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The American Naturalist, Vol. 112, No. 987 (Sep. - Oct., 1978), 833-843.

Vol. 112, No. 987 The American Naturalist September–October 1978

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The shells of freshwater gastropods in comparison to those of most marine snails are generally thin and dull colored, and they are often modestly or not at all ornamented with sculpture. Exceptions to this general conservatism are found in the basins of several large rivers and lakes, the best known being those in Lake Tanganyika. Many authors (Pilsbry and Bequaert 1927; Yonge 1938; Hubendick 1952; Leloup 1953; Beadle 1974) have looked upon these remarkable snails of the Rift Valley lakes of east Africa as forms convergent to marine shelled gastropods and generally attributed such similarities to the high concentration of calcium carbonate, exposure to specific physical conditions (such as deep, quiet water or heavy wave action), rapid speciation rates, or trophic specialization within the lakes.

In this paper, we propose the hypothesis that the morphological elaboration of shell form among many snails of ancient rivers and lakes is associated with the evolution of specialized molluskivorous animals. We also examine the extent of convergence between freshwater and marine forms and briefly explore the generally impoverished and conservative character of freshwater biotas.

SHELL FORM AND PREDATION

On the basis of earlier literature, Vermeij (1974) suggested that strong shell sculpture, occluded apertures, and low spires coupled with a thick shell are effective devices among many marine benthic gastropods in thwarting the attacks of fishes, crabs, lobsters, and other shell-breaking and shell-entering predators. Further work on predation by grapsid crabs on intertidal snails in New Zealand (Kitching and Lockwood 1974) and observations on feeding methods employed by mollusk-eating xanthid and parthenopid crabs in Guam (Vermeij 1975; Vermeij and Zipser, in prep.) suggest that narrow or occluded apertures serve to deter predators from breaking the lip and from pulling soft parts out of the shell. Occluded teeth among land snails have been shown to exclude shell-entering predaceous beetles (for a review, see Solem [1972]). Strong sculpture in the form of ribs, knobs, and spines strengthens the shell and makes it effectively larger and therefore more difficult for a predator to handle (Vermeij 1974).

Several lines of evidence suggest that some similar selective pressures exist among freshwater snails. A large number of different freshwater fishes consume thin-shelled snails such as *Physa* (Carlander 1969; Carothers and Allison 1968). For example, Ivlev (1961) reports a preference by some freshwater fishes (those with pharyngeal teeth, such as carp) for thin-shelled mollusks when given a choice between thin- and thick-shelled individuals. In their study of predation by carp (*Cyprinus carpio*) on gastropods in Skadar Lake, Yugoslavia, Stein et al. (1975) report that the spirally ridged form of

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Pyrgula annulata (Hydrobiidae) is less easily crushed and less frequently eaten than the smooth form of that species. They also found that while comparatively thin-shelled snails such as *Valvata piscinalis* (Valvatidae) less than 3 mm in diameter were swallowed whole and remained intact, larger snails were crushed by the pharyngeal teeth or were not eaten at all. In laboratory studies of carp from Skadar Lake, Covich and Knezevic (in press) found that large-sized individuals of even very thin-shelled species such as *Lymnaea auricularia* (Lymnaeidae) escape frequent predation. Some complexities of fish predation on *Lymnaea* (and many other invertebrates) are reviewed by Macan (1977).

Covich (in press) has obtained similar results on the effects of size, shape, and shell thickness in the laboratory studies of predation by crayfish (Cambaridae). *Procambarus clarkii*, *Procambarus acutus*, and *Procambarus llamasi* readily crushed and ate large numbers of relatively small thin-shelled *Physa gyrina* (Physidae) while the same crayfish rarely broke the thicker shells of the planorbid *Helisoma trivolvis* (also see Deschiens and Lamy [1954]; Piesik [1974]). Studies of turtles (*Pseudemys scripta*) also show the same trend of higher rates of predation on small thin-shelled physids than on large thick-shelled planorbids (Covich, in prep.). Bartonek and Hickey (1969) found that ducklings (*Aythya valisineria* and *A. americana*) in Manitoba could easily crush physids and lymnaeids, but planorbids could not be crushed and were rare in their diet. Small mammals also break gastropod shells they obtain from shallow waters (Parisi and Gandolfi 1974) and probably are capable of consuming larger numbers of thin-shelled species than species with thick shells.

OTHER ANTIPREDATORY ADAPTATIONS

Additional or alternative means of avoiding molluskivores are primarily behavioral and have evolved independently of shell form. There are numerous avoidance behaviors which frequently allow even thin-shelled species with large apertures to escape their predators. Some snails take advantages of spatial-temporal refuges, such as the undersides of large rocks, and forage on open surfaces only at night (see also Ebling et al. 1966; Vermeij 1974). Many thin-shelled pulmonates float quickly to the surface of the water when they release their hold on the substrate after being disturbed by benthic predators. The effectiveness of behavioral refugia for freshwater snails has not been extensively evaluated.

LIFE HISTORY AND PREY-PREDATOR COADAPTATION

Life cycles of some snails, notably freshwater pulmonates, promote rapid growth and maturation as well as high reproductive potential and widespread passive dispersal. Most aquatic pulmonates have life spans of 1 to at most 3 yr (Clarke 1969). These life-history characteristics are typical of species that rapidly colonize relatively temporary waters. In such habitats, it is not adaptive for short-lived species to develop heavy or otherwise armored shells that would impede foraging motility and dispersal. Most predators on snails in temporary fresh waters (birds, leeches, salamanders, sciomyzid flies, ostracods, some Coleoptera) swallow their prey snails whole, enter the shell, or wrench the soft parts out of the shell without breaking it (Fromming 1956; Michelson 1957; Branson 1963; Berg 1964; Eisenberg 1966; McAnnally and Moore 1966; Snyder and Snyder 1969; Sohn and Kornicker 1975; Eckblad 1976). The same appears to be true of some fishes which in temperate lakes and streams feed incidentally on gastropods (Baker 1916, 1918; Grygierek and Wolny 1962; Macan 1966, 1977; Eyerdam 1968; Keast 1970; Ware 1973; Werner 1974; Sadzikowski and Wallace 1976).

In contrast to the thin-shelled, short-lived, and widely dispersed species of temporary waters, snails in permanent aquatic habitats are often prosobranchs with life spans of several years (Kozhov 1963; Dazo 1965; Clarke 1969). The geographic ranges of these species are often small compared to ranges of many pulmonates (Stankovic 1960; Kozhov 1963; Taylor 1966*a*, 1966*b*; Clarke 1969; Davis 1971). Most species in permanent waters have thicker, more armored shells than their counterparts in temporary waters. We believe that this greater development of shell armor evolved partly in conjunction with specialized predators and that life cycles deemphasizing dispersal and promoting outcrossing and longevity have contributed to this coadaptation. This view closely parallels that of Cates (1975) and Rhoades and Cates (1976), Cates and Orians (1975), and Levin (1975) for plant-herbivore interactions. We further contend that predator-prey coadaptation has proceeded furthest or has remained at a higher level in geologically old lakes and river basins, where the most bizarre mollusks are found (see below).

The nature and extent of armor among freshwater mollusks in permanent waters are determined in part by the availability of calcium carbonate. Many authors writing about the conservatism of freshwater snails argued that thick, elaborately sculptured shells can occur only in lakes and the lower courses of large rivers whose waters are rich in calcium carbonate (Adams 1915; Wenz 1921; Haas 1922; Pilsbry and Bequaert 1927). In environments such as mangrove swamps, however, where calcium carbonate is often unavailable, such calcium-conserving methods as inner-whorl resorption and apical decollation (Vermeij 1973) have not precluded the development in several gastropod families of thick shells with dentate apertures. In Lake Baikal, the low temperatures prevailing in this Siberian lake place limits on the development of heavy shells, yet endemic Baikalian snails tend toward gigantism or else are highly ornamented relative to more widespread Palearctic species (Kozhov 1963). Moreover, both Lake Baikal and the equally cold Lake Titicaca contain species exhibiting open coiling (Rex and Boss 1976), a geometrical configuration seemingly incommensurate with the demands of carbonate conservation. Indeed, high-spired shells with a carbonate-demanding morphology (Grous 1974) are all too common in freshwater assemblages among which calcification is often thought of as limiting. Generally we expect mineralogical restrictions on shell architecture to be most relaxed in warm temperate and tropical lakes and large rivers whose drainage basins contain limestone.

THE FAUNA OF ANCIENT BASINS

In this section we summarize the geographical distribution of the morphological devices among freshwater gastropods that are interpreted as having an antipredatory function and examine some cases of possible predator-prey coevolution.

Sculptural elements such as knobs and spines are exceptional among freshwater gastropods, being known only among a small number of prosobranchs and only one pulmonate (*Armiger crista*). Sharp outwardly directed spines or knobs are known in several prosobranch species of: *Clithon* (Neritidae) from the Indo-West-Pacific; *Brotia* (Thiaridae) in Southeast Asia (Brandt 1974; Davis 1971) and India; *Semisulcospira* (Pleuroceridae) in the Lake Biwa area of Japan (Davis 1969); and among eastern North American pleurocerids (some *Io*, *Pleurocera*, *Lithasia*, *Oxytrema*). There are also a number of Southeast Asian hydrobiids with well-developed knobs (Brandt 1974). The Tanganyikan genus *Tiphobia* (Thiaridae) and many populations of the Indo-West-Pacific genus *Thiara* and Madagascan *Melanatria* (Pleuroceridae) possess apically directed spines. Within the prosobranch family Viviparidae, the most highly sculptured and thick-shelled forms evolved (but are now very rare or extinct) in the Coosa River of Alabama (*Tulotoma*) and in various rivers and lakes in Southeast Asia.

The most elaborately sculptured Hydrobiidae, a family of generally inornate snails never exceeding 12 mm in shell length, are found in species from Central America and the West Indies (Covich 1976), the southwestern United States (Taylor 1966*b*), the Mekong River (Brandt 1974), Lake Ohrid (Snegarova 1954; Stankovic 1960; Hadzisce 1956, 1974; Radoman 1973), Lake Titicaca (Haas 1955), and in several spring-fed ponds in the valley of Cuatro Cienegas, Mexico (Taylor 1966*a*). The parallel radiation of shell forms in these hydrobids appears to follow a distinct pattern in several geographically unrelated areas and may be associated with competition for exploiting specific microhabitats (G. M. Davis, in prep.).

With the exception of the Southeast Asian *Rivomarginella* (Marginellidae), which has a long narrow aperture and is one of only two freshwater members of the prosobranch order Neogastropoda (Coomans and Clover 1972) and *Acella haldemani* (Lymnaeidae), no freshwater snails have shells in which the ratios of aperture length : aperture breadth exceeds 2.5. The highest ratios (S) are found in some Brazilian populations of *Aylacostoma* (Thiaridae) ($S = 2.4$), some Philippine species of *Thiara* ($S = 2.1$), and some populations of the pleurocerids *Io* ($S = 2.4$) and *Lithasia* ($S = 2.2$) in the southeastern United States. Furthermore, no freshwater species is known in which the outer lip of the aperture is bordered by occluding teeth. In some tropical Planorbidae, lamellae set deep within the aperture extend from the shell whorl into the shell cavity, but these thickenings are not produced near the growing edge (Richards 1964).

The greatest morphological differentiation among freshwater gastropods has taken place in the Rift Valley lakes of Africa (especially Lake Tanganyika), rivers and lakes of the southeastern United States, the Mekong River, Lake Baikal, Lake Ohrid, Lake Titicaca, and the ponds of Cuatro Cienegas (Coahuila, Mexico). In nearly all these cases, the morphological radiation is within the confines of one or two prosobranch families. Temperate and boreal Planorbidae (*Planorbula armigera* and *Planorbula campestris*) have apertural denticulations on the inner and outer walls about one-quarter whorl back from the aperture. By contrast, the gastropods of African and South American rivers have remained morphologically and taxonomically rather conservative. Thus, elaborate sculpture and thick shells tend to occur most frequently and are most highly developed in river systems and lakes in which mollusks have undergone extensive adaptive radiations.

The limited evidence available suggests that adaptive radiations of specialized molluskivores have often accompanied radiations of mollusks. In the great lakes of Africa, a number of fishes, especially in the family Cichlidae, have become specialized predators of mollusks. They have evolved several mechanisms to this end, including hypertrophied molariform pharyngeal bones, powerful jaws with shell-crushing dentition, and other means for extracting snails from their shells without ingesting the latter (Fryer and Iles 1972; Liem 1973; Greenwood 1974). The reticulately ornamented prosobranch *Melanoides tuberculata* (Thiaridae) has a relatively thick shell, but it is easily crushed by various snail-eating cichlids (Fryer and Iles 1972; Greenwood 1974) and by such noncichlid predators in and around Lake Victoria as the lungfish *Protopterus aethiopicus*, some species of the cyrpinid genus *Barbus*, and species of the mochocid genus *Synodontis* (Corbet 1961). The physical stimulus of breaking hard shells, as well as the high calcium concentration of the diet of the cichlid *Astatoreochromis alluaudi* in Lake Victoria, allows for the development of crushing pharyngeal teeth, which are developed to a far lesser extent in specimens raised on, or naturally feeding upon, a diet of softer food (Greenwood 1974).

Sage and Selander (1975) have proposed that the adaptive radiation of the cichlid genus *Cichlasoma* in the ponds of Cuatro Cienegas is a genetic polymorphism within one species rather than the result of speciation. One of the morphs, with molariform pharyngeal teeth, feeds primarily on mollusks and contains all the known endemic genera of snails in its gut contents (Minckley 1969). Taylor (1966*a*) estimates that about 75% of adult *Nymphophilus* (Hydrobiidae) fall prey to this morph. It is tempting to agree with Taylor's (1966*a*) conjecture that the differentiation among the Cuatro Cienegas snails is related to the adaptive radiation of the cichlid.

In Laguna Chichancanab, a saline lake in the Yucatan Peninsula, four endemic species of the pupfish *Cyprinodon* occur, including one primarily feeding on small snails (R. R. Miller, personal communication to Covich, 1974). Covich (unpublished) collected fish up to 95 mm total length whose stomachs contained numerous snails (especially the hydrobiid *Pyrgophorus coronatus*), along with some ostracods and fragments of *Chara*. Though not endemic to the Chichancanab basin, *Pyrgophorus coronatus* is highly polymorphic there, being characterized by spiral thickenings and rows of sharp spines. These features probably are antipredatory deterrents both to the fish and to the crayfish *Procambarus llamasi.*

In Lake Titicaca (Boliva, Peru) only one of the 10 endemic cyprinodontiform fishes of the genus *Orestias* (*O. luteus*) is known to be a significant predator of snails (Eigenmann and Allen 1942; Tchernavin 1944), though nothing is known of its feeding selectivity. An unusual Titicacan snail predator is the very large frog *Telmatobius culeus*, which apparently does not break the shells of the two gastropod species it consumes (V. H. Hutchison, personal communication to Covich, 1976). Some endemics occur among the gastropods of Lake Titicaca, including a remarkable hydrobiid of the genus *Strombopoma* whose high-spired operculum extends beyond the outer lip of the shell and has the form of a corkscrew (Haas 1955). The adaptive significance of this potential defensive structure is unknown. A remarkably convergent hydrobiid is known from Lake Ohrid (Taylor 1966*a*), whose endemic fauna resembles that of Lake Titicaca in consisting of small species. Nothing is known at present of molluskan predators in Lake Ohrid.

In Lake Baikal, some widespread and endemic fishes are known to include mollusks in their diet (Kozhov 1963), but the specific composition and mode of ingestion are unknown. Similarly, we have little information on the potential of the highly sculpted mollusks in Lake Biwa, but the long history of this lake is currently under active study (Horie 1974). In the river systems of the southeastern United States, some studfishes have molariform teeth with which they presumably crush small mollusks (Thomerson 1969).

COMPARISONS BETWEEN MARINE AND FRESHWATER MOLLUSKS

If the elaboration of shell form among freshwater gastropods inhabiting ancient drainage basins is associated with the coevolution between snails and predators specialized upon them, we must seek an explanation for the much more limited extent of this process as compared with the sea. There are additional perplexing differences in form between marine and freshwater mollusks.

Strong sculpture is far more common and developed to a far greater extent among marine gastropods than among those of even the most diversified freshwater assemblages. Shell apertures with length : breadth ratios (S) that exceed 2.5 are very common among shallow-water marine gastropods, especially on tropical shores (Vermeij 1974). Similarly, occluding teeth impeding entrance into the aperture have evolved in numerous marine families (Vermeij 1974), as well as in such terrestrial pulmonate families as the Endodontidae, Vertiginidae, and Polygyridae. Long apertures among freshwater snails are present only in *Rivomarginella*, while occluded apertures are wholly absent. Even in the Neritidae, which in the sea have many representatives with thickened and dentate outer lips (*Nerita*), freshwater species are characterized by thin, unadorned lips. The shells of freshwater neritids are also generally thinner and the calcareous operculum is thinner and more flexible than those of marine species (Vermeij 1969).

Shell thickening around the apertures of freshwater snails is rare but occurs in some populations of *Biomphalaria* (Richards 1963). However, Bequaert and Miller (1973) conclude that these internal calcareous lamellae or teeth merely store surplus calcium temporarily for later shell growth among young *Biomphalaria havanensis*. They discount the likelihood that this armature affects snail vulnerability to predators or parasites, because many young and most adult snails resorb the teeth. An alternative hypothesis is that these teeth do retard some shell-breaking and shell-entering predators while the snails are small and that once the snails reach adult size they have other modes of escaping predators.

Vermeij (1975) noted that the incidence of planispiral coiling is strikingly higher among freshwater gastropods than among marine Recent forms and that planispiral freshwater snails are much larger than their marine counterparts. It was suggested that, since planispiral coiling is a mechanically weaker configuration than most types of conispiral coiling in which the whorls touch, selection of mechanically strong shells may be less intense in fresh water than in Recent seas. Planispiral coiling is much more frequent among nonboreal snails of temporary fresh waters than among those of large rivers and lakes where specialized molluskivores are more common. Rex and Boss (1974) have summarized the taxonomic distribution of open coiling among Recent gastropods. From their data, it appears that three of the 15 species with this geometry occur in fresh water. There are approximately 3,000 species of freshwater gastropods (estimated from data in Boss [1971]): This means that the incidence of mechanically weak open logarithmic coiling is higher in freshwater assemblages (0.1%) than it is on land or in the sea. This suggestion is strengthened by the contrasts in sculpture and apertural form between marine and freshwater gastropods referred to above. The complete absence of impenetrable apertures among aquatic snails, however, remains perplexing, especially since many snail predators have evolved mechanisms for removing the soft parts from the shell without injuring or ingesting the latter.

There are many more predatory gastropods in marine habitats than in fresh water. Some freshwater species, such as *Marisa cornuarietus* (Demian and Lutfy 1965), *Viviparus georgionus* (Eckblad and Shealy 1972), and *Lymnaea emarginata* (Michelson and DuBois 1974), are known to consume egg masses of other species, but generally there are very few reports of predaceous freshwater gastropods.

Carter (1968) pointed out that, with one exception (*Castalia*), interlocking shell margins and radial ribbing are unknown among freshwater bivalves despite the very widespread occurrence of these features in numerous families of marine clams. Carter believed that interlocking shells were adaptations against predatory starfishes, but since such margins are commonest in the tropics where molluskivorous forcipulate asteroids are rare, it seems more likely that they are primarily effective against the attacks of predatory crustaceans, snails, and birds. In any case, it appears that antipredator features among freshwater clams are less developed than they are in most shallow-water marine habitats. Freshwater mussels, other than *Anodonta*, do have interlocking hinge teeth, and in *Corbicula sluminea* the ventral margin is also crenulated and interlocking.

These and other differences between freshwater and marine communities (table 1) may be explained by historical causes or greater physicochemical limitations in fresh water. Even the oldest aquatic systems are geologically young and transient compared to marine communities. This view, explicitly stated by Hutchinson (1967), implies that there has been insufficient time for coevolution to have given rise to elaborate antipredatory characteristics. Yet, as Fryer and Iles (1972) and Sage and Selander (1975) have

TABLE 1

SUMMARY OF SNAIL-SHELL ARCHITECTURES

CHARACTERISTIC	HABITAT TYPE AND RELATIVE FREQUENCY OF OCCURRENCE				
	Tropical Benthic Marine	Temperate Benthic Marine	Planktonic Marine	Terrestrial	Freshwater
Planispiral coiling	Very rare	Very rare	Common	Common	Common
Open coiling	Very rare	Very rare	Absent	Very rare	Rare
Narrow, elongate aperture	Common	Very rare	Absent	Rare	Very rare
Strong external sculpture	Very common	Rare	Very rare	Rare	Rare
Teeth bordering aperture	Very common	Rare	Absent	Common	Absent
Inflexible opercula	Common	Rare	Absent	Rare	Rare

demonstrated, evolution of trophic adaptations in freshwater animals may be very rapid.

Even under the most favorable conditions in fresh water, calcium carbonate and other limitations may restrict predator-prey coadaptation to relatively modest levels. Such limitations not only may effect the prey but may well restrict the capacities of predators as well. Since temperatures in most bodies of fresh water are lower than those prevalent in tropical sea water, and since muscle power and rate of contraction are strongly temperature dependent in ectotherms, it is plausible that the extent to which predators have been able to improve their effectiveness in dealing with well-armored prey is limited.

Possibly related to such physiological limitations is the absence in fresh water of many predators which in the sea are important molluskivores. These include asteroids, octopods, palinurids, and other lobsters, stomatopods, most crabs, most elasmobranchs, and predatory snails. The predators which replace these marine forms in fresh water (astacuran crustaceans, insects, amphibians) are often smaller and less specialized for predation on hard-shelled invertebrates.

SUMMARY

We have tried to show that freshwater gastropods (especially those in temporary waters) are generally less well adapted to avoid predation by crushing or other shell destruction than are most benthic marine snails. The sturdiest freshwater snail shells occur in ancient lakes and rivers, but even here such common marine antipredatory characteristics as narrow and dentate apertures are wholly absent. Limitations on calcification may be in part responsible for this greater conservatism of freshwater as compared to marine gastropods, but many architectural types incommensurate with the demands of carbonate conservation are common among freshwater snails. Low temperatures in many freshwater systems may also place severe metabolic limitations on specialized trophic linkages among both molluskan prey and their predators.

ACKNOWLEDGMENTS

We wish to thank K. Brown, D. A. Livingstone, and R. A. Stein for their comments on a previous draft. J. D. Allan, G. M. Davis, E. H. Michelson, and I. Rubinoff suggested several references. This study was supported in part by National Science Foundation grant BMS 75-01010. We also appreciate G. E. Hutchinson's help and initial guidance.

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