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Distribution of Adaptations: A Comparison between the Functional Shell Morphology of Freshwater and Marine Pelecypods

GEERAT J. VERMEIJ
ELIZABETH C. DUDLEY

Department of Zoology
University of Maryland
College Park, Maryland

I. Introduction

Biogeography is usually understood to be the study of the distribution of organisms on a geographical scale. Its chief aims are the recognition of, and explanation for, recurring patterns in the distribution of species. Explanation typically takes the form of historical reconstruction of geographical changes that have led to the present configuration of land masses and water bodies. Relationships between habitable area and species number have also been important, as have correlations between geographical range and such physical characteristics as temperature, seasonal fluctuation, and precipitation.

A less well known aspect of biogeography is the study of the distribution of adaptations. Just as there are patterns in the distribution of species, there are

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regularities in the distribution of adaptations. These regularities can be used in the formulation of hypotheses about the geographical distribution of selective agencies that have been important in the evolution of organisms (Vermeij, 1978).

This kind of biogeography requires an understanding of *functional morphology*, the study of the relationship between an organism's form and its mode of life and habitat. Few groups have been more thoroughly studied in terms of functional morphology than the Pelecypoda. This group can therefore serve as a model for the formulation and evaluation of hypotheses about the geographical distribution of the factors that make animals in one part of the world look different from those in another.

Our objective in this chapter is to apply what is known about the functional shell morphology of the pelecypods to the study of differences between marine and freshwater habitats. Several lines of evidence point to the possibility that biological agents of selection are less pervasive or have elicited less specialized adaptations in freshwater organisms than in marine ones. Vermeij and Covich (1978) showed, for example, that several antipredatory features which are widespread in marine gastropods, especially in warm waters, are rare or absent in the several groups which have invaded fresh water, whereas characteristics associated with mechanical weakness and therefore with vulnerability to predators are common in freshwater gastropods. A narrow aperture, or one thickened on the outer lip by constricting teeth, is known in only one freshwater genus, the marginellid neogastropod *Rivomarginella* from southeast Asia. Shells with an *umbilicus,* a cavity formed on the shell's base when the whorls are loosely coiled and incompletely overlapping, are very frequent in freshwater gastropod assemblages (see also Vermeij, 1975). Additional evidence for a reduced role of biological agencies in fresh water comes from studies of bioturbation and bioerosion. Sediment-disturbing organisms influence freshwater sediments to a depth of little more than 0.5 m, whereas in the sea their activities penetrate to depths of 3 m or more (Chamberlain, 1975; McCall and Tevesz, 1982; Thayer, 1983). Organisms which erode calcareous rocks and skeletons chemically or mechanically are highly diverse and ecologically important in the sea, but practically unknown in fresh water. Sticklebacks (Gasterosteidae) have fewer and usually shorter spines in freshwater populations than in marine populations of the same species (Gross, 1978; Reimchen, 1983). This may mean that predators against which the spines are effective (birds and fishes) are less common or less capable in fresh water than in the sea.

If biological agents of selection are of diminished importance in fresh water, nonbiological agencies may be correspondingly more important. Physical events which could exercise control over population size, and which consequently might effect selection, include seasonal temperature changes, flooding, and ice formation. Dangers against which freshwater animals might be expected to show adaptations include desiccation when falling water levels leave animals stranded and fast currents and shifting sediments during storms or floods.

After reviewing briefly some aspects of the functional morphology of the shells of burrowing pelecypods, we shall try to show that most antipredatory and some sediment-related adaptations are rare and very poorly developed in freshwater pelecypods as compared to the widespread occurrence of these characteristics in marine forms. We shall also explore geographical differences among freshwater assemblages from different parts of the world.

II. Functional Shell Morphology

The functional shell morphology of pelecypods has been treated in detail by Stanley (1969, 1970, 1975, 1977a,b, 1981), Runnegar (1974), Carter (1968), Vermeij (1978), and Vermeij and Veil (1978), among others. We offer a brief summary of their conclusions in order to make the comparisons between freshwater and marine clams meaningful.

The following traits are known to promote burrowing rate in pelecypods: a narrow, smooth, bladelike or disc-shaped shell; the presence of a *lunule* (cavity in front of the umbones); a strong ligament; extensive mantle fusion in association with a eulamellibranch gill (that is, the capacity to expel water forcefully to achieve downward penetration); certain forms of oblique external sculpture; and sculpture in which the dorsal or posterior slopes of ridges are steeper than the ventral or anterior slopes. The last-mentioned asymmetrical sculpture also increases the capacity of the clam to anchor itself in the sediment. Features which prevent sediment erosion around the posterior end of a clam whose shell is buried just beneath the sediment surface include a narrow elongated (rostrate) anterior end and a broad posterior end which is laterally expanded and which is set off from the rest of the shell by a distinct keel or angulation. Anchorage is enhanced by the presence of strong concentric or radial sculpture, an inflated or globose shell form, and thick heavy valves. Thickening of the valves toward the anteroventral region, which usually is the part of the shell lying farthest from the sediment surface, probably also improves anchorage. Deep burial also enhances stability in the sediment. At least in marine clams, it is often associated with a thin-walled shell, reduced hinge dentition, and presence of a persistent posterior gape through which the exhalant and inhalant siphons protrude.

Among the features which enhance resistance to shell-crushing and valve-shearing predators are thickened valves, ribs which cause the surface of the shell to be corrugated, denticles or crenulations on the inner valve margin, and a well-developed hinge with interlocking teeth and sockets. Pelecypods in which the margin of one valve overlaps the other along the ventral or posterior edge are capable of sustaining shell fracture without loss of the capacity to retain a tight seal when the valves are shut (Vermeij, 1983). The presence of a persistent posterior, anterior, or ventral gape between the valves indicates that the soft tissues cannot be concealed completely within the valves. It is a characteristic

that is often associated with an environment in which predators are rare or absent (Vermeij and Veil, 1978).

It is important to emphasize that almost all the inferred relationships between pelecypod form and habit come from studies of marine clams. Despite the attention which they have received from systematists, freshwater pelecypods are extremely poorly known animals. Trueman (1968) showed that burrowing in the European unionacean *Margaritifera* is like that in marine clams, but we remain uninformed about the life habits of most freshwater pelecypods. It is becoming clear that some burrowing species deviate from the usual pelecypod habit of keeping the posterodorsal or posterior end of the shell uppermost when the shell is buried. When North American species of *Lampsilis* expose movable mantle flaps, presumably in order to attract host fishes for the parasitic larvae, both the anterior and posterior ends of the shell extend above the sediment surface (Kraemer, 1970). Some species of *Pisidium* lie buried with the ventral margin uppermost (Meier-Brook, 1969). We have seen the North American *Elliptio complanatus* (Say 1822) buried in the standard fashion with the anteroposterior axis more or less perpendicular to the sediment surface, but with the posterior end jutting 2–3 cm above the sediment. This kind of partial burial without byssal attachment is exceedingly rare in marine clams. The dearth of information on the biology of freshwater pelecypods forces us to approach their functional shell morphology with great caution and not a little skepticism.

III. Shell Form in Freshwater Clams

In order to assess the incidence and geographical distribution of features related to burrowing, anchorage, and predation in freshwater pelecypods, and to compare the latter with marine clams, we surveyed the known freshwater pelecypods at the U.S. National Museum of Natural History at the generic level for the presence or absence of hinge teeth, crenulated or scalloped margins, posterior and anterior gapes, truncated posterior surfaces, overlapping valve margins, and external sculpture. We supplemented this survey with analyses of monographs of freshwater pelecypods of South America (Parodiz and Bonetto, 1963) and Thailand (Brandt, 1974).

An analysis of the occurrence of various predation-related and sediment-related traits in freshwater pelecypod faunas is set out in Table I. Similar data for several shallow-water marine assemblages are included for comparison. The marine assemblages were collected by Vermeij.

Consider first some traits which are known or inferred to deter shell-breaking or shell-entering predators. As Carter (1968) has already pointed out, no freshwater pelecypod can be described as having an evenly denticulated or crenulated inner valve margin of the type that is so common in marine cardiids, carditids,

TABLE I

Occurrence of Various Adaptations in Freshwater and Marine Pelecypod Assemblages

Region	Percentage of genera bearing adaptations[a]						
	N	C	Sym	Obl	T	H	G
Freshwater assemblages							
Africa	27	3.7	0	0	3.7	15	18
South America	24	17	0	0	13	17	46
Southern and eastern Asia	60	5	0	0	0	12	25
Thailand	23	0	0	0	0	17	26
North America	52	21	0	0	21	5.8	33
Shallow-water marine assemblages							
Guam	25	36	28	28	12	4	4
Playa Venado, Panama	24	46	33	17	21	0	17
Las Lajas, Panama	13	62	46	15	62	0	15
Western Florida	26	42	35	7.8	0	3.8	23
New Jersey	12	33	8.3	0	0	0	42
Friday Harbor, Washington	25	32	24	0	0	0	36

[a] N, number of genera; C, crenulated or scalloped valve margin; Sym, symmetrical radial or concentric ridges; Obl, oblique or asymmetrical sculpture; T, truncated posterior surface; H, hinge-teeth lacking; G, gaping.

venerids, donacids, and arcids. Various forms of radial ornamentation are known in the young stages of many Unionacea, but this sculpture usually is lost in the adult shell. Coarse folds characterize a minority of Unionacea; they may make the posterior or posterodorsal edge of the shell wavy or scalloped, but we doubt that they contribute much to the prevention of valve shearing. Even in North America, where the incidence of scalloped margins is highest (21%), such margins are poorly represented in comparison to the high incidence of crenulated margins in most temperate and especially tropical marine assemblages. Genera with well-developed posterior scalloping include *Spathopsis* in Africa; *Arcidens, Megalonaias, Arkansia, Plectomerus, Tritogonia, Quincuncina, Quadrula, Cyprogenia, Amblema, Rotundaria,* and *Schalenaias* in North America; and *Lamprotula* and *Gibbosula* in China.

By contrast, the incidence of posterior and anterior gapes is high in most freshwater assemblages. Frequencies of gapes in fresh water are comparable with those in temperate marine assemblages, but generally higher than in those of the shallow-water marine tropics. Examples of gaping include the African genera *Mutela, Spathopsis, Cameronia, Pseudomutela,* and *Chilidonopsis* (a bizarre clam with an elongated delicate shell in which a strong anteroposteriorly oriented keel terminates posteriorly in an outwardly or downwardly directed spine); the South American *Leila, Haasica, Tamsiella, Mycetopoda, Mycetopodella, Fos-*

sula, Monocondylaea, Castalia, and *Castalina;* the Asian *Gibbosula, Lanceolaria, Diplasma, Physunio, Pseudobaphia, Balwantia, Solenaia, Hyriopsis, Cristaria, Novacula, Sinovaculina, Pharella,* and *Tanysiphon;* and the North American genera *Decurambis, Arcidens, Lasmigona, Plethobasis, Canthyria, Actinonaias, Leptodea, Potamilus, Ligumia, Lampsilis,* and *Cumberlandia.*

Nearly all shallow-burrowing marine pelecypods have well-developed teeth in a taxodont or heterodont hinge. Although hinges of deeper-burrowing species are often reduced, such species rarely lack teeth altogether. Freshwater pelecypods, by contrast, often have no hinge teeth. This condition is seen in *Anodonta* of the Northern Hemisphere; *Mutela* and related genera in Africa; *Mycetopoda* and *Mycetopodella* in South America; *Simpsonella, Balwantia, Solenaia,* and *Pilsbryoconcha* in southern Asia; and *Anodontoides* and *Gonidea* in North America. Many unionids, especially in North America, have strong divergent schizodont teeth in the hinge, and some African mutelids (*Cameronia* and especially *Pleiodon*) have secondarily evolved a coarsely toothed taxodont hinge.

Overlapping margins are known in some Recent marine Arcidae, Pectinidae, Cucullaeidae, Donacidae, Petriocolidae, Corbulidae, and Thraciidae (Nicol, 1958; Morton, 1978, 1981; Reif, 1978; Coan, 1983; Vermeij, 1983). In fresh water, such margins are found only in some byssally attached Dreissenidae and in the Erodonidae, a small family, related to the Corbulidae, from South America and New Guinea.

We have not assessed the incidence of lunules in freshwater clams. Although the presence of a lunule enhances burrowing capacity in marine species which burrow by means of forward and backward rocking of the shell (Ansell, 1961; Stanley, 1970, 1975), most lunule-bearing species are slow burrowers. Moreover, it is often difficult to distinguish the lunule on the shells of freshwater clams, either because the anterolateral hinge teeth whose growth generates the lunule are absent, or because the umbones are heavily eroded.

Truncated posterior surfaces are common in some tropical marine pelecypod assemblages, particularly in those from coarse or well-sorted sand. They are unknown from muddy environments and from cold-temperate shores. In fresh water, truncated posterior surfaces that are set off by a keel or angulation from the rest of the shell are found at a rather low frequency in North and South America, and not at all in Asia or Africa. Good examples are seen in the South American genera *Castalia, Callonaia, Paxyodon,* and *Diplodon,* and in North American species of *Truncilla, Alasmidonta, Bullella, Pegias, Quadrula, Plectomerus, Canthyria, Plagiola,* and *Lampsilis.* The southern Asian taxon *Acuticosta* has a distinct angulation in the early stages of growth, but this keel is lost in the adult shell.

Oblique sculpture and asymmetrical sculpture are completely unknown in freshwater pelecypods. Among marine species such sculpture is found only in sandy habitats in warm water, and not at all in muddy environments and in cold water.

Symmetrical sculpture, which promotes stability of the shell in the sediment, is also extremely rare in freshwater pelecypods. Many Unionacea are characterized by irregular ridges which are oriented parallel to the hinge line. In others, sculpture consists of tubercles or large rounded knobs arranged in irregular rows on the middle or posterior part of the valves. Examples of the latter sculpture are seen in North American species of *Quadrula, Megalonaias, Rotundaria, Plethobasis, Cyprogenia, Obliquaria,* and *Dromus;* and in the Chinese *Lamprotula.* These types of tuberculate and knobby sculpture are virtually unknown in marine pelecypods. Slender spines are known in one North American genus (*Canthyria*), in which they are arranged in one or more rows on the central part of the valves, anterior to a weakly developed angulation. Nothing is known of the functional significance of these unique forms of sculpture.

One very striking feature of the great majority of freshwater pelecypods is that the anterior or umbonal part of the shell is thicker than the posterior part. This condition is carried to an extreme in adult *Lamprotula* of China and *Megalonaias, Amblema, Fusconaia, Lexingtonia, Plethobasis, Pleurobema,* and *Dromus* of North America, in which the umbo is close to the greatly thickened anterior end. Superficially, these heavily weighted clams remind us of large Silurian pentameracean brachiopods. Anterior thickening seems to be characteristic of all Unionacea, even of such thin-shelled genera as *Mutela, Anodonta, Solenaia,* and *Diplasma.* It is also seen in the West African donacid *Galatea.* Shell thickness tends to be more evenly distributed on the valves of marine pelecypods. In particular, the posterior part of most shallow-burrowing species is not markedly thinner than the anterior end, and umbonal weighting of the type seen in *Lamprotula* is very rare. Some marine arcids, such as the mangrove-associated West African *Senilia* and the West American *Grandiarca,* have distinctly thicker anterior than posterior ends; so do the brackish-water North American mactrid *Rangia* and the mangrove-associated Indo-West-Pacific *Gafrarium tumidum* (Linné 1758). Some marine lucinids and venerids have the central portion of the valves distinctly thickened in relation to the anterior and posterior ends. Kitchell et al. (1981) have associated this syndrome with resistance to drilling predation. Central thickening, like drilling, is unknown in freshwater pelecypods.

The development of a dorsally directed, thin, winglike expansion of the valve behind the umbo is another characteristic that is commonly observed in freshwater Unionacea. Its functional significance is completely unknown. Wings are found in the African *Spathopsis;* in the South American *Prisodon, Paxyodon,* and *Diplodon;* in species of the Asian genera *Physunio, Hyriopsis,* and *Cristaria;* and in the North American genera *Lasmigona, Amblema, Leptodea,* and *Potamilus.* The most extreme development of the wing is seen in *Hyriopsis* and *Potamilus.* In these genera, the posterodorsal margin of each valve is folded in on itself, so that the medial, as well as the outer, face of the wing of each valve is composed of outer shell material. Few marine burrowing clams have postum-

bonal wings, and in none are the wings of the two valves separated. We have seen wings in the marine tellinid *Tellidora* and in some species of the garid genus *Tagelus*.

IV. Geographical Differences among Regions

We alluded several times in the preceding section to strong latitudinal differences in the incidence of various traits that are related to predation and to the shell's stability in the sediment in marine clams. Geographical differences also exist in fresh water, but the effect of latitude is probably weaker.

North America exhibits the highest frequencies of traits associated with resistance to predators (scalloping of the posterior margin) and stability in the sediment (truncated posterior surfaces). This region also has the lowest incidence of one of the predation-vulnerable features (toothless hinge). This observation is suprising in view of the fact that the North American sample consists entirely of temperate genera, whereas the African and Asian samples are composed chiefly of tropical taxa. It must be remembered, however, that most of the North American genera are from the central and southern United States, where summers are essentially tropical. Gastropods from this region also show some antipredatory specializations that are rare elsewhere (Vermeij and Covich, 1978).

As noted by others (Pilsbry and Bequaert, 1927), the pelecypod fauna of the great Rift Lakes of Africa does not stand out in terms of morphological uniqueness. Most of the species are relatively thin-shelled and of typical rounded to oblong shape without significant sculpture or posterior angulation. The gastropods of these lakes (especially those of Lake Tanganyika) are often highly convergent to marine species in external form and to some extent in sculpture, but they too tend to be thin. The freshwater gastropods of southern Asia and North America surpass their African counterparts in the incidence of antipredatory traits, although some characteristics which are common antipredatory adaptations in marine species are rare or absent even in these regions (Vermeij and Covich, 1978).

Geographical differences in the form of freshwater molluscs may be tied more to history than to latitude. The North American and Asian faunas may have had a longer and less tumultuous history than did those elsewhere. Although antipredatory and some stability-related traits are rare even in the oldest freshwater faunas, favorable mutations have had a longer time to arise and to become established in North America and Asia. The sharp latitudinal differences in the sea, which are highly temperature-dependent, may be blurred in fresh water because the difference in temperature during the season of greatest biological activity between waters at different latitudes may not be great.

V. Selection in the Freshwater Environment

Our observations on the spectrum of shell shapes in freshwater pelecypods are consistent with the findings of Vermeij and Covich (1978) for freshwater gastropods. Together, they suggest that predators have been of little evolutionary consequence for most freshwater molluscs.

The widespread occurrence, even in tropical fresh waters, of persistently gaping valves implies that selection in favor of tight closure has often been weak or absent. Predators should therefore find it easy to detect diagnostic metabolites and to trace them even to clams whose shut valves gape. In fact, North American species of *Lampsilis* and other genera draw attention to themselves by exposing movable mantle flaps from the posterior end, presumably in order to attract the fishes that serve as hosts for glochidium larvae (Kraemer, 1970). Without some auxiliary chemical defense, such provocative behavior involving soft tissues would be unthinkable in marine pelecypods.

Rapid escape from predators also seems to have been unimportant to freshwater clams. Swimming and leaping are unknown, as is sculpture which enhances rapid burrowing or effective anchorage in the sediment during the act of burrowing. Some freshwater pelecypods are flattened or even bladelike, but it is not known whether these shapes are associated with rapid burrowing.

Resistance to various forms of subjugation by predators is also poorly expressed in most freshwater pelecypods. Some species have effective hinge teeth, and in others the scalloping of the posterior margins may contribute to valve strength and alignment, but the evenly spaced denticles or riblets that adorn the inner valve margin of many marine clams are completely unknown in freshwater species. The incidence of toothless hinges, by contrast, is very high compared to that in the sea. Many freshwater clams have thick valves, but the distribution of thickness across the valves is not what we would have expected if thickening were an adaptive response to shell-breaking predation. Most marine predators, including shell breakers, are most active at the sediment surface and in the top few centimeters of sediment (Woodin, 1978; Vermeij, 1978; Blundon and Kennedy, 1982); yet, the thinnest portion of the vast majority of freshwater pelecypod valves is the posterior end, which lies closest to the sediment surface, whereas the thickened anterior end is usually the most deeply buried (and therefore least vulnerable) part of the shell.

In order to seek independent evidence on the importance of shell breakage as a factor in the evolution of freshwater clams, we examined more than 3700 valves (equivalent to 1850 individuals) of North American Unionacea at the U.S. National Museum of Natural History for the presence of repaired injuries which could have been caused by nonlethal attacks of shell-breaking predators or by the hooves of cattle or other large animals (Stone et al., 1982). As discussed at length by Vermeij (1983), the presence of a repaired injury indicates that the

pelecypod was the object of an unsuccessful attempt by some agent or agency to break the shell, and that the animal was capable of tolerating a temporary break in the seal between the valves when the latter were shut. Morphological resistance to breakage is unlikely to evolve if the incidence of repaired breaks is low (Vermeij, 1982).

Only 1 of 126 populations belonging to 77 species of North American unionaceans had a high frequency of nonlethal breakage. In this sample (*Leptodea fragilis* Rafinesque 1820 from Denton County, Texas, 23 valves), we found about 12 nonlethal breaks (frequency of repair, 0.52). Repair in the remaining samples was exceedingly rare. We uncovered only 3 instances of clearly repaired breakage: one in *Actinonaias carinata* (Barnes 1823) and 2 in *Quadrula pustulosa* (Lea 1831). All injuries occurred on the posterior half of the shell. The 15 observed injuries thus affected less than 1% of the individuals which we sampled.

The incidence of nonlethal (repaired) breaks in marine pelecypods is also low, but it is generally higher than in freshwater species. In a preliminary survey, we have identified 44 scars in 18 samples belonging to 13 species of shallow-burrowing tropical species from shallow waters. The overall frequency of repair in the 295 individuals is 0.15 scars per individual. For 16 samples of byssally attached temperate Mytilidae belonging to 4 species, the frequency was 0.12 scars per individual (43 scars in 362 individuals). Pliocene pelecypods from the upper Yorktown Formation at Rice's Pit, Virginia, had an overall frequency of 0.021 scars per individual (23 scars in 1058 individuals) (Vermeij, in preparation). Even this very low value is more than twice that in the freshwater pelecypods which we examined from North America.

In our survey of North American Unionacea, we encountered two kinds of external shell deformation which we have not seen in marine pelecypods. One type consists of evenly rounded depressions up to 2 mm in diameter. The second type is a larger depression marked by parallel striations oriented in an oblique or radial direction (Fig. 1). The inner valve surface is often deformed at the same site. Only 4 of the 531 examples of these two types of deformation were on the anterior half of the valve. We do not know whether the deformations were associated with valve breakage, but it seems likely that there was temporary injury to the mantle edge. The cause of the deformations remains a complete mystery. We have seen no published reports about them, despite the frequent occurrence of these deformations. If injury to the mantle is involved, its frequency in the Unionacea which we studied is very high (0.29 deformations per individual), suggesting that freshwater species have a considerable tolerance for injury to the soft tissues. Temperate marine clams often survive attacks by predaceous fishes on the siphons (Edwards et al., 1970; de Vlas, 1979; Peterson and Quammen, 1982). These injuries leave no trace on the shell and are perhaps repaired while the siphons are sealed inside the shut valves. We suspect that
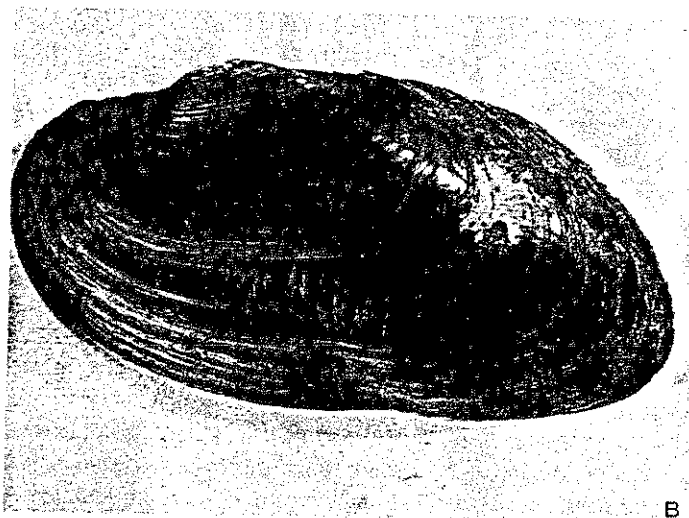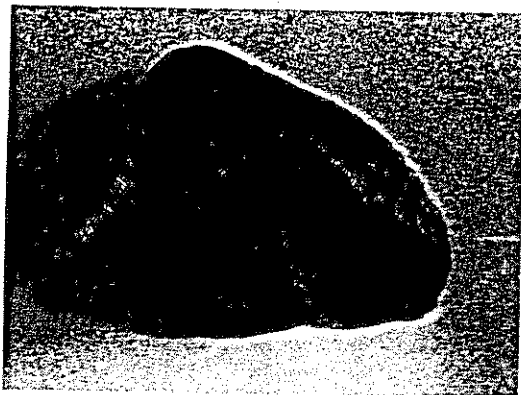
Fig. 1. Unionids with external deformations discussed in the text. (A) *Pleurobema clava* (Lamarck 1819). USNM 592350, Scioto River, southern Ohio. (B) *Uniomenes tetralasma* (Conrad). USNM 504854, Lincoln, Nebraska. [Photographs: M. G. Harasewych.]

injuries to the mantle make marine pelecypods, especially tropical ones, vulnerable to predators which identify their prey chemically. Such injury, as well as valve breakage which results in exposure of tissues to the external environment, is likely to be a greater liability for most marine pelecypods than for freshwater clams (Vermeij, 1983).

Remarkably little is known about the nature or the ecological impact of preda-

tors of freshwater pelecypods. Birds, mammals, and fishes are probably the chief predators of the larger species (Pilsbry and Bequaert, 1927; Corbet, 1961; Root, 1963; Snyder and Snyder, 1969; Maassen, 1977; Turner and Roberts, 1978; Hulscher, 1981), but small pisidiids and corbiculids may fall victim to crayfishes (Covich et al., 1981), amphibians (Gill, 1978), and leeches (McKee and Mackie, 1979; Wrona et al., 1979). Large species are usually taken without injury to the valves, either by penetration between the valves (with the aid of the bill in the case of birds, for example) or by exhumation followed by desiccation on the shore so that the valves open. Snyder and Snyder report that predaceous birds in Florida occasionally inflict damage to species of *Anodonta* and *Villosa*, and Maassen (1977) inferred that the damage he saw on the ventral edge of the valves of *Anodonta* in the Netherlands was done by muskrats (*Ondatra zibethica*). Most analyses of shell middens which are thought to have been accumulated by muskrats have not revealed shell damage (Bovbjerg, 1956). Potential shell-breaking predators do occur in fresh water, but they are probably substantially weaker than typical marine shell breakers. These predators include dracaenid and varanid lizards (Pilsbry and Bequaert, 1927; Rand, 1964; Dalrymple, 1979), various fishes (Corbet, 1961; Fryer and Iles, 1972; Liem, 1973; Liem and Osse, 1975), turtles (Snyder and Snyder, 1971; Mahmoud and Klicka, 1979), crayfishes (Covich et al., 1981), and perhaps freshwater crabs.

Many predators which in the sea are diverse and ecologically important are unknown in fresh water. Drilling predation by octopods and gastropods has never been observed in freshwater environments. Predaceous sea stars (asteroids), stomatopods, palinurid and nephropid lobsters, xanthid and calappid crabs, and gastropods are exclusively marine (Vermeij, 1978; Vermeij and Covich, 1978).

All the available evidence—shell morphology, incidence of repaired breaks, and the nature of freshwater predators on molluscs—suggests strongly that predation in general, and shell breakage in particular, affects freshwater pelecypods to a much smaller degree than marine clams. Although our understanding of freshwater pelecypods and their relationships with other organisms is still extremely rudimentary, we believe that this hypothesis is unlikely to be falsified by additional much-needed data.

Stability of the shell in the sediment would seem to be of overriding importance to species living in rivers which are subject to periodic torrential flow and to large-scale movement of sediment. Sculpture which stabilizes many marine species is unknown in freshwater forms. Freshwater pelecypods show only two of the several possible characteristics that enhance stability in the sediment. These are scour-resistant broad posterior surfaces that are set off by a keel or angulation, and anterior thickening of the valves. The latter characteristic is particularly common.

It is odd that anterior thickening should be relatively rare in marine pelecypods, and that flattened posterior surfaces are confined among recent species

to tropical and warm-temperate areas. After all, midlatitude storms are well known to exhume thousands of marine clams and to hurl them onto ocean beaches, where they subsequently die in great numbers. Biological factors may dictate which of the methods of achieving stability is used. If escape from predators is important, as it is for many marine species, a heavily weighted shell would not be advantageous, but a flattened posterior surface might not impose a significant hindrance. Rapidly burrowing donacids, in fact, often have markedly truncated posterior surfaces. An uneven distribution of valve thickness is probably also ineffective against shell-breaking and drilling predators, which are more important in the sea than in fresh water. In order to protect against these predators, the valves should be of more or less equal thickness throughout or thickest in the central portions. It is obvious that we still know very little about the merits of alternative adaptive pathways for achieving a given adaptation in the various habitats that pelecypods occupy.

Tevesz and McCall (1979) have pointed out that North American Unionacea are much less specific to sediments of a given grain size than are temperate marine pelecypods. Most Unionacea occupy a great diversity of substratum types, ranging from mud to pebbles, whereas many temperate and most tropical marine clams are specialized to a limited range of sediment grain sizes. As Lamont (1934) and Stanley (1970) have shown, the size and spacing of external ridges are often related to the average grain size of enclosing sediment in marine species. Sculpture in sand-dwelling forms is, for example, usually either much coarser or much finer than that of mud-dwelling species. The wide range of substrata occupied by freshwater pelecypods may therefore be inconsistent with the evolution of evenly arranged and evenly spaced radial and concentric ridges, because the scale of the sculpture may be appropriate for only a few of the sediments typically occupied by the species. This possibility, of course, begs the question of the broad substratum tolerance of freshwater pelecypods. This again may be related to the strikingly different biological environment of freshwater as compared to marine clams (Tevesz and McCall, 1979).

VI. Possible Artifacts

Much of the present discussion about freshwater pelecypods has highlighted the Unionacea and to a lesser extent the Corbiculacea, which are by far the largest groups of pelecypods in fresh water. Given this emphasis on only two groups, it is worth considering whether the observed peculiarities of freshwater clams are simply artifacts of these particular superfamilies (and particularly of the Unionacea), or whether the trends also characterize other groups which have invaded fresh water.

Besides the primarily freshwater Unionacea and Corbiculacea, several pri-

marily marine superfamilies contain a few freshwater representatives. They include the Arcacea (*Scaphula* in the Arcidae), Mytilacea (*Arcuatulus* and *Limnoperna* in the Mytilidae), Dreissenacea (*Dreissena, Sinomytilus,* and related genera of the Dreissenidae, which may be related to the Corbiculacea), Cardiacea (*Monodacna* and related Adacnidae), Veneracea (*Glauconomya* in the Glauconomidae), Tellinacea (*Galatea* in the Donacidae, and *Elizia* in the Garidae), Solenacea (*Pharella* in the Solenidae, and *Novacula* and *Sinovaculina* in the Novaculidae), Mactridae (*Tanysiphon* in the Mactridae), Myacea (*Erodona* and related Erodonidae), Pholadacea (*Martesia* in the Pholadidae, and *Nausitoria* in the Teredinidae), and Pandoracea (*Guianadesma* in the Lyonsiidae) (Yonge, 1949; Owen, 1959; Hutchinson, 1967; Morton, 1970, 1973, 1981; Brandt, 1974).

The characteristics which are rare in freshwater pelecypods generally are also rare or absent in the groups which have secondarily invaded fresh water, even though marine representatives of these superfamilies often do possess the characteristics in question. Many arcids, for example, have evenly spaced radial ribs which often cause the inner margins of the valves to be crenulated. The south Asian freshwater genus *Scaphula,* however, has either very weak radial ribs or none at all and has smooth inner valve margins. *Donax* and related marine genera in the Donacidae usually have evenly denticulated valve margins, but the West African freshwater genus *Galatea* does not. Almost all Cardiacea have plicate or denticulate valve margins, and many have radial ribbing, which in some sand-dwelling species is ornamented with dorsally directed scales or spinelets. In *Monodacna* from eastern Europe, however, the ribbing and crenulations are obsolete. We infer from these observations that the rarity or absence of certain shell characteristics in freshwater pelecypods is a biologically significant phenomenon and not a phylogenetic artifact.

Further support for this conclusion comes from the Unionacea themselves. Many species have radial ornamentation or pustules in the early postlarval stages. Neoteny, a well-known and widespread phenomenon throughout the animal kingdom in general, and the Mollusca in particular, could be a developmentally "easy" pathway for the retention of these juvenile characteristics in the adult stage if such sculpture were advantageous; yet this retention is rare. That the Unionacea are potentially morphologically diverse is suggested by the independent evolution of cemented oysterlike forms in Africa (*Etheria*), South America (*Acostaea*), and India (*Pseudomuelleria*) (Yonge, 1962, 1978). We see no developmental reason why the Unionacea failed to evolve certain traits that are phylogenetically widespread in marine pelecypods.

VII. Summary and Conclusions

Freshwater pelecypods differ in many important morphological ways from marine ones. Traits which in many marine pelecypods confer resistance to preda-

tion, promote escape from predators, or enhance stability of the shell in the sediment are either rare or absent in freshwater clams. They include evenly spaced radial or concentric ribs, asymmetrical or oblique sculpture, crenulated or scalloped inner valve margins, and a broad scour-resistant posterior surface set off from the rest of the shell by a keel or angulation. Repaired breaks, which indicate the potential for evolving resistance to shell breakage, are also extremely rare in freshwater pelecypods. Persistent posterior gapes and toothless hinges, characters associated with poor valve closure and poor alignment, are common in freshwater clams. Anterior thickening of the valves, which promotes stability of the shell in the sediment, is very common in freshwater species but rare in marine ones. These observations suggest that predation in general, and shell breakage in particular, has been of little evolutionary consequence for freshwater pelecypods. The possibility that the contrast between freshwater and marine clams is an artifact of the overwhelming dominance of the freshwater fauna by Unionacea and Corbiculacea is discounted by the observation that freshwater representatives of nine primarily marine superfamilies are similar to the primarily freshwater Unionacea and Corbiculacea in lacking many of the features which are diagnostic of related marine forms.

Stanley (1977a) and Vermeij (1983) have emphasized that most of the antipredatory traits of marine pelecypods evolved after the Paleozoic era. Earlier pelecypods were therefore morphologically, though not taxonomically, comparable to freshwater clams. This similarity, as well as the reduced importance of bioerosion and bioturbation in freshwater communities as compared to marine ones, points to the interpretation that freshwater assemblages are adaptationally (but again not taxonomically) archaic. If so, there is even more reason than the usual lament about the insufficiency of available data to study freshwater biotas and the biological interactions in them.

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