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THE ADAPTATION OF BIVALVE MOLLUSCS TO OLIGOHALINE AND FRESH WATERS: PHYLOGENETIC AND PHYSIOLOGICAL ASPECTS[1]

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ABSTRACT

The phylogenetic distribution of freshwater bivalve molluscs is not uniform. One subclass, Paleoheterodonta, contains about 1600 freshwater species and only one marine genus. The numbers of freshwater species in the subclasses Pteriomorphia and Heterodonta are about 5 and 275, respectively. This disparity could be correlated with differences in the osmoregulatory physiology of brackish water and freshwater bivalves in these subclasses. We review, in brief, what is known about the physiological adaptations in bivalves that might be related to their success in invading fresh waters.

Several generalizations emerge from our analysis of the available data. First, a tolerance of very dilute media, including distilled water, by bivalves is associated with a decreased tolerance to media of high salinity. Second, the degree of euryhalinity among bivalves appears to be correlated with neither the size of the intracellular free amino acid pool, nor with the rate of change in the pool during acclimation to increased or reduced ambient salinity. Third, the decreased tolerance to concentrated media manifest in paleoheterodont bivalves may be correlated with a diminished capacity for hyperosmotic cellular volume regulation. Fourth, hypercalcemia in response to dilute media appears to be a common occurrence among heterodont species, but is less common in pteriomorph species; hypercalcemia may play a role in the relatively greater success of the former taxon in colonizing fresh waters.

KEY WORDS — bivalve, osmoregulation, physiology, ecology.

INTRODUCTION

Animals adapted to fresh water, or to dilute brackish waters, lose salts and gain water continuously, and a number of physiological mechanisms serving to reduce or compensate for these passive fluxes have arisen among aquatic animals. These physiological adaptations include reduction of the blood osmolality, production of a hypotonic urine, reduction of epithelial permeability to ions and water, and extra-renal uptake of ions. Through geological time, the larger phyla that now contain freshwater or brackish water species have each given rise to multiple, independent colonizations of these dilute habitats. It follows that the physiological adaptations characteristic of animals living in dilute waters should not be uniformly distributed, and that the capacities of these mechanisms should vary widely among oligohaline and freshwater species.

This expectation has been thoroughly discussed by Kirschner (1979) in terms of the arthropods. For example, whereas crayfish have comparatively low blood osmolality and produce hypo-osmotic urine, freshwater crabs of the genus *Potamon* have a relatively high blood osmolality and produce an isosmotic urine. These crabs are less permeable to water, but more permeable to ions, than are crayfish. There is, then, no single suite of identical mechanisms common to all freshwater arthropods.

The colonization of fresh and dilute brackish waters by bivalve molluscs has been desultory, occurring in different periods, places and phyletic lines. The systematic and geographical distributions of living bivalves reported to occur in very dilute

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waters (*i.e.*, < 1 ‰) are collected in Table 1. Most freshwater bivalves (more than 20% of the Class) are in two taxa - the subclass Paleoheterodonta and the heterodont family Pisidiidae - both quintessentially well-adapted to fresh water. Throughout their life cycles, these animals are found only in persistently fresh waters (or, rarely, in very stable, very dilute brackish water); their tolerance for increased salinity is extremely limited, and their reproductive mechanisms are attuned to fresh waters. The Pisidiidae contain no brackish water or marine species, and the Paleoheterodonta are, except for perhaps five marine species of *Neotrigonia* in the enigmatic Family Trigoniidae, also limited to fresh water. The paleoheterodonts and pisidiids have undergone extensive speciation, and the lack of brackish water species in either group suggests that their colonization of freshwater habitats occurred in relatively ancient times.

The remaining bivalves that occur at the interface between fresh and brackish waters are, with one exception, in the subclasses Pteriomorphia and Heterodonta. Both of these groups contain many brackish water species, but very few pteriomorphs have colonized fresh waters (Table 1). This paucity of freshwater pteriomorphs, relative to the heterodonts, could be due to differences in the adaptive mechanisms distributed in the two subclasses.

Castagna & Chanley (1973) carefully measured the salinity ranges of Chesapeake Bay bivalves, both in the field and in the laboratory; their data support the notion that pteriomorphs and heterodonts respond differently to dilute environments. When these data are plotted with the minimal salinities tolerated in laboratory aquaria as the dependent variable and the field values as the independent variable, the points for the pteriomorph species determine a regression line that is statistically indistinguishable from the isohaline line (Fig. 1). In contrast, the heterodont points are more scattered, the salinity tolerance minima observed in the field are generally higher than those obtained in the laboratory, and the discrepancy between laboratory and field minima increases with environmental salinity.

This analysis suggests that, at the low end of their salinity ranges, the Pteriomorphia are experiencing salt concentrations close to the lowest that they can tolerate under controlled laboratory conditions. Heterodonts, however, tolerate dilutions that are much lower than those occurring in their natural habitats. Thus, the osmoregulatory mechanisms in the two subclasses might well be different in kind or in capacity.

In this brief review, we discuss what is known about the details of osmoregulatory physiology of bivalve molluscs inhabiting oligohaline (*i.e.*, 0.5 to 20 ‰; see Gainey & Greenberg, 1977) or fresh (*i.e.*, < 0.5 ‰) waters. We attend, in particular, to comparisons between pteriomorphs and heterodonts.

SALINITY TOLERANCE

Although the proposition has not been systematically studied, survival in very low salinities appears to be related to reduced tolerance for high salinities. Consider the following series of examples: paleoheterodont clams tolerate distilled water until they die from starvation, but cannot survive osmolalities above 100-200 mOsm (Krogh, 1939; Dietz & Branton, 1975; Gainey & Greenberg, 1977; Deaton, 1981); *Corbicula manilensis* Phillipi survives less well than paleoheterodont clams in

TABLE 1. The systematic distribution of extant bivalve molluscs in very dilute habitats: 1 ‰ to fresh water.

Subclass Order	Family	Genus	Approx. No. Species	Location	Reference
PTERIOMORPHIA					
ARCOIDA	Arcidae	*Scaphula*[1]	2	India, SE Asia	Brandt, 1974; Ram & Radhakrishna, 1984
MYTILOIDA	Mytilidae	*Limnoperna*[1], *Sinomytilus*[2], *Modiolus*[2], *Fluviolanatus*[3], *Arcuatula*[2], *Brachiodontes*[3], *Mytella*[1]	10	India, SE Asia, Australia, Panama Canal	Krishnamoorthi & Rajagopalan, 1969; Mizuno & Mori, 1970; Starobogatov, 1970; Brandt, 1974; Greenberg, 1975; Morton, 1975
PTEROIDA	Isognomidae	*Isognomon*[3]	1	Panama Canal	Rosewater, 1974
PALEOHETERODONTA					
UNIONOIDA	Margaritiferidae[1]				
	Amblemidae[1]				
	Hyriidae[1]				
	Unionidae[1]		1600	Cosmopolitan	Purchon, 1977
MUTELOIDA	Etheriidae[1]				
	Mutelidae[1]				
	Mycetopodidae[1]				
HETERODONTA					
VENEROIDA	Cyrenoididae	*Cyrenoida*[3]	5	W Africa, N America, C America	Moore, 1969; Starobogatov, 1970
	Cardiidae	*Manodacna*[2], *Adacna*[2]	5	Pontocaspian	Romane & Schlieper, 1971
	Mactridae	*Rangia*[3]	2	N America	Hopkins & Andrews, 1970; Andrews, 1981
	Cultellidae	*Neosolen*[3], *Pharella*[3], *Tanysiphon*[3]	3	S Asia, SE Asia	Moore, 1969; Brandt, 1974
	Solecurtidae	*Novaculina*[1]	2	India, S Asia, Thailand	Moore, 1969; Brandt, 1974
	Donacidae	*Egeria*[2], *Iphigenia*[2]	4	W Africa	Purchon, 1963; 1977
	Dreissenidae	*Dreissena*[2], *Mytilopsis*[2]	13	Europe, N America, C America, S America, Africa	Olsson, 1961; Starobogatov, 1970; Keen, 1971
	Corbiculidae	*Corbicula*[2], *Polymesoda*[2], *Batissa*[2]	50	Cosmopolitan	Moore, 1969; Sinclair, 1971; Brandt, 1974
	Pisidiidae[1]	*Bysanodonta, Eupera, Pisidium, Sphaerium*, perhaps others	150	Cosmopolitan	Moore, 1969
	Glauconomidae	*Glauconome*[3]			
MYOIDA	Corbulidae	*Potamocorbula*[1]	1	NE Asia	Hutchinson, 1967; Moore, 1969
	Erodonidae	*Erodona*[1]	2	Amazon, Congo	Hutchinson, 1967; Moore, 1969
	Pholadidae	*Martesia*[3]	1	Borneo	Hutchinson, 1967
	Teredinidae	*Nausitoria*[2], *Teredo*[3], *Psiloteredo*[3]	3	India, SE Asia, Panama Canal	Wright, 1864; Moll, 1936; Hutchinson, 1967; Greenberg, 1975
ANOMALODESMATA					
PHOLADOMYOIDA	Lyonsiidae	*Ostomya*[1]	1	S America	Morrison, 1943; Moore, 1969; Starobogatov, 1974

[1]All species in this taxon reported to live and reproduce in fresh water (<0.5 ‰).
[2]At least one species in this genus reported to live in fresh water, but may also occur in oligohaline brackish water (0.5-20 ‰).
[3]Usual habitat is oligohaline; probably not continuously tolerant to fresh water.

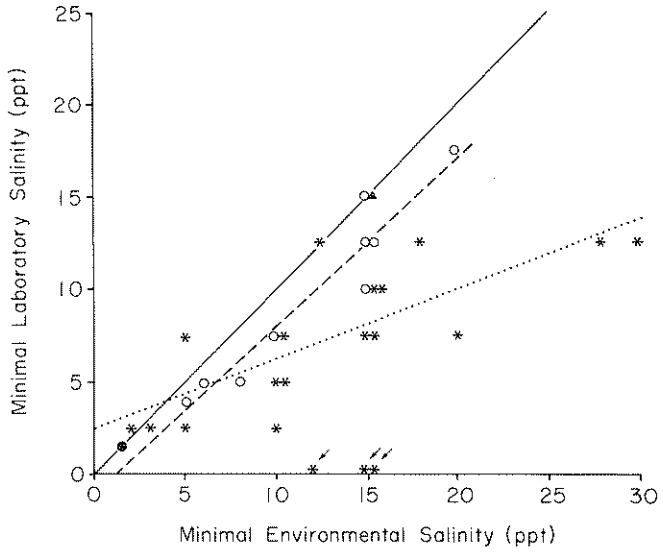

FIG. 1. The relationship between the minimal salinities tolerated by heterodont and pteriomorph bivalves in the laboratory (ordinate) and in the field (abscissa). Symbols: open circle = *Ostrea palmula* (Pteriomorphia), Panama Canal (data from Deaton, 1981); the other points represent Chesapeake Bay species, solid circles = Pteriomorphia, asterisks - Heterodonta, open triangle = *Solemya velum* (Cryptodonta) (data from Castagna & Chanley, 1973). Arrows indicate the *maximum* salinities of three oligohaline heterodonts (*Rangia cuneata*, *Polymesoda caroliniana*, *Mytilopsis leucophaeta*); the minimal laboratory salinity tolerated by these species is fresh water. The solid line is the isohaline line (y = x). Regression lines (dashed) by least squares. For Chesapeake pteriomorphs: y = 0.91x - 1.2, r = 0.96, P < 0.001; the slope and intercept are not significantly different from the isohaline line (P > 0.4). For Chesapeake heterodonts (excluding oligohaline animals): y = 0.37x + 2.6, r = 0.78, P < 0.001; the slope and intercept are significantly different from the isohaline line (P < 0.001, P < 0.05, respectively).

distilled water, but dies in media more concentrated than 400 mOsm (Gainey, 1978; Deaton, 1981); *Limnoperna fortunei* Dunker survives in distilled water for over two months, but has an upper limit of about 600 mOsm (Deaton *et al.*, 1989); *Mytilopsis leucophaeta* Conrad survives in distilled water for a few weeks, but does not survive exposure to 600 mOsm (Deaton *et al.*, 1989); *Rangia cuneata* Gray survives short-term exposure to distilled water, but cannot live above 600 mOsm (Deaton, 1981); and *Polymesoda caroliniana* Bosc cannot tolerate distilled water at all, but survives well in seawater (1100 mOsm) (Gainey, 1978; Deaton, 1981). Marine euryhaline bivalves, such as *Pseudocyrena floridiana* Conrad, *Geukensia demissa* Dillwyn, and *Xenostrobus securis* Linnaeus have a salinity range from 50-100 mOsm to 1100-1400 mOsm (Wilson, 1968; Pierce, 1970; Gainey & Greenberg, 1977). In conclusion, small increases in tolerance to distilled water (*e.g.*, increased survival time) in oligohaline brackish water bivalves that survive quite well in fresh water are apparently correlated with larger decreases in the maximal osmolality tolerated. The narrowing of the tolerance range and the increasing resistance to distilled water culminate in the stenohalinity so marked in the unionids (Gainey & Greenberg, 1977).

VOLUME REGULATION

Any change in the ambient salinity results in a similar change in the osmotic concentration of the body fluids of an osmoconforming animal (Fig. 2). The cells of these animals will shrink or swell depending on the direction and magnitude of the change in hemolymph osmotic concentration. The cells of marine invertebrates are well-known for their ability to adjust to large changes in the ambient osmolality. In bivalves, cellular volume is regulated by the adjustment of a large intracellular pool of free amino acids and by changes in the cytoplasmic concentrations of some ions (Gilles, 1979; Pierce, 1982). The contribution of changes in inorganic ions to volume regulation in bivalves has been studied only in the red blood cell of the ark clam *Noetia ponderosa* Say (Smith & Pierce, 1987); in contrast, amino acid data from a large number of species and a variety of experimental protocols are available. In the following discussion, these data are used to evaluate differences in amino acid-mediated volume regulation among bivalve species.

Size of the Amino Acid Pool

A larger cytoplasmic free amino acid pool has been invoked to explain the lower salinities tolerated by marine euryhaline bivalves relative to marine stenohaline bivalves (Pierce, 1971). The amino acid contents of adductor muscles from various species of bivalves following long-term acclimation to high salinity (listed in Table 2) do not support this notion. There are no clear differences between euryhaline species, such as *Mya arenaria* Linnaeus, *Cardium edule* Linnaeus and *Scrobicularia plana* da Costa, and stenohaline species, such as *Chlamys opercularis* Linnaeus and *Modiolus modiolus* Linnaeus. Furthermore, there are no consistent differences between heterodont and pteriomorph species.

TABLE 2. Amino acid content of adductor muscles from selected bivalve molluscs acclimated to osmotic concentrations approximating the upper limit of their salinity tolerance.

SUBCLASS Species	Habit	(mOsm)	FAA	Reference
PTERIOMORPHIA				
Mytilus edulis	ME	1005	572	1
Crassostrea virginica	ME	1005	610	1
Chlamys opercularis	MS	1005	1070	1
Modiolus modiolus	MS	1005	745	1
HETERODONTA				
Mercenaria mercenaria	ME	1005	675	1
Cardium edule	ME	1005	455	1
Scrobicularia plana	ME	1005	934	1
Mya arenaria	ME	600	738	1
Rangia cuneata	O	630	372	2

Habits: MS = marine stenohaline; ME = marine euryhaline; O = oligohaline (0.5-20 ‰).
Free Amino Acid (FAA) values are μmol/g dry weight.
References: 1 = Shumway *et al.* (1977); 2 = Henry *et al.* (1980)

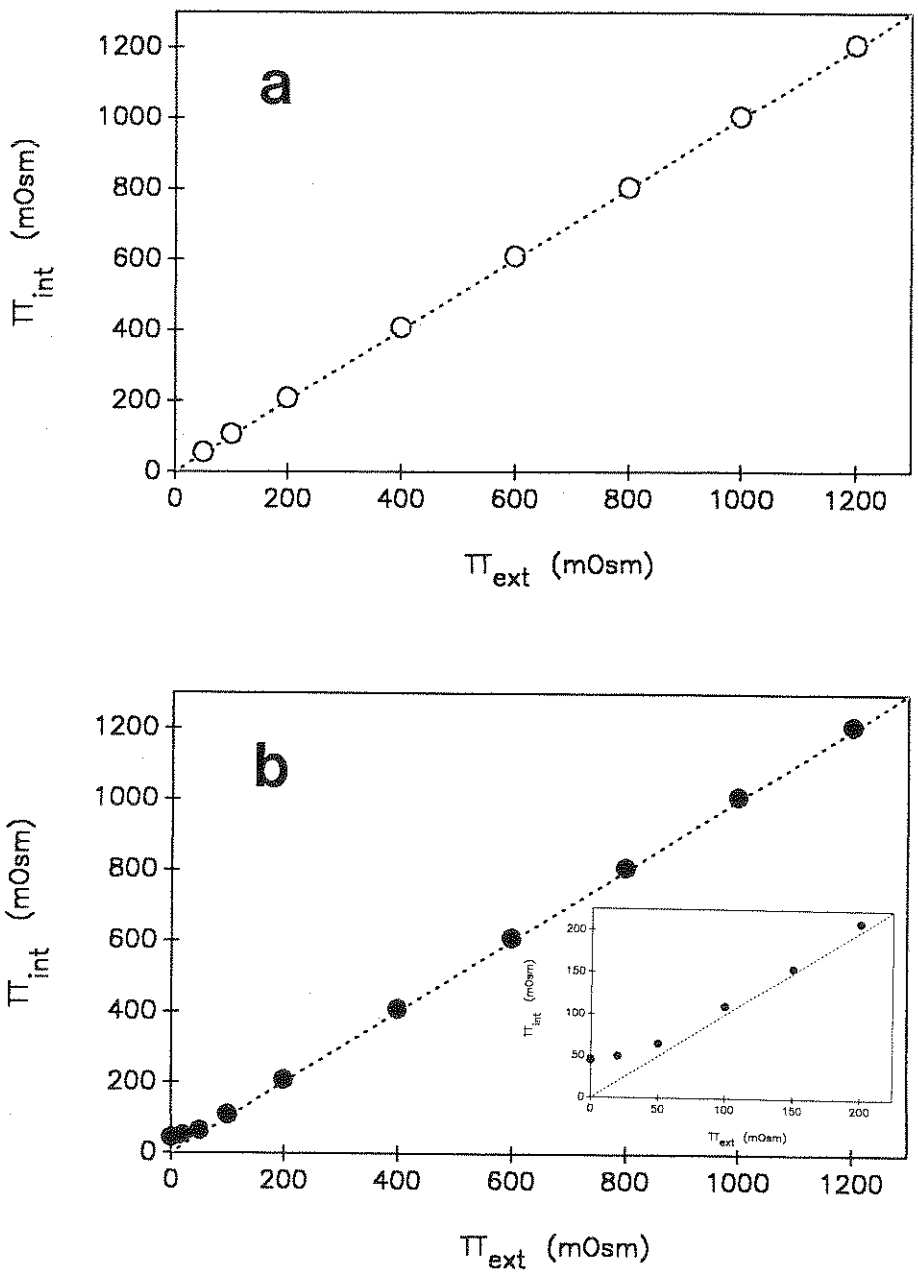

FIG. 2. The relationship between hemolymph osmotic concentration (π_{int}) and the ambient osmotic concentration (π_{ext}) for an osmoconforming (a) and for an osmoregulating (b) bivalve. The dashed line represents the isoosmotic line (*i.e.*, $\pi_{int} = \pi_{ext}$); 0 mOsm = deionized water, 1100 mOsm = seawater (35 ‰).

Capacity for Increase in the Amino Acid Pool

The characteristic inability of many freshwater bivalves to tolerate increases in salinity has been correlated with a decreased capacity for enlargement of the free

amino acid pool in such species (Gainey & Greenberg, 1977). The increases in tissue amino acid levels in a variety of bivalves resulting from increasing the salinity of acclimation are summarized in Table 3. Notwithstanding the diversity of tissues, species, and methodologies used in these experiments, the ratio of the change in amino acid concentration to the difference in osmolality of acclimation provides a rough measure of the capacity of these species to respond to increases in external salinity. *Corbicula manilensis* has the highest such capacity, while *Anodonta cygnea* Linnaeus has the lowest. Although the amino acid increase is low in *A. cygnea*, a unionid, this capacity in other freshwater species (*e.g.*, *Corbicula leana* Prime and *L. fortunei*) and euryhaline marine species (*e.g.*, *Geukensia demissa* Dillwyn, *Mytilus edulis* Linnaeus and *M. arenaria*) are similar. Moreover, *Spisula solidissima* Say, which is stenohaline, has a higher capacity of amino acid increase in response to increased ambient salinity than most of the euryhaline species.

Rate of Change in the Amino Acid Pool

The duration of impairment of cellular function due to osmotic stress depends on the rapidity of volume regulation. The rapidity of volume regulation is partly related to the rate of change in the free amino acid pool. The rates of increase or decrease of cytoplasmic amino acids in response to short-term hyper- or hypo-osmotic stress, respectively, may vary among euryhaline and stenohaline species. These differences, if they occur, could be related to the ability of the animals to adapt to dilute habitats. The available data are not strictly comparable, *i.e.*, the amino acids were measured in various ways, and the species were not all exposed to the same salinity changes. We have nonetheless used these data to examine the variability in the rate of change in the amino acid pool among animals with widely different salinity tolerances.

Rates of Amino Acid Accumulation

The rate of increase in cytoplasmic amino acids for several bivalves exposed to an increase in salinity, but not wedged open during the process, are summarized in Table 4. This rate is highest in *Mytilus arenaria* and lowest in more stenohaline species such as *M. edulis* and *Spisula solidissima*, but the total range of the value is only two-fold.

Rate of Amino Acid Release

Calculated rates of release of amino acids from the tissues of several bivalves exposed to hypoosmotic media are shown in Table 5. In all of the experiments the animals were either wedged open or were unable to close their shells completely (*Mya*). The lowest rate was obtained from *Crassostrea gigas* Thunberg, a euryhaline species. *Mytilus edulis*, with a salinity tolerance range similar to that of *C. gigas*, has a rate of amino acid release that is 4-5 times higher.

Conclusions

The range of salinities tolerated by a marine or brackish water bivalve does not seem to be closely related to the capacity of the tissue amino acid pool to respond to increasing ambient salinity. Still, the inability of some freshwater species (*e.g.*, paleoheterodonts) to tolerate higher salinities is probably explained by a reduced

TABLE 3. Change in the amino acid content of various tissues of selected bivalve molluscs acclimated to high and low osmotic concentration.

SUBCLASS	Species	Habit	Tissue	Low π (mOsm)	Tissue FAA (low π)	High π (mOsm)	Tissue FAA (high π)	Δ FAA/Δ mOsm[1]	Acclimation Measure-ment	Acclimation Timen (days)	Reference
PTERIOMORPHIA	*Geukensia demissa*	ME	Ventricle	380	327	1020	612	0.44	A	70	Baginski & Pierce (1977)
	Mytilus edulis	ME	Whole animal	470	476	940	560	0.18	A	7	Livingstone (1979)
	Limnoperna fortunei	F-O	Mantle	0	7	210	96	0.42	A	24	Deaton *et al.* (1990)
HETERODONTA	*Corbicula manilensis*	F	Foot	15	20	160	197	1.22	A	30	Gainey (1978)
	Corbicula leana	F	Foot	3	40	440	243	0.60	N	5	Matsushima (1982)
	Corbicula japonica	O	Foot	3	48	440	283	0.70	N	10	Matsushima (1982)
	Polymesoda caroliniana	O	Foot	15	27	320	205	0.58	A	60	Gainey (1978)
	Rangia cuneata	O	Adductor	60	61	690	372	0.49	A	42	Henry & Mangum (1980)
	Spisula solidissima	MS	Gill	305	1040	910	1572	0.88	A	6	DuPaul & Webb (1974)
	Mercenaria mercenaria	ME	Gill	305	448	910	657	0.35	A	5	DuPaul & Webb (1974)
	Mya arenaria	ME	Adductor	60	282	630	733	0.79	N	5	Virkar & Webb (1970)
	Mytilopsis leucophaeta	O	Whole animal	0	167	600	590	0.71	A	22	Deaton *et al.* (1990)
PALEOHETERODONTA	*Anodonta cygnea*	F	Adductor	FW*	59	200	124	0.33	N	10	Potts (1958)

[1]Δ FAA/Δπ = (FAA @ high π - FAA @ low π) / (High π - Low π).
*No value given for fresh water; assume 5 mOsm.

Habit: MS = marine stenohaline; ME = marine euryhaline; O = oligohaline (0.5-20 ‰); F = freshwater (<0.5 ‰).
Free amino acid (FAA) values are expressed as μmol/g dry weight. Measurements: A = amino acid analysis; N = ninhydrin positive substances. Some of the values are re-calculated from data expressed as wet weight using data on water content from the referenced publications.

TABLE 4. Rates of amino acid accumulation in the tissues of selected bivalve molluscs exposed to hyperosmotic media.

SUBCLASS	Species	Habit	Tissue	Low π	Tissue FAA (low π)	High π	Tissue FAA (high π)	Time (hr)	Rate	Reference
PTERIOMORPHIA	*Mytilus edulis*	ME	Adductor	470	329	940	446	48	0.005	Deaton *et al.* (1985)
	Geukensia demissa	ME	Gill	380	206	1020	384	48	0.006	Baginski and Pierce (1977)
HETERODONTA	*Spisula solidissima*	MS	Gill	305	1040	910	1199	48	0.005	DuPaul and Webb (1974)
	Mercenaria mercenaria	ME	Gill	305	448	910	612	33	0.008	DuPaul and Webb (1974)
	Mya arenaria	ME	Gill	60	835	630	1131	42	0.012	Virkar and Webb (1970)
	Rangia cuneata	O	Adductor	60	61	690	266	48	0.007	Henry and Mangum (1980)
	Corbicula leana	F	Foot	3	40	440	138	48	0.006	Matsushima (1982)
	Corbicula japonica	O	Foot	3	48	440	147	48	0.006	Matsushima (1982)
	Corbicula manilensis	F	Foot	15	20	160	104	51	0.011	Gainey (1978)
	Polymesoda caroliniana	O	Foot	15	27	320	176	36	0.014	Gainey (1978)

Habits: MS = marine stenohaline; ME = marine euryhaline; O = oligohaline (0.5-20 ‰); F = freshwater (<0.5 ‰).
Tissue free amino acid (FAA) values are μmol/g dry wt.
Rate is (FAA @ high π - FAA @ low π)/time/(high π - low π); units = (μmol/g)/hr/mOsm.

TABLE 5. Rate of decrease in the amino acid content of tissues of selected bivalves exposed to hypoosmotic media.

SUBCLASS	Species	Habit	Tissue	High π (mOsm)	FAA (high π)	Low π (mOsm)	FAA (low π)	Time (hr)	Rate	Measurement	Reference
HETERODONTA	*Corbicula manilensis*	F	Foot	160	197	15	171	4	0.033	A	1
	Polymesoda caroliniana	O	Foot	310	193	15	174	6	0.011	A	1
	Mya arenaria	ME	Adductor	1005	1250	300	1145	6	0.025	N	2
PTERIOMORPHIA	*Mytilus edulis*	ME	Adductor	1005	490	300	330	6	0.038	N	2
	Crassostrea gigas	ME	Adductor	1005	580	300	545	6	0.008	N	2
	Geukensia demissa	ME	Ventricle	1020	740	510	640	8	0.025	A	3

Habits: ME = marine euryhaline; O = oligohaline (0.5-20 ‰); F = freshwater (<0.5 ‰).
Tissue free amino acid (FAA) data from animals that were wedged open; values are µmol/g dry weight.
Rate is (FAA ™ high π - FAA @ low π)/(high π - low π)/time; units = (µmol/g)hr/mOsm.
References: 1 = Gainey (1978); 2 = Shumway *et al.* (1977); 3 = Bartberger and Pierce (1976).

capacity for amino acid-mediated cellular volume regulation. This latter notion is further supported by the slow rate of accumulation of amino acids in the cytoplasm of isolated foot tissue of the unionid mussel *Anodonta woodiana* Lea, and the very low total accumulation in freshwater and brackish water clams in the genus *Corbicula* (Matsushima *et al.*, 1987). The data in Tables 4 and 5 suggest that neither the rate of amino acid accumulation in the tissues during hyperosmotic adjustment, nor the rate of amino acid release during hypoosmotic acclimation, is consistently related to salinity tolerance. Furthermore, these two physiological parameters are not obviously correlated with taxonomy.

OSMOTIC AND IONIC REGULATION

Bivalve molluscs may be divided into physiological groups based on the relationship between the osmolality of their blood and that of the medium. Most bivalves are osmotic conformers: the difference in osmotic concentration (π) between the blood and the medium is small and constant over the entire salinity range (Fig. 2a). Animals that inhabit dilute brackish waters are osmotic regulators in dilute media and osmotic conformers in more concentrated media (Fig. 2b). In these hyper-osmoregulators, the blood π is higher than ambient in dilute media. The major blood cation in bivalves is Na^+, and the major blood anion is usually Cl^-; in some freshwater species, the concentrations of Cl^- and HCO_3^- in the blood are nearly equal.

Hemolymph Osmotic Concentration

Those heterodonts that have been studied are osmotic and ionic regulators in media with an osmotic concentration below 70-100 mOsm (*e.g., Corbicula manilensis, Polymesoda caroliniana, Rangia cuneata, Sphaerium transversum* Say), whereas the many pteriomorph species that are tolerant of media of 100 mOsm or less are osmotic and ionic conformers (*e.g., Ostrea palmula, Geukensia demissa, Xenostrobus securis*) (Wilson, 1968; Pierce, 1970; Dietz, 1979; Deaton, 1981). The only freshwater pteriomorph that has been studied, *Limnoperna fortunei*, is an osmotic and ionic hyper-regulator in media below 60 mOsm (Deaton *et al.*, 1989).

Blood Ions

In paleoheterodont mussels and in heterodont pisidiid clams acclimated to fresh or deionized water, the π of the hemolymph is 45-65 mOsm; blood Na^+ is 15-20 mM, and the concentrations of Cl^- and HCO_3^- are each 10-15 mM (Dietz, 1979). The blood π of other freshwater heterodont clams acclimated to freshwater ranges from 40-65 mOsm: Na^+ is 12-30 mM; Cl^- is 15-25 mM; and HCO_3^- is only 3-6 mM (Dietz, 1977; 1979; Deaton, 1981). Blood bicarbonate has not been measured in a freshwater pteriomorph, but the ionic composition of *Limnoperna fortunei* hemolymph (Na^+ = 20 mM, Cl^- = 9 mM) suggests that the blood HCO_3^- concentration is substantial (Deaton *et al.*, 1989).

Many bivalves, when acclimated to dilute media, exhibit an elevation of the concentration of Ca^{++} in the blood (hypercalcemia). Examples include: euryhaline (*Scrobicularia plana*), oligohaline (*Rangia cuneata, Polymesoda caroliniana, Mytilopsis leucophaeta*) and freshwater (*Corbicula manilensis*) heterodonts (Akberali *et al.*, 1977;

Deaton, 1981; Fig. 3); freshwater pteriomorphs (*Limnoperna fortunei*) (Deaton *et al.*, 1989); and unionid mussels (Murphy & Dietz, 1976). This response declines as tolerance to fresh water increases, and only appears in unionids that have been maintained in distilled water. Euryhaline pteriomorphs - which cannot tolerate fresh water at all (*e.g., Geukensia demissa, Ostrea palmula*) - show no hypercalcemia in dilute media (Fig. 4), so the appearance of this response in *L. fortunei*, though consistent with its freshwater habitat, makes it unique among known Pteriomorphia.

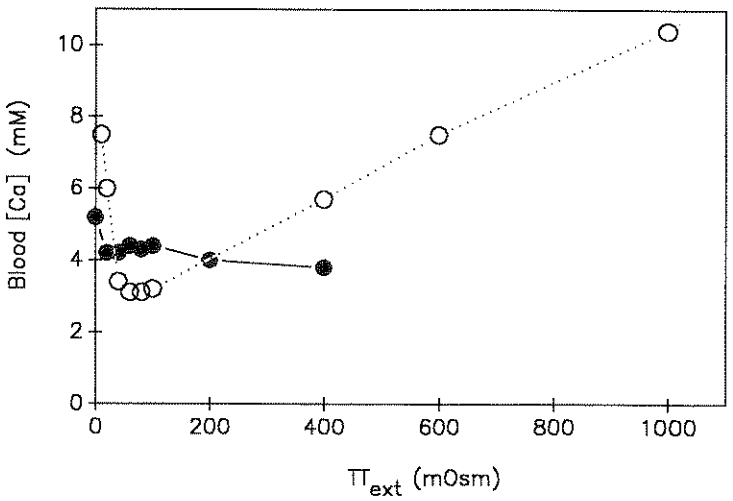

FIG. 3. The relationship between hemolymph Ca^{++} concentration and the ambient osmotic concentration in two heterodont bivalve molluscs. Symbols: open circles = *Polymesoda caroliniana*; solid circles = *Corbicula manilensis* (data from Deaton, 1981). 1100 mOsm = 35 ‰.

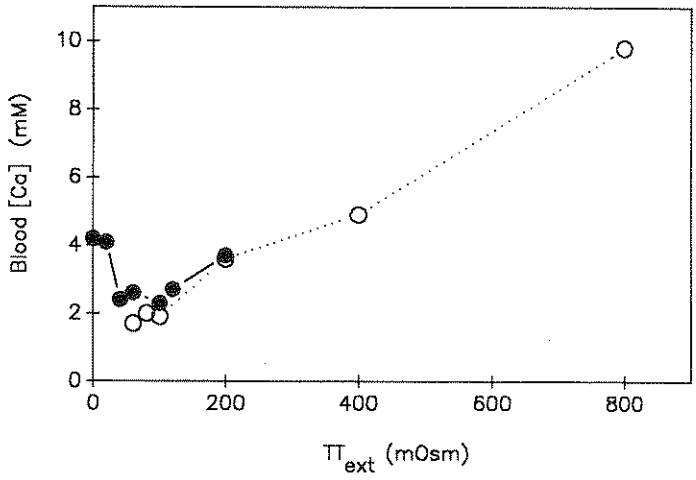

FIG. 4. The relationship between hemolymph Ca^{++} concentration and the ambient osmotic concentration in two pteriomorph bivalve molluscs. Symbols: open circles = *Ostrea palmula* (data from Deaton, 1981); solid circles = *Limnoperna fortunei* (data from Deaton *et al.*, 1990). 1100 mOsm = 35‰.

The elevation of blood Ca^{++} levels in the Heterodonta may underlie the ability of these animals to tolerate salinities in the laboratory that are lower than those in their most dilute habitats (see Fig. 1). The mechanism of action of the hypercalcemia may be related to the ability of Ca^{++} to affect membrane permeability; *i.e.*, the augmented blood Ca^{++} could simply be maintaining blood osmolality despite leakage of Na^{+}, or it could act by reducing the ionic permeability of the epithelium (Swinehart *et al.*, 1980).

Conclusions

Hyperosmotic regulation and hypercalcemia in response to very dilute media appear to be more common among brackish water heterodonts than among brackish water pteriomorphs. These two mechanisms may therefore be a preadaptation for the many colonizations of freshwater by species in the Subclass Heterodonta. By a similar argument, the absence of these mechanisms in most pteriomorphs may underlie their poor representation in the freshwater fauna.

EPITHELIAL PERMEABILITY TO WATER AND IONS

Bivalves in dilute media with blood osmotic and ionic concentrations above ambient, gain water and lose ions by diffusion. The rate of these fluxes is determined by the concentration gradient and by the permeability of the diffusion barrier, the epithelium. Bivalves are covered by an impermeable shell, but the epithelium is generally quite thin.

Prusch & Hall (1978) have shown that the epithelial water permeability of brackish water pteriomorphs (*Geukensia demissa, Mytilus edulis*) is lower than that of either freshwater paleoheterodonts (*Anodonta* sp.) or euryhaline heterodonts (*Mercenaria mercenaria*). The rates of sodium and chloride efflux from *Corbicula manilensis* and *Sphaerium transversum* (Heterodonta) are higher than those of paleoheterodont mussels (Dietz, 1979), suggesting that the latter are less permeable to ions. There is, then, variability in epithelial permeability to ions and water among bivalves tolerant of brackish and fresh waters. The systematic distribution of these differences and their evolutionary significance, if any, are impossible to evaluate without data from freshwater pteriomorph species such as *L. fortunei*.

URINE AND EXTRA-RENAL ION UPTAKE

Freshwater animals produce a urine less concentrated than the blood and take up ions from the medium by active transport in specialized tissues (gills, etc.). These transport tissues are characterized by high activities of ion-specific ATPases.

Paleoheterodont mussels produce a hypotonic urine (Picken, 1937; Hiscock, 1953); the ionic composition has been determined in *Margaritana margaritifera* Schumacher (Chaisemartin, 1968). The urine of other freshwater or brackish water bivalves has not been studied.

The gills of paleoheterodont mussels are sites of independent uptake of Na^{+} and Cl^{-}, and the rates of uptake by isolated gill preparations account for all of the ion uptake measured in intact animals (Dietz, 1985). Ion fluxes of intact *Corbicula manilensis* and *Sphaerium transversum* have been measured (Dietz, 1979), but comparable data from other freshwater species are lacking.

Both Na^+,K^+-stimulated ATPase and Cl^-,HCO_3^--stimulated ATPase have been found in the tissues of bivalve molluscs. The activity of Na^+,K^+-ATPase in the mantle and kidney of a number of freshwater and brackish water bivalves increases when the animals are exposed to dilute salinity. This manipulation results in very little change in the activity of the ATPase in the gill (Saintsing & Towle, 1978; Deaton, 1982). Similarly, exposure of the paleoheterodont *Carunculina texasensis* Lea to distilled water does not affect the enzyme activity in the gill (Dietz & Findley, 1980). The activity of carbonic anhydrase in *Rangia cuneata* gill and mantle tissue increases in animals exposed to lowered salinity (Henry & Saintsing, 1983). This enzyme is probably involved in supplying bicarbonate ions for chloride uptake. Although the gills are certainly important sites of ion uptake in paleoheterodonts, the relative roles of the gills and mantle in the ionic balance of these and other species have not been thoroughly investigated.

SPECIALIZED REPRODUCTIVE MECHANISMS

The parasitic larval forms and brooding behavior in the specialized gill marsupia of paleoheterodonts is well known. Most freshwater bivalve species are ovoviviparous, retaining fertilized embryos through an advanced stage of larval development. Exceptions include *Dreissena polymorpha* Pallas, *Limnoperna fortunei*, and the shipworm *Nausitoria dunlopei* Wright (this latter species is probably not a freshwater animal) (Morton, 1969; Morton, 1987; Barnes, 1987). Ovoviviparity is common among bivalves of all orders, excepting the Nuculoida and the Solemyoida, and occurs in many marine species (Sellmer, 1967). The rapid spread of *D. polymorpha* throughout the rivers and lakes of Europe from the Caspian Sea (Morton, 1970) and its current successful invasion of the Great Lakes (Hart, 1990), is clear evidence that developmental adaptations such as parasitic larvae or brooding are not prerequisites to the successful colonization of fresh water.

PTERIOMORPHS AND HETERODONTS: OTHER PHYSIOLOGICAL DIFFERENCES

Several other physiological and biochemical disparities between the Pteriomorphia and the Heterodonta have emerged, including: the ionic basis of cardiac excitability (Deaton and Greenberg, 1980); the mobilization and storage of intracellular calcium (Koch & Greenberg, 1981); myocardial adenylate cyclase activity (Higgins, 1974); and cholinesterase activity and specificity (Roop & Greenberg, 1976). Attempts have been made to relate these differences to freshwater adaptability (Greenberg & Deaton, 1978), but many such differences could arise between subclasses that have been diverging since the middle of the Ordovician, and they might, or might not, have a direct bearing on salt and water balance.

CONCLUDING REMARKS

Very little is known about the biology of many of the animals in Table 1, and data on salinity tolerance, blood composition, and permeability to water and ions are incomplete or nonexistent. Therefore, many lists of "authentic" stenohaline freshwater bivalves (*e.g.*, Hutchinson, 1967; Purchon, 1979; Table 1) may contain animals that are, upon closer examination, neither stenohaline nor tolerant of fresh

water. For example, when specimens of *Egeria radiata* Linnaeus (a "freshwater" donacid from the lower Volta River in Ghana) were placed in freshwater aquaria, they died with their mantle lobes exposed and swollen, even though clams from the paleoheterodont family Mutelidae in adjacent aquaria suffered no mortality (Purchon, 1963). The freshness of the Volta River at the collection site was confirmed with a hydrometer and by titration, but during the dry season, the river was reported to be "too saline to be drinkable" (Purchon, 1963). Clearly, *E. radiata* has a salt requirement very much like that of the estuarine mussel *Xenostrobus securis*, which occurs in the Swan River estuary in western Australia (see Wilson, 1968); neither of these species is a freshwater animal.

A consideration of the provisionally authentic freshwater bivalves listed in Table 1 suggests that there have been about 13 independent colonizations of this habitat. Of these, four are cosmopolitan in distribution: Paleoheterodonta, Corbiculidae, Pisidiidae and Dreissenidae. The rest are relatively local and are, furthermore, restricted to the tropics: three in West Africa and the Congo, and the rest in the Indo-West-Pacific. Indeed, the few freshwater pteriomorphian bivalves are restricted to the latter region (Table 1). The efficacy of the Indo-West-Pacific region in giving rise to freshwater species could reflect the high diversity of its brackish water species, due in turn to such characteristics as: the large area of estuarine interface between the marine and freshwater habitats; the shallowness of the estuarine salinity gradient; repeated fluctuations in the water levels of the estuaries; and the long-term climatic stability (Hutchinson, 1967; Briggs, 1974; Vermeij, 1978; Davis, 1982).

The physiological bases for the paucity of freshwater pteriomorphs remain obscure. Increases in blood Ca^{++} in response to decreasing ambient salinity, which seem to occur in euryhaline heterodonts but not in euryhaline pteriomorphs, may be important. The relative prevalence of hyperosmotic regulation among brackish water heterodonts and the paucity of osmotic regulation in brackish water pteriomorphs may represent a pre-adaptation for the invasion of fresh waters by members of the former subclass. Other physiological differences seem to be distributed by taxa, but their roles are obscure. Finally, the lack of information about water and ion permeability, urine formation, and other factors involved in osmoregulation precludes any evaluation of their contributions to this striking phylogenetic distinction.

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