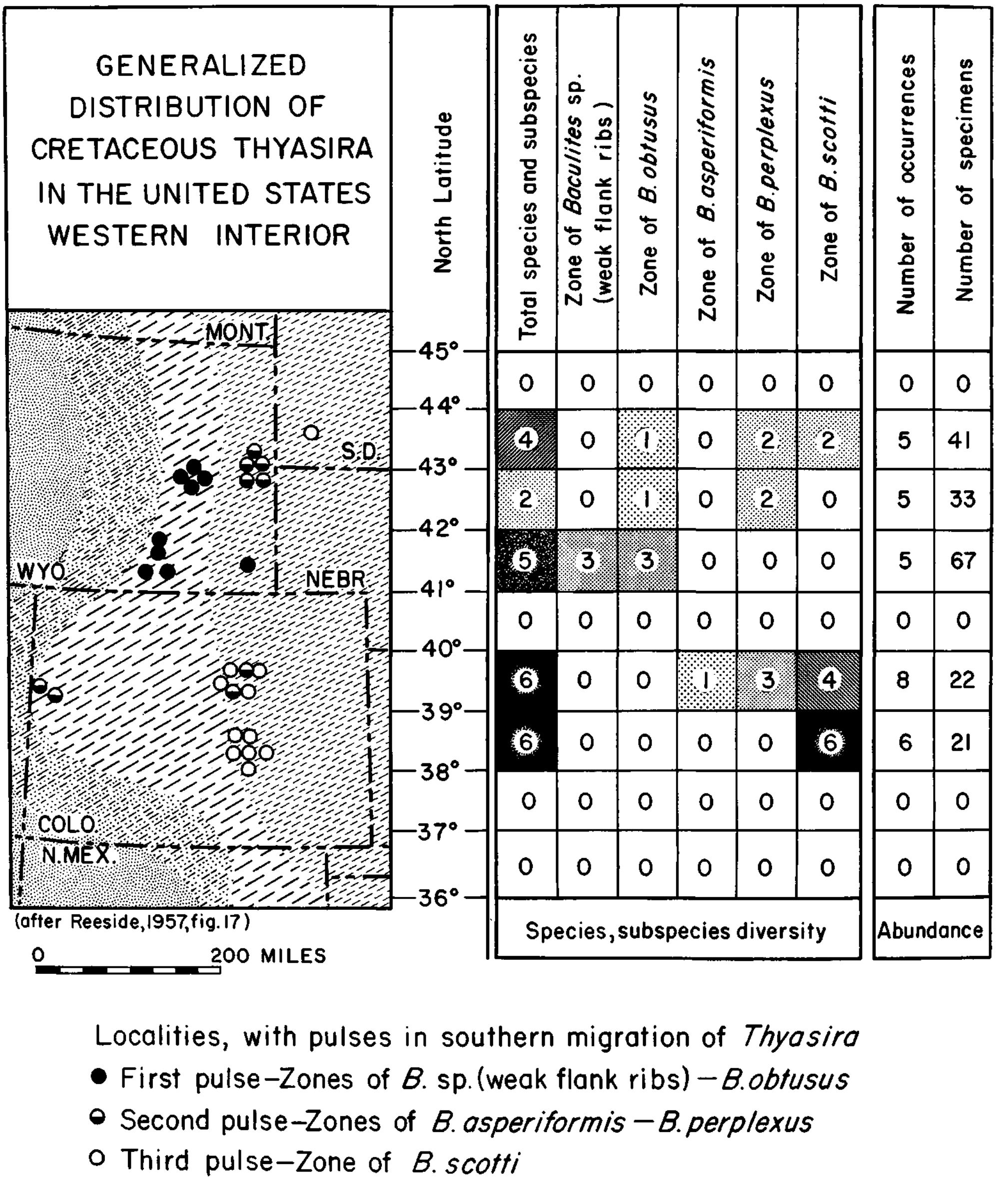
TABLE 1.—*Communities, Biotic Association of Mollusks, and Environmental Characteristics Summarized for Living Thyasira. Families Arranged in Order of Number of Recorded Molluscan Associations.*

ASSEMBLAGE		Arctic Macoma community (Ockelmann, 1958)	Amphiura filiformis community (Petersen, 1913, 1916)	Amphiura chiajii community (Petersen, 1913, 1916)	North Atlantic-Mediterranean assemblages (Allen, 1958)	North Atlantic-Mediterranean assemblages (Allen, 1958)	Astarte crenata community (Ockelmann, 1958)	Arca glacialis-Astarte crenata community (Sparck, 1933)	Boreal Foraminifera community (Thorson, 1957)	Maldane sarsi-Ophiura sarsi community (Thorson, 1957)	Foraminifera community (Ockelmann, 1958)	Amphilepas norvegica-Pecten vitreus community (Petersen, 1913, 1916)	Total for genus	Total for family
		SHALLOWER										DEEPER		
DEPTH RANGE (METERS)		4-50	15-100	15-100	11-140	11-140	25-550	30-550	100+	200-600	200-780	300+		
SUBSTRATE		clay, sandy clay	soft mud	soft clay, silty clay	soft mud	soft mud	soft clay	soft mud	soft mud	soft mud	soft clay	soft mud		
TEMPERATURE		cold	cool	cool	cool	cool	cold	steady negative	cold	cold	cold	cold		
PRODUCTIVITY		low	low-mod.	low	?low	?low	?low	low	low	?low	?low	low		
COMMONLY ASSOCIATED MOLLUSCAN GENERA		11	7	4	3	4	9	4	1	6	5	2	56	
BIVALVIA - TOTAL		11	5	4	3	3	9	4	1	4	5	2	51	
Thyasiridae	Thyasira	X	X	X	X	X	X	X	X	X	X	X	11	12
	Axinopsida	X	--	--	--	--	--	--	--	--	--	--	1	
Nuculidae	Nucula	X	X	X	X	--	X	--	--	X	--	--	6	6
Semelidae	Syndosmya	--	X	X	X	--	--	--	--	X	--	--	4	5
	Theora	--	--	--	--	--	--	--	--	X	--	--	1	
Nuculanidae	Nuculana	X	--	X	--	--	--	--	--	--	--	--	2	4
	Portlandia	--	--	--	--	--	X	--	--	--	X	--	2	
Astartidae	Astarte	X	--	--	--	--	X	X	--	--	X	--	4	4
Pectinidae	Pecten	--	--	--	--	--	--	X	--	--	--	X	2	4
	Propeamussium	X	--	--	--	--	X	--	--	--	--	--	2	
Arcidae	Arca	--	--	--	--	--	X	X	--	--	X	--	3	3
Lucinidae	Lucina	--	--	--	--	X	--	--	--	--	--	--	1	2
	Myrtea	--	--	--	--	X	--	--	--	--	--	--	1	
Cuspidariidae	Cuspidaria	X	--	--	--	--	X	--	--	--	--	--	2	2
Hiatellidae	Hiatella	X	--	--	--	--	X	--	--	--	--	--	2	2
Tellinidae	Macoma	X	--	--	--	--	--	--	--	--	--	--	1	1
Arcticidae	Arctica	--	X	--	--	--	--	--	--	--	--	--	1	1
Cardiidae	Cardium	X	--	--	--	--	--	--	--	--	--	--	1	1
Corbulidae	Corbula	--	X	--	--	--	--	--	--	--	--	--	1	1
Myidae	Mya	X	--	--	--	--	--	--	--	--	--	--	1	1
Limidae	Lima	--	--	--	--	--	--	--	--	--	X	--	1	1
Mytilidae	Dacrydium	--	--	--	--	--	X	--	--	--	--	--	1	1
GASTROPODA - TOTAL		0	2	0	0	0	0	0	0	2	0	0	4	
Turritellidae	Turritella	-	X	--	--	--	--	--	--	--	--	--	1	1
Aporrhaidae	Aporrhais	--	X	--	--	--	--	--	--	--	--	--	1	1
Philinidae	Philine	--	--	--	--	--	--	--	--	X	--	--	1	1
Acteocinidae	Cylichna	--	--	--	--	--	--	--	--	X	--	--	1	1
SCAPHOPODA - TOTAL		0	0	0	0	1	0	0	0	0	0	0	1	
Dentaliidae	Dentalium	--	--	--	--	X	--	--	--	--	--	--	1	1

BIOGEOGRAPHY

Having established a general geographic and environmental correlation in the distribution of Cretaceous and living *Thyasira* (Fig. 95-97), this analysis may be carried one step further with the fossil material. Unlike the living species, the distribution of Cretaceous forms can be analyzed separately in a series of distinct time periods (ammonite zones) and then compared to give a progressive paleogeographic interpretation (Fig. 97).

Thyasira appeared abruptly in the Western Interior Cretaceous and disappeared similarly at the point of its maximum southern migration (Fig. 97). It is limited in the entire Interior Cretaceous to a relatively short sequence of Campanian rocks. Considering the generally widespread warm maritime climate that characterized much of the Cretaceous, and the cool-water temperatures preferred by living *Thyasira,* the most logical interpretation of its brief invasion is that it accompanied a short-term



North Latitude	Total species and subspecies	Zone of *Baculites* sp. (weak flank ribs)	Zone of *B.obtusus*	Zone of *B.asperiformis*	Zone of *B.perplexus*	Zone of *B.scotti*	Number of occurrences	Number of specimens
45°–44°	0	0	0	0	0	0	0	0
44°–43°	4	0	1	0	2	2	5	41
43°–42°	2	0	1	0	2	0	5	33
42°–41°	5	3	3	0	0	0	5	67
41°–40°	0	0	0	0	0	0	0	0
40°–39°	6	0	0	1	3	4	8	22
39°–38°	6	0	0	0	0	6	6	21
38°–37°	0	0	0	0	0	0	0	0
37°–36°	0	0	0	0	0	0	0	0
	Species, subspecies diversity						Abundance	

FIG. 97. Distribution, diversity, and abundance of Western Interior species of *Thyasira* in relation to Late Cretaceous migration pulses and sediment distribution (Kauffman, *11*).

The map (based on REESIDE, 1957, fig. 17) indicates in highly generalized manner the lithologic nature of substrates in early Campanian to initial middle Campanian time (Zone of *Baculites scotti*), patterns representing (in west-to-east sequence) sand, sandy mud, fine gray mud, and fine black mud. A strong preference of Cretaceous *Thyasira* for fine muds without associated coarser clastics is noteworthy, just as in living species (Fig. 94).

The chart shows a shift in southernmost occurrences of *Thyasira* in progressively younger Campanian ammonite-based zones, implying migratory pulses which are keyed to localities marked on the map. Maximum species diversity is found at the southern end of the genus range during each pulse. Close correlation exists between overall latitude distribution and maximum diversity gradients in Cretaceous and Recent species of *Thyasira* (Fig. 95). Constriction of the seaway indicated near the

TABLE 2.—*Abundance of Thyasira and Faunal Associates, Structure of Molluscan Assemblages, and Dominant Lithology at Localities Yielding Thyasira from Upper Cretaceous of Western Interior United States.*

USGS LOCALITIES	D5	D65	D255	D709	D714	D1012	D1215	D1216	D1410	D1564	D1864	D1865	D1866	D2909	D2910	D3256	D3260	D3332	D3933	D3945	D4162	D4747	3763	3779	10459	10666	22838	22840
LITHOLOGY	sh tb	sh sc	sh ic	sh lc	sh lc	sh tb	sh tb	sh ic	sh lc	sh tb	sh ic	sh ic	sh ic	sh ic	sh tb	sh lc	sh ic	sh lc	sh tb	sh lc	sh ic	sh sc	ss	ss s	sh lc	sh sc	sh lc	sh ic
ASSEMBLAGE	H	H	H	D	D	D	D?	D	D	?	H	H	H	?	?	?	?	?	?	D	?	?	?	?	?	?	D	D?
BIVALVIA	1	3	6	2	3	3	4	4	4	3	2	1	1	2	2	3	1	1	4	2	2	3	1	1	2	2	5	4
Thyasira	R	R	C	C	R	R	R	R	C	R	R	C	C	R	R	C	R	R	R	R	C	R	R	C	C	R	R	R
*Inoceramus	-	R	C	-	R	-	R	C	C	-	R	-	-	R	R	R	-	-	C	-	-	R	-	-	-	C	R	R
Lucina	-	-	R	R	R	C	C	C	C	R	-	-	-	-	-	C	-	-	C	R	C	-	-	-	-	-	R	C
*Cymbophora	-	-	R	-	-	R	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-	R	-
Pteria	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-	-	R	-	-	R
"Ostrea"	-	-	R	-	-	-	R	R	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nucula	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-
GASTROPODA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Aporrhais?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-
Lunatia?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-
CEPHALOPODA	2	2	3	3	3	4	3	2	5	1	2	2	2	1	1	1	1	1	1	2	1	1	1	1	2	1	3	2
*Baculites	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	R	C	C	R	C	C	C	C	C
*Hoploscaphites	R	R	R	-	-	-	-	-	-	-	R	R	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
*Didymoceras	-	-	-	C	C	C	-	C	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-
*Oxybeloceras	-	-	-	R	R	C	-	-	R	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-	-	-	R	-
*Anapachydiscus	-	-	-	-	-	R	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R
*Placenticeras	-	-	R	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
*Menuites	-	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
*Scaphites	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-
*Eutrephoceras	-	-	-	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SCAPHOPODA	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Dentalium	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-	-	-
MOLLUSKS-TOTAL	3	5	10	5	6	7	7	6	9	4	4	3	3	3	3	4	2	2	5	4	3	5	2	2	6	3	8	6

*Extinct genus

[EXPLANATION. *Lithology: ic,* ironstone concretions (siderite-limonite); *lc,* limestone concretions, usually argillaceous; *s,* shaly; *sc,* siderite concretions; *sh,* shale, usually dark, noncalcareous, thin-bedded; *ss,* sandstone, usually fine- to medium-grained, argillaceous; *T,* Tepee Butte limestone masses, irregular light-colored argillaceous limestone bodies.

Fossil assemblages: H, Hoploscaphites assemblage; *D, Didymoceras-Oxybeloceras* assemblage; *?* indicates not enough data available to define principal assemblages.

Abundance: R, rare, five or fewer specimens; *C,* common, more than five specimens per collection.

flooding of cool Arctic waters into the central interior or the basin deepened abnormally due to tectonic phenomena for a short period of time so that bottom temperatures came within the range supporting abundant *Thyasira* today, or both influences operated.

As shown in Figure 97, Cretaceous *Thyasira* show three migratory pulses during the Cretaceous. The initial pulse carried them to southern Wyoming, a younger one to central Colorado, and a terminal one to south-central Colorado. In each case they were primarily distributed in clay-mud facies (Fig. 97), and maximum diversity was at the southern end of their range. These pulses are thought to represent steps in the flooding of the interior seaway by Arctic waters; a rate of flooding and faunal migration can thus be calculated since the

FIG. 97. *(Continued from facing page).*

southern margin of the map may account for elimination of the southern tail of the distribution curve in fossil species that normally occurs in Recent species distribution (Fig. 95).

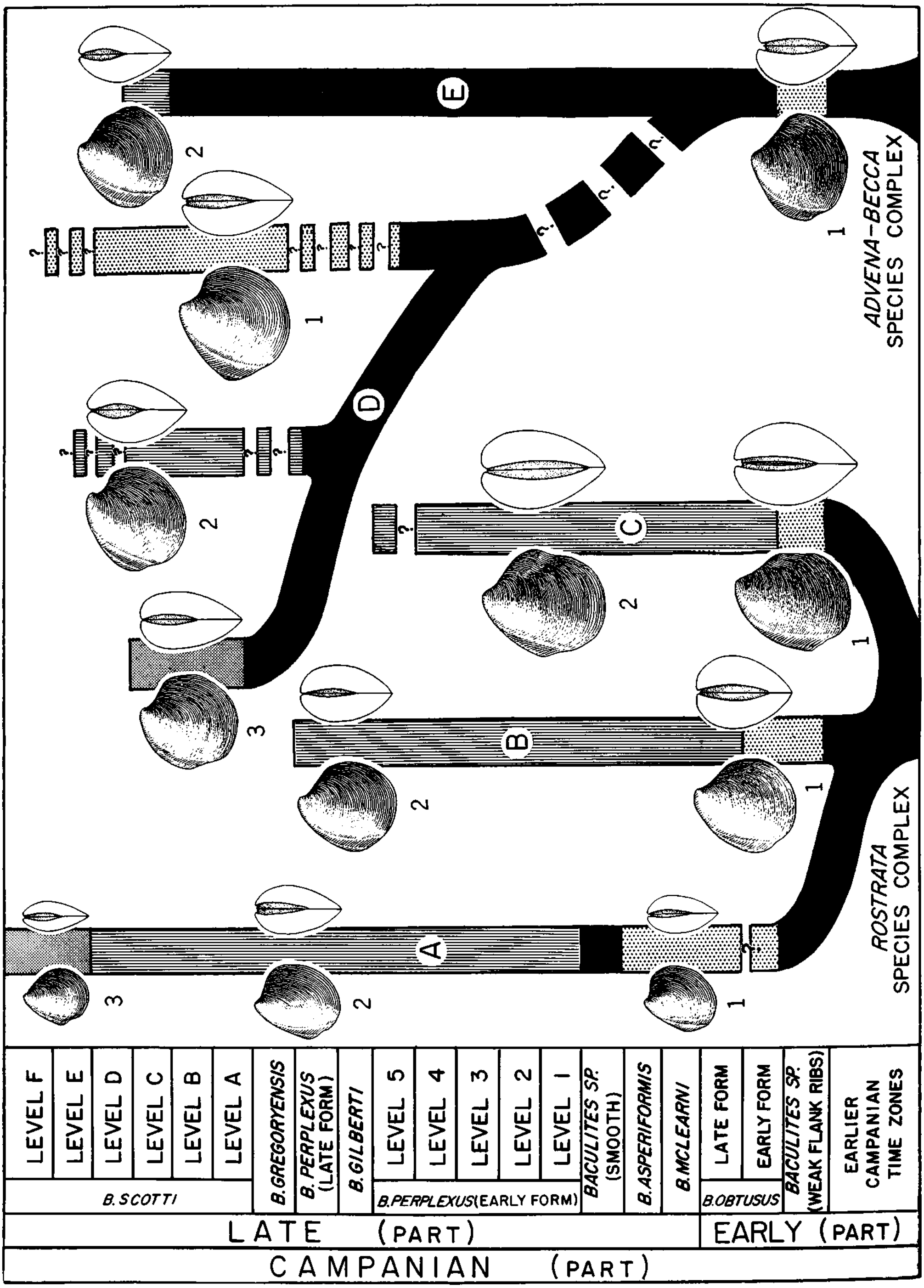


Fig. 98. Phylogeny and evolution of Cretaceous *Thyasira* in Western Interior of North America (Kauffman, *11*).

duration of *Thyasira* in the Western Interior is known. The strange diversity gradient, strongly skewed with the southern tail of the distribution missing, was probably produced by a relatively abrupt transition zone between Arctic and warm southern waters, or by a marked constriction and shoaling of the seaway in southern Colorado, or both. Both factors would have limited southern extension of Thyasiridae because they did not produce environmental situations preferred by *Thyasira* then and now.

COMMUNITY RELATIONSHIPS

Extensive survey of the Recent molluscan literature reveals that living *Thyasira* are abundant only in association with restricted molluscan assemblages of relatively uniform composition. Table I presents a summary of association data for published communities of marine animals containing abundant *Thyasira*. The most diverse associated molluscan assemblage contains 10 genera and 14 species, including *Thyasira* and excluding rare taxa (Arctic *Macoma* community). On the average, only four to five molluscan genera are associated. In the boreal foraminiferal community of OCKELMANN (1958) *Thyasira* is the only abundant mollusk (Table 1). The restricted nature of the assemblages reflects the cool-water environment, low productivity, and chemically unsuitable substrate to which *Thyasira* is so well adapted. Infaunal bivalves strongly dominate the assemblages; gastropods and epifaunal organisms are rare. The most consistent associates of *Thyasira* are other Lucinacea (*Axinopsida, Lucina, Myrtea*—all similarly adapted, like *Thyasira,* to the environment), Nuculanidae *(Nuculana, Portlandia),* Nuculidae *(Nucula),* Semelidae *(Abra* or *Syndosmya, Theora),* Astartidae *(Astarte),* and Pectinidae *(Pecten, Amusium,* or *Propeamussium*). Except for the free-living, swimming pectinids, these are all infaunal filter- and detritus-feeders which show a strong preference for fine-grained substrate. This basic assemblage is not uncommonly supplemented by *Cuspidaria* and *Arca. Turritella* and *Aporrhais* are the most abundant associated gastropods, but still comparatively rare.

Comparison of molluscan assemblages associated with Cretaceous *Thyasira* to those characterizing Recent occurrences reveals an interesting correlation, although it is complicated by the abundance of extinct taxa in the Cretaceous which have no living counterparts (e.g., ammonites, Inoceramidae). Cretaceous molluscan associates are listed in Table 2. Eighteen genera of Cretaceous mollusks, ten of them extinct, occur with *Thyasira* in deposits of the Western Interior. A maximum of ten genera and a minimum of two were found in any

FIG. 98. *(Continued from facing page).*

[Heavy black lines show hypothetical phylogenetic relationships (doubtful where broken, indicating lack of specimens representing lineage in some time intervals). Coarse dotted pattern marks range of oldest subspecies in each lineage. Vertical ruling designates youngest subspecies in each lineage. Fine dotted pattern represents distinct species phylogenetically arranged within lineages from which they were derived. Interrupted and queried portions of ranges denote possible extension of established ranges based on vague stratigraphic data.]

A. Thyasira quadrula lineage, characterized by reduction of the anterodorsal flank, increased inclination of the anterodorsal slope, decrease in convexity and span of apical angle, posterior migration and straightening of primary sulcus, and dorsal migration of primary sulcus notch. [*1, T. quadrula quadrula; 2, T. quadrula arrecta; 3, T. triangulata.*]

B. Thyasira rostrata lineage, characterized by decrease in convexity and in relative size of escutcheon, decrease in relative height and projection of beaks, increase in apical angle with expansion of anterodorsal flank and decrease of anterodorsal slope. [*1, T. rostrata rostrata; 2, T. rostrata cracens.*]

C. Thyasira beauchampi lineage, characterized by decrease in convexity, expansion of anterodorsal auricle and anterior sulcus, decrease in curvature and prominence of beak and umbo, and straightening of primary sulcus with dorsal migration of notch. [*1, T. beauchampi beauchampi; 2, T. beauchampi rex.*]

D. Thyasira becca lineage, characterized by decrease in relative height followed by increase, increase and subsequent decrease in projection of anterodorsal flank, convexity, and beak inclination, posterior migration of primary sulcus, and decrease in projection and angularity of mid-posterior marginal beak in slope. [*1, T. becca becca; 2, T. becca cobbani; 3, T. cantha.*]

E. Thyasira advena lineage, characterized by decrease in convexity, slight increase in height relative to length, posterior migration of primary sulcus, decrease in inclination of beaks, increase in relative projection of beaks and depth of concave notch anterior to them. [*1, T. advena advena; 2, T. advena browni.*]

single occurrence (including *Thyasira*), yielding an average of 4.6 genera (and species) per occurrence. This is comparable with the rstricted nature of modern *Thyasira*-rich assemblages. The diversity is even less if the extinct ammonites, the ubiquitous Mesozoic epifaunal *Inoceramus,* and the mactroid *Cymbophora* (Cretaceous only) are omitted, because they have not been replaced in their niches by living counterparts. Although infaunal bivalves also dominate Cretaceous assemblages with *Thyasira,* epifaunal organisms are more abundant owing to the special adaptations of *Inoceramus* to living on soft mud bottoms, and the surface area for attachment of other epifaunal bivalves *(Pteria, Ostrea)* provided by the large upper valves of flat-lying inoceramids.

Exclusive of extinct mollusks, Cretaceous forms associated with abundant *Thyasira* are taxonomic parallels of living associates. Lucinidae *(Lucina), Nucula, Aporrhais,* and *Dentalium* are among these. The data suggest similar community relationships and environmental control on molluscan diversity and taxonomic representation in *Thyasira*-rich assemblages of the Cretaceous and Recent. This is further evidence for parallel habitat preference and ecologic adaptation in fossil and Recent *Thyasira.* The data further suggest the presence of two basic communities containing *Thyasira* during the Cretaceous, represented by distinct assemblages of mollusks, in particular ammonites. Contrary to popular opinion, the ammonites were probably strongly affected by bottom environments in their distribution; many may have been basically vagrant benthonic organisms. It is considered necessary to include them in the definition of bottom communities.

The first assemblage is characterized by *Hoploscaphites* and *Baculites* without additional ammonites. *Inoceramus* and *Thyasira* are the only commonly associated bivalves. *Lucina* is rare. *Pteria,* scaphopods, and gastropods are known sparingly but exclusively in this assemblage. The second assemblage is characterized by a diversity of ammonites and identified by *Didymoceras* and *Oxybeloceras* without *Hoploscaphites,* gastropods, scaphopods, or *Pteria. Inoceramus, Lucina,* and *Thyasira* are abundant and locally the other associated mollusks are diverse, including *Ostrea, Nucula, Cymbophora,* and *?Lunatia.* Due to the greater diversity and numbers of specimens, as well as the occurrence of *Ostrea* and the mactrid *Cymbophora* in the second grouping, the assemblages are thought to reflect depth zones with the *Didymoceras-Oxybeloceras* assemblage the shallowest. Both are thought to be middle shelf assemblages indicating 200 to 400 feet in depth, using the criteria of KAUFFMAN (1967,*10*).

PHYLOGENY, EVOLUTION, AND INTERPRETATION

The described Cretaceous *Thyasira* from the Western Interior fall into five distinct lineages, each with two or more subspecies and species in evolutionary succession. These can be grouped into two phylogenetic complexes on the basis of gross morphology (Fig. 98). The *Thyasira rostrata* complex includes erect shells elongated along the burrowing axis (height axis); the *T. advena-T. becca* complex includes rounded obese *Thyasira.* Each complex undergoes a principal Campanian radiation (Fig. 98); the *rostrata* complex in the early Campanian, and the *advena-becca* complex in the late Campanian. The pattern of radiation is dissimilar between them in that the late Campanian phase was more abrupt; it was also correlated with the extinction of two major lineages belonging to the *rostrata* complex (Fig. 98), suggesting competition and replacement of the *rostrata* complex by the *advena-becca* complex in the same habitat (as evidenced by similar lithologies containing them).

The members of each lineage are characterized by particular morphologic features, some of which begin to merge toward the point in time of initial radiation of the complex. These characters are shown in Figure 98. The *T. quadrula* species group has reduced beaks and a straight posterior margin (Fig. 98, column A); the *T. rostrata* lineage has inflated shells, dorsally projecting beaks, and rounded posterior margins

(Fig. 98, column B). The *T. beauchampi* lineage includes very large forms with an anterior sulcus (Fig. 98, column C); the *T. becca* lineage has rounded, inflated shells with strongly prosogyrous beaks and an angulate, projecting anterior margin (Fig. 98, column D); and the *T. advena* lineage has inflated rounded shells with a sloping anterior margin and reduced suberect beaks (Fig. 98, column E).

Species co-occurrence is not uncommon among Cretaceous *Thyasira.* In most cases the associated species belong to quite dissimilar lineages; a member of the *rostrata* species complex is found with a member of the *advena-becca* complex in the same concretion, both bivalved and in living position. This situation suggests that the co-occurring species occupied distinct microniches within the primary dark mud habitat. Shell morphology strongly suggests that they were depth zoned. By analogy to living thyasirids and other infaunal Bivalvia, the rounded, inflated shells of the *advena-becca* complex probably belonged to slower and shallower burrowers than the narrower ovate shells of the *rostrata* complex, elongated along the burrowing axis. Where closely related species occur together in the same sediment, one is always very rare and obviously not competing well with its similarly adapted relative in the same niche.

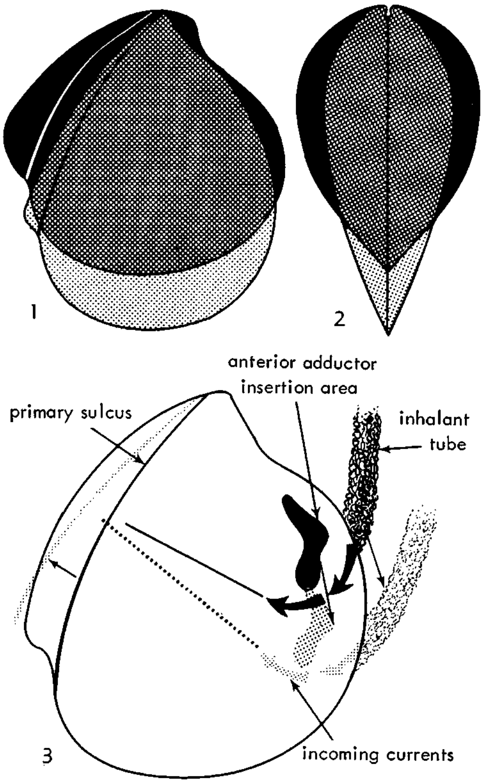


Fig. 99. Main evolutionary trends in Cretaceous *Thyasira* (Kauffman, n).

1. Diagrammatic right lateral view of shell showing decrease in length and flank projection, accompanied by increase in height (burrowing axis) during evolution of older species (black) to younger ones (dotted pattern).
2. Diagrammatic anterior view of shell indicating decrease in convexity during evolution of older species (black) to younger ones (dotted pattern).
3. Diagrammatic view of left valve interior demonstrating ventral migration of anterior adductor insertion area, incurrent channel, connection of inhalant tube, and direction at which incoming currents enter mantle cavity, as well as posterior migration and straightening of primary sulcus and internal fold formed by it. [Solid line connecting incurrent channel with sulcus trace marks approximate direction of water approach to front of gills in early forms. Dotted line indicates same in more advanced forms. Dark areas represent original position and light areas advanced position of features indicated (anterior adductor insertion area, inhalant tube, primary sulcus).]

Evolutionary trends in Cretaceous *Thyasira* from the Western Interior are similar in four of the five lineages; the lineage of *T. beauchampi* shows opposite trends toward widening of the valves and shallow burrowing adaptations. In the lineages of *T. quadrula, T. rostrata,* and less strikingly *T. advena* and *T. becca* (Fig. 98), the principal evolutionary changes through the Campanian are: 1) vertical elongation of the shell along the burrowing axis and consequent reduction of length; 2) decrease in convexity of the valves; 3) decrease on some species of the projection of anterior and posterior flanks and reduction of auricles, where present; 4) ventral and slightly inward shift of the anterior adductor insertion area correlative with reduction of the projecting anterior flank; this brings about ventral shift in the incurrent channel, the point of current entry into the mantle cavity, and the point at which the inhalant tube meets the shell (Fig. 99); and 5) posterior shift and straightening of the primary sulcus with reduction in size of the posterior fold and flank. These are particularly well shown in the *Thyasira quadrula* lineage (Fig. 98, column A).

The interpretation of these trends—the reason for selection of the traits during evolution of the lineages—is perhaps the primary contribution of multifaceted interpretive study as it utilizes all other data. Study of the comparative ecology between living and fossil Thyasiridae, and the nature of the sediment containing Cretaceous species strongly suggests that all lineages were basically adapted for the same habitat and that all members of each lineage occupied this preferred habitat during the Campanian. The evolutionary trends cannot be interpreted in terms of a changing environment, therefore, but rather must be attributed to improved adaptation within the same general habitat. This interpretation is limited only by the gross environmental data available from the study of the containing rock. Based on general analysis of form and function in other Lucinacea (Fig. 90), and in unrelated homeomorphic infaunal bivalves, the evolutionary trends of Cretaceous *Thyasira* can be interpreted as follows:

Vertical elongation along the burrowing axis and complimentary reduction in shell length, projection of auricles or lateral flanks, and shell convexity better adapt the shell to rapid and deep burrowing by streamlining its shape, reducing frictional drag, and increasing its penetration potential when pulled down on the anchored foot. This obviously has high survival value as the thin, weakly hinged shell is highly susceptible to predation or current damage when exposed on the water-substrate interface. This change in shell form brings about the observed downward and inward shift of the anterior adductor insertion area, and the incurrent channel beneath it, because of shortening and rounding of the anterior margin in more advanced species. It also shifts the direction in which incurrent waters enter the mantle cavity from mid-anterior to ventroanterior.

Recalling the critical spatial relationships which must be maintained in the thyasirid shell, 1) the enlarged mantle cavity to receive the coiled foot, 2) the distance between the incurrent waters as they enter the mantle cavity and the gills, and 3) the orientation of the gills relative to the direction in which incurrent waters flood the mantle cavity, it is apparent that all of these would be upset by the change in shell form and shift of the anterior adductor muscle, anterior incurrent channel, and direction of incurrent flow were there not a compensating shift in the soft parts affected.

Posterior migration of the primary sulcus, which internally marks the attachment base of the gills, reflects a posterior shift of the gills internally. This partially or wholly compensates for the loss of space in the mantle cavity produced by lateral compression of the shell and inward shift of the anterior margin and adductor insertion area. Sufficient room for the coiled foot is thus retained. Straightening of the primary sulcus with its posterior migration decreases its slope relative to the horizontal hinge axis. The gills, which buttress against this structure, are thus reoriented with their leading edge facing ventroanteriorly rather than mid-anteriorly. This brings them into proper orientation perpendicular to the new direction of incurrent flow in the younger, more streamlined species. Posterior shift of the gills accompanies inward shift of the anterior incurrent channel through reduction of shell length and anterior flank projection, insuring that the critical spacing between gills and incurrent channel is maintained (Fig. 99).

In summary, adaptation of the shell for more rapid burrowing in *Thyasira* created a spatial imbalance of the feeding and respiration systems internally, in turn creating strong selection pressures for compensatory migration and realignment of the gills. It is postulated that these changes were effected in unison, not singly in any particular order, as a series of interacting selective pressures. The complex structural changes brought about by better adaptation of the shell for burrowing points out that form and function is not a simple study of isolated structures and their operation, but must be considered in terms of interacting morphologic suites performing numerous interrelated functions.

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CLASSIFICATION OF BIVALVIA

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[The American Museum of Natural History and Columbia University] [Chapter revised and slightly expanded from *American Museum Novitates,* no. 2206, 1965, 25 p.]

CONTENTS

INTRODUCTION

The Bivalvia are wholly aquatic benthos which have undergone secondary degeneration from the condition of the ancestral mollusk, possibly, but not certainly, a monoplacophoran-like animal (Yonge, 1953, 1960; Vokes, 1954; Horný, 1960; McAlester, 1966; and others). The changes have involved loss of the head and adoption of

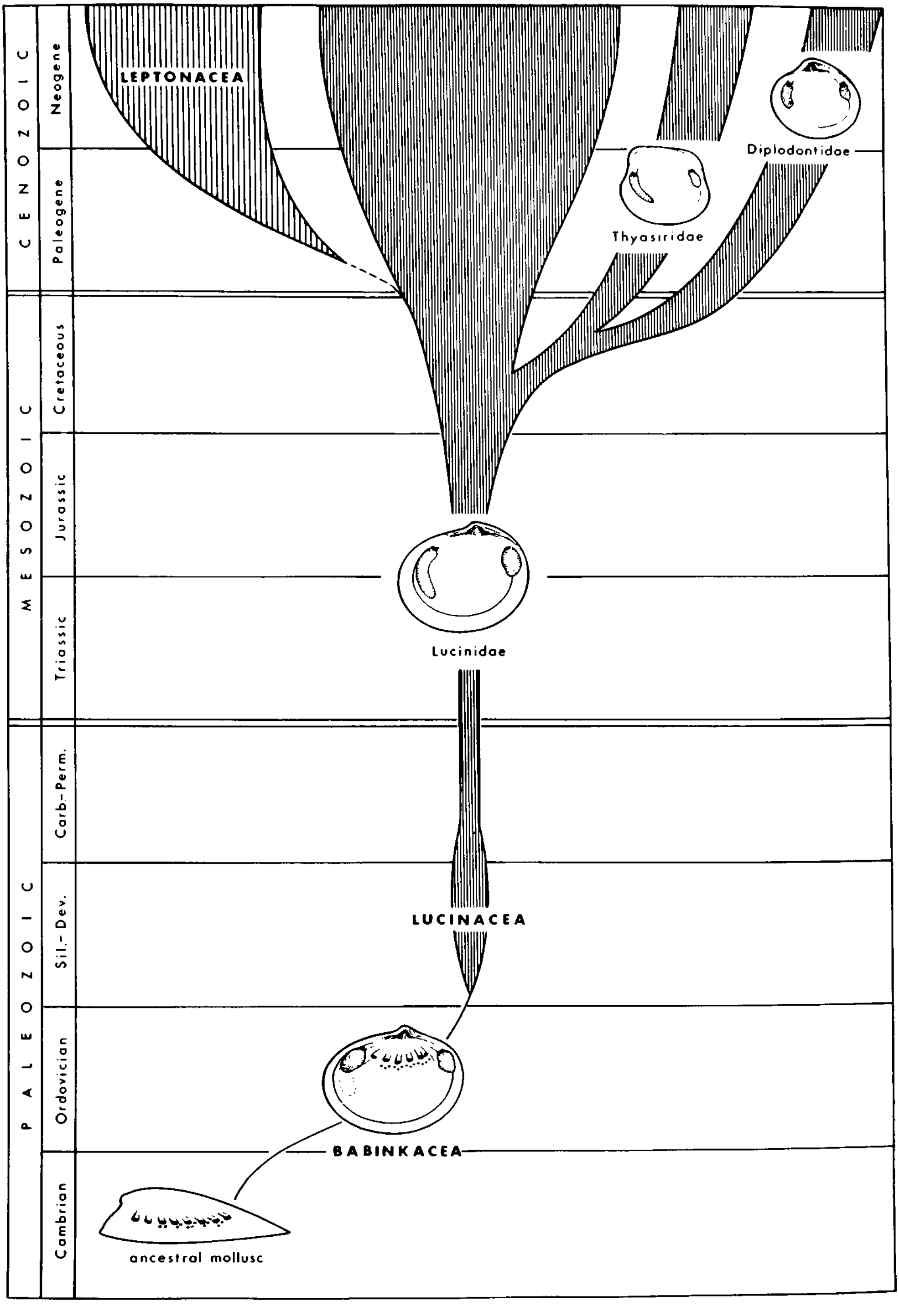

FIG. 100. Hypothetical derivation of certain Bivalvia from monoplacophoran-like ancestor (McAlester, 1966).

a passive mode of life in which feeding is accomplished by filtering of water or sifting of sediment for particulate organic matter (Fig. 100). These adaptations have limited the evolutionary potential severely, and most structural changes have followed variations of rather simple themes. The most evident adaptations have affected articulation of the valves, modes of defense, anchorage, and burrowing, and efficiency in feeding. Habitat preferences are correlated with the availability of food and with chemistry, temperature, agitation and depth of water, and with firmness of the bottom on or within which they live. The morphological clues to genetic affinity are few. Consequently, parallel trends are rife, and it is difficult to arrange the class taxonomically in a consistent and logical way that takes known history into account.

The problem of classifying the bivalves is further complicated by the fact that critical characters sought in fossil representatives commonly are concealed by rock matrix or are obliterated by the crystallization or dissolution of the unstable skeletal aragonite. The problem of studying morphological details is especially difficult among the older fossils which should provide evidence of the relative times of phyletic divergence. Among these, morphological details generally are inadequately known, partly owing to limitations of the materials but even more as the result of insufficient work on the group and lack of application of adequate skills and preparation techniques. In all of the history of work on older bivalves, very few examples of outstanding morphological work on these fossils can be cited. Sound morphological studies, although minimized today, are more than ever needed for understanding ecology of the group and for development of trustworthy classification and phylogenetic interpretation of the bivalves.

The present outline of classification undertakes to synthesize and integrate best features of the most widely used systems. It is neither basically new nor based on adequate morphologic and phylogenetic information. Its superiority over other systems may be claimed on the grounds of simplicity of the adopted nomenclature and the weighing of both anatomical and paleontological data.

It must be stressed that the result is a compromise. No classification of Bivalvia in the present state of knowledge will be wholly acceptable to all students of the group. It is hoped, however, that the arrangement will better serve needs of both neontologists and paleontologists than others that have been suggested.

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DEVELOPMENT OF CLASSIFICATION

FAMILY-GROUP CATEGORIES

Many of the major fossil and living groups of bivalves, now generally regarded as superfamilies, are highly distinctive and accordingly they had been discriminated by the middle of the nineteenth century. Several were known even by vernacular names long before the time of Linné. It is evident that many of the family-group taxa have been astonishingly conservative, with long and continuous records that extend far back into the Paleozoic where well-preserved specimens may be relatively scarce and origins of higher categories are generally conjectural. Where the fossil record is good, abundant evidence shows that general shell characters in many groups have been quite stable through hundreds of millions of years. This fact is contrary to a view sometimes voiced that the soft anatomy is somehow more revealing of affinities than shell morphology and that shell characters alone are inadequate and unreliable as indicators of phylogeny. This view reflects lack of understanding of geologic time and the richness of the fossil record.

SUPRAFAMILIAL CATEGORIES

The building blocks of bivalve taxonomy have been the family groups many of which have not been very controversial. Real difficulties arise, however, when attempts are made to group well-defined superfamilies into orders and subclasses. Excellent reviews of the history of efforts to devise a stable system of bivalve higher categories have been published by HAAS (1929-56), IREDALE (1939), PURCHON (1958), COX (1960), and MORTON (1963), and are not taken up in detail here. It is sufficient to say that, lacking graded morphological series of living or fossil forms suitable for joining many of the family-group taxa, systematists have sought more or less arbitrarily to base ordinal groupings on single-organ systems. But most such traits are now known to be individually plastic and are demonstrably variable within families or even within genera. The experience of more than two centuries of work on the subject encourages the view that a simple keylike classification of the bivalves cannot adequately reflect their relationships at the level of orders and subclasses. Consequently, many of the diagnoses given in this volume are ambiguous and even repetitive.

EARLY SEARCH FOR TAXOBASES

The degree of fusion of the mantle margins, together with the character and number of the resulting apertures or siphons, was regarded by LINNÉ (1758) as a primary basis for the discrimination of orders. In this belief, he was followed for a time by many students: for example, CUVIER (1797, 1800), LAMARCK (1801), DUMÉRIL (1806), FLEMING (1822-28), LATREILLE (1825), D'ORBIGNY (1843-47), WOODWARD (1851-56), ADAMS & ADAMS (1854-58), and ZITTEL (1881-85).

In addition to the presence or absence of well-developed siphons, LAMARCK (1812) stressed the progressive reduction and loss of the anterior adductor muscle in some groups as important and useful, as did PHILIPPI (1853) and ZITTEL (1881-85). GRAY (1821) and LANKESTER (1883) thought that the form and function of the foot furnished a reliable basis for recognition of suprafamilial groups. LINNÉ (1758) and D'ORBIGNY (1843-47) also used the equality or inequality of the valves as a convenient taxonomic criterion. All of these views have influenced the classification herein adopted.

The objective of efforts to classify the Bivalvia was utilitarian, of course, with little thought of phyletic history of the assemblage. The characters enumerated still figure prominently in all classifications but are now generally regarded as supplementary features that may appear independently in unrelated groups. Loss of the anterior muscle (e.g., in Pectinidae and Tridacnidae), or cementation by one valve and acquisition of an oyster-like growth form (e.g., *Ostrea, Hinnites, Mulleria*), are illustrations of parallel adaptations in groups that are otherwise unlike.

CONTRIBUTIONS FROM PALEONTOLOGISTS

STOLICZKA (1870-71), a paleontologist who was impressed by the general stability and homogeneity of form and structure of family groupings of bivalves throughout their history, proposed to base higher categories on overall resemblance to chosen type genus, and on this basis he established nine orders, the names of which were based on the stems of generic names. This taxonomic device had already been experimented with by RAFINESQUE (1815), FÉRUSSAC (1822), and ADAMS & ADAMS (1854-58). Experience showed that it had a sound basis, and the orders of STOLICZKA, with modifications and additions, have become the superfamilies of later workers.

Over the years, the list of generally recognized major groups has grown from the nine orders in STOLICZKA's classification to the 47 superfamilies in the present treatment, with others sure to follow as the study of Paleozoic bivalves progresses. Throughout the nineteenth century the unwieldy number of family-group taxa prompted many efforts to regroup the class into a few convenient morphological divisions.

The paleontologists Neumayr (1884, 1891), Steinmann (1888), Dall (1889, 1895, 1896-1900, 1913), and Douvillé (1896, 1907, 1912, 1913) introduced the historical-phylogenetic point of view into efforts to classify the bivalves. They demonstrated that general shell form and details of the articulating apparatus, that is, the hinge teeth plus the ligament, were commonly quite stable through time, but they also pointed out many exceptions, as for example, the highly variable hinges of the dysodonts and fresh-water mussels (Unionacea). The French paleontologist Bernard (1895, 1896,*4*, 1896,*5*, 1897, 1898) shared these views and made elaborate studies of ontogenies of the hinge in several living bivalves in which he undertook to trace dental homologies among separate major groups. Unfortunately, his work was not well documented and was halted by his early death. This promising field of investigation has been almost totally neglected subsequently, save for a few outstanding exceptions (e.g., Davies, 1935, Casey, 1952) and uncertainties exist about the applicability of some of Bernard's conclusions.

Dall and Douvillé both advocated that close attention should be paid to the entire organism, and they believed that observations on the comparative anatomy of living species could be harmonized with paleontological evidence based on geological chronology and shell characters. To them it was obvious that special consideration must be given to characters that are preserved in the fossil record if the historical facts of bivalve evolution are to be given due recognition in classification.

These authors also made some limited use of the poorly understood differences in shell fabric, or microstructure, later summarized by Bøggild (1930) and Oberling (1955, 1964). Much work remains to be done in this field to sort out the relative influences of phylogeny and ecology in determining the shell microstructure of each group. It seems clear that shell fabric yields important contributory evidence (*e.g.*, unionaceans have prismatonacreous shells; oysters possess prismatofoliaceous calcite shells), but the full phylogenetic implications have yet to be worked out. Unfortunately, original shell microstructures are rarely preserved in bivalves older than Pennsylvanian, and commonly they are destroyed even in geologically quite young fossils. Furthermore, it is now well established that in some groups environmental modifications of shell microstructure have been introduced, whereas in others this microstructure apparently is quite stable. Most of the outlines are yet to be determined.

Douvillé's great contribution was his emphasis on broad adaptive levels in reaching phylogenetic conclusions about the bivalves and he tried to utilize dental homologies indicated by Bernard. In this Douvillé recognized the hazard of confusing examples of similar adaptation with close genetic affinity, and he undertook to make use of all lines of evidence. He did not complete a formal taxonomic arrangement of the bivalves, but his work was incorporated in a classification of Tertiary bivalves by Davies (1935) that stands as a monument to Douvillé. Unfortunately, Davies' work did not incorporate many pre-Tertiary forms, nor will his classification accommodate them.

Douvillé distributed all bivalves among three branches according to three main modes of life. These were 1) "normal" or vagrant epifaunal bivalves, 2) fixed or "sedentary' epifaunal forms, either suspended by a byssus or cemented by one valve for part of the life span, and 3) burrowing, or boring, infaunal bivalves (desmodonts of Neumayr). It was recognized by Douvillé that many members of these branches had undergone secondary radiation leading to structural similarities among unrelated stocks, the details of which he tried to understand by combining studies of comparative anatomy and paleontology (Davies, 1933). Paleontologic and morphologic evidence supports the probable unity of most of his "sedentary" branch, but his "normal" and "burrowing" branches are not very homogeneous either historically or anatomically (Fig. 100). Little is known about the adaptive significance of particular structural types of ornamentation, dentition, ligament, and shell microstructure. And many challenging fundamental prob-

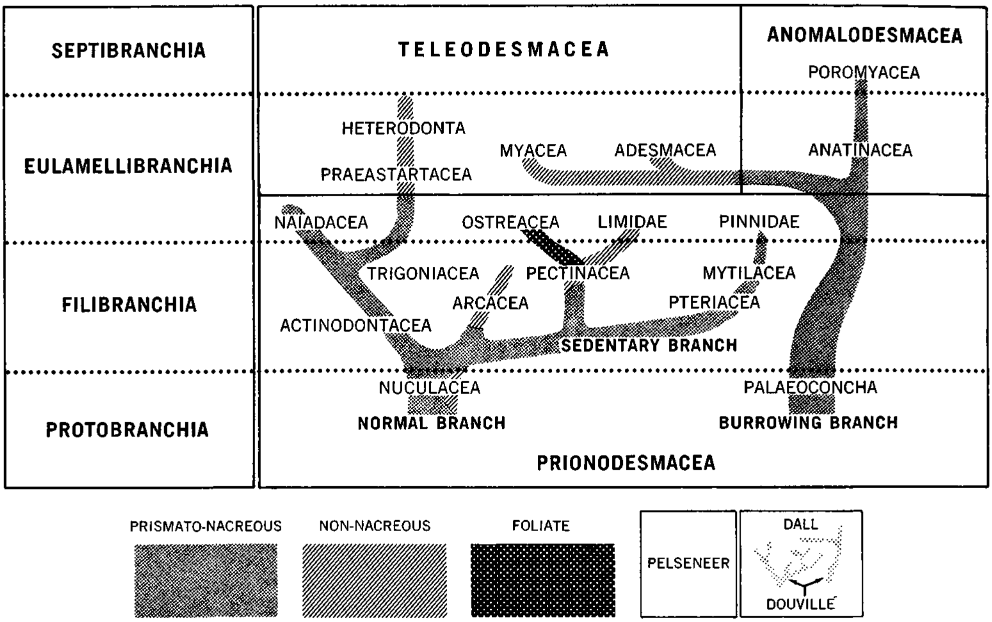

FIG. 101. Schematic comparison of classification of DALL and DOUVILLÉ (based in part on geologic history), with the "horizontal" classification of PELSENEER based mainly on ctenidial grade (Newell, n).

lems of the bivalves are not better understood than they were in the nineteenth century.

PELSENEER SCHOOL

In spite of the considerable amount of paleontologic evidence that was early available and general agreement that a phylogenetic approach to classification must take into account all lines of evidence, there developed a school of anatomists that ignored the fossil evidence and the integrity of superfamilies as defined by aggregate characters and turned to comparative studies of the bivalve ctenidia (Fig. 101) as a primary basis for higher classification (FISCHER, 1880-87; PELSENEER, 1889, 1891, 1906, 1911; RIDEWOOD, 1903).

More recently, ADKINS (1936-38) has classified the bivalves according to whether they possess one or another of two types of laterofrontal cilia on ctenidial filaments. PURCHON (1958) has based a system on stomach type in which he recognized five grades. STASEK (1963) has experimented, as a primary taxobasis, with the degree of association of ctenidia and labial palps (Table 1). The philosophical objection to this approach is that it cannot take into account the total organism, and provides no grounds for recognizing parallel evolution. The practical objection is that reliance on a single anatomical feature generally is not applicable to fossils, and makes no provision for evaluation of paleontologic evidence, the court of final appeal with respect to phylogeny in groups that have a good fossil record.

Studies of comparative anatomy of living species are of biologic interest and of course are essential for phylogenetic conclusions. They are only supplementary, however, and cannot provide needed evidence of the historical course of evolution. RIDEWOOD (1903) showed that a sequence of stages can be recognized in the union of adjacent gill filaments and that identical grades of gill structure have been acquired in bivalves that otherwise are unlike. Furthermore, other bivalves closely similar in many characters may have different grades of ctenidia. For example, the Ostreacea, Pinnacea, and Limacea have gills of eulamellibranch grade, although they have much in common with

TABLE 1. SOME CHARACTERISTICS OF EXTANT BIVALVE SUPERFAMILIES

	Gill Grade				Gill Cilia		Stomach Type					Labial Palps			Shell Microstructure			
Subclasses and Superfamilies	Protobranch	Filibranch	Eulamellibranch	Septibranch	Atkins, Type 1	Atkins, Type 2	Purchon, Type 1	Purchon, Type 2	Purchon, Type 3	Purchon, Type 4	Purchon, Type 5	Stasek, Type 1	Stasek, Type 2	Stasek, Type 3	Nacreous	Cross Lamellar	Foliate	Homogeneous
PALAEOTAXODONTA																		
Nuculacea	x	--	--	--	x	--	x	--	--	--	--	x	--	--	x	x	--	--
Nuculanacea	x	--	--	--	--	--	x	--	--	--	--	--	--	--	--	--	--	x
CRYPTODONTA																		
Solemyacea	x	--	--	--	--	--	?	--	--	--	--	--	--	--	--	--	--	x
PTERIOMORPHIA																		
Arcacea	--	x	--	--	--	x	--	--	x	--	--	--	--	x	--	x	--	--
Limopsacea	--	x	--	--	--	x	--	--	x	--	--	--	--	--	--	x	--	--
Mytilacea	--	x	--	--	x	--	--	--	x	--	--	x	--	--	x	--	--	--
Pinnacea	--	--	x	--	--	x	--	--	x	--	--	--	--	--	x	--	--	--
Pteriacea	--	x	--	--	--	x	--	--	x	--	--	--	--	x	x	x	--	--
Pectinacea	--	x	--	--	--	x	--	--	--	x	--	--	--	x	x	x	x	--
Anomiacea	--	x	--	--	--	x	--	--	--	x	--	--	--	x	--	--	x	--
Limacea	--	--	x	--	--	x	--	--	--	x	--	--	--	--	--	x	--	--
Ostreacea	--	--	x	--	--	x	--	--	x	--	--	--	--	x	--	--	x	--
PALAEOHETERODONTA																		
Unionacea	--	--	x	--	--	--	--	--	--	x	--	x	--	--	x	--	--	--
Trigoniacea	--	x	--	--	x	--	--	--	--	x	--	x	--	--	x	--	--	--
HETERODONTA																		
Lucinacea	--	--	x	--	x	--	--	--	--	x	--	--	--	x	--	x	--	--
Chamacea	--	--	x	--	x	--	--	--	--	x	--	--	x	--	--	x	--	--
Leptonacea	--	--	x	--	x	--	--	--	--	--	--	--	--	x	--	x	--	--
Chlamydoconchacea	--	--	x	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Cyamiacea	--	--	x	--	x	--	--	--	--	x	--	--	--	x	--	x	--	--
Carditacea	--	--	x	--	x	--	--	--	--	x	--	--	x	--	--	x	--	--
Crassatellacea	--	--	x	--	x	--	--	--	--	x	--	x	--	x	--	x	--	--
Cardiacea	--	--	x	--	x	--	--	--	--	--	x	--	x	--	--	x	--	--
Tridacnacea	--	--	x	--	x	--	--	--	--	--	x	--	--	--	--	x	--	--
Mactracea	--	--	x	--	x	--	--	--	--	--	x	--	--	x	--	x	--	--
Solenacea	--	--	x	--	x	--	--	--	--	--	x	--	--	x	--	x	--	--
Tellinacea	--	--	x	--	x	--	--	--	--	--	x	--	--	x	--	x	--	--
Dreissenacea	--	--	x	--	x	--	--	--	--	--	--	--	--	--	--	x	--	--
Gaimardiacea	--	--	x	--	--	--	--	--	--	--	--	--	--	--	--	x	--	--
Arcticacea	--	--	x	--	x	--	--	--	--	--	--	--	--	--	--	x	--	--
Glossacea	--	--	x	--	x	--	--	--	--	--	x	--	x	--	--	x	--	--
Corbiculacea	--	--	x	--	x	--	--	--	--	--	x	--	--	--	--	x	--	--
Veneracea	--	--	x	--	x	--	--	--	--	--	x	--	x	x	--	x	--	--
Myacea	--	--	x	--	x	--	--	--	--	--	x	--	--	x	--	x	--	--
Gastrochaenacea	--	--	x	--	--	--	--	--	--	--	--	--	--	--	--	x	--	--
Hiatellacea	--	--	x	--	--	--	--	--	--	--	--	--	--	--	--	x	--	--
Pholadacea	--	--	x	--	x	--	--	--	--	--	x	--	--	x	--	x	--	--
ANOMALODESMATA																		
Pholadomyacea	--	--	x	--	x	--	--	--	--	--	--	--	--	--	x	--	--	--
Pandoracea	--	--	x	--	x	--	--	--	--	x	--	--	--	x	x	--	--	--
Poromyacea	--	--	--	x	--	--	--	x	--	--	--	--	--	x	x	--	--	--
Clavagellacea	--	--	x	--	x	--	--	--	--	x	--	--	--	x	x	--	--	--

Superfamilies not represented by extant bivalves include the following:

Superfamily	Soft Parts and Shell Microstructure
Ambonychiacea	No information
Archanodontacea	No information
Babinkacea	No information
Conocardiacea	Shell microstructure complex
Ctenodontacea	No information
Cycloconchacea	No information
Cyrtodontacea	No information
Edmondiacea	No information
Hippuritacea	Shell microstructure complex, varying with families
Megalodontacea	No information
Modiomorphacea	No information
Praecardiacea	No information

the Pectinacea, Mytilacea, and Anomiacea, which have filibranch gills. In four families —Arcidae, Anomiidae, Pteriidae (Aviculidae), and Spondylidae—Ridewood found that one or two species had advanced a step beyond the rest of the family. The family-group taxa, based on multiple character complexes, are thereby fragmented.

These facts are adequate evidence of parallel evolution through a series of functional grades and are not indicative of relationship. Pelseneer (1906), in his taxonomic treatment, divided the anisomyarians (considered together with the Arcoida by many paleontologists as a phylogenetic unit) according to grades of gill structure into the Filibranchia and Eulamellibranchia. Later (Pelseneer, 1911), recognizing the incongruity of the resulting associations, he redistributed some of the families in an intermediate group, the Pseudolamellibranchia, which was heterogeneous as regards grade of gill structure, combining families with eulamellibranchiate gills (Ostreidae, Limidae, Pinnidae) and others possessing filibranch gills (Vulsellidae, Pectinidae). Thus, he abandoned gill structure as the primary anatomical basis in favor of overall resemblance. A comparison of Pelseneer's scheme with the classifications of Dall and Douvillé is shown in Figure 101.

A modified version of Pelseneer's 1906 treatment of the bivalves is followed in a leading zoological treatise (Franc, 1960), in which the Filibranchia still contain some forms with eulamellibranch gills (Pinnidae, Limidae, Ostreidae) and the Eulamellibranchia include others with filibranch gills (Trigoniidae). These groups simply illustrate mosaic evolution in which gill characters have evolved at differing rates in different lines. The original purpose of Pelseneer, to provide a simple method of keying the various bivalves according to grade of gill structure, is thus defeated, and there is no semblance of consistency in his search for a natural classification.

HORIZONTAL VERSUS VERTICAL SYSTEMS

In spite of general doubts about the validity of Pelseneer's orders of Bivalvia, Yonge (1959), Cox (1959), Owen (1959), and Purchon (1959), in a symposium on primitive bivalves, recently marshalled evidence of the homogeneity of the bivalves with primitive comblike gills, the Protobranchia, which they proposed to elevate from ordinal status to a subclass of the Bivalvia. All other bivalves they would segregate in one or more additional subclasses. This conclusion, retrograde, I believe, has been adopted by Morton & Yonge (1964). The Protobranchia are based on ctenidial characters shared by the family Solemyidae, and the nuculoids. Otherwise dissimilar, the two groups are characterized by simple gills, which, structurally, are reminiscent of the gills of certain gastropods.

Both *Solemya* and the nuculoids are detritus-feeders, unlike the majority of bivalves which strain suspended material from water. Thus, the protobranchs share in common the quality of primitiveness of the ctenidia. Here similarity ends, however. The nuculoids, clearly a homogeneous group, differ in almost every other feature from *Solemya*. Both groups are extremely ancient, having been separate for at least a half a billion years, and no paleontologic evidence indicates that either was derived from the other. Were they closely related, the fossil record should show some evidence of parallel trends, but the shells have always been quite unlike and remarkably stable.

The Solemyidae and nuculoids apparently have shared the same habitat and apparently have occupied similar niches throughout their known history without any tendency to develop similar shell characters. Since they are unlike morphologically, are not connected by intermediate forms, and have reacted differently within the same habitat, one might infer that in fact they are only distantly related to each other. Classifying these two groups together simply because of similarities in one organ (gill structure) is no more defensible than placing all nacreous shells or all monomyarian shells together. Modern work on the genus *Solemya* tends to emphasize innumerable points of difference from nuculoids. Horizontal classification based on a single-organ system has an element of utility, of course, but it does not reflect the intricacies of phylogeny.

In the light of existing knowledge about the bivalves, an overall phylogenetic classification has not been devised, and experience shows that a simple classification free from innumerable inherent inconsistencies cannot be achieved as yet. Ultimately, the older fossils will provide the needed evidence for grouping morphologically dissimilar superfamilies on the basis of common origin. This may be accomplished only by working upward through genus, family, superfamily, order, and subclass, with a critical eye to the fossil evidence. Phylogenetic relationships are best deduced from the geologic history of the class, and this is poorly known. A wholly satisfactory classification cannot be obtained by arbitrarily forcing family group taxa into ready-made higher categories.

NEUMAYR's and DOUVILLÉ's influence is evident in the great French *Traité de paléontologie* (DECHASEAUX, 1952) and the Russian *Osnovy paleontologii* (EBERSIN, 1960). However, both display extensive modifications necessitated by progress and differing emphases on the subject. DALL's superior knowledge of the bivalves is reflected in his last major revision (1913), and no subsequent student of the group has been able to combine such encyclopedic knowledge and scholarship.

With some noteworthy modifications, the groupings adopted herein are similar to those recognized by L. R. COX (1960), many of which we had discussed together, but the nomenclature is not the same.

CLASS—SUBCLASSES—ORDERS

NAME OF CLASS

Even the name applied to the bivalve mollusks has been a source of widespread disagreement. The malacologists of the world in recent years have been about evenly divided in preferences between the two terms Pelecypoda GOLDFUSS, 1820, and Lamellibranchiata (or Lamellibranchia) DE BLAINVILLE, 1824 (Lamellibranches, 1814), and no possibility of winning universal adoption of either of these two names seems to exist. Following the examples of HAAS (1929-56) and THIELE (1934-35), however, a strong swing now is seen toward compromise on the term Bivalvia LINNÉ, 1758 (YONGE, 1959; PURCHON, 1959; FRANC, 1960; EBERSIN, 1960; COX, 1960; MORTON, 1963; STASEK, 1963; MORTON & YONGE, 1964; VOKES, 1967). This name is not only the oldest formally applied to the class, but it has the merit of possessing a familiar English cognate, "bivalve," which is meaningful to the layman. Generally, there is little confusion with other bivalve groups such as brachiopods and ostracodes (or even some gastropods) which are not customarily termed bivalves without a qualifying adjective. In any case, the name of the class is not intended to be an anatomical description. If desirable, the vernacular terms "pelecypod" or "lamellibranch" may continue to be employed by those who prefer them to "bivalve."

SUBCLASSES

The function of subclasses of Bivalvia is to provide a few major divisions for convenience in discussion and taxonomic sorting and ultimately to distinguish the trunk lines of phylogenetic descent. The last-named objective cannot be fully attained at the present time. The treatment followed here (Fig. 102) recognizes six major divisions, at least two of which (Palaeotaxodonta, Pteriomorphia) are considered by many paleontologists and neontologists to be more or less natural groupings. The other four are probably artificial. The subclasses are named as follows: 1) Palaeotaxodonta KOROBKOV, 1954, 2) Cryptodonta NEUMAYR, 1884, 3) Pteriomorphia BEURLEN, 1944, 4) Palaeoheterodonta NEWELL, 1965, 5) Heterodonta NEUMAYR, 1884, 6) Anomalodesmata DALL, 1889.

PALAEOTAXODONTA

The Palaeotaxodonta comprise the nuculoids, a compact group characterized by a primitive taxodont hinge and protobranch

<table>
<tr><th>DALL, 1913</th><th colspan="2">THIELE, 1934-35</th><th colspan="2">FRANC, 1960</th><th colspan="2">COX, 1960</th><th colspan="2">NEWELL, 1965</th></tr>
<tr><td rowspan="9">PRIONODESMACEA</td><td colspan="2" rowspan="4">TAXODONTA</td><td rowspan="3">PROTOBRANCHIA</td><td>NUCULIDAE
NUCULANIDAE
MALLETIIDAE</td><td rowspan="3">PROTOBRANCHIA</td><td>PALAEOTAXODONTIDA</td><td>PALAEO-TAXODONTA</td><td>NUCULOIDA</td></tr>
<tr><td rowspan="2">SOLEMYIDAE</td><td>LIPODONTIDA</td><td rowspan="2">CRYPTO-DONTA</td><td>SOLEMYOIDA</td></tr>
<tr><td>CRYPTODONTIDA</td><td>PRAECARDIOIDA</td></tr>
<tr><td rowspan="4">FILIBRANCHIA</td><td>TAXODONTA</td><td rowspan="4">PTERIOMORPHIA</td><td>EUTAXODONTIDA</td><td rowspan="4">PTERIOMORPHIA</td><td>ARCOIDA</td></tr>
<tr><td colspan="2" rowspan="3">ANISOMYARIA</td><td rowspan="3">ANISOMYARIA</td><td>ISOFILIBRANCHIDA</td><td>MYTILOIDA</td></tr>
<tr><td>PTEROCONCHIDA</td><td rowspan="2">PTERIOIDA</td></tr>
<tr><td>COLLOCONCHIDA</td></tr>
<tr><td rowspan="8">EULAMELLIBRANCHIA</td><td rowspan="2">SCHIZODONTA</td><td rowspan="7">EULAMELLIBRANCHIA</td><td rowspan="2">SCHIZODONTA</td><td rowspan="8">HETEROCONCHIA</td><td>SCHIZODONTIDA</td><td rowspan="3">PALAEO-HETERODONTA</td><td>TRIGONIOIDA</td></tr>
<tr><td>NAIADIDA</td><td>UNIONOIDA</td></tr>
<tr><td rowspan="4">TELEODESMACEA</td><td>EXTINCT</td><td>EXTINCT</td><td>PANTODONTIDA</td><td>MODIOMORPHOIDA</td></tr>
<tr><td>EXTINCT</td><td>RUDISTES</td><td>PACHYODONTIDA</td><td rowspan="3">HETERODONTA</td><td>HIPPURITOIDA</td></tr>
<tr><td>HETERODONTA</td><td>HETERODONTA</td><td>HETERODONTIDA</td><td>VENEROIDA</td></tr>
<tr><td>ADAPEDONTA</td><td>ADAPEDONTA</td><td>ASTHENODONTIDA</td><td>MYOIDA</td></tr>
<tr><td rowspan="2">ANOMALODESMACEA</td><td rowspan="2">ANOMALODESMATA</td><td>ANOMALODESMACEA</td><td>EUDESMODONTIDA</td><td rowspan="2">ANOMALO-DESMATA</td><td rowspan="2">PHOLADOMYOIDA</td></tr>
<tr><td colspan="2">SEPTIBRANCHIA</td><td>SEPTIBRANCHIDA</td></tr>
</table>

FIG. 102. Comparative classifications of the bivalves. That adapted herein is given in the right-hand column (Newell, n).

ctenidia which function almost solely in respiration. All are soft-bottom detritus-feeders, with representatives of both epifauna and infauna, each with appropriate adaptations. The nuculoids have long been considered to be the most primitive living bivalves, but they are not known to be the most ancient. No direct evidence is found that they gave rise to other radically different morphological types. As DOUVILLÉ (1913) and many others have shown, the taxodont hinge of the Arcidae represents a late development quite unrelated to the nuculoids.

CRYPTODONTA

The Cryptodonta (=Palaeoconcha of authors) are an association of convenience for poorly understood, thin-shelled forms without lateral teeth or well-developed cardinal teeth. Most of the families are limited to the early and middle Paleozoic. *Solemya,* a living protobranch of ancient lineage, is classed as a cryptodont until more can be learned about the Paleozoic forms. It differs morphologically from the nuculoids, and the ctenidia are used in feeding as well as respiration. The cryptodonts were considered by NEUMAYR, DALL, and DOUVILLÉ as primitive burrowers ancestral to many later stocks, but the validity of this idea has been demonstrated only in part. Most lack the siphonal gape of deep burrowers, and some of the forms included in the group even have been regarded by some as bivalved crustaceans.

PTERIOMORPHIA

The Pteriomorphia (=fixed, or sedentary, branch of DOUVILLÉ) are accepted by many paleontologists as a phylogenetic unit. These are the anisomyarians plus the arcoids and Paleozoic cyrtodonts (Fig. 102). Although they are morphologically diverse, the fossil record suggests continuity and common origins for several of the lines. It is possible, as Cox (1960) has pointed out, that the Mytilacea had a separate origin in the Modiomorphidae, a group of the Palaeoheterodonta. The duplivincular grade of ligament is found in many groups of this subclass, but through parallel trends some of the families have attained the alivincular or parivincular grade of ligament. Characteristically, the Pteriomorphia are members of the epifauna, but a few have adopted a boring habit in firm substrates. Many retain the byssus throughout life, a characteristic of very young bivalves of most other groups.

PALAEOHETERODONTA

The Palaeoheterodonta comprise the early Paleozoic actinodonts, unionaceans, and trigoniaceans. This grouping may be artificial, but the later members are alike in possessing free or incompletely fused mantle margins, an opisthodetic parivincular ligament, and prismatonacreous shells. Posterolateral hinge teeth, where present, originate at the beaks and below the ligament. The actinodonts include the oldest known bivalves (Middle Cambrian, Spain; Vogel, 1962). They may have given rise to the Pteriomorphia, Heterodonta, and possibly other groups (Fig. 103).

HETERODONTA

The Heterodonta differ from the Palaeoheterodonta in possessing nonnacreous shells (complex, or crossed lamellar) and more or less fused, siphonate, mantle margins. Posterolateral teeth, where present, commonly originate some distance behind the beaks and ligament. The ctenidia of living representatives are of the eulamellibranch grade. These animals extend far back into the Paleozoic where they merge gradually with the actinodonts. They nestle or burrow in diverse substrates, and their siphons show appropriate adaptations for depth of penetration beneath the surface.

ANOMALODESMATA

The Anomalodesmata generally are siphonate, burrowing forms with prismatonacreous shells, characteristically with an internal resilium, chondrophores, and a lithodesma. In most groups a hinge plate and teeth are weak or lacking.

ORDERS

The long history of work on bivalve classification has been characterized by repeated revisions based on new evidence and new points of view. Usually, new work has resulted in an emendation of the limits of various taxa. Most authors have believed, as did Cox (1960), that extensive emendation renders the old names obsolete. Simpson (1945, p. 32) has commented on this problem:

> To demand a change of name whenever such a shift is made would result in utmost confusion and duplication of terminology, and to change the author and date would be unjust and would obscure the historical origin of names and concepts. The opposite view might logically demand recognizing as author the first student to use a name in precisely its present sense. In most cases this would mean either that the technical authors of many time-hallowed names would change constantly and would tend to be the latest revisers, or that revisers were honor-bound not to change ranks of groups, which would stultify revision.

The problem of obsolescence and repeated replacement of names does not apply to family-group taxa, because they are legally based on type genera. Consequently, anyone may increase or decrease the scope of these taxa without disturbing their nomenclatural stability. They need not retain, even approximately, the limits suggested by the original author, since they are anchored to a nomenclatural type. Obviously, if knowledge is to expand in taxonomy, *a priori* limits cannot be placed on individual taxa. The use of nomenclatural types for orders is a convenient, elastic, and familiar method of insuring stability of nomenclature, while permitting freedom of individual judgment. It obviates any need for rigidly adhering to original definitions or to the endless dropping of names in consequence of emendation. This device has been in steady use for order-group names in many major groups of invertebrates (e.g., brachiopods, cephalopods, coelenterates, echinoids, trilobites, and others), and the practice of anchoring suborders and orders to genera was used for the bivalves by a few nineteenth century taxonomists, as noted above.

Reference to Figure 102 will show that the ordinal groupings adopted here are essentially those of Cox (1960). The changes in names do not require further comment. The number of orders has been reduced from 15 to 14 by reuniting the Ostreacea

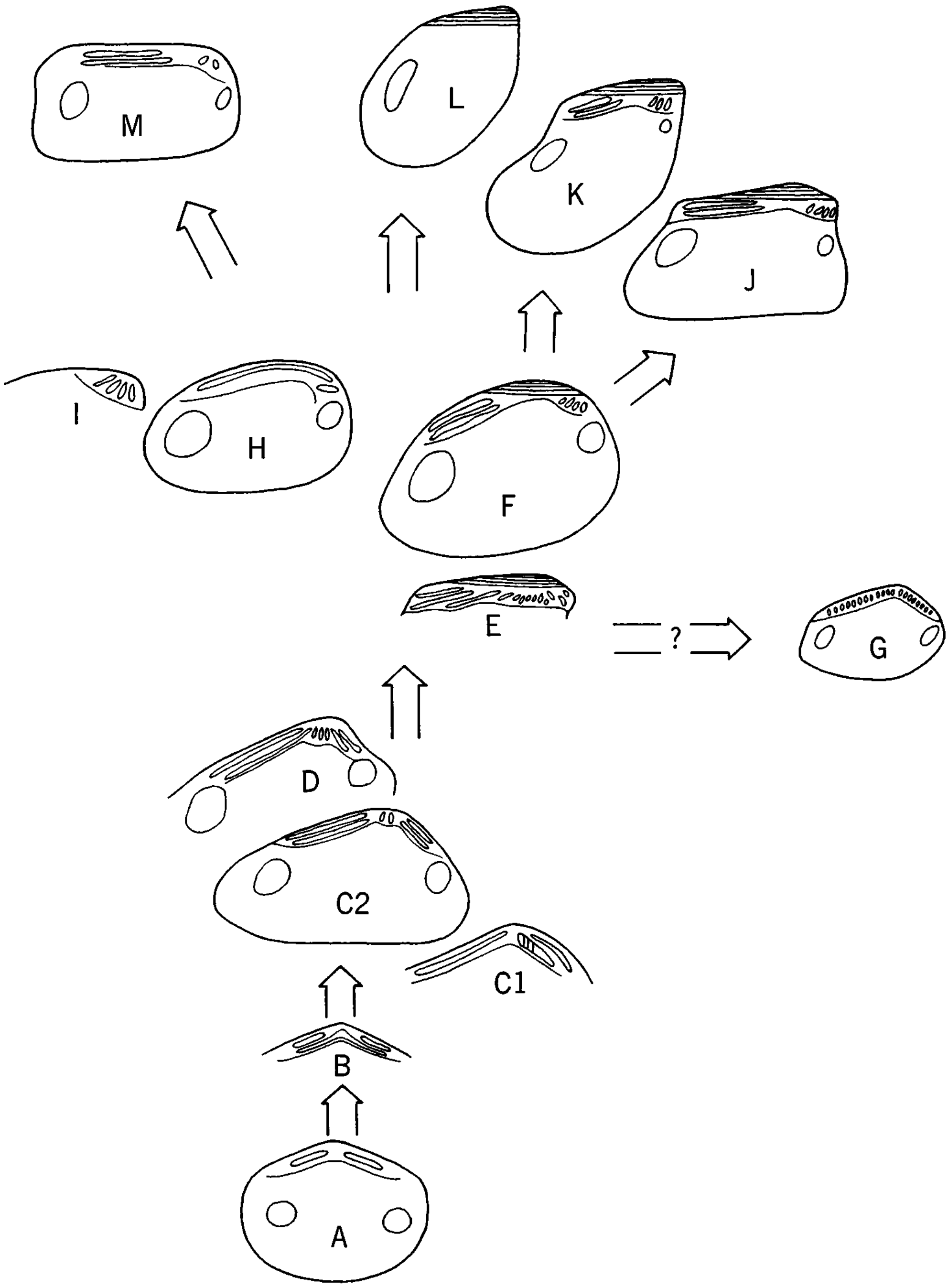

FIG. 103. Conjectural radiation of major groups of bivalves in the Paleozoic (modified from Vogel, 1962). *A, B.* Lamellodontidae, Cambrian. *C1, C2, D.* Hinge types among the Cycloconchidae, Ordovician. *E,F.* Cyrtodontidae, Ordovician. *G.* Nuculoid *(Tancrediopsis),* Ordovician. *H, I.* Modiomorphidae, Ordovician. *J.* Parallelodontidae, Ordovician. *K.* Pterineidae, Devonian. *L.* Myalinidae, late Paleozoic. *M.* Permophoridae, late Paleozoic.

(Colloconchida) with the Pectinacea and related superfamilies on the basis of morphology and paleontologic evidence of close relationship (NEWELL, 1960). Several of the orders contain only one or two superfamilies, but their known history and morphological isolation militate against their being combined at present with other groups. An outline of the subclasses and ordinal group taxa follows.

Among the major classes of mollusks the bivalves have been most neglected and no individual in the world today can claim broad familiarity with fossil and living representatives of the entire class. Consequently, it should not be surprising that myriads of morphologic and taxonomic problems await solution. Much divergence of opinion exists among the many authors of this volume on the bivalves and in his organization of materials submitted by them MOORE has shown great foresight and skill in respecting and preserving divergent judgments whenever feasible. Some genera appear under two or more families with appropriate explanatory notes. Many others are treated as subjective synonyms because of lack of sufficient evidence of consistent morphologic discrimination. Further investigation will show that many such synonymous genera and subgenera might usefully be revived.

A large majority, perhaps one-half of all Paleozoic genera and early Mesozoic genera (including subjective synonyms), are very poorly understood and require intensive study. Additional knowledge of these fossils will affect phylogenetic theories about the class as a whole. RUNNEGAR's (1966) important morphological studies on Australian Permian desmodonts illustrates the urgency of acquiring precise knowledge of the nature of the fossil record. His work has convinced me of the general integrity of the Pholadomyoida, as herein used, even though the taxonomic distribution of the older genera and families remains somewhat conjectural because of lack of accurate morphological data.

MAJOR DIVISIONS OF BIVALVIA

Class **BIVALVIA** (BONNANI, 1681) LINNÉ, 1758, p. 645.

- Subclass **Palaeotaxodonta.** The nuculoids; taxodont, nacreous or crossed lamellar; equivalved.
  - Order **Nuculoida.** Protobranch taxodonts; Purchon type 1; Stasek type 3; a homogeneous group.
- Subclass **Cryptodonta.** *Solemya* plus Paleozoic cryptodonts; edentulous or nearly edentulous; generally equivalve; probably polyphyletic.
  - Order **Solemyoida.** Solemyidae; homogeneous aragonite ostracum; siphonate, burrowing protobranchs.
  - Order **Praecardioida.** Paleozoic cryptodonts, shell margins not gaping; probably a heterogeneous group.
- Subclass **Pteriomorphia.** Cyrtodonts, arks, most heteromyarians; shell structure, ligament, gills, and stomach variable; commonly byssate in adults; general phyletic unity suggested by the fossil sequence.
  - Order **Arcoida.** Isomyarian filibranchs with crossed-lamellar shells; cyrtodonts and prionodonts; generally equivalve; Purchon type 3; Stasek type 3.
  - Order **Mytiloida.** Anisomyarian, generally equivalve, filibranchs and eulamellibranchs with prismatonacreous shells; Purchon type 3; Stasek type 1; characteristically byssate in adults.
  - Order **Pterioida.** Anisomyarian and monomyarian, mainly pleuroconchs and byssate or cemented in adults; pearl clams, scallops, oysters, filibranchs, eulamellibranchs; nacreous, crossed lamellar, or foliate internally; Purchon types 3 and 4; Stasek type 3.
- Subclass **Palaeoheterodonta.** Early actinodonts, unionaceans, trigoniaceans; prismatonacreous; Purchon type 4; Stasek type 1.
  - Order **Modiomorphoida** Newell, new order. Actinodonts; early Paleozoic precursors of most of the orders of bivalves; teeth radial, poorly differentiated, originating at the beaks; equivalved.
  - Order **Unionoida.** Variable upper Paleozoic and post-Paleozoic nonmarine forms, probably derived from the pre-

ceding; eulamellibranchs; Purchon type 4; Stasek type 1, probably polyphyletic.

Order **Trigonioida.** Trigonal marine shells; laterals or pseudolaterals generally lacking; filibranchs; apparently homogeneous.

Subclass **Heterodonta.** Heterodonts; complex crossed-lamellar eulamellibranchs.

Order **Veneroida.** Active heterodonts with differentiated hinge teeth of which laterals rarely reach beaks in adults; Purchon types 4 and 5; Stasek types, 1, 2, and 3; probably polyphyletic.

Order **Myoida.** Asthenodonts with degenerate hinge, generally with siphons and united mantle margins; Purchon type 5; Stasek type 3; probably polyphyletic.

Order **Hippuritoida.** Pachydonts; mainly attached, extinct forms.

Subclass **Anomalodesmata.** Generally fossorial, with poorly developed cardinal teeth, without laterals; mantle margins united; ligament associated in most primitive forms with internal resilium and lithodesma; internally nacreous.

Order **Pholadomyoida.** Burrowers with primitive hinge; eulamellibranchs and septibranchs; Purchon types 3 and 4; Stasek type 3.

Subclass **Uncertain.**

Order **Conocardioida.** Hinge commonly anchylosed in adults; with marked gape at one end and, in some genera, with a calcareous siphonal extension at the other; shell structures with radial pillars appearing at anticardinal margin as interlocking denticulations; musculature poorly known.

OUTLINE OF CLASSIFICATION

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The following outline of the Bivalvia summarizes taxonomic relationships, geologic occurrence, and numbers of recognized genera and subgenera in each suprageneric group from class to subfamily. A single number refers to genera; where two numbers are given, the second indicates subgenera additional to nominotypical ones.

Main Divisions of Bivalvia

- Bivalvia *(class)* (2169;996). *M.Cam.-Rec.*
  - Palaeotaxodonta *(subclass)* (63;40). *Ord.-Rec.*
    - Nuculoida *(order)* (63;40). *Ord.-Rec.*
      - Ctenodontacea *(superfamily)* (6). *Ord.-Carb.*
        - Ctenodontidae (6). *Ord.-Carb.*
      - Nuculacea *(superfamily)* (15;7). *Ord.-Rec.*
        - Praenuculidae (6). *Ord.-Rec.*
        - Nuculidae (9;7). *Ord.-Rec.*
      - Nuculanacea *(superfamily)* (42;33). *Ord.-Rec.*
        - Malletiidae (22;6). *Ord.-Rec.*
        - Nuculanidae (19;27). *Dev.-Rec.*
      - Isoarcidae (1). *M.Jur.-U.Cret.*
  - Cryptodonta *(subclass)* (20;5). *?U.Cam., L.Ord.-Rec.*
    - Solemyoida *(order)* (3;3). *Dev.-Rec.*
      - Solemyacea *(superfamily)* (3;3). *Dev.-Rec.*
        - Solemyidae (3;3). *Dev.-Rec.*
    - Praecardioida *(order)* (17;2). *?U.Cam., L.Ord.-L.Miss.*
      - Praecardiacea *(superfamily)* (17;2). *?U.Cam., L.Ord.-L.Miss.*
        - Praecardiidae (9;1). *?U.Cam., L.Ord.-L.Miss.*
          - Praecardiinae (5). *?U.Cam., L.Ord.-Dev.*
          - Cardiolinae (3;1). *L.Sil.-L.Miss.*
          - Dexiobiinae (1). *?Sil., L.Miss.*
        - Antipleuridae (7;1). *M.Ord.-Dev.*
          - Antipleurinae (3;1). *Sil.-Dev.*
          - Vlastinae (4). *M.Ord.-Dev.*
        - Butovicellidae (1). *Sil.*
  - Pteriomorphia *(subclass)* (490;191). *L.Ord.-Rec.*
    - Arcoida *(order)* (77;29). *L.Ord.-Rec.*
      - Cyrtodontacea *(superfamily)* (12). *M.Ord.-Dev.*
        - Cyrtodontidae (12). *M.Ord.-Dev.*
      - Arcacea *(superfamily)* (39;20). *L.Ord.-Rec.*
        - Arcidae (12;8). *?Trias., Jur.-Rec.*
          - Arcinae (4;6). *?Trias., Jur.-Rec.*
          - Anadarinae (8;2). *U.Cret.-Rec.*
        - Parallelodontidae (11;6). *L.Ord.-Rec.*
          - Parallelodontinae (4). *L.Ord.-U.Jur.*
          - Grammatodontinae (7;6). *?U.Carb., U.Trias.-Rec.*
        - Cucullaeidae (3;2). *L.Jur.-Cret., Rec.*
        - Noetiidae (13;4). *L.Cret.-Rec.*
          - Noetiinae (5;2). *L. Cret.-Rec.*
          - Stiarcinae (5;1). *U.Cret.-Rec.*
          - Trinacriinae (3;1). *U.Cret.-Eoc.*
      - Limopsacea *(superfamily)* (26;9). *L.Perm.-Rec.*
        - Limopsidae (8;1). *U.Trias.-Rec.*
        - Glycymerididae (10;2). *L.Cret.-Rec.*
          - Glycymeridinae (4;2). *Cret.-Rec.*
          - Arcullaeinae (6). *L.Cret.-U.Cret.*
        - Manzanellidae (3). *Perm.-Rec.*
        - Philobryidae (5;6). *Eoc.-Rec.*
    - Mytiloida *(order)* (64;26). *Dev.-Rec.*
      - Mytilacea *(superfamily)* (56;24). *Dev.-Rec.*
        - Mytilidae (53;24). *Dev.-Rec.*
          - Mytilinae (18;6). *?Perm., Trias.-Rec.*
          - Crenellinae (12;5). *U.Trias.-Rec.*

Lithophaginae (4;7). *?Carb., U.Perm.-Rec.*
Modiolinae (19;6). *Dev.-Rec.*
Mysidiellidae (3). *L.Trias.-U.Trias.*
Pinnacea *(superfamily)* (8;2). *L.Carb.-Rec.*
Pinnidae (8;2). *L.Carb.-Rec.*
Pterioida *(order)* (349;136). *Ord.-Rec.*
Pteriina *(suborder)* (298;127). *Ord.-Rec.*
Ambonychiacea *(superfamily)* (53;8). *?L.Ord., M.Ord.-L.Jur., ?U.Jur.*
Ambonychiidae (22;1). *M.Ord.(Chazy.)-U.Dev., ?L.Miss.*
Myalinidae (21;5). *?L.Dev., L.Miss.-L.Jur., ?U.Jur.*
?Lunulacardiidae (9;2). *L.Ord.-Miss.*
Monopteriidae (1). *L.Penn.-U.Penn., ?L.Perm.*
Pteriacea *(superfamily)* (102;21). *Ord.-Rec.*
Pterineidae (21;3). *Ord.-U.Perm.*
Kochiidae (1). *Dev.*
Pteriidae (11;1). *Trias.-Rec.*
Bakevelliidae (17;2). *Perm.-Eoc.*
Cassianellidae (6). *?Perm., Trias.*
Pergamidiidae (4). *U.Trias.-L.Jur.(Lias.).*
Dattidae (1). *U.Trias.(Rhaet.).*
Inoceramidae (16;9). *L.Perm.-U.Cret., ?Oligo.*
Isognomonidae (8;4). *U.Perm.-Rec.*
Pulvinitidae (3). *U.Jur.-Rec.*
Malleidae (14;2). *Jur.-Rec.*
Pectinacea *(superfamily)* (112;75). *Ord.-Rec.*
Pterinopectinidae (7;3). *U.Sil.-L.Perm. (Leonard.).*
Leiopectinidae (3). *Ord.-L.Dev.*
Aviculopectinidae (24). *U.Dev.-U.Jur.*
Aviculopectininae (16). *L.Miss.-U.Jur.*
Streblochondriinae (4). *Miss.-U.Trias.*
Chaenocardiinae (2). *L.Miss.(Visean)-L.Perm.*
Euchondriinae (2). *U.Dev.-U.Perm.*
Deltopectinidae (1). *L.Perm.*
Pseudomonotidae (1). *L.Carb.-U.Perm.*
Posidoniidae (12;1). *L.Carb.-U.Cret.*
Oxytomidae (7;2). *L.Perm.-U.Cret.*
Entoliidae (4;1). *L.Miss.-U.Cret.*
Pectinidae (31;63). *Trias.-Rec.*
Monotidae (2;1). *U.Trias.*
Buchiidae (8). *U.Trias.-Cret.*
Plicatulidae (3;2). *M.Trias.-Rec.*
Spondylidae (1;2). *Jur.-Rec.*
Terquemiidae (5). *?L.Perm., Trias.-U.Jur., ?Cret.*
?Dimyidae (2). *M.Jur.-Rec.*
Family Uncertain (1). *U.Trias.*
Anomiacea *(superfamily)* (10;11). *?Perm., Cret.-Rec.*
Anomiidae (10;11). *?Perm., Cret.-Rec.*
Limacea *(superfamily)* (21;12). *L.Carb.-Rec.*
Limidae (21;12). *L.Carb.-Rec.*
Ostreina *(suborder)* (51;9). *U.Trias.-Rec.*
Ostreacea *(superfamily)* (51;9). *U.Trias.-Rec.*
Gryphaeidae (22;6). *U.Trias.-Rec.*
Gryphaeinae (6;2). *U.Trias.(Rhaet.)-U.Jur. (Kimmeridg.).*
Pycnodonteinae (4;3). *L.Cret.-Rec.*
Doubtful genus (1).
Exogyrinae (11;1). *M.Jur.(Bajoc.)-Mio.*
Ostreidae (26;3). *U.Trias.-Rec.*
Ostreinae (13;1). *L.Cret.-Rec.*
Lophinae (6;2). *U.Trias.-Rec.*
Doubtful genera (7). *U.Cret., L.Oligo.-Eoc.*
Chondrodontidae (1). *L.Cret.(Alb.)-U.Cret. (Turon.).*
?Lithiotidae (2). *L.Jur.(L.Lias.).*
Palaeoheterodonta *(subclass)* (284;125). *M.Cam.-Rec.*
Modiomorphoida *(order)* (40;2). *M.Cam.-L.Perm., ?U.Perm.*
Modiomorphacea *(superfamily)* (33;2). *L.Ord.-L.Perm., ?U.Perm.*
Modiomorphidae (33;2). *L.Ord.-L.Perm., ?U.Perm.*
Cycloconchacea *(superfamily)* (7). *M.Cam.-U.Dev.*
Cycloconchidae (2). *Ord.*
Lamellodontidae (1). *M.Cam.*
Allodesmatidae (3). *M.Ord.-U.Sil.*
Carydiidae (1). *L.Dev.-U.Dev.*
Unionoida *(order)* (184;105). *?M.Dev., U.Dev.-Rec.*
Archanodontacea *(superfamily)* (2). *U.Dev.-L.Perm.*
Archanodontidae (2). *U.Dev.-L.Perm.*
Anthracosiacea *(superfamily)* (17;1). *?M.Dev., Carb.-Perm., ?Jur.*
Anthracosiidae (4). *Carb., ?Perm.*
?Microdontidae (3). *Perm.*
Palaeomutelidae (2;1). *?U.Carb., Perm.*
?Ferganoconchidae (1). *Jur.*
?Pseudocardiniidae (6). *Jur.*
Family Uncertain (1). *?M.Dev.*
Unionacea *(superfamily)* (159;104). *?Perm., Trias.-Rec.*
Margaritiferidae (1;3). *U.Cret.-Rec.*
Unionidae (133;91). *Trias.-Rec.*
Unioninae (60;40). *Trias.-Rec.*
Quadrulinae (22;9). *L.Cret.-Rec.*
Anodontinae (9;11). *U.Cret.-Rec.*
Alasmidontinae (6;8). *U.Oligo.-Rec.*
Lampsilinae (20;16). *?Trias., L.Oligo.-Rec.*
Hyriinae (16;7). *Cret.-Rec.*
Mutelidae (14;9). *?Trias., Cret.-Rec.*
Etheriidae (3;1). *Plio.-Rec.*
?Desertellidae (1). *L.Cret.(?Alb.).*
?Pachycardiidae (5). *Perm.-U.Trias., ?L.Jur.(Lias.).*
?Actinodontophoridae (2). *Perm.-U.Trias.*
Superfamily and family uncertain (6). *Trias.-Cret.*
Trigonioida *(order)* (60;18). *?M.Ord., Dev.-Rec.*
Trigoniacea *(superfamily)* (60;18). *?M.Ord., Dev.-Rec.*
?Lyrodesmatidae (1). *M.Ord.-U.Ord.*
Myophoriidae (13). *Dev.-U.Trias., ?L.Jur.*
?Scaphellinidae (1). *L.Perm.*

- Trigoniidae (41;18). *M.Trias.-Rec.*
- ?Trigonioididae (2). *L.Cret.-U.Cret.*
- Family Uncertain (2). *Cret.*
- Heterodonta *(subclass)* (1001;582). *M.Ord.-Rec.*
  - Veneroida *(order)* (789;529). *M.Ord.-Rec.*
    - Babinkacea *(superfamily)* (1). *M.Ord.*
      - Babinkidae (1). *M.Ord.*
    - Lucinacea *(superfamily)* (99;38). *Sil.-Rec.*
      - Lucinidae (55;30). *Sil.-Rec.*
        - Lucininae (19;16). *L.Jur.-Rec.*
        - Myrteinae (9;2). *L.Jur.-Rec.*
        - Milthinae (14;8). *Sil.-Rec.*
        - Divaricellinae (7;4). *L.Eoc.-Rec.*
        - Doubtful genera (6). *Mio.-Rec.*
      - Thyasiridae (9;4). *M.Trias.-Rec.*
      - Mactromyidae (13;1). *Dev.-Rec.*
      - Fimbriidae (9). *Carb.-Rec.*
      - Ungulinidae (11;3). *U.Cret.-Rec.*
      - Doubtful genus (1). *Rec.*
      - Cyrenoididae (1). *Rec.*
    - Chamacea *(superfamily)* (3;3). *?U.Cret.-Rec., Paleoc.*
      - Chamidae (3;3). *?U.Cret.-Rec., Paleoc.*
    - Leptonacea *(superfamily)* (99;24). *?Cret., Paleoc.-Rec.*
      - Erycinidae (15;4). *Paleoc.-Rec.*
      - Kelliidae (16;5). *Paleoc.-Rec.*
      - Leptonidae (7;4). *?Cret., Paleoc.-Rec.*
      - Montacutidae (33:5). *Eoc.-Rec.*
      - Galeommatidae (24;6). *U.Eoc.-Rec.*
      - Doubtful genera (4). *Rec.*
    - Chlamydoconchaecea *(superfamily)* (1). *Rec.*
      - Chlamydoconchidae (1). *Rec.*
    - Cyamiacea *(superfamily)* (32;3). *Jur.-Rec.*
      - Cyamiidae (9). *Mio.-Rec.*
      - Turtoniidae (1). *Mio.-Rec.*
      - Sportellidae (13;3). *Jur.-Rec.*
      - Neoleptonidae (9). *Plio.-Rec.*
    - Carditacea *(superfamily)* (74;20). *?Ord., Dev.-Rec.*
      - Permophoridae (19;1). *?Ord., ?Dev., L.Carb.-U.Cret.*
        - Permophorinae (11). *?Ord., ?Dev., L.Carb.-L.Jur.*
        - Myoconchinae (8;1). *?M.Dev., Perm.-U.Cret.*
      - Carditidae (36;16). *Dev.-Rec.*
        - Carditinae (2;1). *Paleoc.-Rec.*
        - Carditamerinae (16;8). *U.Trias.(Carn.)-Rec.*
        - Miodomeridinae (2;2). *Paleoc.-Rec.*
        - Palaeocarditinae (4). *L.Dev.-L.Jur.*
        - Venericardiinae (3;3). *?U.Cret., Paleoc.-Rec.*
        - Carditesinae (5;2). *L.Cret.-Rec.*
        - Thecaliinae (2). *Rec.*
        - Subfamily uncertain (2). *L.Cret.-Mio.*
      - Condylocardiidae (16;3). *Eoc.-Rec.*
        - Condylocardiinae (11;1). *Eoc.-Rec.*
        - Cuninae (5;2). *M.Eoc.-Rec.*
      - Family uncertain (3). *L.Carb.-L.Perm.*
    - Crassatellacea *(superfamily)* (69;28). *Ord.-Rec.*
      - Astartidae (37;22). *?M.Ord., Dev.-Rec.*
        - Astartinae (23;13). *?M.Ord., Dev.-Rec.*
        - Eriphylinae (10;4). *Dev.-Eoc.*
        - Opinae (7;5). *Dev.-U.Cret.*
      - Crassatellidae (15;6). *Dev.-Rec.*
        - Crassatellinae (11;5). *Dev.-Rec.*
        - Scambulinae (4;1). *L.Cret.-Rec.*
      - Cardiniidae (9). *Ord.-Rec.*
      - Myophoricardiidae (3). *Trias.*
      - Hippopodiidae (2). *?Dev., L.Jur.-U.Jur.*
    - Cardiacea *(superfamily)* (66;59). *U.Trias.-Rec.*
      - Cardiidae (23;42). *U.Trias.-Rec.*
        - Cardiinae (8;12). *U.Trias.-Rec.*
        - Trachycardiinae (3;6). *?Eoc., Oligo.-Rec.*
        - Fraginae (4;5). *Oligo.-Rec.*
        - Protocardiinae (4;17). *U.Trias.(Rhaet.)-Rec.*
        - Laevicardiinae (4;2). *Eoc.-Rec.*
      - Lahilliidae (1;1). *U.Cret.-Mio.*
      - Lymnocardiidae (42;16). *Mio.-Rec.*
        - Lymnocardiinae (9;12). *Mio.-M.Plio.*
        - Didacninae (11;2). *L.Plio.(Pont.)-Rec.*
        - Paradacninae (6). *Plio.*
        - Adacninae (10;2). *U.Plio.-Rec.*
        - Pseudocarditinae (1). *Plio.*
        - Subfamily uncertain (5). *Mio.-Plio.*
    - Tridacnacea *(superfamily)* (6;2). *?U.Cret., Tert.-Rec.*
      - Tridacnidae (6;2). *?U.Cret., Tert.-Rec.*
    - Mactracea *(superfamily)* (46;47). *U.Cret.-Rec.*
      - Mactridae (27;46). *U.Cret.-Rec.*
        - Mactrinae (15;37). *U.Cret.-Rec.*
        - Lutrariinae (5;4). *Mio.-Rec.*
        - Pteropsellinae (3;3). *Eoc.-Rec.*
        - Zenatiinae (4;2). *Eoc.-Rec.*
      - Anatinellidae (1). *Rec.*
      - Cardilliidae (3). *?Eoc., Oligo.-Rec.*
      - Mesodesmatidae (15;1). *Eoc.-Rec.*
        - Mesodesmatinae (8;1). *Eoc.-Rec.*
        - Davilinae (2). *Rec.*
        - Erviliinae (5). *Pleist.-Rec.*
    - Solenacea *(superfamily)* (12;5). *L.Cret.-Rec.*
      - Solenidae (2;2). *L.Eoc.-Rec.*
      - Cultellidae (10;3). *L.Cret.-Rec.*
    - Tellinacea *(superfamily)* (71;125). *U.Trias.-Rec.*
      - Tellinidae (26;75). *L.Cret.-Rec.*
        - Tellininae (15;58). *L.Cret.-Rec.*
        - Macominae (11;17). *Eoc.-Rec.*
      - Donacidae (7;13). *U.Cret.-Rec.*
      - Psammobiidae (11;21). *U.Cret.-Rec.*
        - Psammobiinae (10;15). *U.Cret.-Rec.*
        - Sanguinolariinae (1;6). *Mio.-Rec.*
      - Unicardiopsidae (1). *M.Jur.-U.Jur.*
      - Quenstedtiidae (1). *L.Jur.-M.Jur.*
      - Icanotiidae (2). *Cret.(Hauteriv.-Maastricht.).*
      - Scrobiculariidae (2). *Eoc.-Rec.*
      - Semelidae (8;8). *Eoc.-Rec.*
      - Solecurtidae (6;3). *L.Eoc.-Rec.*
        - Solecurtinae (4;3). *L.Eoc.-Rec.*
        - Novaculininae (2). *Rec.*
      - Sowerbyidae (2). *?Trias., U.Jur.*

Tancrediidae (5;5). *U.Trias.-U.Cret.*
Doubtful Tellinacea (2). *Permo-Trias.*
Dreissenacea *(superfamily)* (3;3). *Eoc.-Rec.*
Dreissenidae (3;3). *Eoc.-Rec.*
Gaimardiacea *(superfamily)* (5). *Mio.-Rec.*
Gaimardiidae (5). *Mio.-Rec.*
Arcticacea *(superfamily)* (58;12). *M.Dev.-Rec.*
Arcticidae (30;7). *U.Trias.-Rec.*
Bernardinidae (2). *Rec.*
Euloxidae (2). *Mio.*
Kelliellidae (7;1). *Tert.-Rec.*
Neomiodontidae (6). *L.Jur.-U.Cret.*
Pollicidae (2). *U.Cret.*
Ptychomyidae (1;1). *?U.Jur., L.Cret.-U.Cret.*
Trapeziidae (7;3). *?L.Cret., U.Cret.-Rec.*
Mecynodontidae (1). *M.Dev.*
Glossacea *(superfamily)* (18;12). *U.Trias.-Rec.*
Glossidae (2;6). *Paleoc.-Rec.*
Dicerocardiidae (8). *U.Trias.-U.Cret.*
Ceratomyopsidae (2). *M.Jur.-U.Jur.*
Vesicomyidae (6;6). *Oligo.-Rec.*
Corbiculacea *(superfamily)* (23;22). *?L.Jur., M.Jur.-Rec.*
Corbiculidae (19;16). *?L.Jur., M.Jur.-Rec.*
Pisidiidae (4;6). *?U.Jur, Cret-Rec.*
Veneracea *(superfamily)* (101;126). *L.Cret.-Rec.*
Veneridae (95;118). *L.Cret.-Rec.*
Venerinae (8;6). *M.Eoc.-Rec.*
Circinae (3;10). *Paleoc.-Rec.*
Sunettinae (2;2). *Eoc.-Rec.*
Meretricinae (9;6). *U.Cret.-Rec.*
Pitarinae (26;36). *L.Cret.-Rec.*
Samarangiinae (1). *Rec.*
Dosiniinae (2;11). *U.Cret.-Rec.*
Cyclininae (5;2). *L.Cret.-Rec.*
Gemminae (4). *Eoc.-Rec.*
Clementiinae (4;2). *U.Cret.-Rec.*
Tapetinae (19;21). *L.Cret.-Rec.*
Chioninae (12;22). *M.Eoc.-Rec.*
Petricolidae (3;7). *Eoc.-Rec.*
Cooperellidae (1;1). *Mio.-Rec.*
Glauconomidae (1). *Rec.*
Rzehakiidae (1). *M.Mio.-U.Mio.*
Myoida *(order)* (88;46). *Carb.-Rec.*
Myina *(suborder)* (39;31). *Perm.-Rec.*
Myacea *(superfamily)* (29;27). *U.Jur.-Rec.*
Myidae (6;7). *Paleoc.-Rec.*
Corbulidae (17;20). *U.Jur.-Rec.*
Corbulinae (7;18). *U.Jur.-Rec.*
Caestocorbulinae (1;1). *L.Cret.-Eoc.*
Corbulamellinae (1). *Cret.*
Lentidiinae (1;1). *Paleoc.-Rec.*
Pachydontinae (2). *Oligo.-Plio.*
Subfamily uncertain (5). *U.Cret., Oligo.*
Erodonidae (1). *Eoc.-Rec.*
?Pleurodesmatidae (1). *U.Oligo.-Mio.*
Raetomyidae (2). *Eoc.*
Spheniopsidae (2). *M.Eoc.-Rec.*
Gastrochaenacea *(superfamily)* (4;1). *U.Jur.-Rec.*
Gastrochaenidae (4;1). *U.Jur.-Rec.*
Hiatellacea *(superfamily)* (6;3). *Perm.-Rec.*
Hiatellidae (6;3). *Perm.-Rec.*
Pholadina *(suborder)* (49;15). *?Carb., Jur.-Rec.*
Pholadacea *(superfamily)* (49;15). *?Carb., Jur.-Rec.*
Pholadidae (28;7). *?Carb., Jur.-Rec.*
Pholadinae (7;4). *Cret.-Rec.*
Martesiinae (16;2). *?Carb., Jur.-Rec.*
Jouannetiinae (3;1). *U.Cret.-Rec.*
Xylophagainae (2). *U.Cret.-Rec.*
Teredinidae (21;8). *?Cret., Paleoc.-Rec.*
Teredininae (10;2). *Eoc.-Rec.*
Bankiinae (4;6). *Paleoc.-Rec.*
Kuphinae (1). *?Eoc., Rec.*
Subfamily uncertain (6). *U.Cret.-Rec.*
Hippuritoida *(order)* (129;6). *M.Sil.-U.Cret.*
Megalodontacea *(superfamily)* (14;3). *M.Sil.-L.Cret.*
Megalodontidae (14;3). *M.Sil.-L.Cret.*
Hippuritacea *(superfamily)* (115;3). *U.Jur.-U.Cret.*
Diceratidae (8). *U.Jur.-L.Cret.*
Diceratinae (1). *U.Jur.*
Heterodiceratinae (3). *U.Jur.-L.Cret.*
Plesiodiceratinae (2). *U.Jur.*
Epidiceratinae (2). *U.Jur.*
Requieniidae (8;2). *U.Jur.-U.Cret.*
Monopleuridae (8). *L.Cret.-U.Cret.*
Caprotinidae (8). *L.Cret.-U.Cret.*
Caprinidae (23). *L.Cret.-U.Cret.*
Hippuritidae (12). *U.Cret.*
Radiolitidae (39;1). *L.Cret.-U.Cret.*
Radiolitinae (14;1). *L.Cret.-U.Cret.*
Biradiolitinae (7). *U.Cret.*
Sauvagesiinae (7). *L.Cret.-U.Cret.*
Lapeirousiinae (8). *U.Cret.*
Subfamily uncertain (3). *U.Cret.*
Family uncertain (9). *L.Cret.-U.Cret.*
Anomalodesmata *(subclass)* (113;54). *?L.Ord., M.Ord.-Rec.*
Pholadomyoida *(order)* (113;54). *?L.Ord., M.Ord.-Rec.*
Edmondiacea *(superfamily)* (2). *U.Dev.-U.Perm.*
Edmondiidae (2). *U.Dev.-U.Perm.*
Pholadomyacea *(superfamily)* (58;8). *?L.Ord., M.Ord.-Rec.*
Orthonotidae (2). *M.Ord.-M.Dev.*
Grammysiidae (16;1). *?L.Ord., M.Ord.-U.Perm.*
Megadesmidae (6;2). *U.Carb.-Perm.*
Pholadomyidae (25;5). *Miss.-Rec.*
Burmesiidae (2). *U.Trias.-L.Jur.(Lias).*
Ceratomyidae (5). *U.Trias.-U.Jur., ?Mio.*
Myopholadidae (1). *M.Jur.(Bathon.)-L.Cret. (U.Alb.).*
Pleuromyidae (1). *U.Trias.-L.Cret.*

- Pandoracea *(superfamily)* (27;23). *U.Trias.-Rec.*
  - Pandoridae (1;5). *Oligo.-Rec.*
  - Cleidothaeridae (1). *Mio.-Rec.*
  - Laternulidae (7;2). *U.Trias.-Rec.*
  - Lyonsiidae (5;4). *Eoc.-Rec.*
  - Margaritariidae (1). *Mio.*
  - Myochamidae (2;2). *Mio.-Rec.*
  - Periplomatidae (2;6). *U.Cret.-Rec.*
  - Thraciidae (8;4). *Jur.-Rec.*
- Poromyacea *(superfamily)* (23;17). *Cret.-Rec.*
  - Poromyidae (6;4). *Cret.-Rec.*
  - Cuspidariidae (7;7). *U.Cret.-Rec.*
  - Verticordiidae (10;6). *Paleoc.-Rec.*
- Clavagellacea *(superfamily)* (3;6). *U.Cret.(Turon.)-Rec.*
  - Clavagellidae (3;6). *U.Cret.(Turon.)-Rec.*

Subclass Uncertain (1). *M.Ord.-U.Perm., ?U.Trias.*
- Conocardioida *(order)* (1). *M.Ord.-U.Perm., ?U.Trias.*
  - Conocardiacea *(superfamily)* (1). *M.Ord.-U.Perm., ?U.Trias.*
    - Conocardiidae (1). *M.Ord.-U.Perm., ?U.Trias.*

Bivalve genera uncertainly assigned to families (192).

Class, order, and family uncertain (68).

Genera of doubtfully molluscan affinities (22).

Unrecognizable genera (10).

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