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The varix: evolution, distribution, and phylogenetic clumping of a repeated gastropod innovation

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A recurrent theme in evolution is the repeated, independent origin of broadly adaptive, architecturally and functionally similar traits and structures. One such is the varix, a shell-sculpture innovation in gastropods. This periodic shell thickening functions mainly to defend the animal against shell crushing and peeling predators. Varices can be highly elaborate, forming broad wings or spines, and are often aligned in synchronous patterns. Here we define the different types of varices, explore their function and morphological variation, document the recent and fossil distribution of varicate taxa, and discuss emergent patterns of evolution. We conservatively found 41 separate origins of varices, which were concentrated in the more derived gastropod clades and generally arose since the mid-Mesozoic. Varices are more prevalent among marine, warm, and shallow waters, where predation is intense, on high-spired shells and in clades with collabral ribs. Diversification rates were correlated in a few cases with the presence of varices, especially in the Muricidae and Tonnoidea, but more than half of the origins are represented by three or fewer genera. Varices arose many times in many forms, but generally in a phylogenetically clumped manner (more frequently in particular higher taxa), a pattern common to many adaptations.

ADDITIONAL KEYWORDS: evolutionary trends – fossil record – Gastropoda – shell sculpture – snails.

INTRODUCTION

The repeated appearance of similar adaptations has been seen throughout evolution. Leaves, secondary growth leading to woodiness, and winged fruits are all examples convergent evolution among plants. Snake-shaped vertebrates, crab-shaped crustaceans, bivalved lophotrochozoans, and coloniality are among the hundreds of cases in animals (Conway Morris, 2003; Vermeij, 2006).

Important as these manifestations of convergent and parallel evolution are for understanding the history of adaptation, much remains to be learned about how, when, where, and in which clades the trait or structure in question was acquired and became established. Are there particular times, ecological circumstances, or adaptive predispositions within clades that increase the chance that similar, widely beneficial adaptive traits evolve?

In earlier work on envelopment of the shell by the mantle or foot in gastropods, Vermeij (2005a) suggested that many traits or conditions with multiple independent origins are unevenly distributed among major clades. In some subclades, the trait appears repeatedly, whereas in many others it rarely or never evolved, a pattern of parallel evolution referred to as phylogenetic clumping (Vermeij (2005a). Although this pattern may be widespread, questions remain about (1) whether phylogenetic clumping is the rule for innovation and (2) the extent to which factors such as adaptive predisposition, time of origin, and geography contribute to it.

Answering such questions requires robust phylogenetic hypotheses about clades that are large enough to include multiple instances of a trait's appearance, as well as a reliable, thoroughly documented fossil record where traits can be recognized in extinct taxa. These sources of data can identify clades and circumstances in which the trait or feature under investigation did not evolve despite the likely benefits of the innovation.

The convergent structures we consider in this paper are shell sculpture: ontogenetically repeated varices, which are external shell thickenings (ribs, ridges, or flanges) parallel to the outer lip and more prominent

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*Corresponding author. E-mail: NicoleBWebster@gmail.com than other collabral sculptural elements (Fretter & Graham, 1962; Spight & Lyons, 1974). Varices form part of the passive external armour in many gastropods (Vermeij, 1995). As with many other evolutionary innovations, varices only arose in a few gastropod clades. To assess the conditions under which varices evolved, and the selective agents that favoured their establishment, we documented the number of phylogenetically independent origins and tracked the fates of clades in which varices became established.

Varices take two broad forms that are not mutually exclusive. The first and most common is the terminal varix (Vermeij, 1995). This thickening grows at the apertural margin in a snail with terminal growth, demarcating the end of spiral shell growth and defending the mature aperture. In contrast, many groups have more than one varix on the shell, with periodic thickenings occurring throughout ontogeny, whether the snail has determinate growth or not (Vermeij, 1995). In this paper, we focus on the second form – multiple varices, rather than terminal varices – and will hereafter refer to them simply as varices unless they are specifically identified as terminal varices.

Several questions motivated this research. First, what are the different types and variations of varix structure in gastropods? Second, what are the possible functions of varices? Third, what is the evolutionary history of varices: How many different gastropod taxa bear varices? How are varix-bearing taxa distributed phylogenetically? How do varix-bearing clades differ from other major clades lacking varices? What insights do varices provide regarding the generality of phylogenetic clumping and the repeated appearance of an evolutionary innovation?

MATERIALS AND METHODS

To characterize varices and to establish their phylogenetic, spatial, and temporal distribution, we conducted a large-scale survey of the taxonomic literature on living and fossil gastropods, supplemented with an examination of all shell-bearing gastropods in the Vermeij collection, as well as the Jim van Es (JVM) and Leslie Atkins collection from the University of Alberta. These were supplemented with online catalogues of shells: Gastropods.com (Hardy, 2016), Gastropoda Stromboidea (Wieneke *et al.*, 2016), and Digital Murex (Watters, 2016). Using our definition of a varix (see below), we consider a gastropod as having varices if at least some individuals of that species bear varices. We therefore excluded all species bearing a single (terminal) varix or a single reflected or internally thickened adult outer shell lip. We also excluded cases in which occasional growth pauses were marked by a pronounced but unthickened growth line, as well as species bearing axial lamellae (see below).

Savazzi & Sasaki (2004) defined three terms for different types of sculptural alignment, based on their presumed mechanism of alignment. As the underlying mechanism for alignment is unknown, including whether the shell itself provides feedback to maintain patterning, we chose not to follow their definitions. They use the term juxtaposition to mean sculpture that is aligned between whorls without specifying the mechanism, but we prefer the term synchronized for the same effect. Here synchronized sculpture indicates a sculpture pattern where varices are aligned between whorls, regardless of presumed mechanism, rather than sculpture that is aligned due to feedback from other shell features. We use the term periodic to suggest that a growth pause occurs after varix formation, whereas Savazzi & Sasaki (2004) used the same term to indicate sculpture that is produced at regular intervals due to an endogenous or exogenous timer.

The tree used in this paper was created based on expert opinion to merge and expand existing molecular and morphological phylogenies (Nützel, 1998; Colgan *et al.*, 2007; Ponder & Lindberg, 2008; Barco et al., 2010, 2015; Oliverio & Modica, 2010; Aktipis & Giribet, 2011; Dayrat *et al.*, 2011; Puillandre *et al.*, 2011; Simone, 2011; Strong *et al.*, 2011; Zou, Li & Kong, 2011; Takano & Kano, 2014; Galindo *et al.*, 2016), as a comprehensive gastropod phylogeny with sufficient resolution or sufficient varicate taxa is not yet available. Taxa were included either due to the presence of varices or as large or important avaricate groups to show where varices are absent. We aimed to make conservative estimates of relationships, especially relating to the number of origins of varices or when phylogenies disagreed. Number and timing of varix origins were also informed by the fossil record and information published by experts on the various clades. No analysis was performed.

RESULTS

TYPES AND VARIATIONS OF VARICES

Here we define a varix as follows: a varix is an axial (or collabral = parallel to the apertural margin) thickening on the outer shell surface that differs from other axial sculptural elements on the same shell such as individual growth lines, ribs, or lamellae by being thicker, abaxially more elevated, wider, and spatially further apart than smaller elements (Figs 1, 2). In most cases, therefore, species with varices possess two sizes of axial sculpture. Unlike lamellae, where growth after the varix is discontinuous, shell deposition generally continues on the apertural side of a varix.

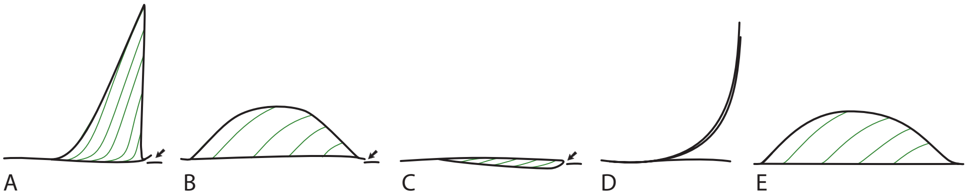


Figure 1. Cross-sectional outlines of different axial shell sculpture. (A) A thick varix with a triangular shape and erect lip, where shell is deposited on both sides of the varix, similar to *Ceratostoma*. (B) A rounded varix with erect lip, similar to *Cerithium*. (C) An internal varix with internal thickening and terminal scar, reminiscent of *Eulimidae.* (D) A thin lamella (not a varix) with no shell deposition or erect lip on the apertural side and lacking an intervarical rib, reminiscent of *Trophon.* (E) A rib (not a varix) with a smooth apertural edge. Green lines indicate theoretical, successive accretionary layers; arrows indicate breaks in shell secretion causing a 'scar' or erect lip.

Furthermore, many varices appear to be associated with a pause in growth – although this has not been tested in most cases – and usually terminate in an erect lip, such that further shell growth appears after an axial scar that marks growth arrest. This characterization of varices is purely descriptive and implies nothing about function or about the mode or timing of formation.

In a few cases, such as the ocenebrine muricid genus *Namamurex* (Pliocene of South Africa) and the ellobiid genera *Pythia* and *Ellobium*, varices occur in the absence of coaxial sculpture other than growth lines. We consider these taxa varicate because of the consistent placement of axial thickenings and their close similarity to varices on species that do also have smaller ribs or lamellae.

Varices vary considerably in form, placement, and number per whorl, and there are other superficially similar sculpture types that we do not consider varices (Fig. 3). Most true varices are rounded thickenings to varying degrees, but in some groups (especially Muricidae) they can be sharply angled, lamellose, and recurved, often bearing elaborate spines that may branch via the elaboration of spiral sculpture. In a few cases, these varices appear more as internal thickenings of the shell, with external scars denoting their location (i.e. some Eulimidae, Cancellaridae, and *Pythia*). Varices are usually distributed on both the spire and last whorl of the shell, either scattered (asynchronous varices) or precisely positioned to align between whorls (synchronous varices). We call these multiwhorl varices. Alternatively, varices appear in specific locations relative to a terminal aperture, generally placed dorsally or ventrolaterally on the last whorl. We call these subterminal varices, which are probably functionally analogous to dorsal or lateral knobs, at least in some cases (see below).

In addition to excluding species with a single terminal varix, cases in which the mantle- or foot-covered adult shell develops lateral thickenings (callus) are not included. These are produced by preferentially depositing shell material along the periphery of the ventral side. This condition, which causes the shell to appear dorsoventrally flattened, is widespread in cypraeoideans (Foin, 1989) and marginellids and in the Oligocene to Miocene stromboidean *Orthaulax*. These thickenings differ from varices in that they are secondarily formed once spiral growth of the shell has ceased, rather than being sculptural elements produced at the outer lip during spiral growth.

A special case we also excluded consists of a dorsal or lateral hump or knob in the adult shell, formed approximately at 90° or 120° from the aperture (although the actual angle varies considerably; Sälgeback & Savazzi, 2006). This feature resembles a varix because it is substantially more elevated than other nodes or tubercles and it is confined to the dorsal or lateral side of the adult shell, but it differs from a true varix in being axially short and thus not formed as an elaborated rib or lamella. In most cases, one dorsal knob per shell is present (e.g. many strombids and nassariids), but for a few groups (e.g. Muricidae and Cassidae) a dorsal knob can form at earlier growth stages.

FUNCTION

Many functions have been proposed for shell sculpture, most of which centre around defence by reducing the risk of predation in some way (Carter, 1967; Spight & Lyons, 1974; Vermeij, 1974, 1982, 1995; Palmer, 1979; Miller & LaBarbera, 1995; Donovan, Danko & Carefoot, 1999; Sälgeback & Savazzi, 2006). Varices may aid in defence in a number of ways. First is deterrence – spines and ridges are painful to soft-mouthed predators. Second is obstruction – large structures prevent gape/claw-limited predators from getting a grip on the shell. These two functions are most effective when the sculpture is large, as in muricid-type varices, or specifically placed, as in synchronized varices or knobs on the last whorl. Third

Figure 2. Examples of varices. (A) Ellobiidae: *Pythia scarabaeus* (L., 1758), lateral view. (B) Ellobiidae: *Ellobium auris-judae* (L., 1758), dorsal view. (C) Epitoniidae: *Cirsotrema varicosum* (L., 1822) JVM3131, lateral view. (D) Eulimidae: *Melanella martinii* (A. Adams in Sowerby, 1854) JVM1093, apical view; (D') Lateral view. (E) Batillariidae: *Pyrazus ebeninus* (Bruguière, 1792), oblique apical view. (F) Cerithiidae: *Cerithium eburneum* Bruguière, 1792, JVM1132, apical view. (G) Potamididae: *Cerithideopsis californica* (Haldeman, 1840), apical view. (H) Strombidae: *Laevistrombus canarium* (L., 1758), O365(D-58), apertural view. (I) Cassidae: *Phalium areola* (L., 1758), JVM851, apical view. (J) Bursidae: *Crossata ventricosa* (Broderip, 1833), apertural view, arrowhead; hollow varix. (K) Pseudomelatomidae: *Imaclava* sp., apertural view. (L) Drilliidae: *Imaclava pilsbryi* Bartsch, 1950, JVM3053, lateral view. (M) Muricinae: *Chicoreus nobilis* Shikama, 1977, apertural view. (N) Aspellinae: *Aspella pyramidalis* (Broderip, 1833), JVM1488, apical view. (N') Dorsal view. (O) Typhinae: *Haustellotyphis cumingii* (Broderip, 1833), JVM1362, apertural view. (P) Ocenebrinae: *Eupleura nitida* (Broderip, 1833), JVM1504, apertural view. (Q) Colubrariidae: *Colubraria tortuosis* (Reeve, 1844), apertural view. (R) Columbellidae: *Strombina fusinoidea* Dall, 1916, JVM1634, apical view. (S) Photinae: *Phos senticosus* (L., 1758), JVM1676, dorsal view. (T) Cancellariidae: *Bivetiella cancellata* (Linnaeus, 1767), JVM2879, apertural view. Scale bars: 5 mm; arrows indicate one (not all visible) varix. JVM and O represent the University of Alberta collection specimen numbers, specimens without collection numbers come from the Vermeij collection.

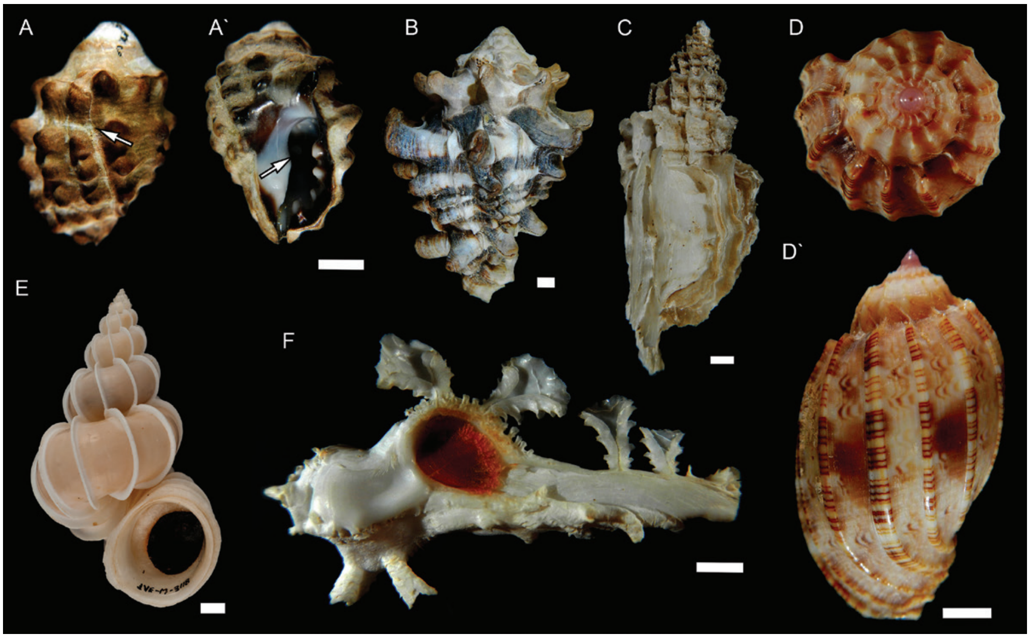


Figure 3. Varix-like sculpture not considered to be a true varix. (A) Ergalataxinae: *Tenguella granulata* (Duclos, 1832) dorsal view, with scar-like rib (arrow). (A') Apertural view, showing previous apertural teeth associated with scar-like rib (arrow). (B) *Vasum turbinellus* (L., 1758), dorsal view. (C) Trophoninae: *Nipponotrophon stuarti* (E. A. Smith, 1880), lateral view. (D) Harpidae: *Harpa amouretta* Röding, 1798, apical view. (D') Dorsal view. (E) Epitoniidae: *Epitonium scalare* (L., 1758), JVM3118, apertural view. (F) Muricopsinae: *Homalocantha anatomica* (Perry, 1811), apertural view. Scale bars: 5 mm. JVM and O represent the University of Alberta collection specimen numbers, specimens without collection numbers come from the Vermeij collection.

is structural – shell thickenings reinforce the shell and help prevent catastrophic breakage by slowing shell crushing, impeding shell peeling, preventing crack propagation, or increasing the force or work required to break the shell. Defence through structural reinforcement generally applies to all forms of shell sculpture; however, we predict that the extra thickening of varices is more effective than other types of shell sculpture, although this has not been tested experimentally. Vermeij (1982) observed that all unsuccessful attacks by calappid crabs on varicate gastropods involved a subterminal varix that prevented a peel or other breakage from extending up the spire.

The synchrony of varices between whorls has an added defensive advantage by allowing additional stress relief between whorls (Savazzi & Sasaki, 2004). Synchrony also ensures specific placement of varices relative to the aperture: A varix across from the aperture will specifically obstruct the grip of predators peeling the aperture, and a dorsal varix can help prevent shell crushing by increasing effective diameter. Synchronous shell growth ensures this is always the case (Savazzi & Sasaki, 2004) except for short periods of shell growth interspersed with long pauses.

Varices may have a few other special functions. In some groups, such as Personidae and Eulimidae, varices are associated with changes in the direction of the shell-coiling axis, although the relationship between these two factors is unclear. Varices may help breakup the outline of the shell, and promote epibiont growth to increase shell camouflage (Carefoot & Donovan, 1995; Vermeij, 1995). Another possible function of varices, specifically tested in the muricid *Ceratostoma foliatum* (Gmelin, 1791), is to aid in righting the shell after falling (Palmer, 1977; Carefoot & Donovan, 1995; Sälgeback & Savazzi, 2006). The angular distribution of varices may make the shell more likely to land upright. More generally, a dorsal protrusion prevents the shell from landing upside down, thus reducing the righting time, which is also thought to apply to the dorsal knob in strombids, cassids, and other groups (Savazzi, 1991). The curved spiny varices of *Murex pecten* Lightfoot, 1786 may act as a cage that can trap mobile prey (Paul, 1981), or they may help prevent the snail from sinking into the sand or mud by distributing the weight of the shell over a broader area, which might apply to other soft-sediment dwelling species with broad varices (including the terminal varices of apporhaids) (Seilacher & Gunji, 1993).

Varices may also allow a different form of shell growth: periodic growth via rapid growth spurts, which has several advantages over continuous/constant growth. Periodic growth minimizes the period of vulnerability by allowing the snail to build up resources for another growth spurt while the aperture is defended by a varix. In contrast, continuous growth involves more time spent when either the aperture is relatively weak or the cost of producing a constantly thick shell is relatively high. Other shell structures, including siphons and a crenulated outer lip (for clamping the shell onto rock), can be formed discontinuously in varicate gastropods (Seilacher & Gunji, 1993; Sälgeback & Savazzi, 2006; Vermeij, 2014). With periodic growth, the siphon is functional most of the time, without needing constant remodelling. This is especially true for the upturned siphons of muricids, cerithiids, personiids, tonnoids, and some nassariids – all groups with varices. This is less applicable to species with straight siphons that can more easily be grown continuously without constant remodelling.

TAXONOMIC SURVEY OF VARICES

VETIGASTROPODA

Few examples of varices occur in basal gastropods, an observation consistent with the general lack of high relief sculpture, which has been partially attributed to a reduced ability to resorb shell material (Vermeij, 1977). However, two inarguable vetigastropod clades include varicate gastropods: the Seguenzioidea and Discohelicidae (Fig. 4; Table S1).

Three genera within Seguenzioidea are varicate – *Onkospira* from the Middle Jurassic (Bathonian) to the Early Cretaceous and perhaps the Late Cretaceous (Kase, 1984; Das, Bardhan & Lahiri, 1999), *Agathodonta* from the Early Cretaceous (Herbert, 2012), and *Calliovarica* from the Early Eocene (Vokes, 1939; Beu & Maxwell, 1990; Hickman & McLean, 1990; Stilwell, 2014). They have been assigned to Eucyclidae (*Onkospira*) or Chilodontidae (*Agathodonta* and *Calliovarica*) and have simple, low rounded varices. Although nothing is known about the phylogeny of these varicate taxa, we take the conservative position that the varicate condition evolved only once in the Seguenzioidea. Significantly, although a terminal varix occurs in several living genera of Chilodontidae (Herbert, 2012), no living Seguenzioidea have multiple varices.

Within the Discohelicidae, *Colpomphalus dupinianus* (d'Orbigny, 1842), from the Hauterivian, is one of the rare cases of varices found on a nearly planispiral shell in gastropods (Kollmann & Fischer, 2005; Ferrari, 2014).

HETEROBRANCHIA

The near complete lack of varices in heterobranchs is interesting and likely related to their general lack of shell sculpture. In nonmarine groups, this is normally attributed to reduced predation pressure, with other possible factors being the increased cost of a weighty shell on land and reduced calcium availability (Vermeij, 1987).

ACTEONIDAE

Varices were just recently described in two genera of Acteonidae, *Hemiauricula* and *Nucleopsis* from the Eocene (Salvador & Cunha, 2016). These consist of weak thickenings and an associated axial scar, with up to three per shell, generally on the last few whorls. These two genera were united as the some members of a redefined Liocareninae. Living acteonids are generally infaunal predators of polychates, so thicker varices may be impractical, and their relationship to other heterobranchs is still in flux, although they are generally considered basal (Salvador & Cunha, 2016).

ELLOBIIDAE

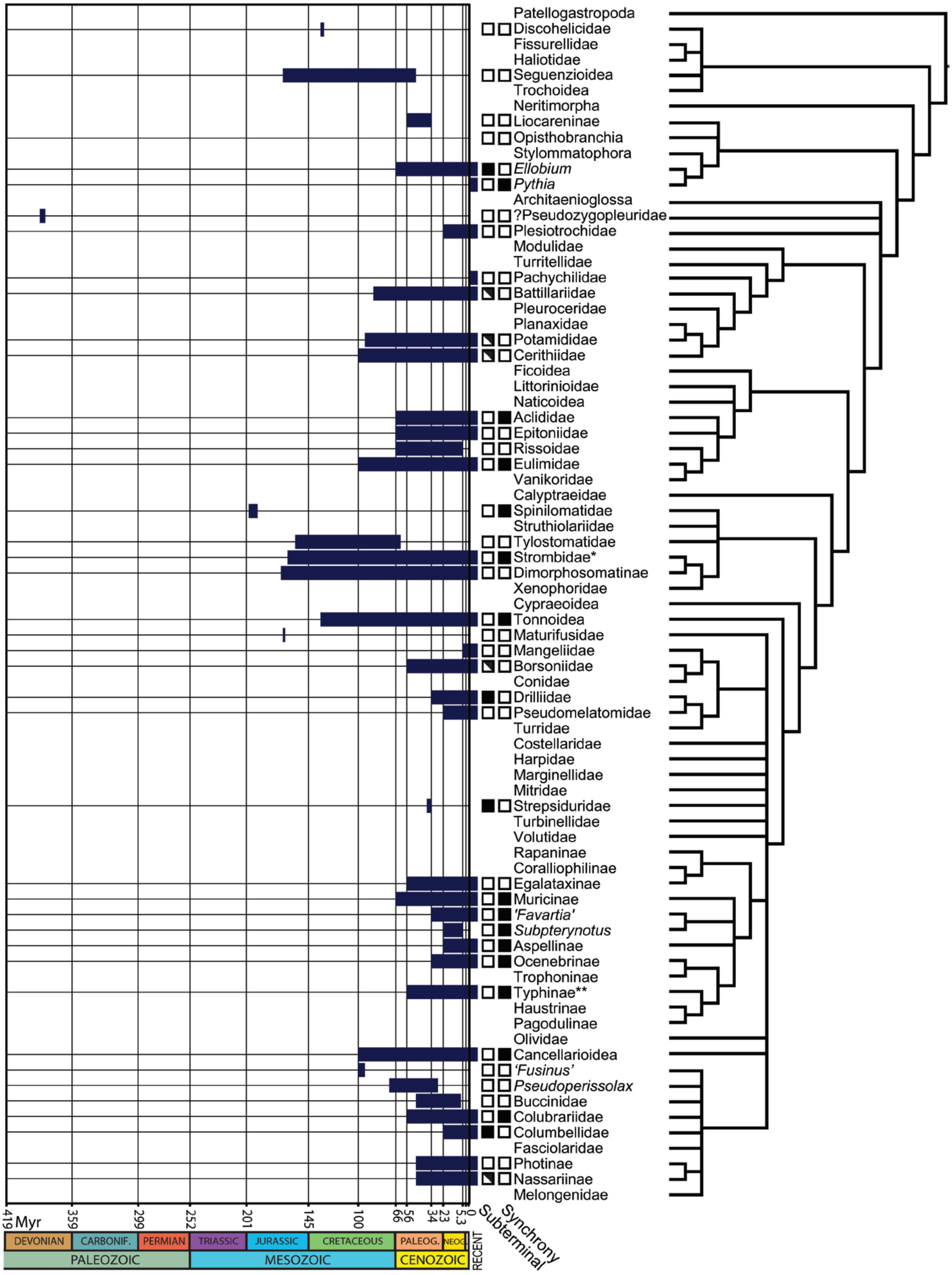
Interestingly, both of the varicate taxa in the Ellobiidae, the Recent genera *Pythia* and *Ellobium*, co-occur with land crabs in near-shore environments (Raven & Vermeulen, 2007). Neither group has elaborate shell thickenings, and both are placed in different ellobiid clades (Martins, 2007), suggesting separate origins.

In *Pythia*, the varices are similar to those of eulimids, with two axially thickened scars 180° apart, matching the dorsoventral flattening of the shell (Fig. 2A). The varices of *Ellobium* are quite different, with a dorsal subterminal varix behind the mature aperture, with the same thickened edge (Fig. 2B). This varix appears in *E. aurisjudae* (L. 1758), *E. aurismidae* (L. 1758), and *E. scheepmakeri* (Petit de la Saussaye, 1850), but is not present in all individuals. It may be that individuals without varices have not yet reached the appropriate ontogenetic stage, or it could be a polymorphic trait. The earliest *E. olivaeformis* (Briart & Cornet, 1873) from the Early Paleocene is not described with varices (Thorsten, 2002).

CAENOGASTROPODA

?Pseudozygopleuridae

Spanionema is the earliest known genus with varices, from the Givetian (Middle Devonian). The varices are irregularly placed and relatively pronounced (Knight *et al.*, 1960; Heidelberger, 2001). The relationships of this genus are uncertain, but it clearly represents a separate origin of varices, with no known varicate relatives.


Patellogastropoda
Discohelicidae
Fissurellidae
Haliotidae
Seguenzioidea
Trochoidea
Neritimorpha
Liocareninae
Opisthobranchia
Stylommatophora
Ellobium
Pythia
Architaenioglossa
?Pseudozygopleuridae
Plesiotrochidae
Modulidae
Turritellidae
Pachychilidae
Battillariidae
Pleuroceridae
Planaxidae
Potamididae
Cerithiidae
Ficoidea
Littorinioidae
Naticoidea
Aclididae
Epitoniidae
Rissoidae
Eulimidae
Vanikoridae
Calyptraeidae
Spinilomatidae
Struthiolariidae
Tylostomatidae
Strombidae*
Dimorphosomatinae
Xenophoridae
Cypraeoidea
Tonnoidea
Maturifusidae
Mangeliidae
Borsoniidae
Conidae
Drilliidae
Pseudomelatomidae
Turridae
Costellaridae
Harpidae
Marginellidae
Mitridae
Strepsiduridae
Turbinellidae
Volutidae
Rapaninae
Coralliophilinae
Egalataxinae
Muricinae
'Favartia'
Subpterynotus
Aspellinae
Ocenebrinae
Trophoninae
Typhinae**
Haustrinae
Pagodulinae
Olividae
Cancellarioidea
'Fusinus'
Pseudoperissolax
Buccinidae
Colubrariidae
Columbellidae
Fasciolaridae
Photinae
Nassariinae
Melongenidae
419 Myr
359
299
252
201
145
100
66
56
34
23
5.3
0
Synchrony
Subterminal
DEVONIAN
CARBONIF.
PERMIAN
TRIASSIC
JURASSIC
CRETACEOUS
PALEOG.
NEOG.
RECENT
PALEOZOIC
MESOZOIC
CENOZOIC

Campaniloidea

The clade Campaniloidea is mostly free of varicate species, but Harzhauser (2014) noted the presence of varices (one to two per whorl) in the Early Miocene plesiotrochid *Plesiotrochus inopinatus* Cossmann, 1910 from the Quilon Formation of India. A second Recent species *Plesiotrochus* aff. *acutangulus* (Yokoyama, 1924) was described by Janssen, Zuschin & Baal (2011) with very weak varices. These occurrences leave open the possibility that more species in this group will be found to have varices.

Epitoniidae

The state of varices in this family, which originated in the Cretaceous, is complicated. Most species have a number of axial elements on each whorl that generally align from one whorl to the next. These vary from striations to alate lamellae, which we do not consider to be varices (Fig. 3E). In most cases, we determined these to be ribs or axial lamellae; however, some species, like many *Cirsotrema*, *Epitonium*, *Opalia*, and *Amaea* have distinct rounded varices interspersed with the other ribs, the earliest being from the Paleocene (Abbott, 1974; Kilburn, 1985; Lozouet *et al.*, 2001) (Fig. 2C). These varices are not synchronized, and whether they represent growth stoppages is unknown.

Eulimidae

The Eulimidae (L. Cretaceous- Recent) are almost exclusively echinoderm parasites, with a generally polished, high-spired shell. The varices of eulimids are atypical of gastropods as a whole. In most species, varices appear as periodic axial scars on the shell associated with an internal thickening. In many cases, they are synchronized between whorls, with only one per whorl, although some have two per whorl, and the degree of synchrony varies (Fig. 2D). For example, not all specimens of *Melanella martini* (A. Adams in Sowerby, 1854) have synchronized varices (Savazzi & Sasaki, 2004). The varices of eulimids are associated with a growth hiatus and subsequent thickening of the aperture. Interestingly, some eulimids are sequential hermaphrodites, and a varix is associated with the transition from male to female (e.g. *Apicalia*) (Warén, 1983). All eulimids with the characteristic curved shell possess a varix every 360°, although the inverse is not true, – not all species with this pattern have curved shells (Savazzi & Sasaki, 2004). The curving of the shell may be accomplished by slight changes to the axis of coiling at each growth hiatus. The internal nature of the varices helps maintain the ultra-smooth texture of the shell while still providing a thickened aperture during growth stoppages and periodic structural support. Some genera, such as *Auriculigerina*, *Chileutomia*, and *Oceanida*, have more expanded varices, which correspond to a more flaring aperture (Warén, 1983; Lozouet, 1999; Landau & Marquet, 2001; Garilli & Messina, 2006).

Aclididae

This family is poorly known, but some members of *Aclis* have varices strongly reminiscent of those seen in Eulimidae (Bertolaso & Garilli, 2009). *Aclis aurisparva* Bertolaso & Garilli, 2009 has scar-like varices on the upper whorls, and further down the spire they become more wing-like processes. The placement of this family is uncertain, but it does have an affinity with Eulimidae, although this may be plesiomorphic (Takano & Kano, 2014). Further complicating the matter, the family Aclididae is also not well defined and may be paraphyletic (Warén, 1983).

Rissoidae

Warén (1983) mentions that 'rissoinids' have internal varices, similar to those of Eulimids, but does not provide details. A single genus *Pseudotaphrus* has occasional varices on its smooth shell, generally on the last whorl (Ponder, 1984). These are similar in appearance

Figure 4. Examples of varices. A) Ellobiidae: *Pythia scarabaeus* L., 1758, lateral view. B) Ellobiidae: *Ellobium aurisjudae* L., 1758, dorsal view. C) Epitoniidae: *Cirsotrema varicosum* L., 1822, JVM3131, lateral view. D-D') Eulimidae: *Melanella martinii* A. Adams in Sowerby, 1854, JVM1093, apical view (D), lateral view (D'). E) Batillariidae: *Pyrazus ebeninus* Bruguière, 1792, oblique apical view. F) Cerithiidae: *Cerithium eburneum* Bruguière, 1792, JVM1132, apical view. G) Potamididae: *Cerithideopsis californica* Haldeman, 1840, apical view. H) Strombidae: *Laevistrombus canarium* L., 1758, O365D-58., apertural view. I) Cassidae: *Phalium areola* L., 1758, JVM851, apical view. J) Bursidae: *Crossata ventricosa* Broderip, 1833, apertural view, arrowhead: hollow varix. K) Pseudomelatomidae: *Inquisitor* sp., apertural view. L) Drilliidae: *Imaclava pilsbryi* Bartsch, 1950, JVM3053, lateral view. M) Muricinae: *Chicoreus nobilis* Shikama, 1977, apertural view. N) Aspellinae: *Aspella pyramidalis* Broderip, 1833, JVM1488, apical view. N') Dorsal view. O) Typhinae: *Haustellotyphis cumingii* Broderip, 1833, JVM1362, apertural view. P) Ocenebrinae: *Eupleura nitida* Broderip, 1833, JVM1504, apertural view. Q) Colubrariidae: *Colubraria tortuosis* Reeve, 1844, apertural view. R) Columbellidae: *Strombina fusinoidea* Dall, 1916, JVM1634, apical view. S) Photinae: *Phos senticosus* L., 1758, JVM1676, dorsal view. T) Cancellariidae: *Bivetiella cancellata* Linnaeus, 1767, JVM2879, apertural view. Scale bars = 5 mm; arrows indicate one (not all visible) varix. JVM and O represent the University of Alberta collection specimen numbers, specimens without collection numbers come from the Vermeij collection.

to the varices in *Ellobium* in that they appear as a stoppage of growth with associated apertural thickening, followed by a short period of spiral growth to a new aperture. Unlike *Ellobium*, their placement does not appear consistent enough to warrant the label of a dorsal varix.

These four families, Aclididae, Eulimidae, Epitoniidae, and Rissoidae, cluster relatively closely on the phylogeny of Takano & Kano (2014), but phylogenetic relationships remain uncertain. With the exception of Aclididae and Eulimidae, each family differs quite widely in how varices are expressed. This morphological difference supports four separate evolutionary origins, especially considering the rarity of varices in Rissoidae, Epitoniidae, and Aclididae.

Cerithioidea

Varices appear to have originated four times independently in the Cerithioidea, because the basal-most cerithioideans do not have varices (Strong *et al.*, 2011). Rounded, unsynchronized varices that extend up the spire evolved once in Potamididae (Turonian-Recent) (Saul & Squires, 2003; Reid *et al.*, 2008) and once in the clade including Cerithiidae, Litiopidae (*Alaba* and *Gibbarissoia*), and Diastomatidae (Paleocene-Recent) (Houbrick, 1981; Strong *et al.*, 2011). In many cases, these varices are lighter in colour compared to rest of the shell. The third origin is in the Batillariidae and the fourth in *Faunus ater* (L. 1758) (Pachychilidae).

Broad, lateral, subterminal varices are also found in many species of Potamididae, Cerithiidae (not Alabininae), Pachychilidae (*Faunus*), and Battilariidae (Fig. 2E–G). A few cerithiines, including *Clypeomorus*, can also have a dorsal subterminal varix (Houbrick, 1985, 1991; Ozawa *et al.*, 2009; Strong *et al.*, 2011).

Many Mesozoic cerithioids are difficult to assign to specific families, so varix origins in these families are unclear. The earliest potamidid with a ventrolateral varix is *Cedrosia pacifica* Saul & Squires, 2003 (Late Cretaceous), although many Mesozoic potamidids are also avaricate (Saul & Squires, 2003). The earliest batillariid found was *Pyrazus partschi* (Zekeli, 1852) from the Late Cretaceous, while the first without varices *?Echinobathra* is mid-late Cretaceous (Ozawa *et al.*, 2009). In the paraphyletic cerithiidae (Ozawa *et al.*, 2009), *Cryptaulax* is found in the Triassic without varices, while the varicate taxon *Hemicerithium? interlinea* (Cragin, 1893) occurs in the Cenomanian (Early Late Cretaceous) (Stephenson, 1952; Sälgeback & Savazzi, 2006).

Faunus ater has a subtle ventrolateral varix not mentioned by Houbrick (1991). *Faunus* is reconstructed as the basal genus, as well as the sole brackish water representative of the freshwater Pachychilidae (Köhler & Glaubrecht, 2010). Earlier fossil pachychilids, including other *Faunus*, do not show varices, so this may be a separate and Recent origin of varices (Pacaud & Harzhauser, 2012).

Stromboidea

Varices occur widely in the Stromboidea. Most are enlarged rounded ribs, but some are adorned with spines, as in the aporrhaids *Spiniloma* and *Spinigeropsis* (Spinilomatidae) of the Early Jurassic, *Pietteia* (Dimorphosomatinae) of the Middle Jurassic, and *Diempterus* (Aporrhainae) of the Late Jurassic (Kollmann, 2009; Gründel, Nützel & Schulbert, 2009). In most aporrhaids, varices occur at half-whorl intervals, but in some aporrhaids and most strombids, varices are more closely spaced and confined to the spire whorls (Fig. 2H).

Largely based on Kollmann's (2009) fossil-based evolutionary scenario, we infer three independent origins of varices in the Stromboidea. No varices occur in the oldest member of the group, the genus *Dicroloma* (Aporrhainae) of the Early Jurassic (Sinemurian) (Kollmann, 2009; Gründel *et al.*, 2009). Varices evolved first in *Spiniloma* (Spinilomatidae) during the Sinemurian, separately in *Pietteia* (Dimorphosomatinae) in the Middle Jurassic, and a third time in a lineage of Aporrhainae including the Late Jurassic genera *Dicroloma* and *Diempterus*. According to Kollmann's (2009) scenario, in the Aporrhaidae, the varices of the Early Cretaceous (Barremian) to Recent Arrhoginae (observed in the genera *Arrhoges*, *Graciliala*, *Latiala*, and *Mexopus*) were inherited from dimorphosomatine ancestors, as were varices in some members of the Anchurinae (*Drepanochilus* and *Helicaulax*), which originated in the Barremian. The varicate Rostellariidae (Campanian Late Cretaceous to Recent) are diphyletic with separate origins in the varicate Arrhoginae (*Graciliala* and *Latiala*). The Strombidae of the Cenozoic are derived via the Rimellinae from the *Calyptraphorus* group of Rostellariidae (Kronenberg & Burger, 2002; Kollmann, 2009).

Finally, varices occur in the Late Mesozoic family Tylostomatidae (genera *Pterodonta* and *Tylostoma*). These varices are visible on the internal moulds (steinkerns), with generally two per whorl (Squires & Saul, 2004). Although Bandel (2007) considers them stromboids, Kollmann (2009) rejects this hypothesis on the grounds that a rostrum and an expanded outer lip, both characteristic of Stromboidea, are absent. Squires & Saul (2004) place this family as Caenogastropoda *incertae sedis*. The phylogenetic placement of Tylostomatidae remains doubtful, but we maintain its placement in the Stromboidea for now and consider their varices to have arisen separately.

Many stromboidean clades lack varices. In Kollmann's (2009) scenario, some of these clades are derived from nonvaricate Aporrhainae. These include the subfamilies Pterocerellinae and Harpagodinae. A loss of varices apparently occurred in some Dimorphosomatinae and in its derived clade Pugnellinae, as well as groups within the subfamilies Anchurinae and Arrhoginae, and separately in the temperate southern-hemisphere Struthiopterinae, which Kollmann (2009) derives from varicate Anchurinae. Within Strombidae, true varices have been lost in such genera as *Euprotomus*, *Harpago*, *Lambis*, *Lobatus* (some species), *Mirabilistrombus*, and *Tricornis*, but how often the loss of varices occurred in this group or in the Aporrhaidae remains unclear. The living southern-hemisphere family Struthiolariidae and the Paleocene to Recent tropical Seraphsidae likewise lack varices, but the absence of a phylogenetic hypothesis prevents conclusions about whether this absence is primary or secondary.

Tonnoidea

Most tonnoid families have varices. In most cases, these follow a synchronized pattern of either varices every 240° (generally in Cassidae, Cymatiinae, Personidae, and some Tonnidae) or 180° (generally in Bursidae and Ranellinae) (Savazzi & Sasaki, 2004). The varices are generally robust, sometimes with a spiny posterior canal as in bursids, true spines as in *Bufonaria echinata* (Link, 1807), alate extensions like *Gyrineum* or *Cymatium*, or associated with a callus as in personids and some cassids. Most are thick and rounded with a prominent adapertural scar (Fig. 2I). Interestingly, in some tonnoids, such as *Crossata* (Bursidae), the sculpture is not represented by thickenings, but rather by hollowed out distortions that are later filled in (Fig. 2J). This is seen in bursids and 'ranellids', but not yet observed for personids or cassids. In the Tonnidae, we have identified only a single species, *Malea elliptica* Pilsbry and Johnston, 1917 where varices have been observed (Beu, 2010). Interestingly, some families that have been placed as basal tonnoids, Eosassiidae (Aptian-Albian), Mataxidae (Campanian to M. Eocene), and Paladmetidae (L. Cretaceous) do not have strongly synchronized varices, suggesting that synchrony arose after the evolution of varices, although their true affinities are controversial (Sohl, 1964; Beu, 1988; Gründel, 2001; Bandel & Dockery, 2012). A single Early Cretacous (Hauterivian?) origin of varices in the Tonnoidea seems likely, with subsequent losses within most families. A recent phylogeny found that all tonnoid families are monophyletic, except 'Ranellidae', and supports a monophyletic Tonnoidea with a presumed single origin of varices (Strong *et al.*, 2016). Stephenson (1952) mentions that the holotype of the basal tonnoid *Caveola pinguis* has a varix approximately dorsal, but this is probably not a subterminal varix because later he mentions that varices are occasional in this species.

Laxton (1970) described the growth of varices in some New Zealand 'ranellids', and described a pattern of growth similar to muricids. The shell grows quickly from one varix to the next, leaving a thin sector of shell which is then reinforced during a growth hiatus after the varix has formed. The first occurrence of early varices during growth is related to food availability, with individuals exposed to fewer resources growing varices on earlier whorls than those with more food. He also noted that although 'adults' did hide and fast while growing intervarical regions, the juveniles did not, presumably to enable faster growth.

As in eulimids, the varices of personids indicate regions where the axis of coiling changes, and in both cases, the ancestral unbent shell is reconstructed as varicate. Causation is unclear, however. If changes in the axis of coiling require a growth hiatus, varices may simply be a product of the temporary growth arrest.

NEOGASTROPODA

Maturifusidae

The family Maturifusidae comprises one core genus *Maturifusus* (Mid Jurassic to Late Cretaceous) and one or two additional genera according to various interpretations (Guzhov, 2001; Kaim, 2004; Gründel, 2005). All have axially sculptured siphonate shells. A single species, *Astandes ticurelatus* (Gründel, 2001), from the Bathonian (Middle Jurassic) of Germany, has some axial ribs enlarged as varices (Gründel, 2001), although these are not evident in the figures of Kaim (2004). The family is interpreted as either a stem group for neogastropods (Guzhov, 2004; Blagovetshenskiy & Shumilkin, 2006) or as ancestral to the clade Latrogastropoda of Riedel (2000), which includes the siphonate Tonnoidea and Neogastropoda as well as Naticoidea, Cypraeoidea, and related clades (for discussion see also Gründel, 2005; Kaim & Beisel, 2005; Bandel & Dockery, 2012). We interpret the appearance of varices in *M. ticurelatus* as separate from that in Tonnoidea and the various neogastropod clades in which varices occur because of the long time gap between the Bathonian and the earliest varices in undoubted latrogastropods (Hauterivian, Early Cretaceous).

Strepsiduridae (= Strepturidae Cossmann, 1901)

The neogastropod family Strepsiduridae (Early Eocene to Recent) contains mostly species with a single terminal varix, including species of *Strepsidura* and the Pliocene to Recent genus *Melapium* (Vermeij, 1998). A Late Eocene species from Colombia described as *Peruficus olssoni* by Clark in Clark & Durham (1946) and tentatively assigned to *Streptostyla* by Woodring (1973), has a subterminal varix placed either 180° or 270° from the outer-lip varix in the two specimens of the type lot examined by GJV at the University of California Museum of Paleontology, Berkeley.

Conoidea

Varices occur only sparsely in the extremely diverse clade Conoidea. *Varicobela* in the Borsoniidae (Eocene-Oligocene), *Tenaturris* in Mangeliidae (Miocene-Recent), and several species of *Inquisitor* (Pseudomelatomidae, Eocene-Recent; Fig. 2K) have occasional, unsynchronized varices in the form of broader ribs (Powell, 1966; Ladd, 1982). A subterminal dorsal varix is also found in the recent *Darbya* (Borsoniidae). Various tropical West Atlantic drilliids show a dorsal varix: *Agladrillia*, *Clathrodrillia*, *Imaclava*, *Fenimorea*, and *Syntomodrillia* (Powell, 1966; Woodring, 1970; Fallon, 2016) (Fig. 2L). When comparing species with convincing varices to related species, some sister taxa have near-varices that either cannot be clearly distinguished from ribs, are too close to the aperture to separate from terminal varices, or do not span the whorl to distinguish from a dorsal knob.

This pattern of scattered species bearing varices suggests at least four varix origins within Conoidea, although further phylogenetic analyses will be required to estimate exactly how many. Notably, despite the high spire and regular ribbing in Turridae, Terebridae, Clavatulidae, and Clathurellidae, we identified no members with varices, nor within the lower spired but hyperdiverse Conidae. Furthermore, those taxa with varices have remained surprisingly species poor.

Muricidae

Species of Muricidae bear the most stereotypical and elaborate varices. They are currently divided into eleven subfamilies (Barco et al., 2010, 2012), five of which we consider to be completely lacking varices: Rapaninae, Coralliophilinae, Trophoninae, Haustrinae, and Pagodulinae. All the other subfamilies have at least a few members with varices (Fig. 2M–P). Many species have axial lamellae rather than varices, such as those in the Trophoninae, with very thin lamellae that lack the robustness, intervarices, and the spacing of varices (Fig. 3C). The earliest varicate muricid is the Early Paleocene genus *Timbellus* (Merle, Garrigues & Pointier, 2011) with three or four synchronized varices on each whorl. Although the subfamily to which *Timbellus* belongs is unclear, Barco *et al.* (2012) suggests it may fit with the typhines. We estimate seven origins of varices in the Muricidae, but the lack of subfamilial trees makes this a broad estimate at best, with clear evidence of phylogenetic clumping. These seven origins are one each for Muricinae, Ocenebrinae, Ergalataxinae, Typhinae + Tripterotyphinae, and Aspellinae, as well as two origins within the Muricopsinae.

Muricid varices are in most cases synchronized between whorls and, if not, are generally evenly spaced. One of the key features of Muricids is the intervarical ribs. Nearly all varicate species have a regular number of ribs interspersed between varices. This pattern often arises gradually during growth from a juvenile pattern where all axial elements appear as ribs or lamellae. As the snail grows, the elements differentiate into regularly spaced, more elaborate varices, with intervarical ribs (Spight & Lyons, 1974). Although many *Hexaplex* lack intervarical ribs, these ribs are usually present on earlier whorls and intermittently present on the last whorl (Merle *et al.*, 2011). Generally, muricid varices grow episodically, with short intense spurts of shell growth completing an intervarical region and varix, followed by periods of quiescence where shell growth is limited to reinforcing the new shell segment (MacKenzie, 1961; Inaba, 1967; MacGinitie & MacGinitie, 1968; Spight, Birkeland & Lyons, 1974; Spight & Lyons, 1974; Illert, 1981). Some authors report snails going into hiding and/or not eating during bursts of shell growth (Inaba, 1967), but this is not true in the laboratory for *Ceratostoma foliatum* (Pers. Obs., NBW).

Muricid varix morphology has four distinctive features. First is the base of the varix, which can be rounded (as in *Haustellum*) or asymmetrical with a gradual adapertural side and abrupt abapertural side (as in *Typhis* and *Hexaplex*). Second is height variation, from low structures (*Hexaplex*) to extended (most *Timbellus*). Third is edge shape, which ranges from relatively smooth (*Ceratostoma* and *Haustellum*) through varying degrees of spinosity (*Murex*) including branching spines (*Chicoreus*). Last is the degree to which the spiral cords are emphasized in the varix, from very pronounced, forming a corrugated edge (*Ceratostoma*), to low spiral cords that are barely evident (*Siratus*). All of these parameters combine in various ways to describe the full diversity of varices in the Muricidae (Powell, 1927; Marwick, 1934). The most common pattern is three varices per whorl, but two, four, and sometimes six per whorl also occur. In an extreme case, the genus *Muricanthus* (Muricinae) can have 12 varices per whorl.

The Ergalataxinae have a few varicate members: *Ergalatax*, *Cronia*, and *Phrygiomurex*, as well as the fossil taxa *Odontopolys* and *Lyropupura*, which are related to the nonvaricate *Vitularia*, and *Daphnellopsis* and *Lindapterys* whose relationships are poorly understood (Palmer, 1937; Lozouet, Ledon & Lesport, 1994; Claremont *et al.*, 2013). The origin of the Ergalataxinae is difficult to determine, but appears to have been in the Eocene (Vermeij & Carlson, 2000; Claremont *et al.*, 2013), with multiple varicate taxa from that time (*Daphnellopsis*, *Odontopolys*, *Morula purulansis* Martin, 1914, and *Lyropupura*). Ergalataxine varices are generally low and rounded, while they are flared in *Lyndapterys* and are mostly synchronized with two per whorl, even in the earliest *L. vokesae* Petuch, 1987 (E. Miocene) (Lozouet *et al.*, 1994). In some taxa, such as *Tenguella* and *Morula spinosa* (H. Adams & A. Adams, 1853), individuals have evidence of a growth stoppage prior to the aperture that resembles a varix. This may be a polymorphic trait in these species or could be due to failed predation events altering shell growth. Some shells show remnants of apertural teeth inside the shell at these locations, which we believe supports the latter hypothesis (Fig. 3A).

Few Muricopsinae have true varices, despite having some of the most elaborate axial sculpture among muricids. Most species actually have impressively elaborate lamellae like the seemingly impossible branching club lamellae in *Homalocantha anatomica* (Perry, 1811) and its relatives (Fig. 3F). Three groups show true varices: *Subpterynotus textilis* (Gabb, 1873), with three alate synchronized varices per whorl and identifiable intervarical nodes (E. Miocene – Pliocene) (Vermeij, 2005b). The other varicate genera belong to the *Favartia* complex*:* *Pygmaepterus menoui* (Houart, 1990), some similar species and several *Caribiella*. We believe these represent two separate origins, based on the distinct morphology of *Subpterynotus*. This subfamily was deemed polyphyletic by Barco *et al.* (2010), and a great deal of uncertainty about generic placement remains.

Only in the Typhinae, which arose in the Early Eocene, and the very similar Tripterotyphinae, do all members appear to have varices (D'Attilio & Hertz, 1988). These subfamilies have similar large alate varices with a distinct intervarical anal tube. Only the most recent excurrent tube is open; previous ones are filled in during growth of the next varix. Shells in these subfamilies can have two to five varices; *Distichotyphis* for example has two varices per whorl, but most have three to four varices aligned per whorl.

Most Muricinae have varices, and the few exceptions are generally fossil groups that may be more properly considered Muricidae *sensu lato*, or stem muricids (*Attiliosa*, *Bouchetia*, *Calotrophon*, *Crassimurex*, *Eopaziella*, *Flexopteron*, *Nucellopsis*, *Paziella*, *Poirieria*). Truly spiny varices, epitomized by *Murex pecten*, only occur within the muricines. *Bolinus*, with generally five to seven varices on the last whorl, has an interesting trend where the two earliest species, *B. beyrichi* (?L. Eocene – E. Oligocene) and *B. submuticus* (Early-Mid Miocene) (Grateloup, 1846), are the most variable in the number of both varices and intervarical ribs, a pattern that we would expect if varices arise before the canalization of their positioning.

Although the validity of the Aspellinae, all of whom have varices, is contested, we have kept it separate here (Barco *et al.*, 2010; Houart & Héros, 2013). *Aspella* bear two varices per whorl, on the edges of the dorsoventrally flattened shell. This genus arose in the Late Oligocene with *A. subanceps* (Merle *et al.*, 2011). Varix number is more variable in *Dermomurex s.l*, with two to eight varices on the last whorl, depending on the species. On earlier whorls, these are interspersed with intervarical ribs, which fade away gradually, and in some species, the number of varices also gradually decreases (Vokes, 1985). *Viator* has the largest number of varices (eight), while *Gracilimurex* only has two per whorl. The varices are aligned either with previous varices or previous intervarical ribs (Vokes, 1985). *Dermomurex* is the oldest genus, with *Dermomurex s.s*, *Takia*, and *Viator* extending back to the Early Oligocene (Merle *et al.*, 2011). *Ingensia* has four varices on the last whorl and is most similar to *Dermomurex*, and no fossils are known (Houart, 2001). These genera are united by a thick intritacalx (an outer calcareous shell layer, above or replacing the periostracum), and low, rounded, smooth varices.

It is difficult to separate the varicate and nonvaricate Ocenebrinae into clear clades without a broad phylogeny of this morphologically diverse subfamily. The earliest appear in the Early Oligocene, while Ocenebrinae probably arose near the Middle Eocene (Vermeij & Vokes, 1997; Merle *et al.*, 2011). Although two varicate taxa included in the phylogeny of Barco *et al.* (2010), *Eupleura nitida* (Broderip, 1833) and *Ocinebrellus inornata* (Récluz, 1851) (called *Ceratostoma* in Barco *et al.*, 2010), were not sister taxa, we feel greater taxon sampling will be required to answer this question. About half of ocenebrine genera have varices, and only *Ocinebrina* and *Ocenebra* appear to have both varicate and nonvaricate species, with a high degree of variability, even intraspecifically. Interestingly, the only muricid with a subterminal varix that we encountered was *Ocinebrina paddeui* Bonomolo & Buzzurro, 2006, which occasionally produces a single dorsal varix, about half whorl back from the aperture (Bonmolo & Buzzurro, 2006). Ocenebrine varices can vary from low and rounded in *Ocinebrina edwardsii* (Payraudeau, 1826) (these are only occasional) to the huge alate varices of *Pteropurpura* and *Ceratostoma*. Most have three varices aligned per whorl, except *Eupleura*, with two varices along the plane of the dorsoventrally flattened shell, and *Ceratostoma rorifluum* (Adams & Reeve, 1849), with four.

Buccinoidea

The relationships of the Buccinoidea are still debated, but we identified six or seven separate origins of varices, one for each of Buccinidae, Colubrariidae, Columbellidae, two in the Nassariidae (Nassarinae and Photinae), as well as a separate origin for *'Fusinus' fluminis* (Stephenson, 1952) from the Cenomanian, which may in fact be a basal neogastropod, and *Pseudoperissolax* (L. Cretaceous – E. Oligocene), whose affinity is still in flux. Squires (2015) placed *Pseudoperissolax* in the Muricinae, but we agree with Beu (Pers. Comm.) and prefer to place this as a buccinoid until further information is available.

Very few Buccinidae possess varices. Only a few fossil species, *Euthria elatior* (Cossman & Pissarro, 1901) from the Middle Eocene and *Euthria varicifera* (Peyrot, 1928) from the Tortonian, showed some irregularly placed varices.

Most Colubrariidae have broad rounded varices, the oldest of which are found in *Metula silvaerupis* (Harris, 1899) from the Early Eocene. Many have nearly to fully synchronized varices between whorls, generally 240° apart, especially in *Colubraria*, *Metula*, and *Cumia*, although the degree of synchrony is variable both within and between species. *Colubraria tortuosa* (Reeve, 1844) is of particular note, as the apex is often twisted or bent, with varices almost 360° apart (Savazzi & Sasaki, 2004) (Fig. 2Q). As in Eulimidae and Personidae, the twisting line of varices matches closely with the concave portion of the spire's twist.

Most Columbellidae also lack varices. Only some members of the *Strombina* group (Early Miocene-Recent) have dorsal and/or ventrolateral varices (Jung, 1989) (Fig. 2R).

Although taxonomists have only reported varices in a few members of the Nassariinae, both fossil and Recent, close inspection reveals that many species are varicate. In nearly all cases, a single lateral varix is present, in addition to the terminal one. Species of *Plicarcularia* usually have a dorsal hump, and *Varicinassa* has multiple varices. The earliest varicate nassariine is *Buccitriton* from the M. Eocene, and species with one or more subterminal varices are clustered in some genera of the recently reorganized Nassariinae: *Buccitriton*, *Nassarius s.s.* from the Indo-West Pacific, and the sister genera *Phrontis* and *Tritia* (Galindo *et al.*, 2016). Although these varicate clades are not perfectly clustered as sister taxa in the phylogeny, we suggest a single origin is appropriate for this subfamily.

Some Photinae bear varices. One is *Tritiaria* from the Middle Eocene, although the oldest, *T. cerralvensis* Gardner 1945 from the Paleocene, which is dubiously attributed to the genus, lacks varices (MacNeil & Dockery, 1984). A few low varices up the spire occur in *Antillophos*, *Europhos*, *Cymatophos*, *Metaphos*, *Philindophos*, and *Phos* (Fig. 2S).

Other nassariid subfamilies lack varices altogether: Bulliinae, Buccinanopsinae, Cylleninae, and Dorsaninae. The nonvaricate condition also applies to stem-group nassariids of the Early Cenozoic in such genera as *Keepingia*, *Molopophorus*, *Colwellia*, *Desorinassa*, *Thanetinassa*, and *Whitecliffia*, some of which may be synonyms of each other, further suggesting that the varicate condition in Nassariidae may have arisen at least twice, once in Photinae and once in Nassariinae.

Cancellariidae

Many Cancellariidae have varices (Fig. 2T), including most Plesiotritoninae and a few Cancellariinae, although varices are lacking in Admetinae. The oldest varicate and nonvaricate species are found in the Maastrichtian Plesiotritoninae (U. Cretaceous), with a general trend of reducing varices in the Recent taxa of this subfamily compared to extinct Cancellariinae (Beu & Maxwell, 1987). Most species of Plesiotritoninae have a few varices scattered up the spire, while a few are at least partially synchronized, as in *Tritonoharpa* (Lozouet *et al.*, 2001; Landau, La Perna & Marquet, 2006).

Lacking Varices

A few groups that we consider nonvaricate have variously been claimed to have varices. One example is the Harpidae, with elaborate ribs, but they generally lack intervarical elements (Fig. 3D). Recently Merle & Pacaud (2004) described the major and minor varices in *Eocithara,* which we consider to be sharp ribs rather than varices. In the Turbinellidae, the knobby ribs of *Vasum turbinellus* (L. 1758) resemble varices, but again lack the intervarical elements (Fig. 3B). The elaborate sculpture in the terrestrial prosobranch family Diplommatinidae we consider lamellae and are generally termed commarginal ribs (Liew *et al.*, 2014)

Other Molluscs

Although we did not complete a thorough review, and despite some sculpture types that appear reminiscent of varices in ammonoids and bivalves, we found clear examples of varices in none of the other molluscan clades, nor in brachiopods.

Ammonoidea

Many ammonoids have periodic constrictions – grooves in the shell that appear to cut through other ribs and are sometimes associated with distinct shell thickenings (Arkell, Kummel & Wright, 1957). Shell thickenings are also found as internal ridges or pseudo-constrictions, without external structures (Westermann, 1990; Bucher *et al.*, 1996). These periodic shell thickenings are thought to indicate episodic growth and have occasionally been called varices, but are generally called constrictions (Seeley, 1865; Moore, Lalicker & Fischer, 1952; Bucher *et al.*, 1996). Many constrictions clearly share ontogenetic similarity with gastropod varices and could be termed varices. All ammonoid constrictions are regularly spaced – although not necessarily synchronized between whorls – with a set number of interribs. This is almost certainly due to the septa and sutures present in ammonoids, but not in gastropods. Another major form of ammonoid shell sculpture similar to varices is megastriae, distinct radial elements that include a discontinuity in shell secretion (Bucher & Guex, 1990; Bucher *et al.*, 1996). The most intriguing type of megastriae are the parabolae of Phylloceratoidea, Lytoceratoidea, Perisphinctoidea, and the simpler flares of some Lytoceratoidea (Radtke, Hoffmann & Keupp, 2016). Although in most cases these structures are worn smooth, they were often large, sometimes undulating or spiny extensions of the shell. Cross sections of the shell reveal a discontinuity, a presumed hiatus in growth, and share many features in common with varices, especially those of muricids (Radtke *et al.*, 2016). Interestingly, it appears that these apertural flares were sometimes resorbed altogether, with the outer most edge falling off as an intact ring of shell, as seen in *Lytoceras* (Seilacher & Gunji, 1993; Radtke *et al.*, 2016). Megastriae are not generally synchronous, but may relate to periods of rapid growth (Bucher & Guex, 1990). Just like many muricids, juvenile megastriae are not as complex and may not clearly fit the definition, as they show an ontogenetic progression.

In at least some cases, both ammonoid constrictions and megastriae share sufficient similarities with our definition to be considered varices, although an exhaustive search, and perhaps a much better understanding of ammonoid shell growth, would be necessary to firmly establish where the boundaries lie.

Some clear varix examples include most members of Ancyloceratidae (E. Cretaceous) showing periodically thickened 'major' ribs interspersed with smaller ribs (Arkell *et al.*, 1957). *Acantholytoceras longispinus* (Uhlig, 1883) (E. Cretaceous, Barremian; Lytoceratidae) has some striking spines on each constriction, although tubercles are found on the constrictions in a few other genera, and in *Hyphantoceras* (L. Cretaceous, Turonian-Santonian; Nostoceratidae), the constrictions are thin and flaring (Arkell *et al.*, 1957).

Several families of Ammonitina with periodic 'major' ribs fit the varix pattern, such as Puzosiinae (Hauterivian-Maastrichtian), Holcodiscidae (E. Hauterivian-L. Barremian), and Cheloniceratinae (Barremian-L. Aptian). Several of these ammonite groups show loose or irregular coiling in contrast to gastropods, where no varices are known among groups with loosely coiled shells.

Bivalvia

Although we will not discuss the entire diversity of bivalve shell sculpture, a few groups of bivalves have sculpture more or less reminiscent of varices. In the Trigoniidae some species, such as *Myophorella montanaensis* (M. Jurassic, Callovian), have sharp commarginal ribs on part of the shell which White (1880) (in Imlay, 1964) termed varices. These are clearly not varices, however, as they do not extend the breadth of the shell. The Spondylidae have spectacular spiny projections, but these cannot be seen as varices because they do not connect along the growth axis into a single unit and they appear more as separate spines along ribs. A few venerids such as *Hysteroconcha* possess strong commarginal ribs (and spines, but fewer of them), but lack intervarical elements or evidence of periodicity. The sculpture most reminiscent of varices is found in the coarse commarginal nodes of *Swiftopecten swiftii* (Bernardi, 1858) and a few fossil pectinids, which appear as periodic commarginal thickenings, mainly on the right valve; however, these are pleats in the shell rather than thickenings (Hertlein & Grant, 1972) and so do not fit our definition of varices.

DISCUSSION

FREQUENCY OF ORIGIN

Given their obvious functional advantages (Carter, 1967; Spight & Lyons, 1974; Vermeij, 1974, 1982, 1995; Palmer, 1979; Miller & LaBarbera, 1995; Donovan *et al.*, 1999; Savazzi & Sasaki, 2004; Sälgeback & Savazzi, 2006), it is not surprising that varices have evolved multiple times in many lineages of gastropods and that many varicate lineages have diversified into large clades. The repeated evolution of adaptive traits is a recurrent theme in evolution (Vermeij, 2006), reflecting not only a predisposition towards a common constructional mechanism of the trait, but also the wide range of circumstances in which varices confer a survival advantage. As indicated earlier, this advantage derives from the greater resistance of the shell to durophagous predators that break the shell, attack by way of the aperture, or attack an overturned animal that cannot right itself.

The distribution of varicate gastropods in space and time is highly consistent with the interpretation of varices as passive antipredatory armor. The varicate condition is particularly common and well developed in gastropods from warm shallow marine waters where predation pressure is high. It is rare in temperate, polar and deep marine habitats, unknown in freshwater, and almost unknown on land. This follows the patterns of other features such as small or narrow aperture, thickenings bordering the apertural rim, and a high spire associated with deep retraction of the soft parts. The variety and degree of elaboration of varicate shells greatly expanded from a modest beginning in the mid-Mesozoic. The most elaborate varices (in muricine muricids) arose in the interval from the Oligocene to the Recent. These spatial and temporal patterns parallel the evolution and distribution of predators, especially those that break shells or enter via the shell's aperture (Vermeij, 1977, 1995, 2015).

Curiously, with the lone exception of the Middle Devonian genus *Spanionema*, the varicate condition did not develop during the Middle and Late Paleozoic. Beginning in the Silurian and continuing episodically in the Mid- and Late-Paleozoic, shell-breaking predators evolved and diversified in many clades (Signor & Brett, 1984). Yet gastropods evolved few of the antipredatory adaptations that became so prominent in Late Mesozoic and Cenozoic times (Vermeij, 2015). Although the power and diversity of these later predators likely exceeded those of their Paleozoic counterparts (Vermeij, 1977, 1987, 1995), small gastropods would surely have benefited from effective armor, including varices, even against relatively weak enemies. One possible explanation is that varices could deter a predator visually by clearly displaying its shell defences prior to contact, and that visually hunting, larger predatory fishes and crustaceans did not become important agents of antipredatory selection for bottom-dwelling gastropods until the Late Mesozoic. To test this hypothesis, it will be important to evaluate the sensory capabilities of predators as well as the mechanics of jaws and claws. Alternatively, Paleozoic gastropods may not have had the capacity to make varices, or perhaps lacked the ability to remove them efficiently to make way for further shell growth. The sculpture normally found in these groups is either restricted to the last whorl, or the upper part of the whorl, as in many Middle and Late Paleozoic gastropods, where they don't have to be removed to permit further shell growth (Vermeij, 1977).

EVOLUTIONARY HISTORY OF VARICATE GASTROPODS

We conservatively estimate that shells with nonterminal varices evolved independently 41 times. Many more origins might be inferred as our understanding of gastropod relationships improves, and as new taxa are described. Mapping the varicate condition onto a composite evolutionary tree of gastropods (Fig. 4) shows that independent origins of varices are highly concentrated in a few large clades, especially in Sorbeoconcha. Multiple origins are known in such relatively restricted clades as Cerithioidea, Stromboidea, Muricidae, Buccinoidea and Conoidea. No cases have come to light in Patellogastropoda, Pleurotomarioidea, and Neritimorpha; and only one each is known for Rissooidea, Vetigastropoda, Campaniloidea, and Heterobranchia. The distribution of varicate gastropods is therefore highly phylogenetically clumped.

As is the case for other minor but functionally beneficial innovations in gastropod shell architecture (Vermeij, 2001, 2005a, 2007), clades with the varicate condition often remained at low diversity and had a geologically brief tenure. Of the estimated 41 origins of the varicate condition, at least 21 (51%) are represented by three or fewer genera, and at least eight (20%) contain varicate taxa from only one geological stage. Notably, seven of nine (78%) origins of the varicate condition during or before the Early Cretaceous failed to stimulate diversification. Only two early clades, the Dimorphosomatinae + derived Stromboidea and the Tonnoidea, achieved diversity levels of ten or more genera, always during the Cenozoic.

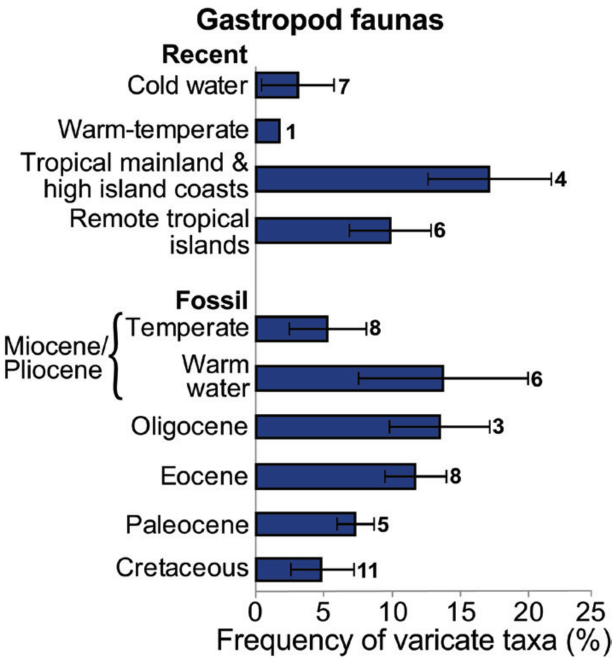


Figure 5. Percentage of varicate gastropod species in various faunas (see Table S2). Error bars are SD., numbers indicate number of localities included.

GEOGRAPHIC DISTRIBUTION OF VARICATE GASTROPODS

Gastropods with the varicate condition are overwhelmingly found in warm shallow marine waters (Fig. 5). Although a few muricids, epitoniids, ranellids, and bittiine cerithiids occur in cold waters, no varicate clade is known exclusively from or evolved in environments outside the tropics. A survey of Recent gastropod faunas (Table S2) revealed a well-defined latitudinal (and therefore temperature) gradient in the incidence of varicate taxa, with the highest frequencies occurring in the tropics (Fig. 5). The high frequency of varicate taxa in the tropics is due largely to a few diverse clades, especially Cerithiidae, Tonnoidea, and Muricidae.

With two marginal exceptions, shells with multiple varices are unknown in gastropods living in freshwater or on land. The exceptions are the genus *Faunus* in the cerithioidean family Pachychilidae, which has very weak rounded varices and which is found in brackish coastal waters of the Indo-Malayan region; and the genus *Pythia* (Ellobiidae), an Indo-West Pacific group with marine larvae and nearshore terrestrial adult stages. The absence of varicate taxa in freshwater is especially surprising because of the high diversity of freshwater Cerithioidea. This clade has many marine representatives with varices, but no freshwater species – not even those in the Great Lakes of Africa or major river systems around the world – have varices. Whether this absence is primary or derived is not known.

Species with a dorsal knob or hump are exclusively tropical or warm-temperate in distribution, and almost all are sand-dwellers. This distribution is considerably more restricted than that of species with a dorsal varix, as seen in many temperate and tropical rock-dwelling muricids and in the intertidal rocky-shore and mangrove-associated cerithiid genus *Clypeomorus*.

Most varicate gastropods are of Late Mesozoic and Cenozoic age. A single varicate genus, the pseudozygopleurid *Spanionema* from the Givetian stage of the Middle Devonian, is from the Paleozoic. No Late Paleozoic or Triassic varicate gastropods have yet come to light.

Data in Table S2, summarized in Fig. 4, indicate a very low incidence of varicate taxa in the Cretaceous, a slightly higher incidence in the Paleocene, and values reaching modern tropical frequencies by the Late Eocene. The low Cretaceous values generally lie in the range of Miocene to Recent temperate to cold-water faunas. Our evidence indicates that the Paleogene rise in the incidence of antipredatory varices in warm-water faunas parallels increases in other armor- and speed-related shell traits (Vermeij, 1995).

Growth hiatus between varices

In many muricids and ranellids, growth stops for a period after a varix is completed, although juveniles appear to grow continuously from one varix to the next (Inaba, 1967; MacGinitie & MacGinitie, 1968; Laxton, 1970; Spight *et al.*, 1974). Varices are generally assumed to be associated with periodic growth in all groups, but this has not been widely tested. The advantage is obvious because they would have a robust apertural defence for a long time. Subterminal varices, whose morphology and placement generally do not suggest a robust aperture, but rather an accessory thickening for the mature last whorl, do not have this advantage.

If the growth of varices is periodic, most specimens should have an apertural varix, as intervarical regions are grown quickly, and the majority of time is spent between growth spurts (Webster & Palmer, 2016). Two surveys suggest varices may not always be associated with periodic growth. First, we did a small survey of *Cerithium coralium* Keiner 1841, a species with both rounded varices up the spire (not completely aligned), and a ventrolateral varix. Of 20 juveniles examined from a single population, only one specimen had an apertural varix, suggesting that varices are not associated with a significant growth hiatus in this species. In contrast, the related *Cerithideopsis californica* (Haldeman, 1840), with more prominent rounded varices, and no obvious lateral varix, showed a greater tendency toward a growth hiatus. Of 31 juveniles examined, 48% had an apertural varix. How and when varices grow during ontogeny appears to vary. We predict that a growth hiatus is related to the degree of synchrony, rate of growth, and the size of varices. Webster & Palmer (2016) examined sculpture growth in *Nucella lamellosa* (Gmelin, 1791) (Ocenebrinae), a species that sometimes grows numerous elaborate lamellae, and found no evidence of a significant growth hiatus, supporting the idea that these muricid lamellae are different structures than the superficially similar varices.

Traits associated with the evolution of varices

Varices occur widely across the Gastropoda, mainly within the Caenogastropoda, and mainly in predatory groups, but also in herbivorous and detritivorous cerithioideans and stromboideans. Varices are found in snails from rocky, sandy, and muddy substrates, as well as in small and large species. Are varices associated with particular forms of shells or other ecological characteristics? Most species with terminal growth have some form of terminal apertural varix, and only these clades show a subterminal varix, although not all do. The majority of species with multiple varices have high-spired shells, but numerous exceptions exist: The Cassidae are a major low-spired, varicate exception, while many groups with the highest spires, Terebridae, Turridae, Turritellidae Cerithiopsidae, Triphoridae, and Pyramidellidae, lack varices altogether. Withdrawal ability also correlates with the presences of varices. Both a fast and deep withdrawal decrease the effectiveness of shell peeling, and varices can hamper further peeling. The presence of sculpture on the shell also may increase the chance of evolving varices. If varices are elaborated ribs, ribs must already be present on the shell to develop into varices. Many groups with regular ribs do not have varicate members, such as the Costellariidae, and many of the conoidean families.

Harper (1997) suggested a correlation between a thin periostracum and sculpture in bivalves, and the same correlation may loosely apply in gastropods. Muricids and cassids have very thin or nonexistent periostraca;

however, ranellids have a prominent periostracum, and all have prominent varices. Testing this correlation in gastropods would require a more in-depth survey of periostracal properties in relation to shell sculpture.

Curiously, very few land or freshwater snails possess nonterminal varices. This could be due to a number of factors. From a cost perspective, the added shell of a varix would be more costly in these often calcium poor environments (Fournié & Chétail, 1984; Palmer, 1992). Land snails also generally (1) have a thick periostracum, which may limit sculpture formation (Harper, 1997), (2) have less well defended shells, (3) are thought to be under a lower level of predation pressure, and (4) withdraw slowly (Vermeij, 1995). Despite all this, terminal varices are quite common in pulmonate snails. Notably, the two pulmonates with varices are both found near-shore with crab predators, and the sole varicate member of the freshwater Pachychilidae is found in brackish water.

EVOLUTIONARY ORIGIN OF VARICES

Varices could arise via two hypothetical trajectories, and either could have occurred among the 41 separate origins. First, varices could have evolved by elaboration of existing periodic shell sculpture in ribbed ancestors. This appears to have occurred in many muricids (and ranellids), where the ratio of varices and intervarical ribs varies through ontogeny or between species, sometimes in clear repeated patterns as in *Hexaplex* or *Dermomurex*. This hypothesis would predict a gradual increase in varix prominence over evolutionary time, and some cerithiids with weak intermittent varices may indicate an early form.

Second, varices could have evolved from repeated growth of a single ancestral terminal varix. In this scenario, periodic varices arise via duplication of a terminal varix during development or via a transition from determinate to indeterminate growth, while still maintaining the apertural varix. This would be akin to peramorphy, a form of heterochrony where maturity is delayed and adult structures (the varices) are further developed (in this case repeated) throughout ontogeny (Gould, 1977). This hypothesis follows the morphological ‘countdown pattern’ explored by Seilacher and Gunji (1993), where a series of iterative structures from the adult shell form prior to the terminal aperture. These structures arise evolutionarily ‘backwards’, starting at a terminal varix and rewinding ontogenetically. The countdown pattern clearly applies to subterminal varices, but it is less clear which patterns of multiwhorl varices may have arisen this way. *Ellobium* exhibits a possible ancestral state for this scenario, where a second apertural varix appears to grow after the first, creating an identical dorsally placed varix.

These two hypotheses yield different predictions for the fossil record. The first requires ribbed ancestors, while the second requires heterochrony or a countdown. Varices have arisen independently many times, and both of these origins seem likely in multiple cases.

SYNCHRONY OF VARICES BETWEEN ADJACENT WHORLS

In many groups, varices are synchronized: aligned with one another in adjacent whorls. This synchronization implies a developmental mechanism to rigidly control varix placement. Clearly, synchrony must have evolved after the origin of varices, but many puzzles remain about how snails maintain the synchrony of varices. Various models have proposed either an activation-inhibition system, a sensory feedback mechanism from previous varices, some way to sense rotation of the shell as the weight of one varix tips the shell balance point, or some combination of these mechanisms (Seilacher & Gunji, 1993; Hammer, 2000; Savazzi & Sasaki, 2004). How the first varix is positioned remains unclear. In many muricids, early whorls have a different sculpture pattern that gradually transitions to the adult form (Spight *et al.*, 1974; Vokes, 1985; Merle *et al.*, 2011), so the synchrony develops gradually. A synchrony of 240° (three varices in two whorls) challenges the tactile/feedback hypothesis because the mantle at the aperture cannot possibly extend back a full whorl to line up a future varix, so other mechanisms must be invoked.

Almost all regular patterns of varix synchrony exist. Some line up on each whorl, whether 360°, 180°, 120°, 90°, or 60° (equivalent to one to six varices per whorl), with three per whorl (120°) the most common. Some groups alternate whorls, with 240° between varices. Each of these patterns lends itself to specific functions (Savazzi & Sasaki, 2004). Eulimids and colubrariids with one varix per whorl often have a curved columella, and the varix may be a point at which the axis of coiling changes. By keeping the change in inclination to the same part of the whorl, the shell develops a curve rather than wobbling at random between whorls. Similarly, many groups with two varices per whorl are dorsoventrally flattened along the varices (*Pythia*, *Biplex*, *Eupleura* and *Aspella*). Three varices per whorl (120°), three per two whorls (240°), and the rare four per whorl (90°) have a similar advantage with a varix always placed laterally to the aperture, similar to a subterminal lateral varix. Shells with three varices per whorl also always have a dorsal varix, increasing the effective diameter of the shell and aiding in shell righting (Savazzi & Sasaki, 2004). As varix number per whorl increases, synchronization would seem to be less important, as varices are so close together.

For a single dorsal or lateral subterminal varix, synchronization is clearly not an issue; however, the position of single varices is always relative to the aperture, so some mechanism to control their placement is necessary. Presumably some manifestation of the terminal countdown mechanism allows this precise placement of varices (Seilacher & Gunji, 1993).

CONCLUSIONS

The term varix encompasses a broad category of shell sculpture that has arisen at least 41 times evolutionarily. As we predicted, these origins of varices were phylogenetically clumped and found mostly in derived gastropods, with most origins occurring during or after the Late Cretaceous. While no single pattern could explain how, when, or where this innovation evolved, a few clear patterns emerged: (1) like other defensive structures, varices were more common in shallow, warm, marine environments, in which predation is intense; (2) high-spired shells and shells with collabral ribs were more likely to have varices; (3) although many groups with varices failed to diversify, varices were correlated with diversification in some groups, especially the Tonnoidea; and (4) the presumed morphological preadaptations and ecological conditions for varices differed between clades, demonstrating the multitude of pathways to produce this innovation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Supplementary Table S1. List of varicate clades including varix types, synchrony present, and time ranges in each presumed separate origin. See text for terms.
Supplementary Table S2. Incidence of varicate species in various faunas.