Chapter 8

Environmental Relationships of Shell Form and Structure of Unionacean Bivalves

MICHAEL J. S. TEVESZ and JOSEPH GAYLORD CARTER

1. Introduction

Most fossil and Recent freshwater bivalves are members of the Unionoida and Corbiculacea, with the great concentration of genera (>150) and species (several hundred) occurring in the unionoid superfamily Unionacea [Permian (?), Triassic-Recent (Haas, 1969)]. Unionaceans are found worldwide in diverse freshwater habitats and show a remarkable amount of inter- and intraspecific shell form variability (see, for instance, Grier,

MICHAEL J. S. TEVESZ ● Department of Geological Sciences, The Cleveland State University, Cleveland, Ohio 44115. JOSEPH GAYLORD CARTER ● Department of Geology, University of North Carolina, Chapel Hill, North Carolina 27514

1920a–c; Stratton, 1960; Haas, 1969; Clarke, A. H., 1973; Tadić, 1975; Johnson, 1978). Much of the available freshwater bivalve literature relevant to the theme of this volume is concerned with analyzing the environmental relationships of this variability in the unionacean families Unionidae and Margaritiferidae. The balance of this literature pertains largely to obtaining information from distinctive "growth bands" and shell microstructure.

First, we will discuss the relationship between shell form and environment, paying particular attention to intraspecific variants that appear to be consistently correlated with physical ecological factors. Because form and environment are correlated in unionaceans, tracing certain morphological changes among Recent and fossil populations provides a way of inferring corresponding environmental changes. We will also investigate the general environmental factors that permit the maintenance of the great morphological variability of unionaceans. Understanding these factors may provide information that may allow accurate reconstructions of ancient aquatic ecosystems and thus increase the resolution by which we may infer environmental change through geological time.

Second, we will investigate the nature and origin of growth bands and try to identify what kinds of information they contain concerning the history of a bivalve and its environment. Growth bands appear as dark rings on the shell surface and as distinctive lines observable in shell cross sections.

Finally, we will provide an explanation of the environmental significance of unionacean shell microstructure and the periostracum. Because these are important features, about which there is little literature, we will present new data and interpretations to help complete the understanding of the shell structure of this group.

2. Unionacean Form

The literature on the ecological significance of shell form in unionaceans can be roughly divided into two categories. The first category is comprised of papers that describe correlations between shell form (usually size, outline, and proportions) and habitat (often generally designated as "lake," "large stream," "small stream," and the like). The second category consists of finer-resolution studies that attempt to explain the relationship of a specific aspect of the shell (say, the thickness of an individual valve) to a particular aspect of the environment (e.g., water hardness). We will discuss form–habitat relationships first.

2.1. Form–Habitat Relationships

Ball (1922) and Eagar (1948) provided, for their time, up-to-date reviews of an extensive, largely anecdotal literature on form–habitat relationships in unionaceans. Eagar's review concisely summarized previously published observations (including those of Ball) on the habitat relationships of shell outline and proportions. This summary included the following general observations (also see his references):

Obesity [measured as T/L (see Figs. 1 and 2A)]

1. Many species, when traced within a single stream, tend to increase in obesity downstream.
2. In a given species or considering a stream fauna as a whole, obesity is positively correlated with stream size and negatively correlated with water velocity.
3. In a given species, lake forms tend to be more obese than river forms.

Size [often measured as L (see Fig. 1)]

1. Small-stream or creek species are smaller than those characteristic of large rivers.
2. While within-individual species size may increase upstream, the entire fauna often seems to show a size increase in a downstream direction.
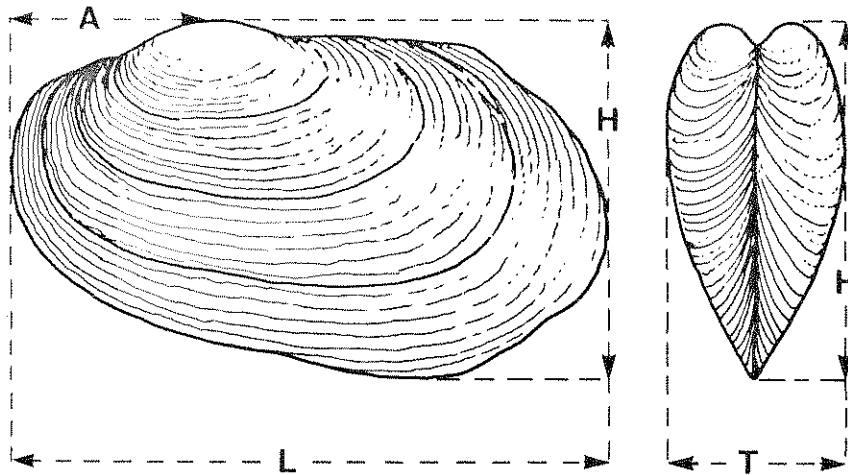

Figure 1. Morphometric definitions. (A) Anterior-to-umbo distance; (L) length; (H) height; (T) shell thickness. For lateral view outline: up = dorsal; down = ventral; left = anterior; right = posterior.
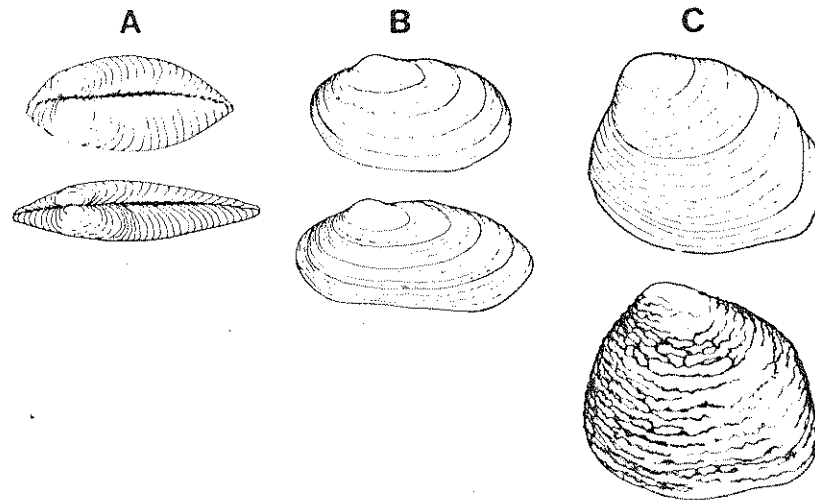
Figure 2. Intraspecific variations. (A) Obesity differences in *Elliptio complanata* (modified from Clarke, A. H., and Berg, 1959); (B) height differences in *Lampsilis radiata siliquoidea* (modified from Baker, 1928); (C) ornamentation differences in *Nyassunio nyassaensis* (modified from Haas, 1936).

3. Individual members of species occupying exposed positions in lakes are generally smaller than individual members of the same species occupying other habitats.

Height [measured as H (See Figs. 1 and 2B)]
1. Both inter- and intraspecifically, there tends to be an increase in relative height in species inhabiting lakes or slow-moving bodies of water compared to forms inhabiting more rapidly moving water.

Shell Outline
1. Both inter- and intraspecifically, curved or well-rounded ventral borders, a long line, and an expanded or well-developed posterior end appear to be more typical of forms living in large lakes, rivers, or slow-flowing bodies of water.
2. Alternatively, forms with a curved dorsal margin and straight or reflected ventral margin are generally found in relatively small streams or swift-flowing water.

These conclusions have generally been substantiated by subsequent studies. Some examples are given below.

A. H. Clarke (1973) found the largest *Lampsilis radiata siliquoidea*, *Ligumia recta*, and *Proptera alata* in the rivers of the Canadian interior basin. Lakes, by contrast, contained mainly smaller forms. Similarly, Harman (1970) mentioned that *Elliptio complanata*, *Anodonta grandis*, and

Lampsilis radiata were smaller in the deep, cold Finger Lakes of New York than in warmer, nutrient-rich streams. A. H. Clark (1973) further noted that such species as *Fusconaia flava*, *Quadrula quadrula*, and *Amblema plicata* were often more obese in larger streams and less obese in smaller streams in the southern part of their range. However, both large- and small-stream forms were relatively compressed when they occurred in northern regions. This, he suggested, may be a general trend among unionids.

More correlations between obesity (and other morphometric features) and latitude were observed by Cvancara (1963). *Lampsilis ventricosa*, *L. ovata*, and *L. excavata* from different latitudes were measured and the data represented on scatter plot diagrams (e.g., his Figs. 3 and 4). These diagrams showed that the values for height/total length and width/total length (= obesity as used here) increased toward lower latitudes. Although all three "species" did not reflect these trends individually, Cvancara suggested that further research could demonstrate that the three forms may represent only one species.

On the subject of length/height proportions, A. H. Clarke (1973) stated for certain *Anodonta* that values of the anterior-to-beak/length ratio were highest in specimens collected from large-lake habitats. Hendelberg (1960), after measuring the length/height ratio of 112 *Margaritifera margaritifera* from a Swedish river and then discussing literature relevant to the environmental "meaning" of the ratio, concluded that this meaning was still obscure. But he mentioned that pearl fishers along this river, Pärlälven, referred to anteroposteriorally elongate shells with concave ventral margins as "rapid shells." Similarly, Dell (1953) observed an increase in the height/length ratio from running-water to standing-water habitats in the genus *Hyridella* from New Zealand. Finally, Cvancara (1972) showed a trend of decreasing shell height with depth in *Anodontoides ferussacianus* and *Lampsilis radiata siliquoidea*, but not in *Anodonta grandis*, in Long Lake, Minnesota.

One aspect of the shell that influences form, but was not covered in the review by Eagar (1948), is shell sculpture. The most dramatic examples of habitat-correlated variability in this feature were reported by Haas (1936, 1969). Within single species of African unionaceans, he found lake-dwelling forms strongly sculptured and stream-dwelling forms smooth (Fig. 2C). However, Ortmann (1920) found no definite trends in this feature among species inhabiting the Ohio drainage region.

If a major change occurred in a particular environment, how quickly would the change be reflected in the shell form of the resident unionids? The damming of a river and subsequent formation of a reservoir provide, in the minds of some workers (Baker, 1928), a "natural experiment" whereby the response of a unionid fauna to rapid environmental change

may be observed. Generally, such a change causes the local extinction of most of the original stream-dwelling unionids (Isom, 1971; Harman, 1974). Nevertheless, Baker (1928) showed for some man-made lakes in Wisconsin that *Anodonta grandis* and *Lampsilis radiata siliquoidea* apparently tolerated this kind of environmental change. Moreover, the surviving populations of both species showed shell-form differences compared to conspecific stream-dwelling forms. For example, compared to the riverine morphs, *A. grandis* in the new lakes were relatively short and wide; *L. siliquoidea* from the impoundments were relatively laterally compressed and high. Apparently, the populations surviving in the newly created lakes quickly assumed some of the shell proportions characteristic of typical lake-dwelling forms.

Evidence casting doubt on the generality (and, perhaps, validity) of Baker's findings was presented by van der Schalie (1936) when he described the riverine morph of *Lampsilis ventricosa* inhabiting Carpenter Lake, Michigan. He concluded that this unusual form–habitat association was caused by humans introducing into the lake fish parasitized by glochidia larvae derived from river-dwelling unionids.

Because human interference is thus a potential source of influence in these "natural experiments" (also see Kessler and Miller, 1978), the usefulness of unionacean shell form in documenting or inferring rapid environmental change is still unknown.

Knowledge of general form–habitat relationships of Recent unionaceans has been used extensively in paleoecological studies. Early studies employing this information include those of Davies and Trueman (1927) and Leitch (1936). The most prominent and prolific writer of late has been Eagar (e.g., 1948, 1953, 1974). These works all have a common focus, since they deal mainly with Carboniferous, nonmarine (fresh or brackish water or both) unionoid (but nonunionacean) bivalves of the family Anthracosiidae.

Eagar's work is the most detailed. Typically, he presents literature summaries of form–habitat information for modern unionaceans. Also, he describes the shell form in the fossil unionoids and places them in a stratigraphic setting. He then uses Recent form–habitat information along with stratigraphic information to help reconstruct the habitat and life position of the fossil forms. With this information, he can infer environmental changes among strata.

A common deficiency of most form–habitat studies of Recent and fossil unionoids is that the functional meaning of the form–habitat correlations is not well understood. The absence of precise ecological data has forced workers interested in discerning habitat controls on unionid proportions, size, and outline to make numerous assumptions concerning the nature of the habitat in which the bivalves were found. Large streams and lakes,

for instance, are assumed to have soft, muddy substrata and slow currents. By comparison, small streams are thought to have coarser bottoms and swift currents. Through the same reasoning, individual streams are considered to take on "large-stream" or "lake" characteristics toward the mouth and "small-stream" characteristics toward the source.

Working with such premises, Wilson and Clark (1914) suggested that the typically compressed form of small-stream unionaceans was adaptive for crawling in gravel and withstanding strong currents. Also, they believed that the more obese forms of large rivers were adapted, through their low bulk density, to soft bottoms and weak currents. A. H. Clarke (1973) cautiously suggested that perhaps more obese specimens had a low surface area/volume ratio and thus were less likely than narrower forms to be dislodged from sediments by shifting currents that occur in lakes during storms. In rivers, compressed forms oriented parallel to the current were presumably less susceptible to disinterment than inflated forms.

It would be easy to propose several more hypotheses to explain form–habitat relationships of the unionacean shell, provided enough assumptions were made about the habitat. But as Ball (1922) pointed out, accurately generalizing the ecological conditions in a given freshwater body is difficult, not only because conditions vary within the environment, but also because the bivalves may inhabit an atypical portion of the environment. For example, large streams may have extensive areas of sand and gravel bottoms, and obese forms from these streams are likely to occur in such areas. Also, Fisher and Tevesz (1976) observed that while most of the bottom of Lake Pocotopaug, Connecticut, is soft mud, the great majority of unionid bivalves in that lake are restricted to a narrow band of coarse, hard substratum encircling the lake at depths of less than one meter.

We conclude that unionacean shell proportions, size, and outline are correlated with broad aspects of the environment. Thus, particularly in paleoecological studies, unionacean shell form may be a useful indicator of environmental change. Nevertheless, at present, functional morphological explanations of these form–habitat correlations are largely speculative.

2.2. Other Factors

Temperature is the most extensively studied environmental factor known to influence the shell. Its relationship to shell growth and size has been particularly well documented by Howard (1922) for North American unionids, by Negus (1966) for British unionids, and by Alimov (1974) for Russian freshwater bivalves (including unionids). In general, unionids

from temperate climates grow only during the warmer months (e.g., April–October), and within the same general kind of habitat, specimens living in warm waters often grow faster and attain larger sizes than those living in cold waters (also see Harman, 1970).

   The presence of "lime" or "hard water" is often correlated with valve thickness. A. H. Clarke (1973), for one, found that hard water often supported heavier specimens of certain species. Additionally, McMichael (1952, p. 351) reported for Australian unionaceans that "mussels from rivers whose waters are poor in lime are often quite thin and weak, while the same species from a river rich in lime will have a strong, thick shell." Similarly, Coker et al. (1921) explained the presence of thin, highly etched shells in eastern North American unionids as being caused by relatively acidic water (Fig. 3A).
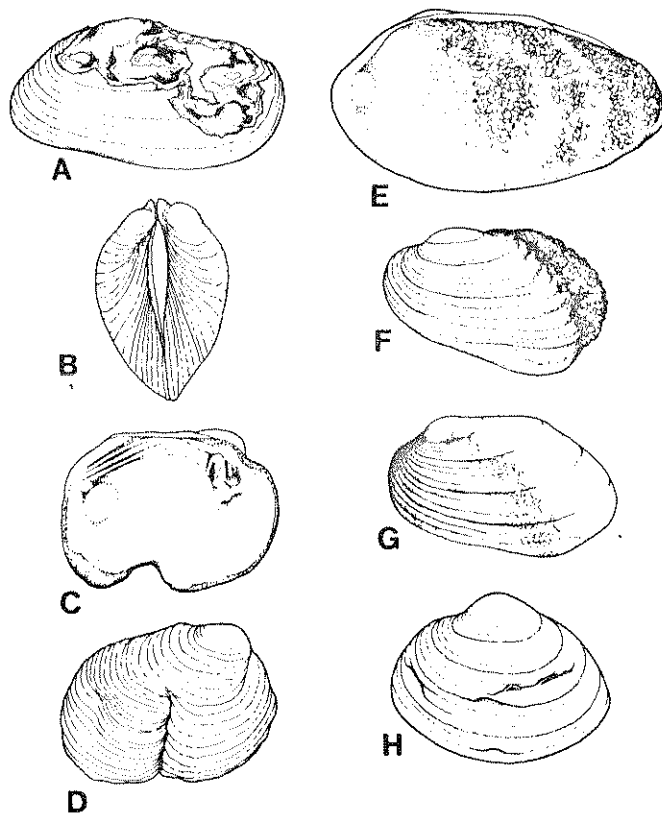

Figure 3. Shell aberrations. (A) Etching by acidic water; (B) gaping margins; (C) notched outline (after Coker et al., 1921); (D) furrowed shell surface (after Coker et al., 1921); (E) abscessed shell; (F) algal-related protuberances; (G) eroded shell posterior; (H) repaired shell

Agrell (1949) believed "trophic degree of the environment" to be related to shell form. For Swedish unionids, he found that such features as anterior development, relative height, and obesity are positively correlated with trophic degree. In the same general geographical area, Björk (1962) found growth rate higher and "quantitative development" better in streams with a relatively high trophic degree and relatively hard water.

A particularly detailed study by Green (1972) showed a complex of environmental factors correlated with the condition of individual shell features. Through use of a multivariate statistical approach, he demonstrated that low-NaCl, high-alkalinity-relative-to-pH environments were inhibited by relatively thick-valved *Lampsilis radiata siliquoidea*. Conversely, specimens from high-NaCl low-alkalinity-relative-to-pH environments were characterized by thin valves. His statistical analysis also showed an inverse relationship between size and water turbulance. Moreover, he showed that such factors as shell height, overall shell thickness, and inside shell volume were conservative morphological variables with respect to measured environmental varaiables.

Certain shell-form aberrations can be directly linked to particular environmental causes. Gaping margins (Fig. 3B), a permanently notched outline (Fig. 3C), and a furrowed surface (Fig. 3D) were attributed by Coker et al. (1921) to an infestation of the mantle by parasitic mites.

These workers also explained that massive, asymmetrical protuberances on the external surface of mussels from lakes were formed as a result of accumulated lime and algae (Fig. 3F). Algae growing on the tip of the shell exposed above the substratum also produce an eroded shell surface (Fig. 3G).

Decksbach (1957) described inner shell surfaces that become abscessed when sedimentary particles were trapped between the mantle and shell. Extensive abscessing produced a shell with irregular outlines (Fig. 3E). Shell breakage and repair also produces aberrantly formed or marred shells [personal observation (Fig. 3H)]. One would intuitively feel that such breakage would be expected to be most prevalent in physically rigorous environments associated with hard substrata.

2.3. Sexual and Ontogenetic Variability

Unionaceans, especially those belonging to the subfamily Lampsilinae, are often markedly sexually dimorphic in shell features. For example, Ball (1922) showed that male or female forms of various species differed markedly in obesity. Also, Brander (1956) and Johnson (1978), among

others, observed that such features as size and the development and shape of the posterior margin were often sexually controlled (Fig. 4).

Ontogeny has similarly marked effects on shell morphology. Both Ball (1922) and Ortmann (1920) found young unionids to be more obese than older specimens. Also, many of the environmentally distinctive aspects of form become apparent only after a bivalve has reached sexual maturity. Thus, spatial segregation of age classes or sexual morphs could produce a morphologically distinctive grouping that might be correlated with, but not necessarily causally related to, environmental factors.

As a final caveat, consider the remark by Eagar (1948) that changes in one shell dimension are often accompanied by perhaps compensating changes in others. Height, for example, generally is positively correlated with obesity (also see Tolstikova and Orlov, 1972; Hendelberg, 1960). This morphological covariance adds to the difficulty in discriminating between fortuitous, as opposed to causally related, correlations between form and environment.

While the genotypic and phenotypic controls on specific aspects of morphological variability in unionaceans are still incompletely known, it is nevertheless possible to provide an explanation of why this extensive variability can be maintained. Vermeij (1974) concluded from his analysis of an extensive literature that a decrease in competition often resulted in an increase in diversity within a higher taxon. At lower taxonomic levels, abnormalities and variants survived in species that either were under low levels of competition or predation or were relatively unspecialized.

Unionaceans live in environments in which competition and predation levels are low, and unionaceans may also be considered unspecialized with respect to the utilization of resources such as food and sub-
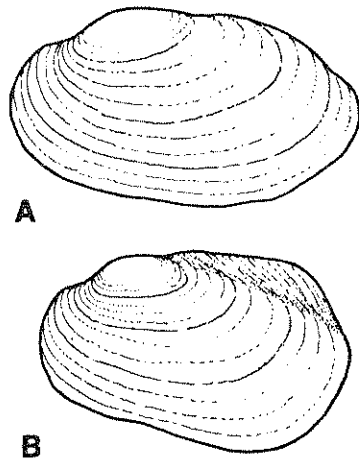

Figure 4. Sexual dimorphism in *Lampsilis radiata siliquoidea.* (A) Male; (B) female.

stratum or space (Coker *et al.*, 1921; Tevesz and McCall, 1978, 1979). Thus, it may be inferred that low biotic selective pressure, an inherent feature of their environment, is one of the factors that permits the maintenance of unionacean variability. In addition, the lack of specialization for particular resources in this group may also be related to low selective pressures. For example, numerous authors (see the reviews by Diamond, 1978; Tevesz and McCall, 1978, 1979) have shown that reduced levels of competition and predation often resulted in decreased specialization (niche-width expansion) of various species. This has been particularly well demonstrated in comparing mainland (high competition) vs. island (low competition) bird populations

This relationship among morphological variability, degree of specialization, and selection pressure has important paleoecological implications. The tendency among paleontologists in reconstructing ancient ecosystems has often been to gather life-habit information from Recent environments and apply this information directly to reconstruct the life habits and community dynamics of fossils. If, however, predation and competition levels of the modern environments differ significantly over geological time, then the "transferred-ecology" approach could lead to erroneous paleoecological inferences. It is therefore important to try to reconstruct these selective pressures directly from the fossils and their associated rock strata (Tevesz and McCall, 1978, 1979). In this respect, a thorough knowledge of the inter- and intraspecific variability of the fossil assemblage may prove informative.

3. Growth Banding

3.1. Origin of Bands

Examination of the outer surface of unionacean valves almost always reveals conspicuous dark-colored bands that extend circumferentially from the umbo and are similar in form to a view of the shell outline normal to the saggital plane. These bands may be divided into two varieties: wide, darker, macroscopically obvious bands occurring at fairly regular intervals and fainter, less dark, more irregularly spaced bands (Fig. 5). The same structures are also represented as dark lines in valve cross sections.

The significance and mode of formation of these bands were extensively discussed by Coker *et al.* (1921) (but also see, for example, von Hessling, 1859; Hazay, 1881; Israel, 1911; Ekman, 1905; Lafevre and Curtis, 1912; Isley, 1914; Altnöder, 1926; Crowley, 1957). Coker and his colleagues found that picking up a mussel and measuring it (i.e., disturbing it) invariably caused a band to be formed on the shell before shell growth
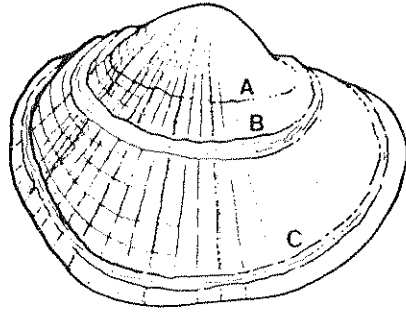
Figure 5. Annual (B, C) and pseudoannual (A) growth bands.

was resumed. On the basis of this observation and subsequent analysis of valve cross sections, they explained the formation of the bands as follows: The unionid shell grows by the deposition of successive laminae of $CaCO_3$ from the surface of the mantle, and the growing edges of the shell are deposited by the mantle margin. However, if the mantle margin withdraws within the shell, away from the growing edge, then when the new layers of prismatic shell and periostracum are deposited, they are not continuous but are overlapped by the old shell and periostracum (Fig. 6). This doubling-up of layers, a result of mantle retraction and reextension, produces the visual appearance of a dark "band" on the shell. The faint, irregularly spaced, "pseudoannual" type of band may be explained in this way.

Coker *et al.* (1921) further believed the darker, more regular bands to be formed by growth retardation due to repeated disturbance by low temperatures. They reasoned that if these bands are similarly formed and the discontinuity of the outer layers is caused by the withdrawal of the mantle because of cold weather, then one would expect several overlapping shell layers before a winter season, because the onset of seasonal cold weather is preceded by alternate warm and cold periods. Thus, these darker bands, or annual rings, are the result of frequent growth interruptions that produce multiple "doublings-up" of the shell along growth edges (Fig. 7).
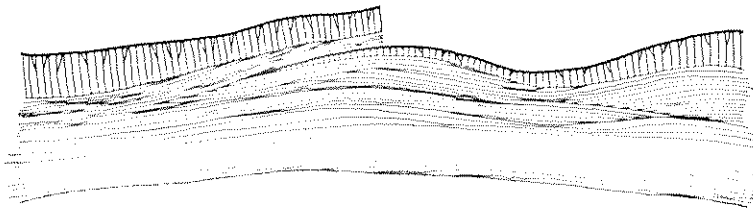

Figure 6. Cross-sectional view of pseudoannual band. Vertical elements: prisms; horizontal elements: nacre. After Coker *et al.* (1921).
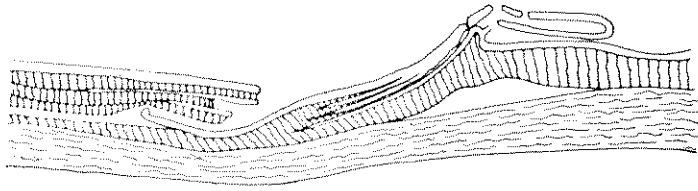
Figure 7. Cross-sectional view of annual band. Upper clear areas: periostracum; vertical elements: prisms; horizontal elements: nacre. After Coker et al. (1921).

3.2. Band Information

Several techniques make it easy to discriminate between the "annual" and "pseudoannual" bands of unionaceans (see Appendix 1.A.4). Thus, absolute age information is readily available for species from temperate latitudes. This information, in conjunction with information on population densities and shell weights and dimensions, has been used by many workers to infer life-history parameters such as growth rates, population age structure, annual production, recruitment and mortality rates, and season of death (see particularly Negus, 1966; but also see, among many others, Chamberlain, 1931; Tudorancea and Florescu, 1968a,b, 1969; Tudorancea and Gruia, 1968; Magnin and Stanczykowska, 1971; Harangy et al., 1964, 1965; Ray, 1977).

The life-history information that may be obtained because these bands yield absolute age information again exemplifies how unionaceans are potentially useful in monitoring environmental change. For example, because much information is already available on unionacean population age structure and mortality rates, new information on population dynamics that differs substantially from long-term averages may possibly be related to a change in the environment, for instance, the introduction of a pollutant. Also, once the typical season of death in certain unionaceans has been established, one could analyze the season of death from shells in a suspected "kill" and make inferences as to whether or not the mortality was natural or caused by an unusual modification of the environment.

An interesting way of relating environmental temperature change to band information also comes from the work of Negus (1966). In a very informative diagram (her Fig. 10), she plotted average percentage of departure from mean growth for a particular bivalve year class against the average departure from mean average temperature during growing season for each calendar year. This plot showed that slower growth during a particular year, as reflected by relatively closely spaced annual bands, was generally associated with a relatively cool growing season for that

year. These findings invite speculation that unionaceans may be used as relative paleothermometers. However, Stansbery (1970) found that unionids inhabiting deep water and fine-grained sediments in lakes (i.e., according to him, a situation associated with reduced current) tended to grow slower, live longer, and show less ontogenetic change in growth rate than specimens from shallower depths. Thus, the spacing of annual bands may also be related in part to the physical rigor of the habitat.

Grier (1922) and Brown et al. (1938) noted the regular spacing and distinctness of all bands in lake-dwelling, as opposed to stream-dwelling, unionids. This condition resulted from a paucity of pseudoannuli on lake-dwelling forms. Stansbery (1967) explained that the stabilizing effects of a large lake ensured gradual uniform temperature changes, thereby largely eliminating the rapid temperature fluctuations that are an important cause of pseudoannual band formation. Thus, the number of pseudoannuli produced per year per unionid is inversely related to the temperature stability of the environment. This, in turn, is often related to the size, depth, and circulation patterns of a given body of water.

Because unionids concentrate trace elements, the shell, like that of other bivalves, is a repository of chemical information. If it were possible to analyze the concentration of various substances in an individual annual layer, then the shell might provide a chronological record of relative concentrations of those elements or compounds in the ambient environment. The presence of growth bands and their organic component help to facilitate such analyses. According to Sterrett and Saville (1974), several interruptions in the formation of the shell in the spring and fall produce an area of discontinuity visible as a dark line. The greater amount of periostracum at this border results in an area higher in protein than in other parts of the shell. Theoretically, if the shell is baked at high temperatures, the protein of the periostracum will ash, and the CaCO₃ will not, leaving a weak spot or crack that delineates part of the shell formed in a single growing season. A methodology for separating the annual layers based on this reasoning has been used by Nelson (1964) and Sterrett and Saville (1974) (see Appendix 1.A.4). The ease with which these layers may be separated makes the chemical concentrations in the shell for particular years readily analyzable and thus facilitates monitoring yearly changes in the chemical environment. The significance of these chemical concentrations in bivalves in general is discussed in Chapter 4.

Counting growth bands on the shell surface and in shell cross sections is not the only way of determining absolute age and thus the population dynamics of unionaceans. European workers have frequently employed the method of Wellmann (1938), whereby annuli are counted on the ligament (see, for example, Björk, 1962; Hendelberg, 1960). However, this method is limited in usefulness because annuli on the ligament are de-

stroyed by erosion of the anterior portions of the ligament, which is a common phenomenon in unionaceans. This makes it necessary to estimate lost information. Over the long term, this method suffers because the entire ligament is much more easily destroyed than the shell.

Finally, the study of the significance of unionacean growth bands has been confined mainly to temperate latitudes, where seasonal cold stops growth for prolonged periods and is responsible for annual band formation.

But what about warmer climates? To the best of our knowledge, the significance of growth banding in tropical unionaceans is little studied. Warm-climate unionids do form distinctive bands, but the causes behind the formation of these bands are different than for temperate species. For example, McMichael (1952, p. 351) mentions the following regarding Australian unionaceans: "During severe droughts, the rivers and creeks dry up, and the shells may become dormant. Fresh water mussels will then bury deeply into the mud and their shells will cease growing, becoming thickened at the edge. When rain comes again, the shells may emerge and grow quickly, leaving a thick growth line on the shell which marks the dormant period."

Other seasonal effects in the tropics, such as extensive rain, could also conceivably cause growth interruptions. Stream-dwelling unionids, for instance, could be subjected to the effects of abnormally high amounts of suspended particulate matter during repeated floods caused by monsoons. A prolonged stormy season could likewise cause lake-dwelling forms to be subject to abnormally long periods of agitated conditions. These and related phenomena could disturb the mussel enough to cause repeated and prolonged retractions of the mantle, thus producing a thick and distinctive band. Therefore, it is necessary to know the general climatic setting from independent evidence (e.g., temperate vs. tropical) before growth bands on unionaceans can be accurately interpreted.

4. Ecological and Evolutionary Significance of Unionacean Shell Microstructure

Unionaceans have a primitive shell microstructure consisting of outer prismatic and inner nacreous shell layers, with the former deposited on a nonreflected shell margin. They probably inherited this microstructure from the Trigoniacea, a superfamily inhabiting marine and estuarine environments and now restricted to only a few Indo-Pacific species (Cox, 1960; Newell and Boyd, 1975). Unlike other major groups of freshwater bivalves (e.g., Corbiculacea, Dreissenacea), the Unionacea have apparently never evolved crossed lamellar microstructure, and have retained

an outer simple prismatic to composite prismatic shell layer comparable to that in many Trigoniacea (Boggild, 1930; Beedham, 1965; Taylor et al., 1969, 1973; Cox, 1969; Tolstikova, 1972, 1973, 1974; Newell and Boyd, 1975). The Unionacea are likewise conservative in terms of the variability of their shell microstructure. Despite their considerable generic diversity, unionaceans show only minor interfamilial differences in this feature, represented largely by changes in the internal arrangement of the outer layer prisms and by the occurrence of adventitious thick organic (conchiolin) laminae within the nacreous layer of certain species (Tolstikova, 1974).

Like the shell of most other bivalves, the unionacean nacroprismatic shell provides protection of the soft parts, support of the ctenidia and viscera, an assist in burrowing, and a source of $CaCO_3$ for buffering metabolic acids during periodic anaerobic metabolism. In terms of protection, their nacreous microstructure may have been retained because of its relatively high mechanical resiliency in comparison with certain other common inner-layer microstructures [e.g., complex crossed lamellar and homogenous (see, for instance, Taylor and Layman, 1972)]. Many unionaceans inhabit streams, and their shallow burrowing habit exposes the shell posterior to physically rigorous conditions, especially during floods. Unionaceans may additionally have retained a primitive nacroprismatic shell microstructure because this offers maximum protection of their shell from dissolution in fresh water. Their vertical to reclined outer layer prisms show relatively thick interprism organic matrices, and the horizontal organic laminae separating nacreous laminae may likewise retard shell dissolution. Perhaps the most important adaptations of unionacean shells, with regard to preventing shell dissolution, are their persistent periostracum and occasional deposition of thick, horizontal laminae within the nacreous layer.

4.1. Periostracum and Shell Protection

The adaptive value of the unionacean periostracum for preventing exterior shell dissolution is clearly seen where this layer is abraded. In this case, dissolution of the underlying prismatic and nacreous layers occurs. This results in solution pits on the shell exterior, some of which penetrate through most of the shell thickness at the umbos (Figs. 3A and 8). Thick periostraca are rarely encountered in the Unionacea, but most species in this superfamily show a periostracum of intermediate thickness in the adult shell. By the present definition, intermediate-thickness periostracum is between 15 and 50 μm as measured near the margin of the adult shell. Thin periostraca (<15 μm) are equally rare in this superfamily.

Figure 8. N
(Gould) fre
(A) Aragon
inae sporac
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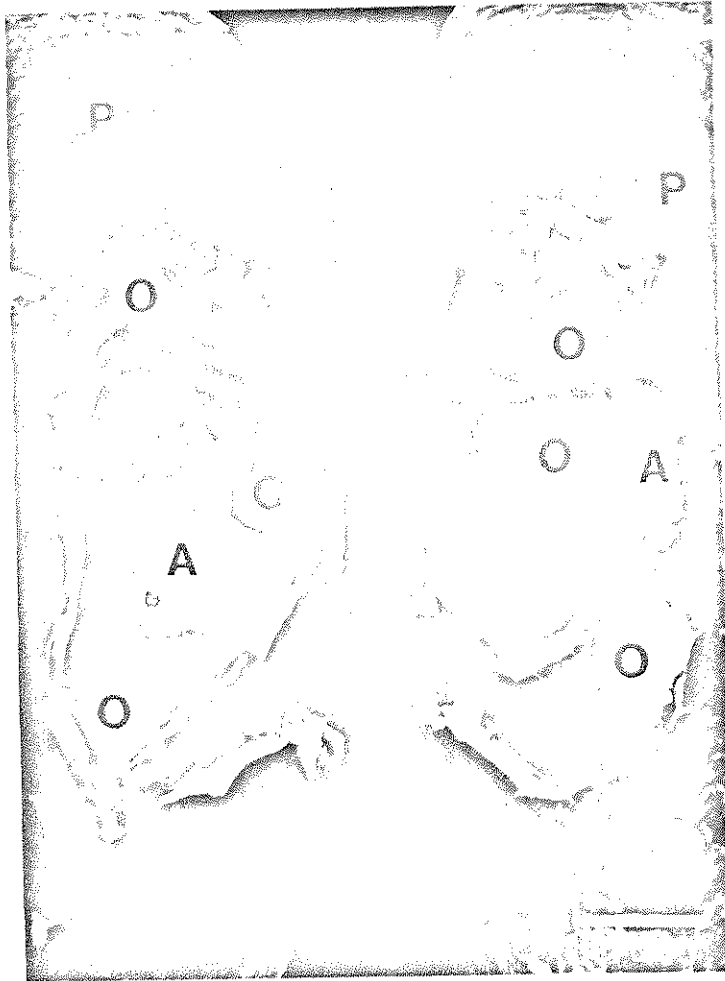thinner
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Figure 8. Natural dissolution of the shell exterior in the margaritiferid *Margaritifera falcata* (Gould) from the Ozette River, Washington. Yale University Peabody Museum No. 10158. (A) Aragonitic prismatic and nacreous shell layers; (O) prominent adventitious organic laminae sporadically distributed among the nacreous laminae; (P) periostracum. Scale bar: 1.0 cm.

This uniformity of periostracal thickness probably reflects the fact that thinner periostraca are not sufficiently protective, whereas thicker periostraca tend to peel away from the shell exterior after repeated desiccation.

Compared with most other bivalves, many unionaceans are remarkable for the resistance of their periostracum to peeling and cracking after
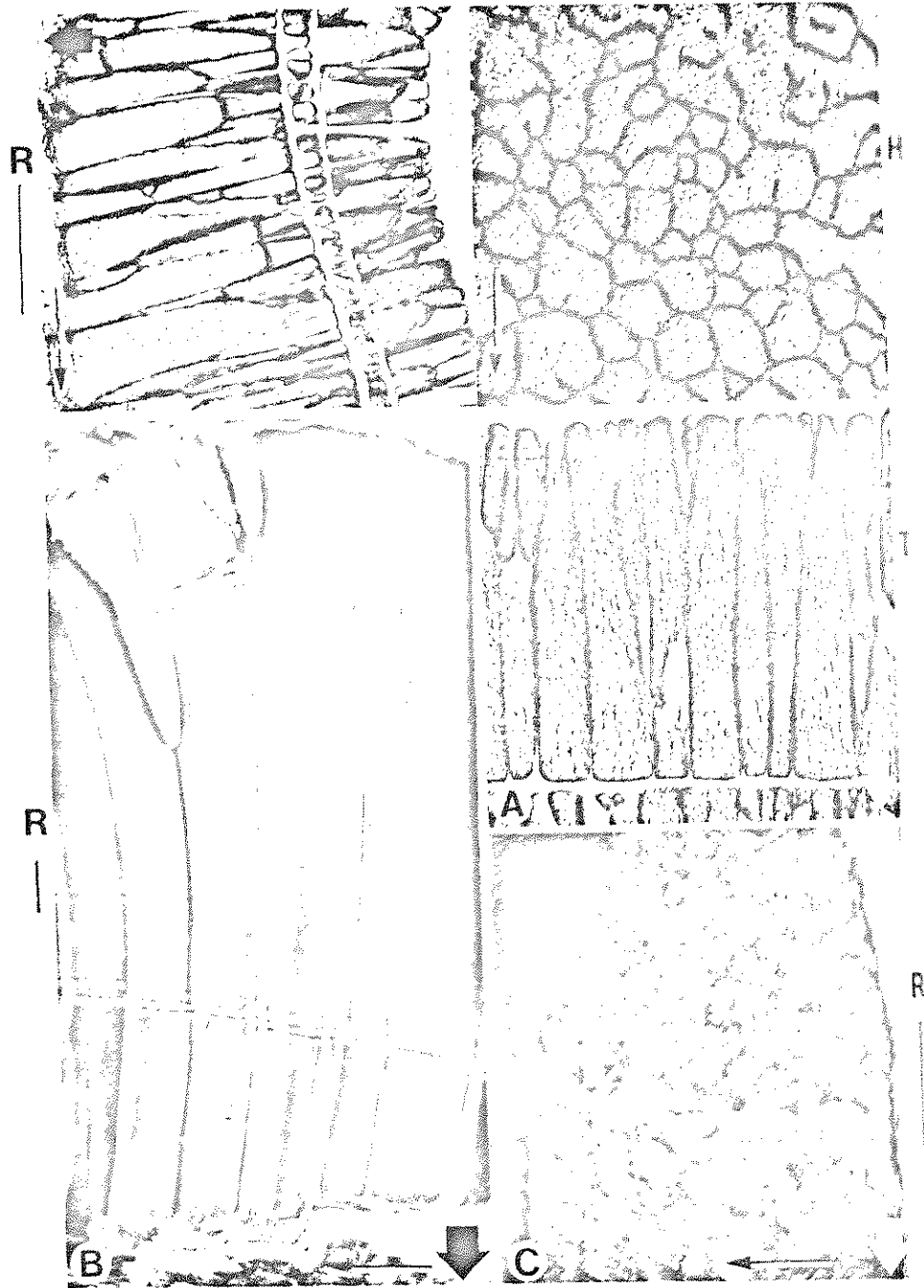
drying. Two other bivalve surperfamilies show this property, i. e., certain representatives of the Mytilacea and, to a lesser degree, the Trigoniacea. In mytilids such as *Mytilus edulis* Linnaeus, resistance to desiccation peeling is improved by the incorporation of fluid-filled vacuoles in the center of the periostracal layer. These vacuoles maintain the moisture of the periostracal layer with subaerial exposure, thereby preventing differential contraction of the outer and inner periostracal sublayers (Carter, 1976). In contrast, trigoniacean and unionacean periostraca are typically nonvacuolated, but they show a strong structural bond with the underlying prismatic layer. As described by Taylor *et al.* (1969) and illustrated in Figs. 9 and 10, the unionacean (and trigoniacean) periostracum conforms with the end of the prisms and extends deeply into the prismatic layer. This forms a strong bond between these two layers and retards peeling when the exterior of the periostracum contracts through drying. Consequently, even air-dried museum specimens of most unionacean species resist periostracal peeling and cracking, except for the species with unusually thick periostracal layers (e.g., certain *Cumberlandia* and *Amblema*). In nonunionacean and nontrigoniacean bivalves with nonreflected shell margins (e.g., most Mytilacea, Ostreacea, Pectinacea, and Myacea), the initial spherulites of the outer prismatic shell layer are deposited on a more or less planar inner periostracal surface. In these instances, the periostracum supports the initial spherulites and excludes environmental contaminants, but it does not envelop the ends of the prisms, nor does it extend into the prismatic layer to the extent that this occurs in the Unionacea and Trigoniacea (see, among others, Clarke, G. R., 1974).

The trigoniacean periostracum is generally thinner over the prism ends than in the Unionacea. Additionally, the trigoniacean periostracum does not extend as deeply into the outer prismatic shell layer. It therefore seems likely that the trigoniacean periostracal–prism relationship provided only a preadaptation for the evolution of a typical unionacean periostracum–prism layer bond. Interestingly, aside from thickening the periostracum and bonding this more strongly with the underlying prismatic shell layer, unionaceans have tended to reduce the prominence of apical

Figure 9. Outer prismatic shell layer in the unionid *Elliptio complanata* (Solander) from the Sangerfield River near Hamilton, New York. University of North Carolina No. 4923. The three photographs in the upper and middle right parts of the plate (A) comprise a three-dimensional view of the prismatic layer in the shell posterior, viewed in radial vertical (R), transverse vertical (T), and horizontal (H) sections (acetate peels of polished and etched sections). Scale bars: 50μm. (B, C) Two photographs representing radial vertical fractures through the outer prismatic shell layer viewed by scanning electron microscopy. The thick arrows indicate the direction toward the depositional surface; the thin arrows indicate the direction toward the posterior shell margin. Scale bars: 2 μm.

bosses that characteristically occur on the ends of trigoniacean prisms. These apical bosses are generally pyramidal and often structurally distinct from the underlying prism columns (see Taylor et al., 1969; Newell and Boyd, 1975). Loss or reduction of these structures is adaptive in freshwater bivalves because it reduces the likelihood of exposure of the shell $CaCO_3$ as a result of abrasion over the apical bosses. On the basis of this evolutionary trend, it may be possible to identify fossil trigoniaceans evolving microstructural adaptations for life in acidic fresh water. These transitional trigoniacean–unionacean species should show progressive reduction of their prism apical bosses and increased separation of their outer prism columns, i.e., indicative of a more deeply penetrating periostracal layer.

4.2. Adventitious Interior Conchiolin Layers

Thick, horizontal laminae of organic material (conchiolin) occur as adventitious sublayers within the nacreous layers of a large number of unionaceans. These sublayers can occur sporadically over the interior surface of the valve, but they are most commonly observed as irregular patches in or near the umbonal cavity. In addition, these organic deposits are most commonly found among unionaceans with relatively thin shells in the umbonal area (e.g., in thin-shelled species of the genera *Alasmidonta, Cristaria, Iridina, Elliptio,* and *Margaritifera,* but less commonly in thicker-shelled species of the genera *Pleurobema, Plethobasus,* and *Obovaria*). These organic sublayers can be deposited in response to shell penetration through chemical dissolution or as responses to contaminants entering between the shell and mantle (e.g., extraneous water, sediment, or other material entering through an abnormal separation between the mantle margin and the shell margin). Beedham (1965) suggested that inner-layer conchiolin patches in older *Anodonta* are secreted in response to outside water moving through cracks in the anterior part of the hinge. Beedham states that in *Anodonta,* secretion of the conchiolin patches is followed by the secretion of an underlying prismatic layer prior to resumption of normal nacre deposition. This sequence is identical to that which develops in the repair of damaged shell margins in this genus (Beedham, 1965). In the case of certain deeply eroded *Margaritifera falcata* (Gould), the distribution of the interior conchiolin patches clearly indicates that they are being deposited as a reaction to deep solution pitting

Figure 10. Scanning electron micrographs of radial vertical fractures through the outer prismatic shell layer of the unionid *Obliquaria reflexa* Rafinesque from the Meramec River, St. Louis, Missouri. Yale University Peabody Museum No. 9749. The periostracum appears in the upper part of (A). A higher magnification of the prism fracture in (B). The thick arrows indicate the direction toward the depositional surface; the thin arrows indicate the direction toward the posterior shell margin. Scale bars: 5 μm (A, B) and 1 μm (C).

over the umbos. But in other *M. falcata*, and in many other thinner-shelled unionaceans, similar but less abundant organic patches can be observed even in shells lacking appreciable umbonal dissolution. In some instances, these patches are superficially smooth and do not extend to the shell margins or hinge, suggesting that they have not been deposited in response to water leakage or a foreign body contaminant. Thus, it appears likely that unionaceans can deposit patches of adventitious conchiolin near their umbonal region as a safeguard against possible deep umbonal dissolution, in addition to utilizing the same strategy to seal over complete shell penetration and foreign contaminants. In some instances, these prophylaxis conchiolin layers can be distinguished from damage-response layers by their lack of an underlying prismatic layer prior to the resumption of normal nacre deposition.

The deposition of prophylaxis and damage-response conchiolin layers in unionacean shells can grossly alter the total shell conchiolin/$CaCO_3$ ratio. This fact must be considered when conchiolin/$CaCO_3$ ratios (or "scleroprotein"/$CaCO_3$ ratios) are utilized as indicators of paleosalinity, as attempted by Kolesnikov (1970). It may be that prophylaxis conchiolin layers are deposited by certain species with greater frequency and in thicker layers in more acidic freshwater environments. However, this aspect of their formation has yet to be investigated, and is at present entirely speculative.

4.3. Evolutionary Limitation of Shell Form

In addition to protecting the shell valves from exterior dissolution, the unionacean periostracum forms a water-tight seal at the shell margins on shell closure. This aids in water retention within the mantle cavity in species periodically exposed to subaerial conditions, and it effectively excludes unfavorable water conditions when these arise. The gasketlike role of the unionacean periostracum is especially useful because these species have tapering (i.e., nonreflected) shell margins. Consequently, without a periostracal seal, minor damage to their thin margins could seriously impair their ability to seal the mantle cavity and protect their mantle margins on shell closure. Bivalves with nontapering (i.e., reflected) shell margins can secrete a thick shell margin, thereby reducing the likelihood of shell-margin breakage (e.g., *Mercenaria* and many other Veneracea), and thus generally show only a thin periostracum.

It is possible that the Unionacea have been evolutionarily limited to a tapering shell margin because of their unique periostracum–prism adaptation for preventing periostracal peeling. With a fully reflected shell margin, a unionacean would necessarily deposit its outer prismatic shell

layer directly on the curved surface of the previously deposited prismatic layer, rather than on the underside of the periostracum. Consequently, it would be impossible for such a unionacean to develop a deep interpenetrating bond between the outer ends of the simple prisms and the periostracal layer. Their periostracum, as in veneroid bivalves with fully reflected shell margins, would then be more prone to peeling and cracking on desiccation. Most living veneroid bivalves with fully reflected shell margins are seldom exposed to such conditions, but air-dried museum specimens are evidence of the transient bond between their periostracum and the underlying shell. Inasmuch as strongly crenulated shell margins and sharp ornamental features would increase the likelihood of local abrasion through the periostracum, the subdued ornament typical of unionacean shells may likewise be attributed, in part, to natural selection for resistance to shell dissolution in an acidic environment. Even in comparison with their relatives in the Trigoniacea, the modern and fossil Unionacea show only subdued and generally knobby or rounded ornament with the exception of rare spinose species such as *Canthyria spinosa* (Lea). Utilizing a similar shell microstructure and tapering shell margin, the Trigoniacea have evolved radial costae or plicae, concentric ridges, or even divaricate ornamentation (see, for instance, Newell and Boyd, 1975).

4.4. Periostracal Color and Surface Texture

Two features of the unionacean periostracum that have yet to be analyzed adequately for their ecological and evolutionary significance are color and exterior surface texture. After studying periostracal color in unionaceans from Lake Erie and the Upper Ohio River drainage system, Grier (1920c) concluded that color variation is often greater than standard species descriptions generally indicate. He suggested that this color variability might be related to aging, water acidity, and water silt content. He noted downstream and aging effects in which yellows and greens darken to deep browns and blacks. Other investigators have noted an aging effect in periostracal color among marine bivalves Ockelmann (1958) described an orange, yellow-brown, or red-brown periostracum in juvenile *Astarte*. In contrast, the periostracum secreted by the adult is darker brown to black. Holme (1959) mentioned a similar aging effect for *Lutraria* in which the periostracum changes from colorless in juveniles to brown when secreted by adults. With regard to salinity, Fischer (1887) noted that olive-green is especially common in freshwater bivalves. Carter (1976) noted that greens are especially common in periostraca of the two largest freshwater bivalve superfamilies (Unionacea and Corbiculacea), and that

greens are also common, but less ubiquitious, among two marine super-families (Nuculanacea and Solenacea). Inasmuch as nuculanacean shells may be exposed to acidic sedimentary environments, and solenaceans often inhabit estuarine environments, the possibility arises that green coloring is more common in all four goups as a result of an acidity or salinity effect. A. H. Clarke (1973) has noted that green coloring in *Anodonta* is associated with muddy substrata. Inasmuch as muddy substrata commonly contain abundant decomposing organic compounds, and a resulting acidic sedimentary environment, this would appear to reinforce the idea of a pH effect on periostracal color.

Periostracal layers in the Unionacea are, by and large, generally superficially smooth and macroscopically featureless, except for occasional wrinkles. However, a number of species, especially in the families Mutelidae and Etheriidae, show radial, concentric, or intersecting microscopic ridges on the surface of the periostracum (Simpson, 1900; Marshall, 1926; Bonetto and Ezcurra, 1965; Carter, 1976). According to Carter (1976), these features are generally expressed only in the surface of the periostracum, and do not represent crenulations affecting the entire thickness of the periostracum. The ecological and evolutionary significance of these structures, like that of periostracal color, has yet be to be documented.

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