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GEOGRAPHICAL VARIATION IN THE STRENGTH OF THAIDID SNAIL SHELLS

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One important selective pressure on molluscan shells is imposed by shell-breaking predators. Direct evidence for this biologically caused mortality comes from field studies of predation (Kitching, Muntz and Ebling, 1966; Kitching and Lockwood, 1974). The intensity of shell breaking is known to be greater in the tropics than in the temperate zones (Vermeij, 1979a). Correspondingly, tropical shells show greater development of traits that confer protection against crushing than do species in colder waters; these features include a globular shape (low spire), strong sculpture and a narrow or occluded aperture (Vermeij, 1978; Palmer, 1979).

In this paper we examine the mechanical resistance of shells to forces similar to those imposed by crushing predators such as fishes and crabs. Using the latitudinally widespread family Thaididae we show that tropical shells are considerably more resistant to cracking than temperate ones, and that this difference is to a considerable extent associated with differences in shell build (the size and shape of the shell) and microstructure.

Materials and Methods

Specimens of *Thais* (= *Nucella*) *lapillus* were collected by J. D. C. at Scarborough, Yorkshire, England, during 1978. Other species were collected by G. J. V. from various parts of the world from 1969 to 1977. The specimens were first boiled briefly until the soft parts could be removed with the aid of a needle, and were then dried at room temperature. They were thoroughly rewetted before testing. Curry (1979) has shown that such treatment is unlikely to have a serious effect on shell strength. The following shell measurements were made: dry mass M; length L (distance from apex to tip of siphonal canal); maximum breadth B. A measure of volume was estimated as $V = L \times B^2$. The acuteness of the shell was expressed as the ratio L/B. The thickness of the shell wall was considered, for comparative purposes, to be represented by the mass to volume ratio (M/V); for convenience this is expressed as $(g/mm^3) \times 10^5$.

Each shell was placed between the metal platens of a Howden compressive testing machine, the apertural side downwards and the dorsum of the shell touching the upper plate. The platens were brought together at the rate of 1 mm per minute. The shells broke within a few seconds. The maximum load borne by the shell was recorded; we call this value the strength. The method of testing we used corresponds reasonably well to the type of force exerted by rays, puffers, and crabs that crush the shell, but not to the peeling action exerted by many crabs (Shoup, 1968). Although not specifically dealing with the latter mode of attack, the method of testing used gives an idea of the general robustness of the shells.

The fracture surface of at least one specimen from each species was examined under a scanning electron microscope. All species showed crossed-lamellar struc-

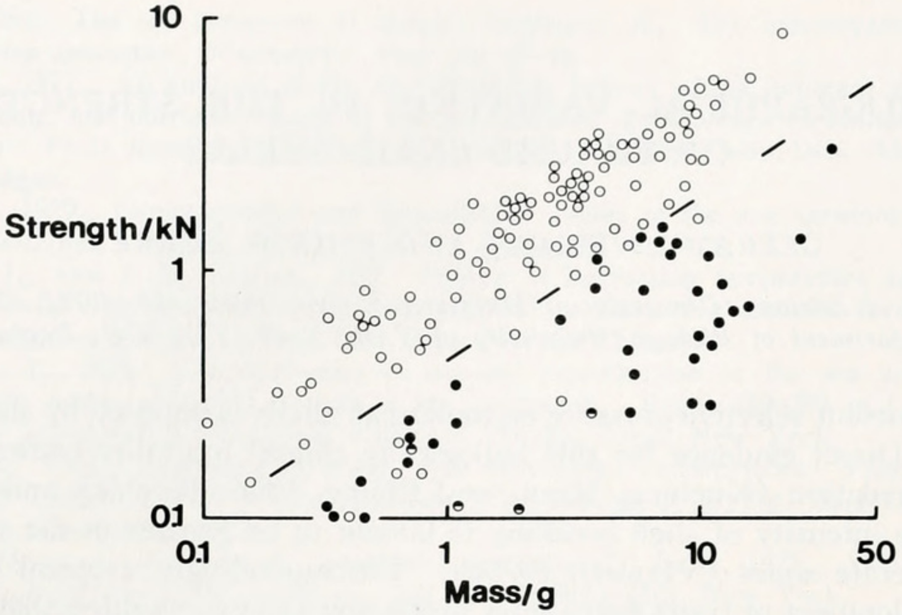

FIGURE 1. Relationship of strength and mass of shells. Open circles—tropical sites; solid circles—temperate sites; half-filled circles—Dakar. The interrupted line is log load (knN) = − 0.3 + 0.67 (log mass (g)).

ture, as would be expected in the Thaididae (Bøggild, 1930). However, in a few specimens it was ill defined, and could be seen only with difficulty. In such cases several specimens of the same species were examined to see whether this was a general phenomenon, or whether it was restricted to a single individual. It seemed always to be characteristic of the species. Some species had a very characteristic layer of calcite on the outer surface of the shell, which looked almost structureless under the scanning electron microscope. Again, according to Bøggild (1930), this is not unexpected. In two species this layer made up a substantial proportion of the whole thickness of the shell: about 30–40%. In the other species the layer was very thin, and has been ignored in the discussion.

The question of whether a shell comes from a tropical or a temperate faunal zone is in most cases easily decided. Only for Dakar (on the bulge of Africa) is there some doubt (Briggs, 1974). Dakar has a minimum sea-surface temperature of about 19° C. This value is intermediate between the minima of other sites that are clearly tropical or temperate.

RESULTS

Figure 1 shows the relationship between strength and shell mass. Note both ordinate and abscissa are on a log scale. Temperate shells are shown by solid circles, tropical shells by open circles. There were 36 shells of *Thais lapillus*. In order that they should not dominate the diagram visually we chose seven randomly. However, *all* shells of this species are included in the calculations and discussion. Expressing shell strength in relation to mass shows, in effect, the amount of protection that can be obtained from a unit mass of shell. In general, if a shell is stronger per unit mass this implies that it is thicker-walled. This is certainly true for *Thais lapillus* studied by Kitching, Muntz and Ebling (1966).

In general, the tropical shells lie above the temperate ones. It is also clear that, although the lower boundary is ill-defined, the upper boundary is quite sharp. This may indicate the maximum strength that can be achieved by a thaidid shell

TABLE I

"Minimum sea temperature"—Data taken from maps in Sverdrup, Johnson and Fleming (1970), except for Eilat (data supplied by Israeli Embassy, London, personal communication) and Panama (data from U.S. National Ocean Survey, 1970).

"Tropical"—Checks indicate certainly tropical, crosses certainly temperate, question marks intermediate. "Above" and "Below"—Number of specimens above and below the interrupted line in Figs. 1 and 2. "Acuteness"—The mean ratio of length to breadth of the specimens. "Thickness"—The mean value of the mass/volume ratio of the specimens.

"Structure"—Checks indicate clear crossed-lamellar structure, crosses indicate indistinct structures; C indicates a thick layer of calcite on the outside of clear crossed-lamellar structures. After the locality name, P indicates Pacific or Indopacific, and A indicates Atlantic.

Species	Locality	Min. Sea Temp.	Tropical	Above	Below	Acuteness	Thickness	Structure
Cymia tectum	Panama P	27	√	2	0	1.20	28	√
Drupa arachnoides	Guam P	27	√	7	0	1.11	38	√
Drupa morum	Guam P	27	√	5	0	1.09	43	√
Drupa ricinus	Guam P	27	√	6	0	1.12	38	√
Drupella alata	Guam P	27	√	2	0	1.85	55	√
Morula fiscella	Guam P	27	√	2	0	1.60	32	√
Morula granulata	Hawaii P	27	√	7	0	1.45	37	√
Morula granulata	Guam P	27	√	9	0	1.48	52	√
Morula granulata	Palau P	27	√	6	0	1.38	55	√
Morula granulata	Eilat P	20	√	5	0	1.51	48	√
Morula uva	Guam P	27	√	2	0	1.41	44	√
Thais deltoidea	Curaçao A	25	√	6	0	1.31	33	√
Thais deltoidea	Panama A	27	√	3	0	1.35	41	√
Thais hippocastanum	Guam P	27	√	2	0	1.23	28	√
Thais kiosquiformis	Panama P	27	√	1	0	1.32	19	√
Thais melones	Panama P	27	√	7	0	1.31	53	√
Thais triangularis	Panama P	27	√	2	0	1.16	37	√
				Mean		1.35	40.1	
Acanthina brevidentata	Panama P	27	√	4	1	1.54	36	√
Thais coronata	Ivory Coast A	24	√	2	2	1.27	37	C
Thais haemastoma	Ghana P	24	√	8	1	1.46	33	√
Thais haemastoma	Costa Rica P	26	√	4	4	1.36	26	√
Thais lapillus	England A	6	x	1	35	1.59	50	x
				Mean		1.44	36.4	
Acanthina calcar	Chile P	14	x	0	4	1.35	41	x
Purpura patula	Curaçoa A	25	√	0	2	1.45	18	√
Thais chocolata	Peru P	17	x	0	2	1.34	28	C
Thais haemastoma	Dakar A	19	?	0	4	1.62	27	√
Thais haemastoma	Peru P	19	x	0	12	1.43	21	√
Thais lamellosa	Washington P	9	x	0	10	1.75	30	x
				Mean		1.49	27.5	

built of crossed-lamellar structure while still allowing some living space inside. The tropical scatter of strengths follows a slope of strength $\propto$ mass$^{\frac{2}{3}}$ fairly closely, and we have arbitrarily divided the scatter into those points that are above and below the line of the equation log load (kN) = $-$ 0.33 + 0.67 (log mass (g)). This is drawn in Figure 1.

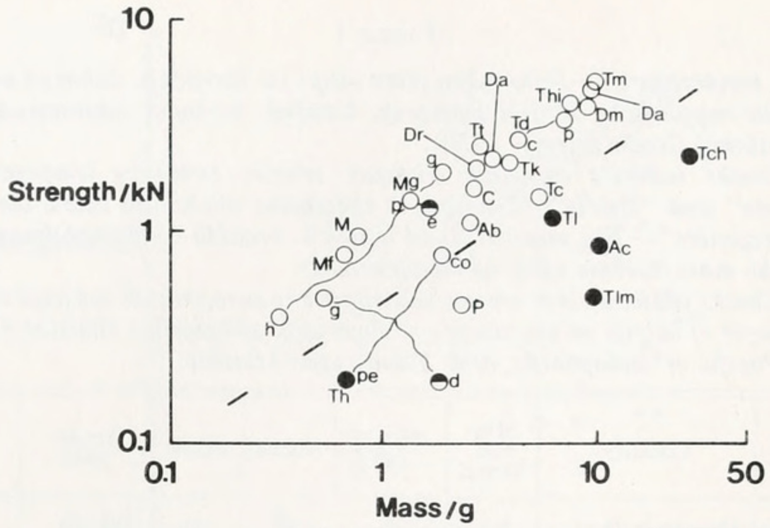

FIGURE 2. Species characterized by medians of load and of mass. Wavy lines join medians of collections made at greatly distant sites. Ab-*Acanthina brevidentata*; Ac-*Acanthina calcar;* C-*Cymia tectum;* Da-*Drupa arachnoides;* Dm-*Drupa morum;* Dr-*Drupa ricinus;* Da-*Drupella alata;* Mf-*Morula fiscella;* Mg-*Morula granulata,* e-Eilat, g-Guam, h-Hawaii, p-Palau; M-*Morula uva;* P-*Purpura patula;* Tch-*Thais chocolata;* Tc-*Thais coronata;* Td-*Thais deltoidea,* c-Curaçao, p-Panama; Th-*Thais haemastoma,* co-Costa Rica, d-Dakar, g-Ghana, pe-Peru; Thi-*Thais hippocastanum;* Tk-*Thais kiosquiformis;* Tl-*Thais lapillus;* Tlm-*Thais lamellosa;* Tm-*Thais melones;* Tt-*Thais triangularis.*

In Table I species, or populations from different localities, are listed alphabetically in three groups: all specimens above the dashed line in Figure 1; some above and some below; all specimens below the line. Of course, the more specimens of a species that are tested, the more likely it is that one or two specimens will stray above or below the line. Figure 2 attempts to demonstrate that this effect is unimportant. Each species is represented by its median value for load and median value for mass. The position of the species medians in relation to the line is seen to accord very well with the proportion of specimens falling above and below the line. From now on we shall call species all of whose shells fall above the line "strong," those that fall below "weak," and those that have specimens above and below "intermediate." This is for convenience only, and of course implies no hard and fast distinctions among species in the different categories.

All the strong species are tropical. Of the weak species, four are temperate, one is tropical, and one comes from Dakar, which might be considered as temperate. Of the intermediate species, three are tropical (*Thais haemastoma* is represented twice) and *Thais lapillus,* a temperate form, has but one shell out of 36 above the line.

The inescapable conclusion from this is that in the Thaididae the tropical shells are stronger than the temperate ones. In general the shells are about four times more resistant to crushing than temperate shells of similar mass.

We have demonstrated geographical differences in shell strength. We consider next what features of the shell may contribute to its strength or weakness. Probably the strongest shape for a shell that must grow like a snail's and which can be attacked from various directions is a thick-walled spheroid. A crude measure of the thickness of the walls is mass/volume. Table I shows that the strong species are in general thicker walled than the intermediate or weak shells. Using the species means as data points, the overall analysis of variance shows a significant difference in the means $F_{2,25} = 3.73$ $P < 0.05$. The strong shells are significantly thicker than the weak shells $F_{1,21} = 7.19$, $P < 0.05$.

There is an indication in Table I that the stronger shells are less acute. Taking species' mean acuteness from Table I as data points, the Mann–Whitney U test for the difference between the strong populations and the others lies on the border of significance ($Z = 1.91$, $P \simeq 0.05$). The difference is certainly not as marked as the difference in mass/volume. The interrelationship of these two variables is shown in Figure 3. The weaker shells are predominantly to the right and bottom of the diagram, showing that in general they are both thin-walled and acute.

The structure of the shell material also shows some relationship with shell strength, in that the three species that had rather ill-defined crossed-lamellar structure were intermediate or weak. There were two species with large amounts of calcitic accretion on the outside of the shell: *Thais coronata* and *Thais chocolata*. These species were intermediate and weak respectively.

Although the mode of fracture of crossed-lamellar structure is not well understood, Currey and Kohn (1976) have shown that the orientation of the lamellae is important in preventing cracks from traveling right through the shell. The ill-defined crossed-lamellar structure seen in three species of thaidids will be less able to interrupt crack travel than the well-defined structures. This will also be true of the calcite coating seen in two species.

Discussion

In general, temperate Thaididae are considerably weaker than tropical ones, and we have also shown features of shell build and microstructure that are at least partially correlated with this. However, the selective reasons for this difference are not clear. Obviously, it should benefit any snail subject to crushing to be resistant to crushing by predators. Vermeij (1977) and Zipser and Vermeij (1978) have produced evidence that, in general, temperate shell crushers are not as strong as tropical ones. Nevertheless, the relatively weak temperate *Thais lapillus* is often killed by its local, relatively weak predators, crabs (Kitching, Muntz, and Ebling, 1966). *Thais lapillus* would therefore appear to gain a considerable selective advantage were it to evolve a stronger shell; yet it does not. Mass for mass it is far weaker than tropical shells like *Thais deltoidea* and *Drupa arachnoides*.

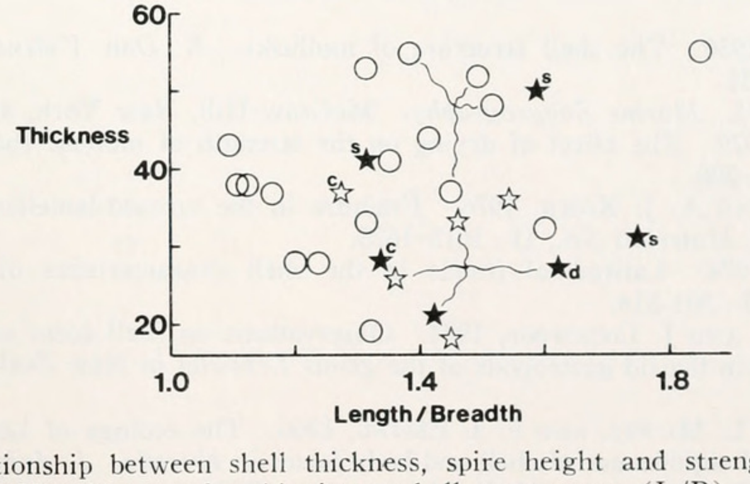

FIGURE 3. Relationship between shell thickness, spire height and strength. Ordinate = Shell thickness: $(M/V) 10^5/g\ mm^{-3}$. Abscissa = shell acuteness: (L/B). Open circles = Strong tropical shells. Open stars = intermediate or weak tropical shells. Solid stars = intermediate or weak temperate shells. d: *Thais haemastoma* from Dakar, s: Species with ill-defined crossed-lamellar structure, c: Species with a thick layer of calcite.

These latter species are relatively thicker-walled, more spherical, and have better developed crossed-lamellar structures. Presumably these shell features are disadvantageous in other ways to a temperate-region species. One disadvantageous feature of these tropical shells is that, being relatively thicker-walled for a given volume, there is less room for the animal inside. Snails of the genus *Conus* have overcome this problem by partially dissolving the interior whorls (Kohn, Myers, and Meenakshi, 1979). Therefore, a tropical snail of given body mass has to build and carry around a more massive shell than does a relative from temperate regions. Building a relatively more massive shell may be more difficult in temperate than in tropical regions. Graus (1974) has shown that in gastropods on the Eastern seaboard of the United States, there is an almost linear relationship between mean "calcification index" (the ratio of shell mass to its internal volume) and the mean water temperature. He suggests that the main reason for this is the relative insolubility of calcium carbonate at high temperatures. This makes it easier to produce calcium carbonate structures at higher temperatures. There is other evidence that this is the case (Vermeij, 1978, pp. 16–19). However, the increased intensity of predation in the tropics must also make strong shells selectively more necessary there. Whether the indistinct shell structure seen in three of the weaker temperate species is adaptive in some way—for instance, by being metabolically cheaper or quicker to lay down—or whether it is imposed on the animal by environmental factors, is unknown.

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Summary

The crushing strength of 170 specimens of shells of 21 species of Thaididae has been measured. In general, the tropical shells are much stronger, mass for mass, than the temperate ones. This strength is achieved mainly by the shells being thicker walled in the tropics, thereby leaving less room for the animal inside.

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