UC Davis UC Davis Previously Published Works

Title

Geography, shell form and opercular thickness in living marine neritid gastropods

Permalink https://escholarship.org/uc/item/1qs1x491

Journal Journal of Molluscan Studies, 84(4)

ISSN 0260-1230

Authors Vermeij, Geerat J Hoeft, Evan

Publication Date

DOI 10.1093/mollus/eyy046

Peer reviewed



Journal of The Malacological Society of London Molluscan Studies

Journal of Molluscan Studies (2018) **84**: 498–500. doi:10.1093/mollus/eyy046 Advance Access publication date: 5 October 2018

RESEARCH NOTE

Geography, shell form and opercular thickness in living marine neritid gastropods

Geerat J. Vermeij¹ and Evan Hoeft²

¹Department of Earth and Planetary Sciences, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA; and ²Department of Evolution and Ecology, University of California, Davis, 2320 Storer Hall, Davis, CA 95616, USA

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

The gastropod operculum is a defensive device that covers the shell's aperture and protects the soft parts when the latter are fully retracted into the shell (Stanley, 1982; Vermeij, 2015). Although it is usually organic in composition, the operculum is calcified in at least sixteen independent clades spanning the Ordovician to the Recent (Checa & Jiménez-Jiménez, 1998; Vermeij, 2015). One of the major clades in which the operculum is a rigid calcified plate is the Neritimorpha, in which the operculum pivots in a hinge-like fashion around the inner (or columellar) edge of the aperture as the soft parts extend out of or withdraw into the shell (Bandel, 2008; Krijnen & Vink, 2009). In the mainly tropical Nerita clade (Frey & Vermeij, 2008), the operculum deters predators and may also prevent desiccation, especially in species living at the upper reaches of marine influence (Vermeij, 1973; Vermeij & Frey, 2008). Here we investigate possible geographical differences in nerite opercular thickness-but find none. We also comment on opercular thickness in relation to apertural characteristics.

In a study of turbinid gastropods, Vermeij & Williams (2007) showed that tropical species in shallow water have thicker opercula than species from temperate coasts of Australia, New Zealand, South Africa and California, and that the thickest (and presumably most protective) opercula occur in the tropical Indo-West Pacific (IWP) region. These findings prompt the question whether similar geographical differences occur in the *Nerita* clade which, like the Turbinidae, has a pantropical distribution with a few temperate taxa in Australasia. An additional question particular to the *Nerita* clade is whether species typical of the high intertidal zone, where the intensity of predation tends to be low, have relatively thinner opercula than species living lower on the shore.

The operculum is only part of the passive protective armament of nerites. The outer lip is part of the first line of defence against shell-breaking predators and is strongly thickened and dentate on its inner side in adults. Moreover, the aperture covered by the operculum is often small, especially in high intertidal species. Relative opercular thickness might be expected to be greater in species with a broader aperture, all else being equal.

We measured minimum and maximum diameter and maximum opercular thickness for 31 species in the *Nerita* clade, using material in the Vermeij collection. These measurements ignored the apophysis protruding from the operculum's adaxial (columellar) side, because it is associated with articulation. Relative opercular thickness (opercular thickness index, OTI) was calculated as the thickness divided by the mean diameter (minimum plus maximum diameter divided by two). Each species was represented by at least four adult individuals. An OTI was then calculated for each species. Unpublished data indicate that relative opercular thickness varies little ontogenetically or among localities. Data for each species were therefore combined even when samples from more than one locality were measured, as was the case for most of the studied species. In order to examine how opercular thickness is related to shell traits, we made the following measurements on adult shells: shell diameter D, outer-lip thickness L and apertural diameter A. From these measurements we calculated relative lip thickness L/D and relative apertural breadth A/D.

Species were divided into four habitat categories as observed by Vermeij (1971a, b, 1973) and Vermeij & Frey (2008): low to mid rocky shore or mangrove; upper rocky or mangrove shore; a broad vertical range on the rocky shore; and sand. Geographically, we considered the IWP and the Atlantic–East Pacific (AEP) regions in the tropics and the temperate Australasian region of New Zealand and eastern Australia. Taxa identified as subgenera in previous studies were considered as full genera here.

As expected, the mean OTI for low to mid-shore nerites in the IWP is higher (mean \pm SD 0.149 \pm 0.17, n = 10) than in the AEP (mean 0.141, n = 3), but the difference is not statistically significant. Contrary to our expectations, the mean OTI of high-shore species in the IWP (mean 0.164 ± 0.42 , n = 10) is higher than for low-shore species, but again the difference is not significant (Table 1). Moreover, the comparison is misleading. The high standard deviation for the high-shore species reflects a trimodal distribution in opercular thickness. Two species (Ritena plicata and 'Nerita' costata) have extremely thin opercula, associated with a very small aperture bordered by large teeth. Three species (Cymostyla quadricolor, C. spengleriana and C. undata) stand out as having exceptionally thick opercula. The five other high-shore species make up the middle third of the distribution. The three upper-shore species in the AEP (mean thickness 0.159) also vary dramatically in OTI, with one species (Nerita versicolor) having a very thin operculum and a small occluded aperture, and two others (N. peloronta and N. scabricosta) having thicker opercula than any low-shore species in either the IWP or AEP.

Four species have broad vertical distributions on the shore and are the only members of the *Nerita* clade in their respective geographical locations. These are *Theliostyla senegalensis* in West Africa, *'Nerita' chlorostoma* at Ilha Fernando de Noronha (Brazil), *Ritena picea* in the Hawaiian Islands (where *R. plicata* is extremely scarce)

RESEARCH NOTE

Habitat and Taxon	Ν	ΟΤΙ	Relative lip thickness	Relative aperture breadth
Indo-West Pacific, low to mid shore				
Theliostyla albicilla (Linnaeus, 1758)	24	0.151	0.13	0.23
Argonerita chamaeleon (Linnaeus, 1758)	5	0.145	0.14	0.23
Theliostyla exuvia (Linnaeus, 1758)	5	0.133	0.08	0.26
Argonerita histrio (Linnaeus, 1758)	8	0.173	0.12	0.24
Amphinerita incerta (von dem Busch in Philippi, 1844)	6	0.133	0.10	0.26
Linnerita litterata (Gmelin, 1791)	8	0.167	0.10	0.26
<i>'Nerita' patula</i> Récluz, 1841	3	0.127	0.09	0.26
<i>Ilynerita planospira</i> (Anton, 1839)	4	0.173	0.12	0.23
Theliostyla sanguinolenta (Menke, 1829)	10	0.141	0.11	0.24
Theliostyla textilis (Gmelin, 1791)	7	0.145	0.11	0.26
Indo-West Pacific, high shore				
<i>'Nerita' articulata</i> Gould, 1848	10	0.152	0.09	0.29
'Nerita' costata Gmelin, 1791	11	0.115	0.13	0.24
Cymostyla guamensis (Quoy & Gaimard, 1834)	5	0.128	0.10	0.24
Amphinerita insculpta (Récluz, 1841)	8	0.163	0.11	0.25
<i>Cymostyla maxima</i> (Gmelin, 1791)	9	0.198	0.13	0.24
Ritena plicata (Linnaeus, 1758)	24	0.100	0.15	0.21
Cymostyla quadricolor (Gmelin, 1791)	7	0.205	0.11	0.28
Cymostyla spengleriana (Récluz, 1843)	10	0.217	0.13	0.24
Amphinerita umlaasiana (Krauss, 1848)	10	0.151	0.10	0.26
Cymostyla undata (Linnaeus, 1758)	12	0.208	0.11	0.26
Indo-West Pacific, broad distribution				
Ritena picea (Récluz, 1841)	10	0.118	0.11	0.26
Indo-West Pacific, sand				
Linnerita polita (Linnaeus, 1758)	16	0.143	0.11	0.26
Atlantic-East Pacific, low shore				
Theliostyla fulgurans (Gmelin, 1791)	7	0.140	0.09	0.26
Theliostyla funiculata (Menke, 1851)	4	0.148	0.13	0.24
Theliostyla tessellata (Gmelin, 1791)	11	0.135	0.10	0.290
Atlantic-East Pacific, high shore				
Nerita peloronta Linnaeus, 1758	21	0.185	0.09	0.32
Nerita scabricosta Lamarck, 1822	24	0.182	0.11	0.26
Nerita versicolor Gmelin, 1791	27	0.091	0.10	0.19
Atlantic-East Pacific, broad distribution				
'Nerita' chlorostoma Lamarck, 1816	5	0.113	0.07	0.29
Theliostyla senegalensis (Gmelin, 1791)	9	0.123	0.09	0.26
Australasia				
Lisanerita atramentosa (Reeve, 1855)	17	0.149	0.13	0.29

and Lisanerita atramentosa in Australia and New Zealand. Their OTI (mean thickness 0.141) lie at or below the mean for IWP and AEP low-shore species.

Three factors could contribute to the lack of geographical and shore-level patterns in relative opercular thickness in nerites. First, there is interspecific variation in the expression of overall passive armour. Species living without other neritids tend to have shells with a thin adult outer lip and a broad aperture, a syndrome that is particularly well exemplified by 'N.' chlorostoma at Fernando de Noronha and T. senegalensis in West Africa (Table 1). Two other species with notably thin shells are 'N.' patula, an IWP species found sheltering beneath boulders, and the high-shore Cymostyla guamensis in the Mariana Islands. Second, this variation could be related to the degree to which nerites depend on escape from as compared with resistance to their chief predators. The relatively unsculptured, elongate shells of Amphinerita incerta, A. umlaasiana, Linnerita litterata and L. polita might imply a greater reliance on escape than on resistance. In contrast, species with a thicker, more strongly sculptured, more broadly ovate to round outline may rely more heavily on shell armour to resist predators. This aspect deserves further investigation. Third, there appears to be variation in the relative roles played by the shell and operculum in passive defence. Both the shell and operculum are relatively thick in such species as Cymostyla maxima, C. quadricolor, C. spengleriana, C. undata, T. albicilla and T. funiculate, whereas the operculum would appear to contribute little to the defence of R. plicata, a species that has an exceptionally thick outer lip and a small aperture.

Little is known about predation on members of the Nerita clade or about the role of the operculum in defence. In Pacific Panama, T. funiculata and N. scabricosta are frequently drilled by, and have escape responses from, the drilling muricid Plicopurpura pansa (Garrity & Levings, 1981). In the Kei Islands of eastern Indonesia, Vermeij (personal observations) found three individuals of the muricid Muricodrupa cariosa drilling three nerites, two C. maxima and one R. plicata. Surveys in Guam and Palau (Vermeij, 1979) indicated low incidences of drilled nerites and frequencies of lethal breakage ranging from 0.16 to 0.83, depending on species and location. An operculum would have offered little protection in any of these cases of predation. Vermeij (1979) collected one R. plicata on the windward coast of Guam in which the operculum had been

broken in two pieces, both still attached to the foot of the living snail. This anecdote shows that opercular damage can occur in life.

The absence of a geographical signal in opercular thickness in nerites contrasts with that in turbinids (see above). IWP turbinids have generally thicker opercula than AEP or temperate species. In nerites, the frequency of repaired injuries on shells is higher in the IWP than elsewhere (Vermeij, 1978), suggesting more intense selection by predators there. The reasons for the absence of a geographical pattern in nerite opercular thickness are unclear. Turbinid opercula are markedly thicker than those of nerites and even the low-shore nerites occupy zones higher on the shore than is typical for turbinids other than IWP species of Lunella. The neritid operculum is plate-like, rather than externally strongly convex as in most turbinids. In this way, it more closely resembles the calcified operculum of naticids. For these flatter, more plate-like opercula, protection from entry by predators by means of a tight fit might be more important and be less tied to opercular thickness than in turbinids, where some evidence points to a role of the operculum in limiting damage to the exposed outer shell lip when the soft parts are withdrawn (Vermeij & Williams, 2007). The thickened outer lip of nearly all nerites likely deters attempts by predators to break the shell, leaving the operculum to close off the soft parts from outside agencies.

As noted by Checa & Jiménez-Jiménez (1998), there is substantial diversity in the forms and functions of gastropod opercula. This diversity points to a greater range of functions—and functional specialization—than is usually considered. Our results, together with previous work, point to the desirability of additional work on the functional morphology and evolution of opercula.

REFERENCES

BANDEL, K. 2008. Operculum shape and construction of some fossil Neritimorpha (Gastropoda) compared to those of modern species of the subclass. *Vita Malacologica*, 7: 21–38.

- CHECA, A.G. & JIMÉNEZ- JIMÉNEZ, A.C. 1998. Constructional morphology, origin, and the evolution of the gastropod operculum. *Paleobiology*, 24: 109–132.
- FREY, M.A. & VERMEIJ, G.J. 2008. Molecular phylogenies and historical biogeography of a circumtropical group of gastropods (genus: *Nerita*): implications for regional diversity patterns in the marine tropics. *Molecular Phylogenetics and Evolution*, **48**: 1067–1086.
- GARRITY, S.D. & LEVINGS, S.C. 1981. A predator-prey interaction between two physically and biologically constrained tropical rocky shore gastropods: direct, indirect and community effects. *Ecological Monographs*, **51**: 267–286.
- KRIJNEN, C.J.M. & VINK, R.J. 2009. The operculum of the genus Nerita. Gloria Maris, 49: 27–56.
- STANLEY, S.M. 1982. Gastropod torsion: predation and the opercular imperative. *Neues Jahrbuch fur Geologie und Paläontologie Abhandlungen*, **164**: 95–107.
- VERMEIJ, G.J. 1971a. Temperature relationships of some tropical Pacific intertidal gastropods. *Marine Biology*, **10**: 308–315.
- VERMEIJ, G.J. 1971b. Substratum relationships of some tropical Pacific intertidal gastropods. *Marine Biology*, **10**: 315–320.
- VERMEIJ, G.J. 1973. Morphological patterns in high intertidal gastropods: adaptive strategies and their limitations. *Marine Biology*, **20**: 319–346.
- VERMEIJ, G.J. 1978. Biogeography and adaptation: patterns of marine life. Harvard University Press, Cambridge, MA.
- VERMEIJ, G.J. 1979. Shell architecture and causes of death in Micronesian reef snails. *Evolution*, **33**: 686–696.
- VERMEIJ, G.J. 2015. Gastropod skeletal defences: land, freshwater, and sea compared. *Vita Malacologica*, **13**: 1–25.
- VERMEIJ, G.J. & FREY, M.A. 2008. Almost terrestrial: small supratidal species of *Nerita* in the western Pacific. *Basteria*, **72**: 253–261.
- VERMEIJ, G.J. & WILLIAMS, S.T. 2007. Predation and the geography of opercular thickness in turbinid gastropods. *Journal of Molluscan Studies*, **73**: 67–73.