

PREDATION AND THE GEOGRAPHY OF OPERCULAR THICKNESS IN TURBINID GASTROPODS

GEERAT J. VERMEIJ¹ AND SUZANNE T. WILLIAMS²

¹*Department of Geology, One Shields Avenue, University of California at Davis, Davis, CA 95616, USA;*

²*Department of Zoology, The Natural History Museum, London, SW7 5BD, UK*

(Received 5 September 2006; accepted 21 November 2006)

ABSTRACT

The heavily calcified opercula of turban snails (Turbinidae) function as passive-defensive structures against predators that break the shell at the outer lip or that enter the shell by way of the aperture. Passive armour generally is more common and much better developed in the tropics than in colder regions. In line with this expectation, the relative opercular thickness of tropical turbinids (mean 0.358 ± 0.045 , 33 species) significantly exceeds that of temperate species (mean 0.300 ± 0.051 , 21 species). Small differences in relative opercular thickness occur among tropical biogeographic regions, but none is significant. Patterns observed among turbinids as a whole also appear in individual clades, indicating that the patterns are not dictated by a phylogenetic signal.

INTRODUCTION

Turban snails are gastropods in the trochoidean vetigastropod family Turbinidae (as defined by Williams & Ozawa, 2006). They have a spirally growing, externally calcified, rigid operculum that completely fills the aperture of the shell when the soft parts are withdrawn (Hickman & McLean, 1990; Checa & Jiménez-Jiménez, 1998). The close fit of the turbinid operculum, together with the fact that turbinids appear to lack escape responses to slow predators such as gastropods and sea stars (personal observations), indicates that the shell and operculum have a passive-protective function against predators that break the shell at the outer lip or enter the shell via the aperture. In contrast to turbinids, members of the related family Trochidae usually have a flexible operculum, and often exhibit well-developed fleeing responses to predatory gastropods and sea stars.

Passive shell defences such as apertural teeth, external tubercles and spines, a narrowly elongate or very small aperture, glossy and slippery external surfaces and high spires associated with deep withdrawal of the soft parts, are generally much more common and much better expressed among tropical species than among temperate and especially polar ones (Vermeij, 1993). Within the tropics, such defences tend to be most common and most highly developed in the Indo-West Pacific, less so in the eastern Pacific and western Atlantic, and least in West Africa (Vermeij, 1993). There is a rise in incidence and expression of armour from deep to shallow water. Vermeij (1993) tentatively suggested that these patterns might also apply to the opercular defence of turbinids. He suspected that tropical species have relatively thicker opercula than temperate ones.

In this paper, we summarize old and new data pertaining to predation on turbinids and some other gastropods with a calcareous operculum, and we test the hypothesis that there exists a trend for tropical, shallow-water turbinids to have relatively thicker opercula than species living in the cool-temperate zones or in deep waters. Opercular thickness and shape may also carry a phylogenetic signal, with more basal lineages of the Turbinidae having thinner opercula than more derived members. We therefore examined the geography of turbinid opercular form in a molecular-phylogenetic framework as established by Williams & Ozawa, 2006 and Williams (2007).

MATERIAL AND METHODS

We measured maximum diameter and maximum thickness of opercula of 54 turbinid species. Relative opercular thickness was calculated as the ratio of maximum thickness to maximum diameter. All material used in this study is in the Vermeij collection and at the U.S. National Museum of Natural History (Washington, D.C.). Temperate and tropical regions are defined following Williams (2007). Every geographic region in which turbinids occur is represented in our sample of species, except tropical West Africa, where only two rare deep-water species of *Bolma* are known (Beu & Ponder, 1979). We sampled 23 species in the tropical Indo-West Pacific, four in the tropical eastern Pacific, six in the tropical western Atlantic, 13 in the temperate southern hemisphere (Chile, South Africa, Australia and New Zealand) and eight in the north temperate zone (the Mediterranean, Japan, Baja California, Gulf of California and California). Most species were represented by multiple samples. In view of the low between-sample variation, we calculated a single mean relative opercular thickness for each species.

If a thick operculum confers protection against shell breakage at the outer lip, we expect a positive correlation between relative opercular thickness and the frequency of repaired shell injuries on the last whorl of the shell. With a thicker operculum, a predator would have a harder time dislodging or otherwise penetrating the opercular defence; damage is limited to the outer lip. Were the opercular thinner, more outer-lip attacks might be expected to succeed. We evaluated this prediction by assessing the frequency of repair (number of repaired shells divided by total number of specimens examined) for 12 shallow-water turbinid species in the Vermeij collection. We combined data from several localities to arrive at a single frequency of repair for each species.

RESULTS AND DISCUSSION

Predation and the calcareous operculum

Evidence for the protective role of calcareous opercula against predators remains largely circumstantial. Taylor & Morton (1996) observed that the predatory muricid gastropod *Reishia clavigera* (Küster) in Hong Kong attacked gastropods whose operculum is flexible by way of the aperture, whereas it drilled

Correspondence: G.J. Vermeij; e-mail: vermeij@geology.ucdavis.edu

Table 1. Mean relative opercular thickness of Turbinidae (cm)*.

Region and species	Location	<i>n</i>	Mean	Clade
Tropical Indo-West Pacific				
<i>Astraliium calcar</i> (Linnaeus, 1758)	Indonesia, New Guinea	8	0.35	1
<i>A. haematragum</i> (Menke, 1829)	Japan	6	0.28	1
<i>A. rhodostomum</i> (Lamarck, 1822) sp. 1	Mariana Islands	2	0.38	1
<i>A. rhodostomum</i> (Lamarck, 1822) sp. 2	Palau	2	0.365	1
<i>A. semicostatum</i> (Kiener, 1850)	India	8	0.33	1?
<i>A. cf. stellare</i> (Gmelin, 1791)	New Caledonia	8	0.355	1?
<i>Lunella (Lunella) cinerea</i> (Born, 1778)	Indonesia, New Guinea	9	0.42	4
<i>L. (L.) coronata</i> (Gmelin, 1791)	Kenya, Madagascar	4	0.40	4
<i>L. (L.) granulata</i> (Gmelin, 1791)	east Asia	2	0.41	4
<i>Turbo (Turbo) petholatus</i> Linnaeus, 1758	western Pacific	8	0.39	5
<i>T. (Lunatica) marmoratus</i> Linnaeus, 1758	western Pacific	6	0.29	5
<i>T. (Marmarostoma) argyrostomus</i> Linnaeus, 1758	Guam	3	0.42	5
<i>T. (M.) 'bruneus'</i> Röding, 1798	Indonesia, New Guinea	27	0.38	5
<i>T. (M.) chrysostomus</i> Linnaeus, 1758	Indonesia, Palau	12	0.38	5
<i>T. (M.) crassus</i> Wood, 1828	New Guinea	7	0.37	5
<i>T. (M.) perspicuosus</i> Iredale, 1929	northern Australia	2	0.36	5?
<i>T. (M.) sandwicensis</i> Pease, 1861	Hawaii	5	0.42	5
<i>T. (M.) setosus</i> Gmelin, 1791	central Pacific	18	0.37	5
<i>T. (M.) sparverius</i> Gmelin, 1791	east Asia	8	0.375	5
<i>T. (s.l.) radiatus</i> Gmelin, 1791	Madagascar, Red Sea	8	0.37	5
<i>Bolma millegranosa</i> Kuroda & Habe, 1958	Japan	1	0.38	2?
<i>B. modesta</i> (Reeve, 1843)	Japan	2	0.29	2
<i>Guilfordia triumphans</i> (Philippi, 1841)	Japan	1	0.22	2
Temperate Indo-West Pacific				
<i>Astraea heliotropium</i> (Martyn, 1784)	New Zealand	15	0.17	2
<i>Micrastraea kesteveni</i> (Iredale, 1924)	southern Australia	5	0.32	2
<i>Astraliium tentorium</i> (Thiele, 1930)	Western Australia	2	0.27	1
<i>Cookia sulcata</i> ([Lightfoot, 1786])	New Zealand	11	0.23	2?
<i>Lunella (Lunella) coreensis</i> (Récluz, 1853)	Japan	3	0.38	4
<i>L. (Ninella) torquata</i> (Gmelin, 1791)	New South Wales	4	0.305	4
<i>L. (Subninella) undulata</i> ([Lightfoot, 1786])	New South Wales	21	0.34	4
<i>L. (s.l.) smaragdus</i> (Martyn, 1784)	New Zealand	57	0.365	4
<i>Modelia granosa</i> (Martyn, 1784)	New Zealand	4	0.32	2?
<i>Pomaulax japonicus</i> (Dunker, 1844)	Japan	1	0.28	3
<i>Turbo (Turbo) jourdani</i> (Kiener, 1839)	Western Australia	1	0.25	5
<i>T. (Batillus) cornutus</i> [Lightfoot, 1786]	Japan	6	0.29	5
Other temperate regions				
<i>Bolma rugosa</i> (Linnaeus, 1758)	Mediterranean	3	0.29	2
<i>Lithopoma (Uvanilla) olivaceum</i> (Wood, 1828)	Baja California	2	0.27	3?
<i>L. (U.) unguis</i> (Wood, 1828)	Baja California	6	0.285	3?
<i>Pomaulax gibberosa</i> (Dillwyn, 1817)	California	5	0.33	3?
<i>Prisogaster elevatus</i> (Souleyet, 1852)	Chile	4	0.28	OG?
<i>P. niger</i> (Wood, 1828)	Chile	10	0.40	OG
<i>Turbo (Callopona) fluctuosus</i> Wood, 1828	Gulf of California	18	0.32	5
<i>T. (Sarmaticus) cidaris</i> Gmelin, 1791	South Africa	2	0.30	5
<i>T. (S.) sarmaticus</i> Linnaeus, 1758	South Africa	6	0.31	5
Tropical eastern Pacific				
<i>Lithopoma (Uvanilla) buschii</i> (Philippi, 1848)	Panama	3	0.33	3?
<i>Turbo (Callopona) funiculosus</i> (Kiener, 1847)	Clarion Island	2	0.35	5
<i>T. (C.) saxosus</i> Wood, 1828	Panama	2	0.37	5
<i>T. (Senectus) squamiger</i> Reeve, 1843	Mexico	4	0.34	5

Continued

Table 1. *Continued*

Region and species	Location	<i>n</i>	Mean	Clade
Tropical western Atlantic				
<i>Lithopoma (Lithopoma) americanum</i> (Gmelin, 1791)	Florida, Bermuda	6	0.385	3
<i>L. (L.) caelatum</i> (Gmelin, 1791)	Caribbean	11	0.37	3
<i>L. (L.) phoebium</i> (Röding, 1798)	Caribbean	5	0.37	3
<i>L. (L.) tectum</i> (Lightfoot, 1786)	Caribbean	2	0.295	3?
<i>L. (L.) tuber</i> (Linnaeus, 1767)	Caribbean	3	0.31	3?
<i>Turbo (Senectus) castanea</i> Gmelin, 1791	Florida, Puerto Rico	15	0.39	5

Abbreviation: OG, outgroup.

? – not tested or not resolved, likely clade placement; *Clade number refers to the five clades identified by Williams & Ozawa (2007).

through the shell of the turbinid *Lunella coronata*. *Dicathais orbita* (Gmelin) in Australia and *Neorapana tuberculata* (Sowerby) in the northern Gulf of California, however, attacked turbinids by way of the aperture, and in doing so often drilled the edge of the calcareous operculum (Taylor & Glover, 1999; Vermeij & Carlson, 2000; Herbert, 2004).

Octopods typically drill their gastropod prey, but first inspect the aperture of gastropods by means of the arms to confirm the shell is occupied (Wodinsky, 1969; Steer & Semmens, 2003). Turbinid species are usually drilled (most often on the body whorl, above the aperture) but the animal may also be pulled out by force, without drilling (Wodinsky, 1978; Loch, 1988; Steer & Semmens, 2003). There are no published data on the effectiveness of the calcareous operculum in preventing successful predatory attacks by octopods nor any studies testing if the presence of a calcareous operculum effects the decision to drill rather than pull the animal out.

One of us (GJV) conducted feeding trials with the predatory gastropods *Cymatium nicobaricum* (Röding) (Ranellidae) and *Nassa sarta* (Bruguère) (Muricidae) in Guam during 1974 and 1975. None of 18 individuals of *Nerita albicilla* Linnaeus, a thick-shelled species with a calcareous operculum, was successfully attacked by three *C. nicobaricum*. Likewise, none of five *N. albicilla* was killed or eaten by two *N. sarta*. By contrast, species of *Morula*, *Drupa*, *Conus* and *Cerithium* were readily consumed by *C. nicobaricum*; and *N. sarta* readily attacked and consumed small cypraeids and trochids. The consumed gastropods often had a very small or narrow aperture, but either lacked an operculum (Cypraeidae) or have a flexible operculum. These data are

Table 2. Frequencies of repaired shell injuries in some turbinid species.

Species	<i>n</i>	Frequency %
Tropical species		
<i>Lunella cinerea</i>	11	56
<i>Turbo 'bruneus'</i>	21	0
<i>T. chrysostomus</i>	25	8.0
<i>T. castanea</i>	24	13
<i>T. perspicuosus</i>	10	10
<i>T. sandwicensis</i>	8	38
<i>T. setosus</i>	19	42
Temperate species		
<i>Cookia sulcata</i>	7	0
<i>Lunella smaragdus</i>	56	16
<i>L. undulata</i>	29	17
<i>Prisogaster niger</i>	42	4.8
<i>Turbo fluctuosus</i>	16	0

therefore consistent with the interpretation that the rigid calcareous operculum of *Nerita* was effective against gastropods that attack their victims by way of the aperture without drilling.

The calcareous operculum may play a role in limiting damage and preventing predation by shell-crushing predators on large individuals. Analyses of shells or fragments no longer occupied by the original gastropod reveal that breakage is a frequent cause of death for tropical shallow-water turbinids. In the Palau Islands, the frequency of lethal breakage among adult turbinids was 100% for *Turbo setosus* ($n = 5$) and 46% for *T. chrysostomus* ($n = 26$) (Vermeij, 1979). Previously unpublished data collected by Vermeij in 1979 indicate frequencies of lethal breakage of 26% for *T. perspicuosus* ($n = 23$) in northern Australia, 50% for *T. 'bruneus'* ($n = 14$) in northern Irian Jaya (Indonesia) and 59% for *T. setosus* ($n = 17$) near the reef edge at Pago Bay, Guam. In feeding trials with the large carpiiid crab *Carpilius maculatus* in Guam (see Zipser & Vermeij, 1978), two individuals successfully attacked and partially consumed *T. setosus* with shell diameters of 56.5 and 58.6 mm, but inflicted only lip damage without penetrating the opercular defence of individuals 68.0 and 71.7 mm in shell diameter.

Opercular geography

Testing for the effect of geography among the tropical biogeographic regions, we find that the greatest relative opercular thickness in turbinids occurs in the Indo-West Pacific (mean 0.361 ± 0.050 , range 0.22 to 0.42, $n = 23$), followed by the western Atlantic (mean 0.353 ± 0.040 , range 0.295 to 0.39, $n = 6$) and the eastern Pacific (mean 0.348 ± 0.017 , range 0.33 to 0.37, $n = 4$) (Table 1). None of these differences is statistically significant.

Differences among temperate regions are also insignificant. North-temperate turbinids from the Mediterranean, Japan, Baja California, Gulf of California and California (mean 0.306 ± 0.036 , range 0.27 to 0.38, $n = 8$) do not differ in opercular thickness from south-temperate species in South Africa, Australia, New Zealand and Chile (mean 0.297 ± 0.059 , range 0.17 to 0.40, $n = 13$; see Table 1).

The surprisingly thick operculum of the Chilean turbinid *Prisogaster niger* (mean 0.40; Table 1) is anomalously high for a temperate species, but it is consistent with the previously unrecognized, yet exceptionally well developed, armour of the shallow-water Chilean molluscan fauna. Among warm-temperate faunas, that of Chile has the highest incidence of muricids with a predation-enhancing labral tooth (Vermeij, 2001; DeVries, 2005), as well as unusually thick-shelled fissurellid keyhole limpets, trochids, muricids and chitons. Although not very rich, the Chilean fauna thus appears to have carried predation-related adaptation further than most other climatically similar faunas. This aspect of Chile's fauna deserves further work.

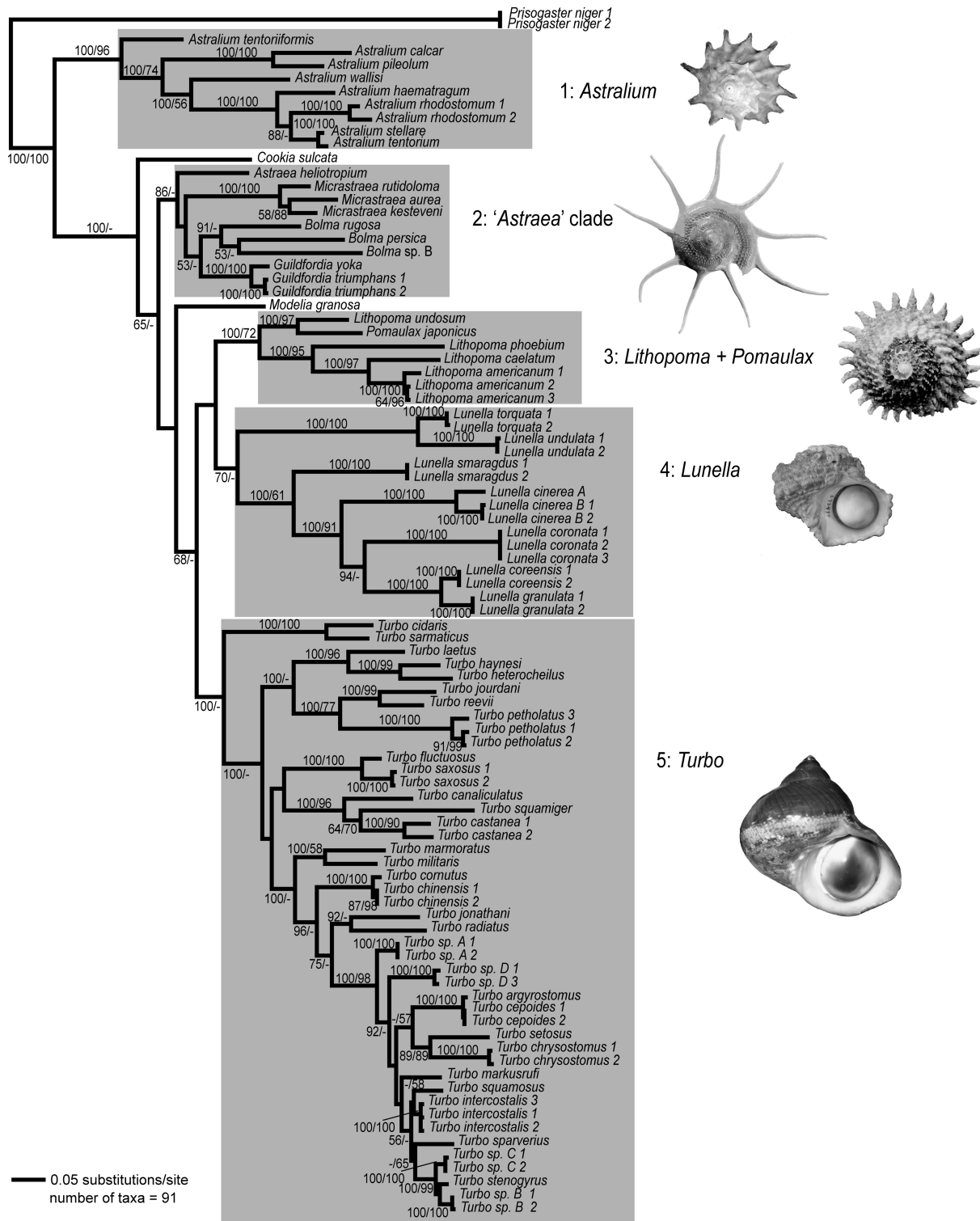


Figure 1. Molecular phylogeny for the turbinid subfamily Turbininae produced by Bayesian analysis for combined three-gene data set (concatenated sequences from 28S rRNA + COI + 16S rRNA). The tree was drawn using *Prisogaster niger* as the outgroup. Support values (from left to right) are posterior probabilities and parsimony bootstrap values. Values <50% are not shown. Methods are discussed in Williams (2007). Photos (from top to bottom): *Astralium calcar*, *Guildfordia triumphans*, *Lithopoma phoebium*, *Lunella coronata* and *Turbo petholatus*. Figure modified from Williams (2007).

The data support our prediction about the effect of temperature. Tropical turbinids have significantly thicker opercula (mean 0.358 ± 0.045 , range 0.22 to 0.42, $n = 33$) than temperate species (mean 0.300 ± 0.051 , range 0.17 to 0.40, $n = 21$) ($P = 0.0001$, two-tailed t -test). Within the tropical Indo-West

Pacific, three of the sampled species from the genera *Bolma* and *Guildfordia* occur in cooler and deeper water than the 20 strictly tropical, shallow-water species discussed above, and have opercula whose thickness (mean 0.297 ± 0.080 , range 0.22 to 0.38, $n = 3$) is similar to that of temperate species.



Figure 2. Examples of turbinid opercula for each clade in Figure 1. Clade 1: **A.** *Astrarium calcar*. **B.** *A. pileolum*. **C.** *A. stellare*. Clade 2: **D.** *Astraea heliotropium*. **E.** *Guildfordia yoka*. **F.** *Bolma rugosa*. Clade 3: **G.** *Lithopoma americanum*. **H.** *L. olfersi*. **I.** *L. undosum*. Clade 4: **J.** *Lunella cinerea*. **K.** *L. smaragdus*. **L.** *L. torquata*. Clade 5: **M.** *Turbo petholatus*. **N.** *T. sarmaticus*. **O.** *T. saxosus*. Outgroup: **P.** *Prisogaster niger*. Scale bars are all 5 mm.

With these three species removed from the tropical sample and included in the temperate group, the difference in opercular thickness between tropical and temperate turbinids is significant at a level of $P = 0.00001$.

Within the eastern Pacific, the four tropical species have relatively thicker opercula than the four species sampled from the cooler sector extending north from southern Baja California and the Gulf of California ($P = 0.039$) (Table 1). These data therefore indicate that turbinids in cooler waters have relatively thinner opercula than those in the warmest tropical waters.

Although a significant difference in the frequency of repair between tropical and temperate shallow-water turbinids could

not be established, the three species with conspicuously high frequencies (*Lunella cinerea*, 56%; *T. sandwicensis*, 38% and *T. setosus*, 42%) all occur in the tropical Indo-West Pacific region (Table 2). The lack of significance of the expected geographic pattern is due to the presence of species without repairs in both the tropics and the temperate zone (Table 2). We interpret these results to mean that, at large sizes, turbinids offer significant, successful resistance to shell-breaking predators, especially in the tropics. The tightly fitting, rigid operculum likely contributes to this resistance, for without the operculum, the unreinforced outer lip together with the large, rounded aperture would probably not prevent a predator from breaking back

the outer shell wall to expose the shell parts or from extracting the soft parts without damaging the shell.

Large turbinid opercula are some of the thickest calcified structures that gastropods produce. The largest, thickest operculum we have measured is that of *T. (Lunatica) marmoratus* (diameter 92.2 mm, maximum thickness 26.0 mm). Maximum absolute opercular thickness is thus highest in the Indo-West Pacific, followed by cold-temperate Australia (22.1 mm in *T. (T.) jourdani*), cold-temperate north California (17.9 mm in *Lithopoma (Megastraea) undosum*, data not shown), the warm-temperate eastern Pacific (11.1 mm in *T. (Callopoma) fluctuosus*), and the western Atlantic (6.0 mm in *Lithopoma (Lithopoma) caelatum*). The geography of maximum opercular thickness therefore does not match the geography of mean relative opercular thickness, but instead reflects the pattern of maximum body size.

The greater relative thickness of tropical turbinid as compared to temperate turbinid opercula is potentially explained by the higher solubility of calcium carbonate, and therefore by the greater energetic expense associated with the precipitation of that mineral, in cooler waters. These considerations led Graus (1974) to predict that shells of cold-water molluscs are thinner and more nearly spherical, meaning that they use a minimum of mineral to enclose a maximum volume. Although thermal dependencies of calcification surely contribute to the context in which selection of shell and opercular traits occurs, we reject them as the primary explanation for the patterns we observe. As noted above, some of the absolutely thickest calcareous opercula are found in temperate turbinids. Moreover, many cold-water gastropods, including some species of the buccinid genus *Neptunea* in the far north, have notably thick shells; and many gastropods in cold marine and fresh waters depart markedly from the spherical form predicted under limits on calcification (Vermeij, 1978, 1993). The weight of circumstantial evidence favours the hypothesis that selection due to various kinds of predators is primarily responsible for patterns in turbinid opercular thickness. Predators collectively appear to exercise less intense selection on cool-water species than on their warm-water counterparts.

The effects of phylogeny

The correlation between relative opercular thickness and temperature that we have uncovered for turbinids as a whole, also appears in individual clades. In Williams' (2007) clade 4 (the *Lunella* clade), the four temperate species (*Lunella corensis*, *L. smaragdus*, *L. undulata*, *L. torquata*; mean 0.348) have thinner opercula than the three tropical ones (*L. cinerea*, *L. coronata*, *L. granulata*; mean 0.410; Table 1, Fig. 1). Tropical Atlantic members of clade 3 (the *Lithopoma–Pomaulax* clade), together with the strictly tropical eastern Pacific *Lithopoma buschii*, have thicker opercula (mean 0.343) than the four north-temperate members (mean 0.291, Table 1, Fig. 1).

Phylogeny may, however, play an important role in some aspects of opercular shape and colour in turbinids. Although there are no significant pairwise comparisons between clades (using a Bonferroni correction), species in Williams' (2007) clade 2 (the *Astraea* clade) and clade 3 (the *Lithopoma–Pomaulax* clade) have generally thinner opercula than members of the *Astralium*, *Lunella* and *Turbo* clades (clades 1, 4 and 5 respectively; Fig. 1). The thinnest opercula are concentrated in clade 2 (the *Astraea* clade), most of whose members are of either temperate or deep-water tropical distribution (Fig. 1). The thickest point of the operculum in clades 1 and 3 is located close to the margin, whereas in the other clades (especially in clades 4 and 5 and in *Prisogaster*) it is more central in position.

Opercula may also be highly sculptured, and the greatest range of variation is observed in clade 5 (*Turbo*), which has opercula with highly polished surfaces, minute granules, large irregular granules and spiral whorls or ribs, all with or without radial lines and central or subcentral pits (Fig. 2). Great variation is also seen in *Lithopoma–Pomaulax* (clade 3) (Fig. 2). Opercula of species belonging to clades 1, 4 and 5 (*Astralium*, *Lunella* and *Turbo*) are often brightly coloured, as are the opercula of some *Bolma* species (in clade 2) (Fig. 2). Other species in clade 2 (*Astraea* clade) and all species in clade 3 (*Lithopoma* and *Pomaulax*) most often have opercula that are white or have very light coloration (Fig. 2). Whether this trend reflects phylogeny or the ecological effect of food substrate or temperature on a biochemical pathway is not known.

Taken together, our results indicate that both temperature and phylogeny affect opercular thickness and shape in turbinids. It remains to be seen if early-diverging turbinid lineages have thinner opercula than later-emerging ones, and if opercular thickness among warm, shallow-water species has increased over Cenozoic time.

A calcified operculum or operculum-like device has evolved independently at least 13 times in gastropods, beginning in the Early Ordovician (Frýda & Rohr, 2006), as well as in cephalopods (Vermeij, 1993; Checa & Jiménez-Jiménez, 1998; Williams & Ozawa, 2006). It will be interesting to see if widespread clades with a calcified operculum, such as Neritopsina, Naticinae and the clade comprising the families Areneidae, Colloniidae and Phasianellidae display similar patterns to those we have found in turbinids.

REFERENCES

- BEU, A.G. & PONDER, W.F. 1979. A revision of species of *Bolma* Risso, 1826 (Gastropoda: Turbinidae). *Records of the Australian Museum*, **32**: 1–68.
- CHECA, A.G. & JIMÉNEZ-JIMÉNEZ, A.P. 1998. Constructional morphology, origin, and the evolution of the gastropod operculum. *Paleobiology*, **24**: 109–132.
- DEVRIES, T.J. 2005. Late Cenozoic Muricidae from Peru: seven new species and a biogeographic summary. *Veliger*, **47**: 277–293.
- FRÝDA, J. & ROHR, D.M. 2006. Shell heterostrophy in Early Ordovician *Macluritella* Kirk, 1927 and its implications for phylogeny and classification of Macluritoidea (Gastropoda). *Journal of Paleontology*, **80**: 264–271.
- GRAUS, R.R. 1974. Latitudinal trends in the shell characteristics of marine gastropods. *Lethaia*, **7**: 303–314.
- HERBERT, G.S. 2004. Observations on diet and mode of predation in *Stramonita biserialis* (Gastropoda: Muricidae) from the northern Gulf of California. *Festivus*, **36**: 41–45.
- HICKMAN, C.S. & MCLEAN, J.H. 1990. Systematic revision and suprageneric classification of trochacean gastropods. *Natural History Museum of Los Angeles County Science Series*, **35**: 1–169.
- LOCH, I. 1988. *Octopus cyaneus* blues. *Australian Shell News*, **64**: 9.
- STEER, M.A. & SEMMENS, J.M. 2003. Pulling or drilling, does size or species matter? An experimental study of prey handling in *Octopus dierythraeus* (Norman, 1992). *Journal of Experimental Marine Biology and Ecology*, **290**: 165–178.
- TAYLOR, J.D. & GLOVER, E.A. 1999. Penetrating the defences: opercular drilling by *Dicathais orbita* (Mollusca: Gastropoda: Muricidae) on the turbinid gastropod *Ninella torquata*. In: *The seagrass flora and fauna of Rottnest Island, Western Australia* (D.I. Walker & F.E. Wells, eds), 177–198. Western Australian Museum, Perth.
- TAYLOR, J.D. & MORTON, B. 1996. The diets of predatory gastropods in the Cape D'Aguilar Marine Reserve, Hong Kong. *Asian Marine Biology*, **13**: 141–166.
- VERMEIJ, G.J. 1978. *Biogeography and adaptation: patterns of marine life*. Harvard University Press, Cambridge.
- VERMEIJ, G.J. 1979. Shell architecture and causes of death in Micronesian reef snails. *Evolution*, **33**: 686–696.

TURBINID OPERCULA

- VERMEIJ, G.J. 1993. *A natural history of shells*. Princeton University Press, Princeton.
- VERMEIJ, G.J. 2001. Innovation and evolution at the edge: origins and fates of gastropods with a labral tooth. *Biological Journal of the Linnean Society*, **72**: 461–508.
- VERMEIJ, G.J. & CARLSON, S.J. 2000. The muricid gastropod subfamily Rapaninae: phylogeny and ecological history. *Paleobiology*, **26**: 19–46.
- WILLIAMS, S.T. 2007. Origins and diversification of the Indo-West Pacific fauna: evolutionary history and biogeography of turban shells (Gastropoda, Turbinidae). *Biological Journal of the Linnean Society* (in press).
- WILLIAMS, S.T. & OZAWA, T. 2007. Molecular phylogeny suggests polyphyly of both the turban shells (family Turbinidae) and the superfamily Trochoidea (Mollusca: Vetigastropoda). *Molecular Phylogenetics and Evolution*, **39**: 33–51.
- WODINSKY, J. 1969. Penetration of the shell and feeding from gastropods by *Octopus*. *American Zoologist*, **9**: 997–1010.
- WODINSKY, J. 1978. Feeding behaviour of broody female *Octopus vulgaris*. *Animal Behaviour*, **26**: 803–813.
- ZIPSER, E. & VERMEIJ, G.J. 1978. Crushing behaviour of tropical and temperate crabs. *Journal of Experimental Marine Biology and Ecology*, **31**: 155–172.