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Gastropod skeletal defences: land, freshwater, and sea compared

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ABSTRACT

Predation is a primary agency of natural selection affecting the evolution of skeletal form in gastropods. The nature of antipredatory defence depends on how predators attack their prey as well as on the types and quantities of resources that are available to the potential victims. Here I review the five main methods of predation on shell-bearing gastropods (swallowing prey whole, apertural entry, drilling, shell breakage, and partial consumption) and 31 categories of shell and opercular defence that are effective at one or more of the three stages of predation (detection, pursuit, and subjugation). These categories are evaluated for marine Palaeozoic, marine Late Mesozoic to Recent, freshwater, and terrestrial environments. The five types of predation are common in most environments, but drilling and partial consumption are absent in freshwater and unlikely in the Marine Palaeozoic, and partial consumption may be rare on land. The fewest specialized defences are found in freshwater, followed by the marine Palaeozoic and Recent terrestrial environments. There has been a sharp rise in the number of defence types and in the degree of antipredatory specialization in marine environments from the Palaeozoic to the Recent, particularly among defences at the subjugation and pursuit phases of attack. The small number of defences and the passive nature of shell-based protective traits in terrestrial gastropods contrast with the high diversity of antipredatory adaptations, including those related to aggression and speed, in other land-dwelling animal clades.

INTRODUCTION

Every organism has enemies – competitors, predators, and parasites and every organism must be adapted to them. In the case of predation, defences of the prey depend both on the prey's physiology – its metabolism, energy budget, and level of activity – and on the abundance and capacities of the predators. The traits of both parties are, in turn, strongly affected by resources and by the medium in which prey and predator live. Compared to air, water has a very high viscosity, density, specific heat, and electrical transmission. Gases like oxygen and carbon dioxide diffuse into and out of living bodies much more readily in air than in water. As a result, resistance to locomotion (through friction drag and pressure drag) is high, gas exchange between the body and its surroundings is slow, heat loss and gain are rapid, and gravitational forces acting on the body are small in water (Denny, 1993; Vermeij & Grosberg, 2010). On the other hand, precipitation of an external mineralized skeleton is energetically more favourable in water (especially seawater) than in air.

Given this mix of different challenges and opportunities for specialization in defence that life in water and life in air provide, it is surprising how little attention has been paid to comparisons of defences on land, in freshwater, and in the sea. For gastropods, antipredatory adaptation was suggested to be much less specialized in freshwater lakes and streams than in the sea (Vermeij & Covich, 1978). Most other comparisons among gastropods from contrasting media have emphasized differences in shell shape without considering underlying functional demands explicitly. For example, whereas marine gastropods cover a very wide spectrum of form in the envelope of functionally permissible shapes, terrestrial gastropods display a bimodal distribution between very low-spired, flattened forms and high-spired, turreted shapes (Cain, 1977a, 1978a, 1978b; Cowie, 1995). The bimodal distribution has been linked to the requirement for gravitational stability on land (Okajima & Chiba, 2011, 2013). Why balance should be more important in terrestrial gastropods than in water-dwelling species living in high turbulence is unclear, suggesting that factors other than stability must be involved.

Here I present some preliminary analyses and ideas concerning gastropod defences on land and in water, with particular but not exclusive emphasis on shell-based traits. As animals that tend to occupy subordinate positions in the food web, gastropods are never apex predators; instead, they are eaten by, and must be defended against, many large and small predators. I shall argue that, despite the generally reduced constraints on physiology in terrestrial as compared to marine organisms, land snails exhibit a narrower range of defensive traits than marine gastropods, and tend even more toward passive defences and less toward active deterrence than their shallow-water marine counterparts. I also explore parallels between land snails and such other terrestrially subordinate animals as isopod and amphipod Crustacea.

PREDATION AND ADAPTATION

Antipredatory traits in prey species are probably universal in animals in general and gastropods in particular. A necessary condition for natural selection in favour of such traits is that attacks by predators fail at one or more steps in the process of locating, capturing, and killing the prey (Vermeij, 1982). If all attacks were successful, selection for characteristics that deter predation could not occur. Populations subject to such successful predation cannot survive in the presence of predators, and either become extinct (probably in a very small minority of cases) or more commonly persist in environments where the predators are rare or absent (Vermeij, 2012a). The only other alternative is for reproductive rates to be so high that the prey population can produce vulnerable offspring faster than the predator population can harvest them. This is the weed solution (MacArthur, 1965), which is not considered further here even though some gastropods may employ it.

METHODS AND CONSTRAINTS OF PREDATION ON GASTROPODS

From the predator's perspective, the act of predation comprises three steps, summarized in Table 1: search and identification, pursuit, and subjugation. From the prey's perspective, these steps correspond respectively to recognition of danger, escape, and resistance. Each step is associated with adaptations that, singly or in combination, increase the likelihood of the predator's securing its victim and decrease the prey's likelihood of being eaten. The two parties are quite literally engaged in a power struggle whose nature and outcome is not only determined by the predator and prey in question, but also by each party's other enemies (Vermeij, 1982, 1987, 2004). Given the universality of predation as a selective agency in the lives and evolution of gastropods, it is not surprising that defence accounts for a substantial component of the high diversity of behaviours and shell forms observed in gastropods in particular and molluscs in general (Vermeij, 1993).

Both predator and prey require good sensory capacities during the first phase of a predatory attack. Selection for long-distance sensation may be more intense for predators than for prey, because search and correct identification of suitable prey must always begin when the predator is not initially in contact with its victim (Vermeij, 1987, 2004). In this connection it is striking that, whereas predatory marine gastropods often rely on long-distance chemical and sometimes visual detection of prey and predators, gastropods with other modes of feeding usually require direct contact before recognizing a threat. Predators at this stage must avoid being detected by their prey. They accomplish this by remaining still (not creating vibrations or turbulence) or moving with as little noise (turbulence) as possible. For the prey, these requirements may be even more stringent. If they rely on camouflage, crypsis, chemical and metabolic inertness, or silence, they must remain at rest for long periods, which in the case of mobile prey may limit feeding, searching for or attracting mates, and even respiration. Specialization for life on or in the bodies of well-protected hosts may reduce contact with potential predators (see below), but given that it almost always implies small size and limited mobility, this pathway of adaptation to the first phase of a predatory attack also places severe constraints on competitiveness. It must be emphasized, however, that such specialization to parasitism, commensalism, and in some cases mutualistic symbiosis is immensely successful, accounting for a large fraction of animal diversity in general and of marine gastropod diversity in particular.

Warning signals are effective adaptations of prey against predators during the first stage of an attack. Warning, however, implies danger to the predator during the subjugation-resistance phase. Honest warnings must therefore always be accompanied by, and indeed be secondary to, effective defences during the final phase of an attack. Phylogenetically, threat displays and such other signals as warning (aposematic) colouration, aggressive sounds, and the release of chemical signals of danger should evolve after the resistance-related defences do. To my knowledge, this hypothesis has not been tested in molluscs.

Aplysiid opisthobranch gastropods and many coleoid cephalopods confuse potential predators by releasing ink (Wood et al., 2010; Love-Chezem et al., 2013; Nusnbaum & Derby, 2010). The ink may in some cases be harmful to the

Type of predation	Palaeozoic marine	Mesozoic to Recent marine	Mesozoic to Recent freshwater	Mesozoic to Recent terrestrial
Swallowing whole	common	common	common	common
Apertural entry	?	common	common	common
Drilling	rare	common	absent	regional
Shell-breakage	?	common	common	common
Partial	present	common	absent	rare

Table 1. Distribution of types of predation on shell-bearing gastropods.

predator. Release of ink must almost always be associated with a well-developed escape response during the second stage of an attack.

The pursuit or escape phase entails locomotion. Predators vary from a sit-and-wait method, associated with short attack distances and very rapid movement of all or part of the body, to a long-pursuit method, which involves outpacing the victim over a comparatively long distance. High speed, agility, acceleration, and maneuverability, together with a highly developed sensory capacity to track prey, are essential for a predator's success during this second phase. For the prey, all these same traits are also useful, but in addition they have the option of making it difficult for the predator to sense their position. This can be achieved by silent movement, including passive descent from a rock or through the water. I have previously noted that maximal locomotor and sensory capacities are greater among predators than among prey (Vermeij, 1987, 2004). This applies even to gastropods: predatory gastropods burrow faster into sand than non-predatory species in the marine tropics (Vermeij & Zipser, 1986b; Dudley & Vermeij, 1989).

The final stage of an attack – subjugation or resistance – has elicited perhaps the greatest variety of adaptive responses. For predators of gastropods, five basic methods have proven effective (Table 1): swallowing or enveloping (and therefore suffocating) a prey whole; entering the prey shell by way of the aperture with part or all of the predator's body, often with the use of force to pull out the edible parts and to pry away the operculum; drilling a hole through the shell wall, following by insertion of the proboscis to scrape or liquefy the edible soft parts; crushing, cutting, or peeling the shell with specialized claws, jaws, beaks, hammer-like organs, anvils, and in the case of at least one nonhuman primate (the long-tailed macaque *Macaca fascicularis aurea*), stone tools; and consumption of exposed parts such as the foot, proboscis, or mantle extensions without killing the prey (Vermeij, 1993; Gumert & Malaivijitnond, 2012; Gumert et al., 2009).

Whole-prey ingestion places strong constraints on the size of prey that can be eaten, because the prey must always be smaller than the predator. It entails a high investment in a capacious mouth and stomach, and for shell-bearing prey it means that the predator takes in an inedible skeleton as well as the soft parts. Large effective size (achieved either by long extensions or by high volume), an odd shape, and the capacity to enter into the shell that is hermetically sealed are options available to prey whose primary predators swallow or envelop their victims whole. Features that make it difficult for the predator to grasp the prey would also be useful, including a slippery or spiny shell, copious mucus, noxious secretions, and especially tenacity (or resistance to dislodgement). These latter traits are also effective against other methods of subjugation.

The ability to ingest prey whole requires few predatory specializations and may well be among the most ancient methods of predation. It is used by predators in all three media, but little is known about how common it is. Of all the methods used by gastropod-consuming predators, whole-prey ingestion or envelopment is perhaps the least well studied.

The other four methods predators use to catch, subdue and feed upon gastropods or other prey enable predators to attack larger prey successfully, because the bulky prey shell is ingested only in pieces or not at all. To varying degrees, these methods involve the use of force. The applied force often comes directly from muscle contraction, which is fast enough and forceful enough implies a high rate of active metabolism. In other cases, work is done when stored energy coupled with a release mechanism deploys a feeding organ at extremely high speed without involving the entire body. Stomatopod crustaceans, for example, either spear or hammer their prey by a millisecond-scale deployment of the maxillipeds, which strike the prey with enormous force (Patek et al., 2004; Patek & Caldwell, 2005; Weaver et al., 2012; DeVries et al., 2012).

Attack via the shell aperture is a common form of predation in all three media. Sometimes the predator uses the whole body to enter the prey shell, but more commonly entry is accomplished by an extensible part of the body such as mandibles, the proboscis, an extrusible stomach (in some sea stars), grasping teeth (in some fishes), claws (crabs and lobsters), or beaks (many birds). Envenomation and anaesthetization, which speed up prey subjugation, represent special cases of apertural entry. To my knowledge, these are employed on other marine gastropods, mainly by other gastropods, especially and most spectacularly by molluscivorous members of the toxoglossan neogastropod family Conidae. Some spiders include gastropods in their diet, although few if any are known to specialize on them, and it is unknown whether they use venom in killing them (Nyffeler & Symondson, 2001). Predatory land snails are not known to use either venom or anaesthetic to disable their gastropod prey.

Although drilling is the oldest documented method of predation of animals, being known from the Ediacaran (545 Ma) tubular fossil *Cloudina* (Bengtson & Zhao, 1992; Conway Morris & Bengtson, 1994), its first known occurrence on gastropods is in the Ordovician (Rohr, 1991). Drilling did not become common or widespread on gastropods until the Campanian (Late Cretaceous) with the evolution of naticid and muricid gastropod predators. Tonnoideans drilling echinoids may also have a Late Cretaceous origin. Octopods have been drilling prey since at least the Early Eocene (Todd & Harper, 2011). On land, the chief culprits appear to be insects (reviewed by Baalbergen et al., 2014), but at least one rathouisiid slug of the genus *Atopos* also employs mechanical drilling on tiny rock-dwelling gastropods in Borneo (Schilthuizen et al., 2006; Liew & Schilthuizen, 2014). Several gastropods including the European oleacinid *Poiretia* and the South African rhytidid *Natalina cafra* (Férussac, 1821) and the European zonitid *Aegopinella* also appear to drill (or at least to decalcify) shells of prey gastropods (Mordan, 1977; Appleton & Heeg, 1999; Helwerda & Schilthuizen, 2014). Drilling by gastropods is unknown in freshwater. In the Miocene Lake Steinheim in Germany, about 5% of gastropods (*Gyraulus* and *Bania*) have small holes (average diameter 0.8 mm), which Rasser and colleagues (2014) persuasively argue are the work of sharp pharyngeal teeth of cyprinid fishes of the genus *Tinca*. Holes in some Caspian molluscs reported by Il'ina (1987) may well have a similar origin.

Shell breakage and repair are known from the Early Cambrian onward. The earliest documentation appears to be for lingulate brachiopods (Zhang et al., 2011), but the earliest recorded case in molluscs is in the Late Early Cambrian (Botoman) limpet-like genus *Marocella* (Skovsted et al., 2007). The oldest repaired gastropods are from the Early Ordovician (Ebbestad & Peel, 1997; Ebbestad, 1998). Judging from the frequencies of predator-induced shell repair, shell breakage increased from the Early Palaeozoic to the Late Carboniferous and again to modern levels in the latest Cretaceous (Vermeij et al., 1981). Breakage in freshwater and terrestrial gastropods seems to be much less frequent than in most modern shallow-water marine environments, but relatively high frequencies of repair in land snails have been documented by Cadée (1995) and for West Indian species of *Cerion* by Quensen & Woodruff (1997). Shell-breaking predators are present in both freshwater and on land, notably among vertebrates (mammals, birds, and lizards) and arthropods (crabs, harvestmen (Opiliones), and pterostichine beetles) (Nyffeler & Symondson 2001; Digweed, 1993; Vermeij & Covich, 1978). By far the most powerful shell-crushers are marine: loggerhead turtles (*Caretta caretta*), gonodactylid stomatopods, crabs (carpiliids, parthenopids, eriphiids, and cancrids), nephropid and especially palinurid lobsters, fishes (labrids, lethrinids, sparids, sciaenids, haemulids, embiotocids, balistids, and especially tetraodontiforms including the spiny puffer *Diodon hystrix*, and myliobatid rays), and the sea otter (*Enhydra lutris*), as well as shell-dropping birds (gulls and crows) (Vermeij, 1978, 1993; Vermeij & Zipser, 2015).

Partial consumption is common both in the sea and to a lesser extent on land. In marine gastropods, the foot of proboscis is frequently nipped by fishes, whereas on land the culprits may be birds. Some gastropods are adapted to partial consumption by autotomizing exposed structures, such as the posterior end in terrestrial slugs and part of the foot in stomatellids, harpids, the olivid *Agaronia*, and some land snails (Stasek, 1967; Miller & Byrne, 2000; Pakarinen, 1994; Rupert et al., 2011; Hoso, 2012a). This ability appears to characterize relatively active gastropods, which can regrow the parts lost to predators quickly.

GASTROPOD SHELL AND OPERCULAR DEFENCES

In Table 2 I offer a qualitative appraisal of the occurrence of 31 categories of shell and opercular defence in gastropods. Some of these defences overlap, and two or more can occur together in the same animal; all refer to adult (or at least post-larval) traits. For each defence, I indicate its relative abundance in marine Palaeozoic, marine Late Mesozoic to Recent, freshwater, and terrestrial environments. By a rare defence I mean one that is found in at most 5% (and usually 1 to 2%) of species. A defence described as common is found in at least 10% of species. Defences labeled as tropical, high-shore, or regional are considered common even if they are not found everywhere. For marine environments, most of what we know about antipredatory adaptation concerns shallow-water species; my assessment of the occurrence of gastropod defences in the sea therefore excludes the deep sea, where most defences seem to have a low incidence and degree of specialization.

Below I discuss these defences. Along the way, I identify many points of ignorance, and I make occasional asides on phylogenetic aspects and other functions of the trait in question.

CAMOUFLAGE WITH EPIBIONTS AND RUBBLE

A partial or complete cover of the shell with organisms can be an effective defence of gastropods, because the presence of epibionts confuses or repels predators. More or less specialized associations between hermit crabs and epizoan sponges, hydroids, sea anemones, zoantharians, and bryozoans are well-known and widespread, and appear to benefit both parties (Williams & McDermott, 2004). In living gastropods these associations with suspension-feeding epizoans are both less widespread and apparently less specialized. Most of the examples that have been described are marine, and with the exception of facultatively sponge-covered species such as the western Atlantic pisaniine buccinid *Solenosteira cancellaria* (Conrad, 1846) (Wells, 1969) and the Indo-West Pacific eucyclid trochoidean *Euchelus atratus* (Gmelin, 1791) (Hickman & McLean, 1990), most occur either in deep water or in the cold southern hemisphere (see Hand, 1975; Hain, 1990; Pastorino, 1993; Luzzatto & Pastorino, 2006; Mercier & Hamel, 2008; Schejter et al., 20011; Zabala et al., 2013). All the gastropods commonly covered in life by these animals are predators. In the shallow-water tropics, especially on reefs, coralline algae frequently coat surface-dwelling gastropods completely (Pl. 1, Fig. 6). Coralline cover protects gastropods from drilling gastropods (Smyth, 1990). In Curaçao and elsewhere, I have observed a strong bromine odor emanating from corallines that thickly encrust shells of living species of *Vasum*, *Leucozonia*, and *Cittarium*, suggesting the possibility of predator repellence. The association between corallines and gastropods is not species-specific for either party and affects both predatory and herbivorous gastropods. Subtidal herbivorous *Littorina littorea* (Linnaeus, 1758) from New England and Canada are thickly encrusted with corallines of the genus *Clathromorphum* and may be camouflaged by this association (Bedard, 1971). Tseng & Dayrat (2014) report that the complete cover of the crevice-dwelling intertidal pulmonate limpet *Trimusculus reticulatus* (G.B. Sowerby I, 1835) by corallines provides excellent visual camouflage.

Two interesting points about dense epizoan cover of shells deserve a brief mention. First, species that habitually have a thick epizoan cover have limited mobility and are often sedentary. The weight of the epizoan cover likely impedes locomotion, and camouflage works best when the

Defence type	Palaeozoic marine	Mesozoic to Recent marine	Mesozoic to Recent freshwater	Mesozoic to Recent terrestrial	Stage
Epizoan or rubble camouflage	common	common	absent	rare	1
Colour as camouflage	?	common	common	?	1
Life with protective hosts	common	common	absent	absent	1
Colour aposematism	?	common	absent	absent	1, 3
Sensation structures	rare	common	rare	rare	1, 2
Chemical deterrence in shell	?	rare	absent	absent	1, 3
Refuge in large size	?	common	rare	common	1, 3
Determinate growth	rare	common	rare	common	1, 3
Episodic growth	rare	common	absent	rare	1, 3
Reversal in coiling	common	rare	common	common	3
Ontogenetic change in coiling	common	rare	rare	common	3
Deep withdrawal, high spire	rare	common	rare	rare	3
Narrowly elongate aperture	rare	common	rare	rare	3
Occluded aperture	rare	common	rare	common	3
Rigid operculum	common	common	common	common	3
Enveloped shell	rare	common	rare	rare	1, 2, 3
Slippery shell	rare	common	rare	rare	3
Ratchet sculpture	rare	common	absent	absent	2
Ribs, tubercles, spines	rare	common	rare	rare	3
Thick shell	rare	common	rare	rare	3
Edge crenulation	rare	common	absent	absent	3
Mucus attachment	?	common	absent	absent	3
Cementation	rare	common	absent	absent	3
Lirae	rare	common	rare	rare	3
Columellar/parietal folds	rare	common	rare	rare	3
Shell-assisted autotomy	?	common	absent	rare	3
Crack-resistant structure	rare	common	common	rare	3
Tough microstructure	common	common	rare	rare	3
Aggressive shell weapon	absent	common	absent	absent	3
Operculum as weapon	?	common	absent	absent	3

Table 2. Gastropod shell defences.

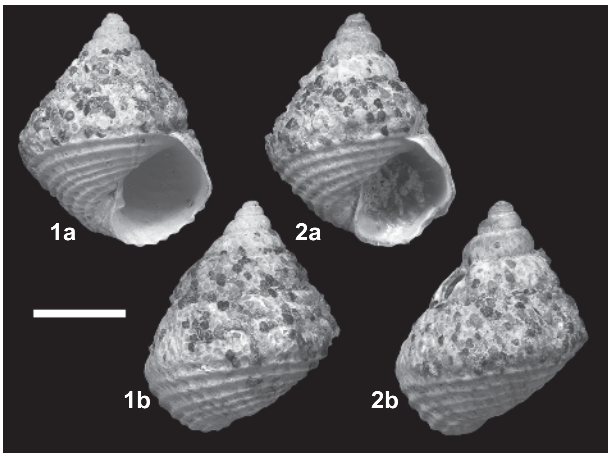
gastropod remains stationary and cannot be detected as a moving target by would-be predators. Second, although high topographic relief on shells would seem to attract settling corallines and suspension-feeding animals by providing depressions, there is no compelling evidence that habitually encrusted gastropods have heavily sculptured shells. Anemone-encrusted species of *Buccinanops* and *Adelomelon* in Argentina are relatively smooth, as are coralline-encrusted *Littorina* and *Trimusculus*. It is possible that initial settlement takes place at the depressed suture-line between whorls, but this has not to my knowledge been demonstrated for any epizoan sponge, cnidarian, or coralline.

Epizoan protection is unknown on land and is extremely rare in freshwater. In the case of land snails, this is not surprising, because all marine non-molluscan epizoan animals are suspension-feeders, which cannot operate effectively in the low-density medium of air unless they build traps for catching flying insects. In freshwater, however, suspension feeders are potentially available as epizoan guests. The only example of freshwater gastropods with non-molluscan epizoans of which I am aware is that of spongilline sponges on species of *Tylomelania* in Lake Poso and the Malili Lakes of Sulawesi, Indonesia (Albrecht & Glaubrecht, 2006). It is noteworthy that substantial escalation between sundathelphusid crabs and molluscs has taken place in these relatively young but deep lakes (von Rintelen et al., 2004). This makes the absence of epizoan-gastropod associations in other large lake systems, such as the rift lakes of East Africa, or in ancient river systems such as the Mekong and Mississippi, all the more surprising, for predator-prey escalation has also occurred to varying degrees in these freshwater systems (Vermeij & Covich, 1978; West et al., 1991; West & Cohen, 1996). Dias and colleagues (2008) report the presence of ciliate protists on the Brazilian ampullariid *Pomacea figulina* (Spix, 1827), but this cover is thin and incomplete.

A related, ancient, and phylogenetically widespread phenomenon is the cementation of rubble or sand grains to the shell exterior, presumably for camouflage. The best known examples are xenophorids, but the habit also occurs in the Miocene to Pliocene turritellid *Springvalea*, the Late Miocene to Pliocene modulid *Psammodulus* (Figs 1-2), the Pliocene trochid *Calliotropis arenosa* Helwerda, Wesselingh & S.T. Williams, 2014, Eocene to Recent scaliolids, and many Palaeozoic gastropods (EI-Nakhal & Bandel, 1991; Vermeij, 2014a; Helwerda et al., 2014; Landau et al., 2014). In contrast to animal-covered gastropods, which are mostly predators, sand-agglutinated gastropods are and were surface grazers or suspension-feeders. To my knowledge, no case of attachment of sand or debris to living gastropods in freshwater has come to light. On land, however, some gastropod shells are routinely covered with adherent debris or limestone dust, as in species of the West Indian annulariid genus *Stoastomops* (Baker, 1962) and Canary Islands rock-dwelling species of the enid genus *Napius* (Yanes et al., 2010) (the latter routinely covered by lichens). As in the case of marine gastropods encrusted by animals and algae, rubble-covered species both on land and in the sea tend to be sedentary and therefore likely to be camouflaged against visual and perhaps in some cases (like me) tactile predators. Whether the shell surface is in any way specialized for the adhesion of particles by providing pits or other secure sites has not been investigated, but no obvious trend in sculpture is discernible.

HOSTS AS SAFE HAVENS FOR GASTROPODS

Many gastropods live on or inside the bodies of other organisms, where experiments show that they achieve relative safety from enemies thanks to the physical or chemical defences of their hosts. The clades containing these parasitic guests are often highly diverse, and tend to be associated with particular host clades. For example, cerithiopsids, triphorids, pseudococculinids, trochaclidids, xeniostomatine calliostomatids and a few fissurellids target sponges (Aren, 1992; Warén & Gofas, 1996; Nützel, 1998; McLean, 2012a). Nematocyst-bearing Cnidaria are occupied by epitoniids (Fig. 3), ovulids (Fig. 4), many muricids (especially Coralliophilinae but also some Rapaninae and Ergalataxinae), calliostomatids, and architectonicids (Robertson, 1970; Nützel, 1998; Reijnen et al., 2010; A. Gittenberger & E. Gittenberger, 2005; A. Gittenberger & Hoeksema, 2013; Bieler, 1988; Lozouet & Renard, 1998; Oliverio et al., 2009; Dolin & Ledon, 2002; Kokshoorn et al., 2007). Echinoderms, which are usually laced with saponins, host more than 1200 species of eulimids



Figs 1-2. *Psammodulus mexicanus* Collins, 1934 with cemented sand grains to the shell exterior. Bocas del Toro, Panama, Early Pliocene. Scale bar: 1 mm. Photo: Sonja Reich.

Fig. 3. *Cirsotrema varicosum* (Lamarck, 1822) under its host sea anemone *Heteractis crispa* including wentletrap eggs (middle, bottom). Indonesia, Spermonde archipelago. Photo: Arjan Gittenberger.

(Warén, 1984; Takano & Kano, 2014). Other less frequently exploited hosts are stomatopods, colonized by *Caledoniella* (Reaka, 1978); pycnogonids (sea spiders), occupied by the Antarctic zerotulid *Dickdellia* (Sirenko, 2000; Schiaparelli et al., 2008); fishes, from which several colubrariids, marginellids, and cancellariids suck blood (Bouchet, 1989; O'Sullivan et al., 1987; Johnson et al., 1995). Bivalve, gastropod, and various worm hosts are attacked by pyramidellids. Parasites that switch hosts and therefore spend time away from protective cover often have thick, well-defended shells, as in the fish parasites and some eulimids; but permanent associates have reduced shell defences, reflecting increased reliance on protection from their hosts.

Associations with potentially well-defended hosts date back to the Middle Ordovician (Baumiller, 1990, 1993, 1996; Baumiller & Gahn, 2002; Baumiller & Macurda, 1995; Gahn & Baumiller, 2003), when platyceratids parasitized crinoid and blastoid echinoderms by drilling. Holes in a Late Cretaceous sea star probably indicate the presence of parasitic eulimids at that time (Neumann & Wisshak, 2009).

Marine algae and seagrass also provide substrata and relative safety for small gastropods, which either feed on their hosts directly or consume organisms growing on the host. These associations may be facultative or obligate (Vermeij, 1992). Fishes and other predators of small gastropod guests are limited in their prey-searching ability in dense vegetation; and predators that use tube feet or a ventral foot for locomotion and attachment, including gastropods and sea stars, are rarely found on marine plants. With the exception of the seagrass-associated Indo-West Pacific cerithiid *Cerithium rostratum* A. Adams in G.B. Sowerby II, 1855 and the less substrate-specific cerithiids of the western Atlantic, gastropdos living on algae and seagrass have almost smooth shells. However, in contrast to gastropods on living animal hosts, vegetation-associated marine species can have relatively robust shells, as in the North Atlantic *Littorina obtusata* (Linnaeus, 1758) (Fig. 5) and in many columbellids, modulids, and gibbuline, teguline, and cantharidine trochoideans. Limpets specialized for life on algae and seagrass, however, have generally thinner shells than their rock-dwelling counterparts. It is possible that, whereas marine vegetation offers clutter as the predominant form of safety, animal substrata impart an additional dimension of safety in the form of chemical or stinging deterrence, which keeps many would-be predators away.

Freshwater and especially terrestrial gastropods are often found on plants. This is the case for freshwater lymnaeids, stream-side succineids, mangrove-inhabiting potamidids and littorinids, and especially for a large number of relatively high-spired arboreal land snails. To my knowledge, none of the terrestrial gastropods has a species-specific association with a plant species, and although some large gastropods living on or near the ground eat living plants, arboreal species consume mainly lichens, fungi, and epiphyllic algae but not the tissues of the trees themselves (Vermeij, 2005b; Meyer et al., 2014).

Arboreal life appears on the whole to confer protection against enemies relative to life on the ground. Species living in trees are subject to predation by snakes, birds and mammals (Smith & Temple, 1982; Hoso & Hori, 2008; Hoso et al., 2007, 2010; Schilthuizen et al., 2007), but I am unaware of snail-eating arboreal insects, or snails. Reid (1992) has shown that the thinner arboreal species of mangrove-dwelling species of the littorinid genera *Littoraria*, *Littorinopsis*, and their relatives live higher on trees and suffer lower rates of predation by crabs than do the thicker-shelled species that live lower down. Tree-dwelling potamidids also have thinner shells than their ground-dwelling counterparts in mangroves and may, like the littorinids, also be subject to a lower intensity of predation.

A special category of gastropods living on safe hosts comprises limpet-like species occupying the outer and some-

Figs 4. *Diminovula culmen* (Cate, 1973) (circa 1 cm) hiding among the branches of the anthozoan *Dendronephthya* sp. at Akber Reef, Raja Ampat, Indonesia. Photo: Bastian T. Reijnen.

Fig. 5. *Littorina obtusa* (Linnaeus, 1758) living low intertidally, well camouflaged on fucoid algae *Fucus spiralis* from Terschelling, The Netherlands. Photo: Gerrit Doeksen.

times the inner surfaces of shells. This habit has evolved many times among patellogastropods, capulids, calyptraeids, hipponicids, siphonariids, and amathinids in the sea. Many cases are known in which young limpets, including the predatory muricid *Concholepas concholepas* (Bruguière, 1789), settle on older, larger individuals of the same species, where they experience less competition or less predation than on adjacent rock surfaces (Branch, 1976; Manriquez et al., 2004). Species of *Scurria* (Lottiidae) and *Sabia* (Hipponicidae) (Pl. 1, Fig. 3; Fig. 6) excavate depressions on the shells of their hosts (Knudsen, 1991; Noda, 1991; Morton, 1998; Vermeij, 1998; Espoz et al., 2004). Several calyptraeids from the Eocene onward have evolved flat to dorsally concave shells suitable for life inside the aperture of hermit-crab-occupied gastropod shells (Baluk & Radwanski, 1985; Vermeij, 1989). The hipponicid *Thylacus cretaceus* Conrad, 1860 inhabited the columellar areas of gastropod shells during the Late Cretaceous of the Gulf Coastal Plain of the southeastern United States (Bandel & Riedel, 1994) and may also have sought refuge in shells occupied by hermit crabs. Compared to their rock-dwelling counterparts, many of which have strongly radially sculptured shells, the shell-associated limpets tend to be smooth. Exceptions are *Sabia* and the juvenile limpets that as adults move from shells to rock. Experiments have demonstrated that life on the shells of living hosts is safer than life on adjacent rock (Mapstone et al., 1984; Vermeij et al., 1987), apparently because predatory gastropods and sea stars do not commonly search host shell surfaces for potential prey.

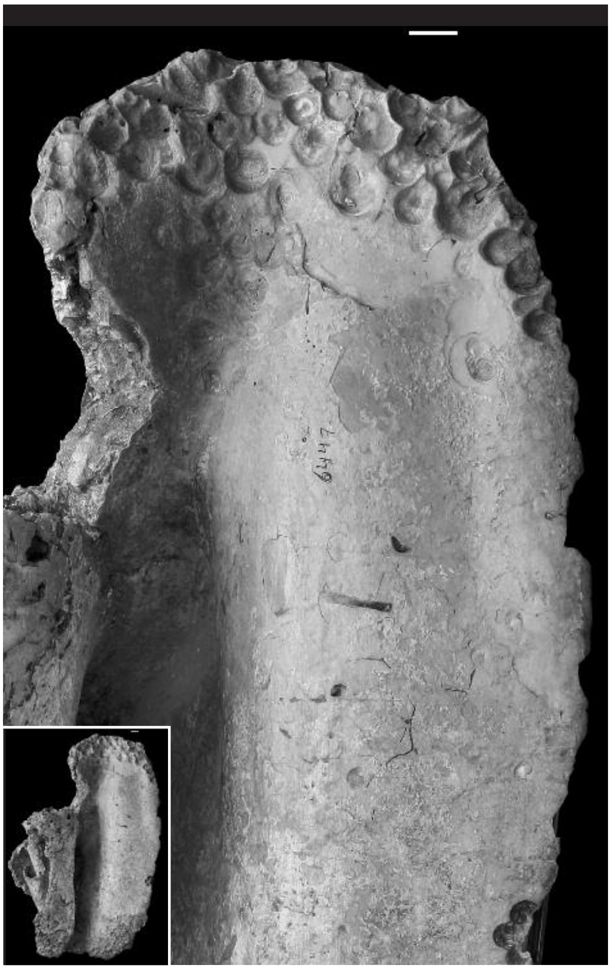


Fig. 6. Imprints of *Sabia* sp. on the outer lip of *Lobatus vokesae* Landau, Kronenberg & Herbert, 2008 from Cañada de Zamba, off Rio Cana, Gurabo formation, early Pliocene. Scale bar: 1 cm. Photo: Jan Johan ter Poorten.

All these cases are marine. I know of just one freshwater limpet that is apparently specialized to live on the shells of living gastropods. In Lake Poso and the Malili Lakes of Sulawesi, the limpet-like planorbid *Protancylus* lives on the shells of *Tylomelania* (Albrecht & Glaubrecht, 2006). Young neritids are carried upstream in rivers on the shells of living conspecific adults of some species in the Indo-West Pacific region (Kano, 2009). Consistent with the absence of limpet-like gastropods on land, there are no known cases of terrestrial gastropods living on host snails.

Shells also offer a degree of safety, and in some cases appear to be modified to carry, the eggs of conspecific gastropods. Eggs attached to the shell exterior are documented for the eastern tropical Pacific pisaniine buccinid *Solenosteira macrospira* (Kamel & Grosberg, 2012); sand-dwelling columbellids of the genera *Bifurcium*, *Cosmioconcha*, *Mazatlania*, and *Strombina* (Cipriani & Penchaszadeh, 1993; Miloslavich et al., 2005; Fortunato et al., 2008; Vermeij, personal observations on *Mazatlania fulgurata* (Philippi, 1846) in Panama); and the dorsanine nassariid *Buccinanops cochlidium* (Dillwyn, 1817) in Argentina (Averbuj & Penchaszadeh, 2010). Umbilical brooding of eggs is known in the North Pacific trochid *Margarites vorticiferus* (Dall, 1873) as well as in species of *Munditia* and in architectonicids (Lindberg & Dobberteen, 1981). Some tropical freshwater neritids carry eggs on the shell exterior (Vermeij, 1969; Maciolek, 1978; Kano, 2009; Kano & Fukumori, 2010). All species that carry eggs either have smooth surfaces or relatively weak sculpture of granules, ribs, or cords.

COLOUR AND PATTERN

Many marine gastropods, terrestrial tree snails, but very few freshwater gastropods are brightly coloured or intricately patterned on their outer shell surfaces. In the few cases where careful observations have been made and experiments have been done, the patterns often make the shells difficult for visual predators to distinguish from the surroundings. This is the case, for example, with the variably coloured and banded *Littorina fabalis* (Turton, 1825) and *L. obtusata* (Linnaeus, 1758) (Fig. 5), which typically live on North Atlantic fucoid algae and which fall frequent prey to fishes, crabs, and perhaps birds (Reimchen, 1979); and for many land snails, which are cryptically patterned either under UV light or in the visible spectrum (Savazzi & Sasaki, 2013). European species of the helicid land-snail genus *Cepaea* are polymoprhic in both colour and in banding and are hunted principally by thrushes (birds of the family Turdidae), which attack at the relatively vulnerable apex by pounding the shell on an anvil, and by small rodents, which attack at the reflected adult outer lip (Reichardt et al., 1985; Rosin et al., 2013). The polymorphism reflects selection for visual crypsis on different backgrounds, and appears to be directed largely at thrushes (Cain, 1977b). Rosin and colleagues (2013) have noted that colour and shell thickness are not independent of each other. In *Cepaea nemoralis* (Linnaeus, 1758), yellow and unbanded shells are more easily crushed than pink and banded morphs. In the intertidal, mangrove-dwelling littorinid *Littoraria pallescens* (Philippi, 1846), the dark morph has a heavier, thicker shell than the yellow morph (Cook & Kenyon, 1993).

In Cypraeidae (cowries), the shell is often vividly coloured and complexly patterned, and the mantle that covers the shell in life may sharply contrast with the colour of the shell, raising the possibility that predators either cannot visually detect or are confused by their cowrie prey (Savazzi, 1998). Species of *Oliva* often match the colour of the sand in which they live, and therefore appear camouflaged to human visual observers (Van Osselaer et al., 2004). Two Indo-West Pacific species, *O. carneola* (Gmelin, 1791) and *O. rufula* Duclos, 1835, may be aposematically coloured, because they produce noxious coloured substances when disturbed (Van Osselaer et al., 2004). The mangrove-dwelling Australian littorinid *Littorinopsis filosa* (G.B. Sowerby I, 1832) is protected to some extent against parasitoid flies by cryptic colouration (McKillup & McKillup, 2002). It must be emphasized, however, that the function of shell colours, particularly those on the interior surfaces of shells, remain largely unstudied.

SHELL FEATURES AND SENSATION

Sampling of water for chemical cues emitted by enemies, food, or mates is important for mobile gastropods that are capable of escaping from predators or moving toward food and potential mates. The siphonal canal at the anterior end of the shell of many gastropods is typically associated with remote olfaction. It occurs in most predatory marine gastropods (neogastropods and tonnoideans) as well as in cypraeoideans and herbivorous cerithioideans and stromboideans and parasitic triphoroideans. The earliest siphonal canals appear in the Ordovician, but their frequency increased during the Late Palaeozoic and especially during the Mesozoic and Caenozoic with the diversification of predatory gastropods (Vermeij, 2007). Beginning in the Late Cretaceous, many gastropods evolved a siphonal canal that not only extends in front of the shell but is also dorsally directed, permitting the snail to place the olfactory osphradium well above the boundary layer near the substrate on which the animal crawls. In this position, odor plumes from further away can be detected more rapidly (Vermeij, 2007). In most species, the siphonal canal remains ventrally open, but it has become a fully enclosed tube in at least 16 Caenozoic lineages (Vermeij, 2007). A fully sealed canal provides additional protection for the sense organs and the feeding proboscis. Extremely long, slender siphonal canals characterize some ranellid, muricine muricid, fusinine fasciolariid, columbariid, and turrid gastropods, all of which evolved after the Cretaceous. These long structures presumably enable gastropods to perceive early warning of impending danger or, more likely, provide access to food items hidden in crevices. It is notably that all gastropods with these extremely long siphonal extensions are slow-moving and have strongly sculptured shells.

In addition to an anterior canal, many siphonate gastropods have a distinct adapical canal or sinus, which often houses additional sense organs. Given their position, these organs likely function chiefly in detecting danger from behind rather than food or mates. Adapical canals or notches are especially well developed in sand-burrowing gastropods, which can detect danger in the water while remaining buried in sand.

Finally, several gastropods with a siphonal canal have developed a sinus situated abapical to the canal. This feature accommodates sensory tentacles and sometimes eyes. The so-called stromboid notch or sinus occurs in strombids and some related groups as well as in photine buccinids, nassariids, cancellariids, some turrids, and some lyriine volutids.

Extensions, embayments, or other elaborations of the apertural rim associated with sensation are found overwhelmingly in marine gastropods. A siphonal indentation has evolved in a small number of hydrobioid gastropods in freshwater, and has been retained from marine ancestors in several other freshwater clades including cerithioideans and the handful of neogastropods that have colonized freshwater (Vermeij, 2007). Whether the canal in these freshwater gastropods functions in chemical detection is unknown.

CHEMICAL DEFENCE OF SHELLS

A potential defence of shells that has rarely been mentioned in the literature is chemical deterrence. Although toxins, mucus, and other noxious substances are widespread in soft-bodied gastropods without shells or with strongly reduced shells that no longer cover the body, as in many opisthobranchs and terrestrial slugs, chemical deterrents incorporated into the external shell seem to be rare. The only credible case in gastropods of which I am aware is the report by Fishlin & Phillips (1980) who showed that the sea star *Leptasterias hexactis* in California is repelled by a substance in the seagrass-feeding lottiid limpet *Lottia paleacea* (Gould, 1853) incorporated into the shell from the host plant. Many patellogastropods and vetigastropods take up pigments and potentially other substances from their algal foods (and from sponges?) into their shell, raising the possibility that chemical shell defence is more widespread than is currently appreciated. Several gastropod clades, including Fissurellidae and some deep-sea taxa, are characterized by shell pores, which in principle could transport chemical agents from the soft tissues to the shell's exterior. No evidence for this has, however, come to light.

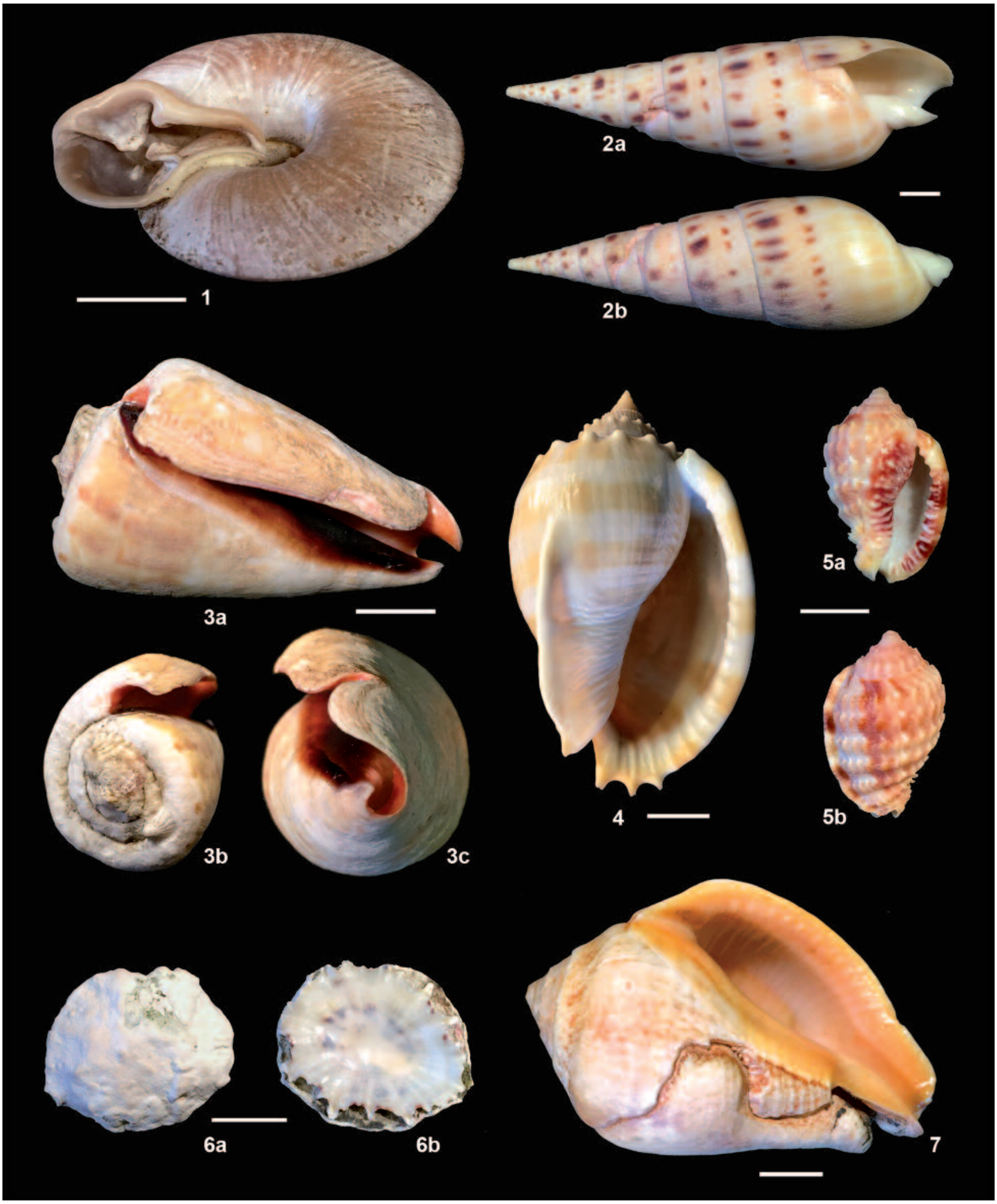


PLATE 1

Figs 1-7. Gastropd shell defences and repairs. **1**. *Labyrinthus plicatus* (Born, 1778), Barro Colorado Island, Panama. Note the aperture which is highly constricted by folds. **2**. *Oxymeris maculata* (Linnaeus, 1758), Tumon Bay, Guam. The high spire permits the soft parts to withdraw deeply into the shell. Note the repair scar on the spire. **3**. *Conomurex luhuanus* (Linnaeus, 1758), Nchesar, Palau. On the spire are two *Sabia conica* (Schumacher, 1817) which form a straight line with the apex. The *Sabia* excavate a deep pit in the shell. Note the narrow aperture with conspicuous adapical canal and abapical stromboid notch. **4**. *Phalium bandatum* (Perry, 1811), Nada, Wakayama, Japan. Note the sharp abapical spines and the upturned, left-directed siphonal canal. **5**. *Morum matthewsi* Emerson, 1967, Fortaleza, Ceará, Brazil. The six spiral bands on the last whorl are strongly ratcheted, with the posterior sides steep and the anterior sides shallow. The axial ribs are also ratcheted, but less so. The strongly reflected outer lip has occluding denticles on its inner side. **6**. *Scutellastra flexuosa* (Quoy & Gaimard, 1834), Togcha Bay, Guam. Coralline algae completely encrust the exterior, and even extend beyond the crenulated rim. As a result, it is completely cryptic on the coralline-encrusted reef margin. **7**. *Volema pyrum* (Gmelin, 1791), Majunga, Madagascar. Note the huge repaired scar and the aperture, which is lirate within. Scale bars: 1 cm.

LARGE BODY SIZE

One of the many benefits of a large shell is invulnerability to most forms of predation. Many species reach a size refuge from their attackers, and many have adapted their growth trajectory to achieve this refugial size quickly. By far the largest gastropods are, and always have been, marine. Already by the Ordovician, the sedentary *Maclurina manitobensis* (Whiteaves, 1890) reached a diameter of 25 cm (Rohr et al., 1992). At least three gastropods of the Late Mesozoic exceeded a shell length of 400 mm, including several Late Jurassic and Cretaceous nerineoideans (Kollmann, 2014), the limpet-like *Gigantocapulus*, and an undescribed species of *Leviathania* (summarized in Vermeij, in review). Caenozoic gastropods are even larger, with Eocene species of *Campanile* and the Recent *Syrinx aruanus* (Linnaeus, 1758) topping the list at lengths of greater than 90 cm (Vermeij, 2011). Gastropods on land and in freshwater reach much smaller maximum sizes. The largest terrestrial gastropod is the fossil *Pebasiconcha immanins* Wesselingh & Gittenberger, 1999 (Fig. 7) from the Miocene of the Pebas Basin of Colombia (256 mm) (Wesselingh & Gittenberger, 1999). The largest freshwater gastropod appears to be the Brazilian ampullariid *Pomacea maculata* (Perry 1810), which reaches a length of 165 mm (Hayes et al., 2012).

It is difficult to assess the abundance of species that rely on large size as an adult defence. When the predator is small, the size at which a prey species becomes immune is also quite small; invulnerability therefore depends on the size and capacity of predators. Nearly all predators are limited by the size of prey they can kill, suggesting that a refuge in large size is the rule everywhere. The only exceptional predator is the recently evolved mammal *Homo sapiens*, which preferentially takes the largest individuals of all gastropods and other molluscs harvested in the wild (Vermeij, 2012). Species that do not reach a refuge in large size can survive only if they inhabit a spatial refuge or if they reproduce at such a high rate that eaten adults are continually being replaced, the classic “weedy” strategy.

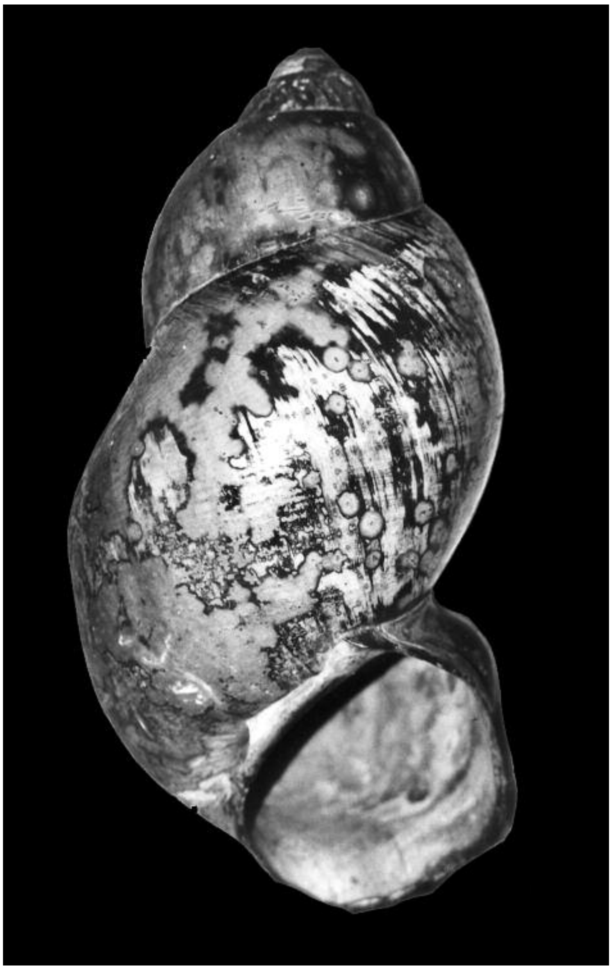


Fig. 7. *Pebasiconcha immanins* Wesselingh & Gittenberger, 1999. Paratype, height 219 mm. Peru, Loreto department, from the vicinity of Pebas. Middle Miocene. Photo: Frank Wesselingh.

SHELL THICKNESS

A thick shell also tends to confer protection against predators, especially against those that break or drill shells. Given that predators' handling time of thicker shells is longer than that of thinner ones, and that attempts to subdue thick-shelled prey more often end in failure (Palmer, 1979, 1985; Kitchell et al., 1981), a thick shell confers a substantial benefit. As with large size, the shell thickness required for resisting predation depends on the capacity of the predators, and is therefore difficult to evaluate in terms of abundance. On the whole, marine gastropods have explored a much greater range of shell thickness than have either freshwater or terrestrial gastropods, reflecting the great importance of shell breakage and drilling in marine environments.

As an aside, it is curious (and never previously commented on) that the thickest gastropod shells are much thinner than their bivalve counterparts. Bivalves with shells 5 cm or more in thickness have evolved in many lineages of oysters and oyster-like bivalves as well as in a few other bivalves beginning in the Permian (Vermeij, 2014a), whereas in gastropods the thickest shells I have seen (cassids and some large strombids) rarely exceed 3 cm in thickness. Even in freshwater, some unionoidean bivalves develop much thicker shells, especially in the anterior region, than gastropods. The reason for this difference remains a mystery. Equally vexing is the observation that the calcareous opercula of turbinids, which can reach a thickness of 20 mm, are thicker than their associated shells.

GROWTH PATTERNS AND COILING

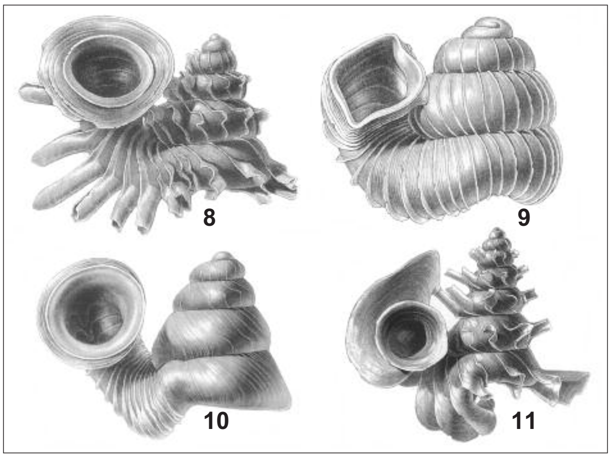
Small (and young) gastropods are almost always more vulnerable to predators than larger older ones. The growth pattern of gastropods often reflects this reality when predation is intense. On land and in many tropical reef-associated gastropods, young gastropods grow fast and have thin shells. Often, especially on reefs, these juveniles occupy environments where predators are scarce or impeded, as is the case beneath boulders and in deep sand. Upon reaching maturity, the shell thickens, and in many cases forms a modified, reinforced apertural rim as spiral growth ceases (Vermeij & Signor, 1992; Irie & Iwasa, 2005). In many marine gastropods, growth is episodic, ceasing at intervals while a reinforced apertural rim is laid down, then growing rapidly before another round of reinforcement begins, leading to the formation of external or internal varices. The period of active growth is typically spent in safe habitats. Determinate and episodic growth were rare during the Palaeozoic and became common only from the Early Jurassic onward, especially in warm marine waters.

The highest incidence of determinate growth was achieved in the Neogene (Vermeij & Signor, 1992). Determinate growth is extremely common in land snails but relatively uncommon in freshwater, and occurs among land snails only in the coastal tropical Pacific ellobiid genus *Pythia*. Episodic growth associated with varices is unknown in freshwater; it may well occur in land snails but has yet to be documented in them.

Throughout their history, most gastropods have been dextrally coiled (right-handed), with the aperture appearing on the right when the shell is held with the apex pointing toward the observer and the aperture facing down; but sinistral species have evolved many times. There are at least 20 separate lineages with sinistral shells in the modern marine fauna (Vermeij, 2002; Bonfitto & Morassi, 2012) and many more in the past (Vermeij, 1975). There are also many instances in freshwater, but the most frequent transitions between dextral and sinistral coiling have occurred among land snails (Vermeij, 1975; Hoso, 2012b; Preece & White, 2008; Webster et al., 2012; Fehér et al., 2013; E. Gittenberger et al., 2012).

Many shell-entering and shell-crushing predators have asymmetrical feeding structures with which they manipulate and subdue shell-bearing prey. Most crabs, for example, have a larger right claw, which differs from the smaller left claw by being specialized for crushing or peeling gastropod shells. Experiments have shown that sinistral gastropods are attacked less successfully by right-handed crabs than are dextral individuals of the same species (Dietl & Hendricks, 2006) and that left-handed crabs have more difficulty attacking dextral gastropods at the aperture than right-handed crabs of the same species do (Shigemiya, 2003). Snakes and water beetles with asymmetrical mouthparts and birds with a right-curving beak have more trouble removing prey bodies from left-handed tree snails and freshwater gastropods than removing the more common right-handed individuals (T. B. Smith & Temple, 1982; Snyder & Snyder, 1969; Inoda et al., 2003; Hoso et al., 2007, 2010; Hoso & Hori, 2008). A shift from dextral to sinistral coiling (and among land snails sometimes in the opposite direction) may therefore provide some antipredatory advantage as long as the new style of coiling remains in the minority among potential prey. A reversal in shell (and body) handedness is, of course, not related to predation alone; it also affects mating success (M. S. Johnson et al., 1977, 1990; E. Gittenberger, 1988; Asami et al., 1998).

Many land snails and some marine ones periodically or terminally change coiling direction during growth. Hoso and colleagues (2008) have shown that the distorted aperture resulting from such shifts is an effective defence of the Japanese land-snail genus *Satsuma* against pareine snakes, which attack their prey by way of the aperture. Such a defence may also explain the bizarre backward-pointing apertures in tiny tropical Asian land snails of genera such as *Plectostoma* and *Opisthostoma* (Figs 8-11; Liew & Schilthuizen, 2014). Similar architectures are frequent in Palaeozoic marine gastropods (Frýda et al., 2002), and in modified form characterize living marine personid tonnoideans, in which periodic shifts in



Figs 8-11. *Opisthostoma* species from Indonesia. **8.** *O. everetti* E. A. Smith, 1893. **9.** *O. goniostoma* Vermeulen, 1994. **10.** *O. hosei* Godwin Austen, 1890. **11.** *O. mirabile* E. A. Smith, 1893. Drawings: Jaap Vermeulen.

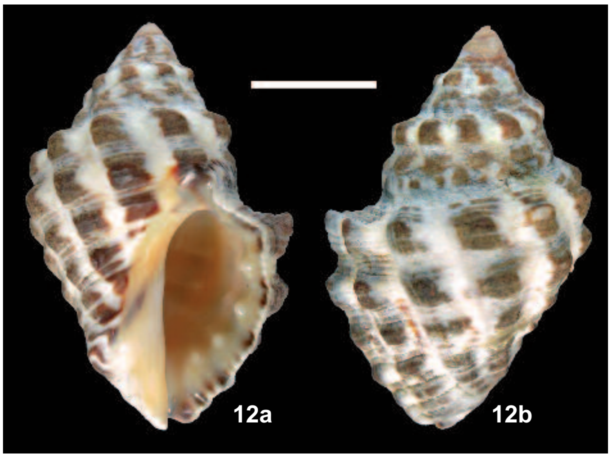


Fig. 12. *Reishia clavigera* (Küster, 1860). Area of Changi, on intertidal rocks, near Changi River, Singapore. Coll. and photo: Roland Houart. Scale bar: 1 cm.

direction are associated with a small, heavily armored aperture (Linsley & Javidpour, 1978). Whether such coiling modifications have any defensive functions is unknown.

DEEP WITHDRAWAL

In many shell-bearing gastropods, the body can be withdrawn more than a full whorl back from the aperture's opening, making it difficult for predators that invade the shell by way of the aperture to reach the soft parts (Signor, 1985; Edgell & Miyashita, 2009). Deep withdrawal is best exemplified in marine terebrids (Pl. 1, Fig. 2), turritellids, and vermetids. In gastropods with this capacity, the spire is high and slender, the aperture is small, and the rate of whorl expansion is low. However, none of these traits necessarily implies deep withdrawal. Marine cerithiids, freshwater cerithioideans, and most high-spired land snails have all these characteristics, but the body typically does not withdraw far from the apertural edge. In the sea, the ability to withdraw far into the shell is common in the tropics, rare in colder waters, and nearly unknown in Palaeozoic taxa. The ability is also rare in freshwater and terrestrial gastropods despite the common occurrence of shell-entering predators in those environments.

NARROW AND OCCLUDED APERTURES

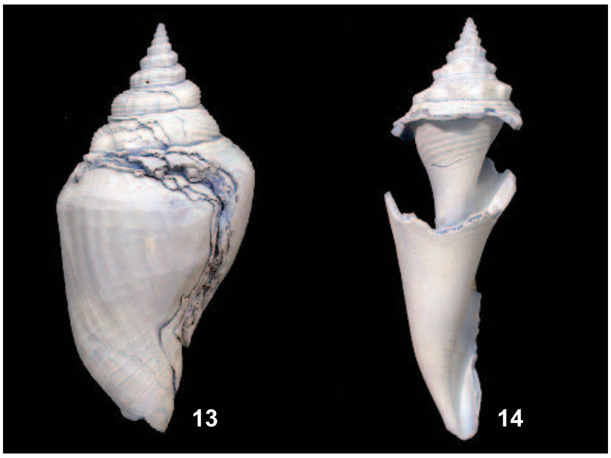
An alternative to deep withdrawal of the body is a narrowly elongate aperture or one that is partially occluded by folds and thickenings ("teeth" or "denticles") on the rim. A narrowly elongate aperture typifies most marine Cypraeoidea, Columbellidae, Mitridae, Costellariidae, Marginellidae, Cystiscidae, Olividae, Volutomitridae, Conoidea, Acteonoidea, and Bulloidea. It does not occur in Vetigastropoda, Neritoidea, Littorininoidea, Cerithioidea, Campaniloidea, Ampullinidae, or Naticidae, and is unknown in Palaeozoic taxa. In freshwater, a narrow aperture is known only in the lymnaeid *Acella* and the marginellid *Rivomarginella* (Vermeij & Covich, 1978), whereas on land it characterizes the taxonomically diverse predatory family Oleacinidae. Apertures with a dentate outer lip and/or a toothed or plicate inner lip are very widespread, especially in Cypraeoidea, Tonnoidea (Pl. 1, Fig. 4), Muricidae, Columbellidae, Mitridae, Costellariidae, Marginellidae, Cystiscidae, and some Neritoidea, Vetigastropoda, and Rissooidea. Apertural armature is extremely common in numerous clades of pulmonate and neritoidean land snails (Solem, 1972) but is essentially unknown in freshwater.

The combination of a rounded aperture and prominent apertural dentition is extremely common in land snails but conspicuously rare in marine gastropods. Tropical high-intertidal neritids are the only marine example that come to mind. Somewhat less obtrusive barriers in round-apertured marine snails occur in a few trochoideans (e.g. *Clanculus* and *Monodonta*) and in a few species of the littorinid genus *Tectarius*.

Marine gastropods with tooth-occluded apertures are unknown in the Palaeozoic and became common only in the Palaeogene, with a further expansion in the Neogene. It is therefore all the more peculiar that the earliest land snails, currently assigned to the ellobioidean pulmonate genus *Anthracopupa* of the Late Carboniferous (Stworzewicz et al., 2009) already had apertural teeth. This kind of apertural defence is therefore unusual among protective measures in having evolved on land before it did so in the sea.

CLOSING DEVICES

The presence of an operculum, a device that closes the shell entrance when the head and foot are withdrawn into the



Figs 13-14. Two fossil specimens (whitened) of *Strombus alatus* Gmelin, 1791 with repaired shell (**13**) and heavily damaged shell (**14**) due to crab attack. Photos: Lisa Whitenack, courtesy Gregory Herbert.

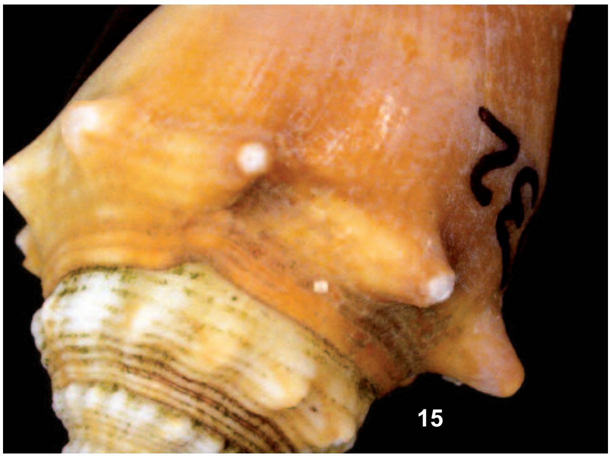


Fig. 15. *Strombus alatus* Gmelin, 1791 with spines broken off by crabs of the genus *Menippe*. Photo: Lisa Whitenack, courtesy Gregory Herbert.

shell, confers protection against predation in three ways. First, if the seal between the operculum and the surrounding shell is complete, the gastropod can survive passage through a predator's digestive system. This form of protection has been documented for gastropods that have been swallowed whole by fishes (Norton, 1988) and birds (Cadée, 2011). It is presumably effective mainly in small gastropods. Second, the operculum bars entry to the aperture by beetles, predatory gastropods, leeches, crabs, birds, and probably other predators (Gibson, 1970; Kasigwa et al., 1983; Snyder & Kale, 1983; Kelly & Cory, 1987). Some predators, when confronted by an operculum, will resort to alternative means of killing the prey, such as drilling through the shell wall or crushing it (Mordan, 1977). The operculum thus slows down the process of subjugation, increasing the probability that the predator will be interrupted and that the prey will ultimately survive. In Hong Kong, for example, the muricid *Reishia clavigera* (Küster, 1860) (Fig. 12) is forced to drill through the shell when confronted with the calcareous operculum of prey *Lunella coronata* (Gmelin, 1791) and *Nerita albicilla* Linnaeus, 1758 – instead of the faster method of entering via the aperture (Taylor & Morton, 1996).

Devices with an opercular function are not unique to gastropods. They have also evolved in Palaeozoic hyoliths and in Palaeozoic and Mesozoic cephalopods. Gastropods have never evolved an operculum that pinches potential attackers, as have some cephalopods and shell-dwelling hermit crabs. As an aside, it is curious that no scaphopod is known to close the shell's wide end with an operculum.

A mineralized structure closing the aperture when the body is withdrawn into the shell is found in many marine, freshwater, and terrestrial gastropods (Checa & Jiménez-Jiménez, 1998). Among marine gastropods, a calcareous operculum characterizes Turbinidae, Tricoliidae, Phasianellidae, and Liotiidae within the clade Trochoidea (Williams & Ozawa, 2006); Neritidae and related families in Neritopsina (Kaim & Sztajner, 2005; Bandel, 2007, 2008; Jagt & Kiel, 2008); and several clades within Naticidae (Huelsken et al., 2008), as well as in some littorinids (the Mariana Islands endemic *Tectarius viviparus* (Rosewater, 1982)) (Reid & Geller, 1997), and vermetids of the Indo-West Pacific genus *Cupolaconcha* (Golding et al., 2014). It also occurs in Palaeozoic macluritids and oriostomatids (Rohr & Boucot, 1985; Rohr & Gubanov, 1997; Rohr & Yochelson, 1999; Yochelson, 1979). None is known in the huge clades Latrogastropoda (neogastropdos, tonnoideans, and related clades) or Heterobranchia. There was also repeated evolution of calcareous opercula in freshwater, as in the Indian littorinid genus *Cremnoconchus* (Reid et al., 2013), the Mesozoic to Early Caenozoic genus *Reesidites* in the extinct family Pliopholygidae (D. W. Taylor, 1966b), bithyniine hydrobiids (D. W. Taylor, 1966a), and Ampullariidae (Taylor, 1966a). Freshwater neritids and some terrestrial helicinids likely inherited their calcareous operculum from their marine ancestors in the Neritopsina. A true calcareous operculum is known among terrestrial gastropods in Helicinidae as well as in Pomatiacidae, Cyclophoroidea. Nonhomologous calcareous closing mechanisms evolved separately in terrestrial clausiliids and the bizarre "camaenid" *Thyrophorella thomensis* Greeff, 1882 (from São Tomé) and urocoptids (Nordsieck, 1982; E. Gittenberger, 1996; Gittenberger & Mordan, 2002; Gittenberger & Schilthuizen, 1996). In all cases, these calcareous structures lie close to the apertural rim when the body is retracted. Two charopid genera from New Caledonia form an organic but greatly thickened operculum-like structure, again nonhomologous with a true operculum (Solem et al., 1984).

A striking characteristic of calcareous opercula in marine vetigastropods, neritids, and naticids is the species-specific colour and sculpture, the latter consisting of ridges, smooth zones, beads, or pustules. This specificity has been described frequently in taxonomic papers, including those on Caenozoic fossils (see e.g. Marincovich, 1977; Hickman & McLean, 1990; McLean & Kiel, 2007; McLean, 2012b; Bandel, 2008; Frey & Vermeij, 2008; Huelsken et al., 2008; Williams, 2008; Vermeij & Frey, 2008; Krijnen & Vink, 2009; Vermeij & Williams, 2007; Pedriali & Robba, 2008). To my knowledge, these characteristics have never been investigated from a functional point of view, but I suspect that species recognition for mating may play an important role in their evolution.

Stage of effectiveness	Number of effective defences				
	Palaeozoic marine	**Mesozoic to Recent marine**	**Mesozoic to Recent freshwater**	**Mesozoic to Recent terrestrial**	**Total**
1	2	8	0	3	9
2	0	4	0	0	4
3	4	23	4	7	25
No data	7	0	1	0	7
Total	6	29	4	8	31

Table 3. Summary of occurrence of shell and opercular defences common in gastropods.

SHELL ENVELOPMENT

A partially or completely enveloped shell is usually associated with relatively fast locomotion. As detailed by Vermeij (2005), this condition evolved approximately fifty times from the Ordovician onward, mainly in Cretaceous to Recent clades but also at least twice in temperate freshwater lineages and two to three times in land snails (see also Frey & Vermeij, 2008; Van Mol, 1978). A common trend in land snails and some marine lineages (especially among so-called opisthobranchs) is the evolution of externally shell-less slugs. This evolution occurs either through internalization of the shell or from a condition in which the external shell is far too small to accommodate the soft body. Envelopment and the evolution of slug-like forms also entails the development of chemical defence, visual camouflage, or aposematically coloured mantle or foot.

A common but by no means universal consequence of shell envelopment by the mantle or foot is that the shell is slippery-smooth, as in many cowries (Cypraeidae) and olivids. This makes the animal difficult for predators to grasp when the soft parts are withdrawn into the shell. A slippery surface can also evolve in lineages without shell envelopment, as in the rissoid genus *Zebina* and the columbellid genera *Conella* and *Nitidella*. A mucus coating would accomplish the same function, and this may be common in some calliostomatid trochoideans, bulloidean opisthobranchs, and some land snails.

EXTERNAL SHELL SCULPTURE

External shell sculpture figures prominently in gastropod shell defence, especially in the sea. Thin, long spines not only make the animal appear much larger than the internal volume of the shell encompasses, but also increase handling time for predators. Gastropods with such spines are known from at least the Silurian (as in *Spineomphalus*) (Rohr & Packard, 1982). Although infrequent in freshwater, they do occur in the southeast North American pleurocerid genus 10, the Mekong River triculine hydrobiid *Pachydrobia spinosa* Poirier, 1881 and *Saduniopsis planispira* Davis, 1979, and the Indo-West Pacific neritid genus *Clithon* (see Vermeij & Covich, 1978; Davis, 1979). In the freshwater thiarid genus *Thiara*, short backward-pointing spines on the spire likely complicate handling by predators. Periostracal spines occur in some small land snails, but to my knowledge no long-spined species are known.

Many types of sculpture strengthen or stiffen the shell through buttressing and by concentrating compressive forces at the thickest parts of the shell. Included in this category are thick spines, knobs, and tubercles, which may be branched as in many muricids; high strap-like or belt-like spiral cords or welts; a dorsal knob or ridge; ribs produced parallel to the contour of the outer lip; varices (periodic thickenings more or less parallel to smaller intervening ribs); and a terminally thickened or reflected outer lip (Pl. 1, Fig. 5). These reinforcing structures are rare in marine Palaeozoic gastropods but became common in the Mesozoic and especially the Caenozoic (Vermeij, 1977; Vermeij & Signor, 1992). Some freshwater gastropods are tuberculate or bear relatively strong cords and ribs, which have been shown to confer protection against shell-breaking predators (Rust, 1997), but varices are unknown, and reinforced stiffening ribs and keels are quite common in gastropods from large river systems and ancient lakes. Reflected or thickened outer lips are also extremely rare in freshwater snails.

Despite these demonstrated advantages of external sculpture, not all sculpture appears to be effective as a defence. In one of the best experimental studies of its kind, Whitenack & Herbert (2015) have shown that robust spines on the body whorl of the Floridian strombid *Strombus alatus* Gmelin, 1791 (Figs 13-14, 15) do not protect adult individuals from large crabs of the genus *Menippe*. In earlier work, we similarly found that the defences of this small strombid *Gibberulus gibberulus gibbosus* (Röding, 1798) – thickened adult lip, narrow aperture, shoulder nodes, and rounded varices – are no match for the lip-peeling crab *Calappa hepatica* (Vermeij & Zipser, 1986a). It may be that, as Whitenack & Herbert (2015) suggest, sculptural and other defences against shell breakage work best against smaller predators, or they may have been effective against powerful predators such as the loggerhead turtle (*Caretta caretta*), which is now rare.

Some sculpture on marine gastropods, particularly from the Eocene onward, aids in burrowing into sand. The anterior flanks of ribs form a low angle to the direction of locomotion, whereas the adapical and abapertural sides are steep. This ratchet effect characterizes many burrowing cerithiids, olivids (with abapical ridges), cassids, mitrids, nassariids, harpids, and acteonids (Vermeij & Zipser, 1986; Vermeij & Dudley, 1989; Signor, 1982a, b, c, 1983; Savazzi, 1989; Savazzi & Pan, 1994). Although this type of sculpture is not found in the fastest burrowers, whose shells tend to be smooth and streamlined (Vermeij & Zipser, 1986; Vermeij & Dudley, 1989), it does reduce backward slippage of the shell during the burrowing cycle. To my knowledge, ratchet sculpture is unknown among freshwater or terrestrial gastropods. It is also rare among cool-water marine snails and entirely absent in polar forms. The scarcity of ratchet sculpture in these environments as well as during the Palaeozoic and Early Mesozoic is attributed in part to the rarity of burrowing in gastropods under these conditions (Signor, 1982; Vermeij, 1993).

SHELL-EDGE CHARACTERISTICS AND TENACITY

Gastropods in many marine groups are characterized by well developed crenulations at the edge of the lip in contact with the hard substratum on which these animals live. Elsewhere I have speculated that these crenulations, which form in various ways, serve to resist dislodgement by waves or predators (Vermeij, 2014b). I noted that such crenulations are unknown in freshwater and terrestrial gastropods. In these animals, as well as in many marine high intertidal littorinids and potamidids, a resting snail is attached to the substratum by a strip or film of dried mucus, potentially aided by the flattened smooth ventral side of the reflected adult outer shell lip. This kind of attachment is more passive than the postulated friction-enhancing lip modifications associated with edge crenulations of many marine gastropods, which must expend muscular power to stay in place during attacks by predators attempting to dislodge their prey.

SHELLS AND AGGRESSION

All of the traits discussed so far can be categorized as passive defences. The shell (and sometimes operculum) can under some circumstances serve as a weapon that functions either in aggressive defence or as an aid in subduing prey (Ankel, 1976). Some limpets, when clamping the shell to the substratum, can pinch off the foot of predatory gastropods by pinning it beneath the shell (Branch, 1979). Stimson (1970, 1973) showed that the large Californian lottiid limpet *Lottia gigantea* maintains intertidal territories by shoving potential competitors away with the thickened anterior portion of the shell. Muricids push competitors away from contested prey (Abe, 1989; Ishida, 2005). Such aggression likely requires both the capacity to anchor the shell against force and the internal musculature to push the shell forward or downward against resisting forces. The heavy shell of species of *Cassis* helps crush the test of prey sea urchins (echinoids) when the gastropod catapults forward and drops the shell onto its prey (Hughes & Hughes, 1981). Many gastropods have an enlarged spine or tooth pointing ventrally toward the substratum at the edge of the outer lip. This so-called labral tooth has been shown to function in penetrating between barnacles' opercular plates and between the valves of bivalves, and may stabilize the predator which the snail is attacking its prey (Wells, 1958; Paine, 1966; Perry, 1985; reviewed in Vermeij, 2001). A row of sharp short spines at the lip edge of some sand-dwelling gastropods may serve a defensive function against potential attackers, although experiments to test this hypothesis have not been done (Vermeij, 2001, 2014b). Labral teeth and rows of downward-pointing apertural spines are unknown in freshwater gastropods. All marine examples, which evolved in some 60 clades (labral teeth) and six clades (rows of spines), are known from the Late Cretaceous onward. I am aware of only one terrestrial genus with a labral tooth, the Jamaican oleacinid *Varicella*.

Several busyconine and fasciolariine gastropods have a notably convex-downward outer shell lip that has been shown to function in opening bivalve prey with tightly closing shells. Although part of the lip is often damaged in the process, it is strongly reinforced and can grow back rapidly (Warren, 1916; Carriker, 1951; Kent, 1983; Dietl, 2003a, b, 2004; Dietl et al., 2010). Convex-lipped predatory gastropods are known from the Late Cretaceous onward.

A few marine gastropods have evolved a sharply pointed operculum whose outer edge bears sharp serrations. A stabbing function for such an operculum seems plausible but has never been experimentally investigated. Opercula of this type are known in many Strombidae and Seraphsidae as well as in some Nassariidae, some deep-water conids, and the xenophorid *Austrophorus* (Tucker & McLean, 1993; Kreipl et al., 1999; Kronenberg & Burger, 2002).

INTERNAL SCULPTURE

The diversity of internal shell features in gastropods is as great as that of external sculpture, but the functional significance of internal folds, lirae (ridges on the inner side of the outer wall), and rows of teeth has received comparatively little attention. Many of these features are, however, familiar to taxonomists: columellar folds, parietal ridges (Pl. 1, Fig. 1), smooth or beaded lirae, and entrance folds to the siphonal canal.

In many trochoidean vetigastropods, an anisotropic microscopic microstructure or obliquely oriented aragonitic blades oriented in such a way that rubbing the palatal side of the aperture toward the rim meets with less resistance than rubbing the surface inward from the outer lip (Wise, 1970; Vermeij, 2005), is a conspicuous feature of the inner side of the aperture's outer wall.

Although columellar folds are common in Palaeozoic to Recent marine gastropods as well as in some land snails, lirae are unknown in the Palaeozoic and are very rare even as late as the Cretaceous. Lirate gastropods in the modern fauna are overwhelmingly tropical in distribution, and most belong to post-Eocene groups (Pl. 1, Fig. 7). I am unaware of any lirate gastropods in freshwater, or on land.

GENERAL DISCUSSION

From the foregoing accounts it is clear that the skeletal defences of gastropods are very unevenly distributed in space and time. Of the 31 types summarized in Table 2, 29 (94%) are common globally or regionally in Late Mesozoic to Recent marine environments, whereas only 4 (13%) are well represented in freshwater, 6 (19%) are common in the marine Early Palaeozoic, and 8 (26%) are common on land (Table 3). Most of these defences in all environments are effective at the subjugation-resistance step of predatory attacks; active responses as reflected in shell and opercular morphology, involving locomotion and aggression, are essentially limited to geologically young marine gastropods.

As has been observed in earlier studies (Vermeij, 1975, 1977, 1993), marine Early Palaeozoic gastropods are architecturally similar to extant gastropods on land. In both groups there is a high incidence of poorly buttressed umbilicate shells; of trochiform, discoidal, sinistral, and planispiral forms; and a low incidence of narrow apertures and crenulated lip edges. Apertural teeth are the only defence type that evolved first in land snails (during the Late Carboniferous) and much later in marine ones. In fact, the main architectural difference between Palaeozoic marine and living terrestrial land snails is the high incidence of folds and denticles around the apertural rim in the latter group.

The heavy emphasis on passive defences in gastropods is to be expected in animals that are not generally known for either speed or aggression. What is surprising, however, is that land snails have remained even more passive than their modern marine counterparts. The low density and viscosity of air, the very high diffusivity of oxygen and carbon dioxide into and out of air-breathing organisms, and the consequent high metabolic rates enabled terrestrial arthropods and vertebrates to explore a much greater variety of defences, particularly those involving locomotion, aggression, and the application of strong forces, than in their marine ancestors. Air-breathing is thus a necessary but not sufficient condition for achieving such active means of antipredatory adaptation. In their passivity, land snails resemble terrestrial isopod and amphipod crustaceans, which likewise rely chiefly on passive defences such as rolling up into a ball and (rarely) toxic secretions.

Another theme that emerges from the foregoing synthesis is the anecdotal nature of much of what we know or can infer about defence in shell-bearing gastropods. Three areas will be important in achieving a deeper understanding: (1) experimental verification of many proposed functions, and quantification of how well defences work in the wild and under the more controlled conditions of laboratory settings against specific predators or classes of predators; (2) observational studies of enemies, that is, a continuing emphasis on natural history, including anecdotal observations; and (3) a systematic and inclusive account of the ecological, geographical, temporal, and phylogenetic distribution of defence types and styles of predation, with particular attention to how often, when and where predation-related traits evolved.

Above all, this review highlights the importance and intellectual challenge of thinking of shells not only as objects to classify, but also as functional structures that work in conjunction with the rest of the body as well as in the context of risks, challenges, and opportunities posed by the environment. Shells offer a molluscan window on the world, the world we live in and the world of the distant geological past.

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REFERENCES

ABE, N., 1989. Interactions between carnivorous gastropods and their sessile animal prey at a rocky intertidal shore. — Physiological Ecology in Japan 26: 1-38.

ALBRECHT, C. & GLAUBRECHT, M., 2006. Brood care among basommatophorans: a unique reproductive strategy in the freshwater limpet snail *Protancylus* (Heterobranchia: Protancylidae) endemic to ancient lakes on Sulawesi, Indonesia. — Acta Zoologica (Stockholm) 87: 49-58.

ANKEL, W.E., 1976. Das Gehäuse der Schnecken als Werkzeug und Waffe. — Natur und Museum 106: 102-111.

APPLETON, C.C. & HEEG, J., 1999. Removal of calcium by *Natalina cafra* (Pulmonata: Rhytididae). — Journal of Molluscan Studies 65: 271-273.

ASAMI, T., COWIE, R. H. & OHBAYASHI, K., 1998. Evolution of mirror images by sexually asymmetric mating behavior in hermaphroditic snails. — American Naturalist 152: 225-236.

AVERBUJ, A. & PENCHASZADEH, P.E., 2010. Reproductive seasonality, oviposition and development of the nassariid whelk *Buccinanops cochlidium* (Dillwyn, 1817) in Patagonia, Argentina. — Journal of Molluscan Studies 76: 25-32.

BAALBERGEN, E., HELWERDA, R., SCHELFHORST, R., CASTILLO CAJAS, R.F., VAN MOORSEL, C.H.M., KUNDRATA, R., WELTER-SCHULTES, F.W., GIOKAS, S. & SCHILTHUIZEN, M., 2014. Predator-prey interactions between shell-boring beetle larvae and rock-dwelling land snails. — PLoS One 9: e100366.

BAKER, H.B., 1962. Puerto Rican land operculates. — Nautilus 76: 16-22.

BAŁUK, W. & RADWAŃSKI, A., 1985. Slipper-limpet gastropods (*Crepidula*) from the Eocene glauconitic sandstone of Kressenberg (Bavarian Alps, West Germany). — Neues Jahrbuch für Geologie und Paläontologie Monatshefte 1985: 237-247.

BANDEL, K., 2007. Description and classification of Late Triassic Neritimorpha (Gastropoda, Mollusca) from the St. Cassian Formation, Italian Alps. — Bulletin of Geosciences 82: 215-274.

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.

BANDEL, K. & RIEDEL, F., 1994. Classification of fossil and Recent Calyptraeoidea (Caenogastropoda) with a discussion on neomesogastropod phylogeny. — Berliner Geowissenschaftliche Abhandlungen (E) 13: 329-367.

BAUMILLER, T.K., 1990. Non-predatory drilling of Mississippian crinoids by platyceratid gastropods. — Palaeontology 33: 743-748.

BAUMILLER, T.K., 1993. Boreholes in Devonian blastoids and their implications for boring by platyceratids. — Lethaia 26: 41-47.

BAUMILLER, T.K., 1996. Boreholes in the Middle Devonian blastoid *Heteroschisma* and their implications for gastropod drilling. — Palaeogeography, Palaeoclimatology, Palaeoecology 123: 343-351.

BAUMILLER, T. K. & GAHN, F.J., 2002. Fossil record of parasitism on marine invertebrates with special emphasis on the platyceratid-crinoid interaction. — Paleontological Society Papers 8: 195-209.

BAUMILLER, T. K. & MACURDA, D.B. Jr., 1995. Borings in Devonian and Mississippian blastoids (Echinodermata). — Journal of Paleontology 69: 1084-1089.

BEDARD, A.A., 1971. *Littorina littorea* (Linnaeus) and some new symbiotic associates. — Research Report of the Manomet Bird Observatory 4: 1-2.

BENGTSON, S. & ZHAO, Y., 1992. Predatorial borings in Late Precambrian mineralized exoskeletons. — Science 257: 367-369.

BIELER, R., 1988. Phylogenetic relationships in the gastropod family Architectonicidae, with notes on the family Mathildidae (Allogastropoda). — Malacological Reviews, Supplement 4: 205-240.

BONFITTO, A. & MORASSI, M., 2012. A new sinistral turriform gastropod (Conoidea: Mangeliidae) from Taiwan. — Zootaxa 1415: 63-68.

BOUCHET, P., 1989. A marginellid gastropod parastizes sleeping fishes. — Bulletin of Marine Science 45: 76-84.

BOUCHET, P. & PERRINE, D., 1996. More gastropods feeding at night on parrotfishes. — Bulletin of Marine Science 59: 224-228.

BRANCH, G.M., 1976. Interspecific competition experienced by South African *Patella* species. — Journal of Animal Ecology 45: 507-520.

BRANCH, G.M., 1979. Aggression by limpets against invertebrate predators. — Animal Behaviour 27: 408-410.

CADÉE, G.C., 1995. Komt schelpreparatie bij landslakken vaak voor? — Correspondentieblad van de Nederlandse Malacologische Vereniging 282: 6-11.

CADÉE, G.C., 2011. *Hydrobia* as "Jonah in the whale": shell repair after passing through the digestive tract of shelducks alive. — Palaios 26: 245-249.

CAIN, A.J., 1977a. Variation in the spire index of some coiled gastropod shells and its evolutionary significance. — Philosophical Transactions of the Royal Society of London B 277: 377-428.

CAIN, A.J., 1977b. The uniqueness of the polymorphism of *Cepaea* (Pulmonata: Helicidae) in western Europe. — Journal of Conchology 29: 129-136.

CAIN, A J., 1978a. The deployment of operculate land snails in relation to shape and size of shell. — Malacologia 17: 207-221.

CAIN, A.J., 1978b. Variation of terrestrial gastropods in the Philippines in relation to shell shape and size. — Journal of Conchology 29: 230-245.

CARRIKER, M.R., 1951. Observations on the penetration of tightly closing bivalves by *Busycon* and other predators. — Ecology 32: 73-83.

CHECA, A.G. & JIMÉNEZ-JIMÉNEZ, A.P., 1998. Constructional morphology, origin, and the evolution of the gastropod operculum. — Paleobiology 24: 109-132.

CIPRIANI, R. & PENCHASZADEH, P.E., 1993. How does *Strombina* reproduce? Evidence from two Venezuelan species (Prosobranchia: Columbellidae). — Veliger 36: 178-184.

CONWAY MORRIS, S. & BENGTSON, S., 1994. Cambrian predators: possible evidence for boreholes. — Journal of Paleontology 68: 1-23.

COOK, L.M. & KENYON, G., 1993. Shell strength of colour morphs of the mangrove snail *Littoraria pallescens*. — Journal of Molluscan Studies 59: 29-34.

COWIE, R.H., 1995. Variation in species diversity and shell shape in Hawaiian land snails: in situ speciation and ecological relationships. — Evolution 49: 1191-1202.

DAVIS, G.M., 1979. The origin and evolution of the gastropod family Pomatiopsidae, with emphasis on the Mekong River Triculinae. — Academy of Natural Sciences of Philadelphia Monograph 29: 1-120.

DENNY, M.W., 1993. Air and water: The biology and physics of life's media. Princeton University Press, Princeton.

DEVRIES, M.S., MURPHY, E.A.K., & PATEK, S.N., 2012. Strike mechanics of an ambush predator: the spearing mantis shrimp. — Journal of Experimental Biology 215: 4374-4384.

DIAS, R. J., D’AVILA, S., WIELOCH, A.H. & D'AGOSTO, M., 2008. Protozoan ciliate epibionts on the freshwater apple snail *Pomacea figulina* (Spix, 1827) (Gastropoda, Ampullariidae) in an urban stream of south-east Brazil. — Journal of Natural History 42: 1409-1420.

DIETL, G.P., 2003a. Coevolution of a marine gastropod predator and its dangerous bivalve prey. — Biological Journal of the Linnean Society 80: 409-436.

DIETL, G.P., 2003b. Interaction strength between a predator and dangerous prey: *Sinistrofulgur* predation on *Mercenaria*. — Journal of Experimental Marine Biology and Ecology 289: 287-301.

DIETL, G.P., 2004. Origins and circumstances of adaptive divergence in whelk feeding behavior. — Palaeogeography, Palaeoclimatology, Palaeoecology 208: 279-291.

DIETL, G.P. & HENDRICKS, J.R., 2006. Crab scars reveal survival advantage of left-handed snails. — Biology Letters 2: 439-442.

DIETL, G.P., DURHAM, S.R. & KELLEY, P.H., 2010. Shell repair as a reliable indicator of bivalve predation by shell-wedging gastropods in the fossil record. — Palaeogeography, Palaeoclimatology, Palaeoecology 296: 174-184.

DIGWEED, S.F., 1993. Selection of terrestrial gastropod prey by cychrine and pterostichine ground beetles (Coleoptera: Carabidae). — Canadian Entomologist 125: 463-472.

DOLIN, L. & LEDON, D., 2002. Nouveaux taxons et discussion de la systématique des genres correspondants d'Ovulidae (Mollusca, Caenogastropoda) de l'Eocène Inférieur de Gan (France). — Geodiversitas 24: 329-347.

DUDLEY, E.C. & VERMEIJ, G.J., 1989. Shell form and burrowing performance in gastropods from Pacific Panama, with comments on regional differences in functional specialization. — Veliger 32: 284-287.

EBBESTAD, J.O.R., 1998. Multiple attempted predation in the Middle Ordovician gastropod *Bucania gracillima*. — GFF 120: 27-33.

EBBESTAD, J.O.R. & PEEL, J.S., 1997. Attempted predation and shell repair in Middle and Upper Ordovician gastropods from Sweden. — Journal of Paleontology 71: 1007-1019.

EDGELL, T.C. & MIYASHITA, T., 2009. Shell shape and tissue withdrawal depth in 14 species of temperate intertidal snail. — Journal of Molluscan Studies 75: 235-240.

EL-NAKHAL, H. & BANDEL, K., 1991. Geographical distribution of the small gastropod genus *Scaliola*. — Micropaleontology 37: 423-424.

ESPOZ, C., LINDBERG, D.R., CASTILLA, J.C. & SIMISON, W. B., 2004. Intertidal limpets of Chile and Peru. — Revista Chilena de Historia Natural 77: 257-283.

FEHÉR, Z., NÉMETH, L., NICOARĂ, A. & SZEKERES, M., 2013. Molecular phylogeny of the land snail genus *Alopia* (Gastropoda: Clausiliidae) reveals multiple inversions of chirality. — Zoological Journal of the Linnean Society 167: 259-272.

FISHLIN, D.A. & PHILLIPS, D.W., 1980. Chemical camouflaging and behavioral defenses against a predatory seas tar by three species of gastropods from the surfgrass *Phyllospadix* community. — Biological Bulletin 158: 34-48.

FORTUNATO, H., PENCHASZADEH, P.E. & MILOSLAVICH, P., 1998. Observations on the reproduction of *Bifurcium bicanaliferum* (Sowerby, 1832) (Gastropoda: Columbellidae: *Strombina*-group) from the Pacific coast of Panama. — Veliger 41: 208-211.

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.

FRÝDA, J., BLODGETT, R.B. & LENZ, A.C., 2002. New Devonian gastropods from the families Crassimarginatidae (new family) and Scoliostomatidae (new family), Royal Creek area, Yukon Territory, Canada. — Journal of Paleontology 76: 246-255.

GAHN, F.J. & BAUMILLER, T.K., 2003. Infestation of Middle Devonian (Givetian) camerate crinoids by platyceratid gastropods and its implications for the nature of their biotic interaction. — Lethaia 36: 71-82.

GIBSON, J.S., 1970. The function of the operculum of *Thais lapillus* (L.) in relation to desiccation and predation. — Journal of Animal Ecology 39: 159-168.

GITTENBERGER, A. & GITTENBERGER, E., 2005. A hitherto unnoticed adaptive radiation: epitoniid species (Gastropoda: Epitoniidae) associated with corals (Scleractinia). — Contributions to Zoology 74: 125-203.

GITTENBERGER, A. & HOEKSEMA, B.W., 2013. Habitat preferences of coral-associated wentletrap snails (Gastropoda: Epitoniidae). — Contributions to Zoology 82: 1-25.

GITTENBERGER, E., 1988. Sympatric speciation in snails; a largely neglected model. — Evolution 42: 826-828.

GITTENBERGER, E., 1996. Adaptations of the aperture in terrestrial gastropod-pulmonate shells. — Netherlands Journal of Zoology 46: 191-205.

GITTENBERGER, E. & MORDAN, P., 2002. The urocoptid closing device: rare and remarkable. — Basteria 66: 123-127.

GITTENBERGER, E., HAMANN, J.D. & ASAMI, T., 2012. Chiral speciation in terrestrial pulmonate snails. — PLoS One 7: e34005.

GITTENBERGER, E. & SCHILTHUIZEN, M., 1996. Parallelism in the origin of the G-type clausilial apparatus (Gastropoda, Pulmonata, Clausiliidae). In Origin and evolutionary radiation of the Mollusca, eds. TAYLOR, J.D., pp. 295-300. Oxford University Press, Oxford.

GOLDING, R.E., BIELER, R., RAWLINGS, T.A. & COLLINS, T.M., 2014. Deconstructing *Dendropoma*: a systematic revision of a world-wide worm-snail group, with descriptions of new genera (Caenogastropoda: Vermetidae). — Malacologia 57: 1-97.

GUMERT, M.D. & MALAIVIJNOND, S., 2012. Marine prey processed with stone tools by Burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. — American Journal of Physical Anthropology 149: 447-457.

GUMERT, M.D., KLUCK, M. & MALAIVIJITNOND, S., 2009. The typical characteristics and usage patterns of stone axe and pounding hammers used by long-tailed macaques in the Andaman Sea region of Thailand. — American Journal of Primatology 71: 594-608.

HAIN, S., 1990. Die beschalten benthischen Mollusken (Gastropoda und Bivalvia) des Weddellmeeres, Antarktis. — Berichte zur Polarforschung 70: 1-181.

HAND, C., 1975. Behaviour of some New Zealand sea anemones and their molluscan and crustacean hosts. — New Zealand Journal of Marine and Freshwater Research 9: 509-527.

HAYES, K.A., COWIE, R.H., THIENGO, S.C. & STRONG, E.E., 2012. Comparing apples with apples: clarifying the identities of two highly invasive Neotropical Ampullariidae (Caenogastropoda). — Zoological Journal of the Linnean Society 166: 723-753.

HELWERDA, R.A. & SCHILTHUIZEN, M., 2014. Predation on Greek *Albinaria* (Pulmonata: Clausiliidae) by *Poiretia* (Pulmonata: Oleacinidae) and by an unknown organism making circular holes: possible drivers of shell evolution. — Journal of Molluscan Studies 80: 272-279.

HELWERDA, R.A., WESSELINGH, F.P. & WILLIAMS, S.T., 2014. On some Vetigastropoda (Mollusca, Gastropoda) from the Plio-Pleistocene of the Philippines with descriptions of three new species. — Zootaxa 3755: 101-l35.

HICKMAN, C.S. & MCLEAN, J.H., 1990. Systematic revision and suprageneric classification of trochacean gastropods. — Natural History Museum of Los Angeles County Science Series 35: 1-169.

HOSO, M., 2012a. Cost of autotomy drives ontogenetic switching of anti-predator mechanisms under developmental constraints in a land snail. — Proceedings of the Royal Society B 279: 4811-4816.

HOSO, M., 2012b. Non-adaptive speciation of snails by left-right reversal is facilitated on oceanic islands. — Contributions to Zoology 81: 79-85.

HOSO, M. & HORI, M., 2008. Divergent shell shape as an antipredator adaptation in tropical land snails. — American Naturalist 172: 726-732.

HOSO, M., ASAMI, T. & HORI, M., 2007. Right-handed snakes: convergent evolution of asymmetry and functional specialization. — Biology Letters 3: 169-172.

HOSO, M., KAMEDA, Y., WU S.-P., ASAMI, T., KATO M. & HORI, M., 2010. A speciation gene for left-right reversal in snails results in anti-predator adaptation. — Nature Communications 1: 133.

HUELSKEN, T., MAREK, C., SCHREIBER, S., SCHMIDT, I. & HOLLMANN, M., 2008. The Naticidae (Mollusca: Gastropoda) of Giglio Island (Tuscany, Italy): shell characters, live animals, and a molecular analysis of egg cases. — Zootaxa 1770: 1-40.

HUGHES, R.N. & HUGHES, H.P.I., 1981. Morphological and behavioural aspects of feeding in the Cassidae (Tonnacea, Mesogastropoda). — Malacologia 20: 385-402.

IL'INA, L. G., 1987. Evidence of boring in shells of brackish-water gastropods. — Paleontological Journal 21: 23-30.

INODA, T., HIRATA, Y. & KAMIMURA, S., 2003. Asymmetric mandibles of water-scavenger larvae improve feeding effectiveness on right-handed snails. — American Naturalist 162: 811-814.

IRIE, T. & IWASA, Y., 2005. Optimal growth pattern of defensive organs: the diversity of shell growth among mollusks. — American Naturalist 165: 238-259.

ISHIDA, S., 2005. Comparison of penetration costs and ingestion speeds among muricid gastropods with different foraging strategies. — Veliger 47: 163-168.

JAGT, J. W.M. & KIEL, S., 2008. The operculum of *Otostoma retzii* (Nilsson, 1827) (Gastropoda, Neritidae; Late Cretaceous) and its phylogenetic significance. — Journal of Paleontology 82: 201-205.

JENSEN, K.R., 1996. Phylogenetic systematics and classification of the Sacoglossa (Mollusca, Gastropoda, Opisthobranchia). — Philosophical Transactions of the Royal Society of London B 351: 91-122.

JOHNSON, M.S., CLARKE, B. & MURRAY, J., 1977. Genetic variation and reproductive isolation in *Partula*. — Evolution 31: 116-126.

JOHNSON, M.S., CLARKE, B. & MURRAY, J., 1990. The coil polymorphism in *Partula suturalis* does not favor sympatric speciation. — Evolution 45: 459-464.

JOHNSON, S., JOHNSON, J. & JAZWINSKI, S., 1995. Parasitism of sleeping fish by gastropod mollusks in the Colubrariidae and Marginellidae at Kwajalein, Marshall Islands. — Festivus 27: 121-125.

KAIM, A. & SZTAJNER, P., 2005. The opercula of neritopsid gastropods and their phylogenetic importance. — Journal of Molluscan Studies 71: 211-219.

KAMEL, S.J. & GROSBERG, R.K., 2012. Exclusive male care despite extreme female promiscuity and low paternity in a marine snail. — Ecology Letters 15: 1167-1173.

KANO, Y., 2009. Hitchhiking behaviour in the obligatory upstream migration of amphidromous snails. — Biology Letters 5: 465-468.

KANO, Y. & FUKUMORI, M., 2010. Predation on hardest molluscan eggs by confamilial snails and its potential significance in egg-laying site selection. — Journal of Molluscan Studies 76: 360-366.

KELLY, P.M. & CORY, J.S., 1987. Operculum closing as a defence against predatory leeches in four British freshwater prosobranch snails. — Hydrobiologia 144: 121-124.

KENT, B.W., 1983. Natural history observations on the busyconine whelks *Busycon contrarium* (Conrad) and *Busycotypus spiratum* (Lamarck). — Journal of Molluscan Studies 49: 37-42.

KITCHELL, J.A., BOGGS, C. H., KITCHELL, J.F. & RICE, J.A., 1981. Prey selection by naticid gastropods: experimental tests and application to the fossil record. — Paleobiology 7: 533-542.

KNUDSEN, J., 1991. Observations on *Hipponix australis* (Lamarck, 1819) (Mollusca, Gastropoda, Prosobranchia) from the Albany area, Western Australia. — [In] Proceedings of the Third International Marine Biological Workshop: The marine flora and fauna of Albany, Western Australia, eds. WELLS, F.E., WALKER, D.I., KIRKMAN, H. & LETHBRIDGE, R., Pp. 641-660. Western Australian Museum, Perth.

KOKSHOORN, B., GOUD, J., GITTENBERGER, E. & GITTENBERGER, A., 2007. Epitoniid parasites (Gastropoda, Caenogastropoda, Epitoniidae) and their host sea anemones (Cnidaria, Actiniaria, Ceriantharia) in the Spermonde Archipelago, Sulawesi, Indonesia. — Basteria 71: 33-56.

KOLLMANN, H.A., 2014. The extinct Nerineoidea and Acteonelloidea (Heterobranchia, Gastropoda): a palaeobiological approach. — Geodiversitas 36: 349-383.

KREIPL, K., ALF, A. & KRONENBERG, G.C., 1999. A new subgenus of the family Xenophoridae Philippi, 1853. — Spixiana 22: 179-180.

KRIJNEN, C.J.M. & VINK, R. J., 2009. The operculum of the genus *Nerita*. — Gloria Maris 49: 27-56.

KRONENBERG, G.C. & BURGER, A.W., 2002. On the subdivision of Recent Tibia-like gastropoda (Gastropoda, Stromboidea), with the recognition of the family Rostellariidae Gabb, 1868, and a note on the type species of *Tibia* Röding, 1798. — Vita Malacologica 1: 39-48.

LANDAU, B., VERMEIJ, G.J. & REICH, S., 2014. Classification of the Modulidae (Caenogastropoda, Cerithioidea), with new genera and new fossil species from the Neogene of tropical America and Indonesia. — Basteria 78: 1-29.

LIEW, T.-S. & SCHILTHUIZEN, M., 2014. Association between shell morphology of micro-land snails (genus *Plectotstoma*) and their predators' predatory behaviour. — PeerJ 2: e329.

LINDBERG, D.R. & DOBBERTEEN, R.A., 1981. Umbilical brood protection and sexual dimorphism in the Boreal Pacific trochid gastropod, *Margarites vorticiferus* Dall. — International Journal of Invertebrate Reproduction 3: 347-355.

LINSLEY, R.M. & JAVIDPOUR, M.D., 1980. Episodic growth in Gastropoda. — Malacologia 20: 153-160.

LOVE-CHEZEM, T., AGGIO, J.F. & DERBY, C.D., 2013. Defense through sensory inactivation: sea hare ink reduces sensory and motor responses of spiny lobsters to food odors. — Journal of Experimental Biology 216: l364-l372.

LOZOUET, P. & RENARD, P., 1998. Les Coralliophilidae, Gastropoda de I'Oligocéne et du Miocéne Inferieur d'Aquitaine (sud-ouest de la France): systématique et coraux hôtes. — Geobios 31: 171-184.

LUZZATTO, D. & PASTORINO, G., 2006. *Adelomelon brasiliana* and *Antholoba achates*: a phoretic association between a volutid gastropod and a sea anemone in Argentine waters. — Bulletin of Marine Science 78: 281-286.

MACARTHUR, R.H., 1965. Patterns of species diversity. — Biological Reviews 40: 510-533.

MACIOLEK, J., 1978. Shell character and habitat of nonmarine Hawaiian neritid snails. — Micronesica 14: 209-214.

MÁNRIQUEZ, P.H., NAVARRETE, S.A., ROSSON, A. & CASTILLA, J.C., 2004. Settlement of the gastropod *Concholepas concholepas* on shells of conspecific adults. — Journal of the Marine Biological Association of the United Kingdom 84: 651-658.

MAPSTONE, B.D., UNDERWOOD, A.J. & CREESE, R.G., 1984. Experimental analyses of the commensal relation between intertidal gastropods *Patelloida mufria* and the trochid *Austrocochlea constricta*. — Marine Ecology Progress Series 17: 85-100.

MARINCOVICH, L. Jr., 1977. Cenozoic Naticidae (Mollusca: Gastropoda) of the northwestern Pacific. — Bulletins of American Paleontology 70: 169-494.

MCKILLUP, S.C. & MCKILLUP, R.B., 2002. Flies that attack polymorphic snails on coloured backgrounds: selection for crypsis by a sarcophagid parasitoid of *Littoraria filosa*. — Biological Journal of the Linnean Society 77: 367-377.

MCLEAN, J.H., 2012a. Detrital feeding in *Xeniostoma inexpectans*, a new genus, new species, and new subfamily Xeniostomatinae of Calliostomatidae (Gastropoda: Vetigastropoda), hosted by hexactinellid sponges of the Aleutian Islands, Alaska. — Nautilus 126: 89-97.

MCLEAN, J.H., 2012b. New species and genera of colloniids from Indo-Pacific coral reefs, with the definition of a new subfamily Liotipomatinae n. subfam. (Turbinoidea, Colloniidae). — Zoosystema 34: 343-376.

MCLEAN, J.H. & KIEL, S., 2007. Cretaceous and living Colloniidae of the redefined subfamily Petropomatinae, with two new genera and one new species, with notes on opercular evolution in turbinoideans, and the fossil record of Liotiidae (Vetigastropoda: Turbinoidea). — Paläontologische Zeitschrift 81: 254-266.

MERCIER, A. & HAMEL, J.-F., 2008. Nature and role of newly described symbiotic associations between a sea anemone and gastropods at bathyal depths in the NW Atlantic. — Journal of Experimental Marine Biology and Ecology 358: 57-69.

MEYER, W.M., GARY, D.T.A., YEUNG, N.W., DIRKS, C., LEUNG, K., LEON, J.A., RESSLER, D.T. B., CURRY, P.A. & HAYES, K.A., 2014. Native arboreal land snails in the Mt. Kaala Nature Area Reserve, Oahu, Hawaii, have similar plant preferences: implications for conservation. — Journal of Molluscan Studies 80: 469-472.

MILLER, J. A. & BYRNE, M., 2000. Ceratal autotomy and regeneration in the aeolid nudibranch *Phidiana crassicornis*. — Invertebrate Biology 119: 167-176.

MILOSLAVICH, P., CARBONINI, C.K., DIAZ, J.M. & ARDILA, N.E., 2005. Spawn of *Amphissa* sp. and *Cosmioconcha* sp. (Caenogastropoda: Columbellidae) from the Colombian Caribbean. — Nautilus 119: 157-163.

MORDAN, P.B., 1977. Factors affecting the distribution and abundance of *Aegopinella* and *Nesovitrea* (Pulmonata: Zonitidae) at Monks Wood National Nature Reserve, Huntingdonshire. — Biological Journal of the Linnean Society 9: 59-72.

MORTON, B., 1998. The occurrence of *Hipponix conicus* (Gastropoda: Hipponicidae) on intertidal Muricidae in Vietnam. — Journal of Molluscan Studies 64: 129-133.

NEUMANN, C., & WISSHAK, M., 2009. Gastropod parasitism on Late Cretaceous to Early Paleocene holasteroid echinoids – evidence from *Oichnus halo* isp. n. — Palaeogeography, Palaeoclimatology, Palaeoecology 284: 115-119.

NODA, H., 1991. Fossil homing scar of gastropod *Hipponix* (*Malluvium*) *lissus* from the Pliocene Shinzato Formation in Okinawa Prefecture, southwestern Japan. — Annual Report of the Institute of Geoscience, University of Tsukuba 17: 43-47.

NORDSIECK, H., 1982. Die Evolution des Verschluß-apparats der Schließmundschnecken (Gastropoda: Clausiliidae). — Archiv für Molluskenkunde 112: 27-43.

NORTON, S. F., 1988. Role of the gastropod shell and operculum in inhibiting predation by fishes. — Science 241: 92-94.

NUSNBAUM, M. & DERBY, M.D., 2010. Effects of sea hare ink secretion and its escapin-generated components on a variety of predatory fishes. — Biological Bulletin 218: 282-292.

NÜTZEL, A., 1998. Über die Stammesgeschichte der Ptenoglossa (Gastropoda). — Berliner Geowissenschaftliche Abhandlungen E 26: 1-229.

NYFFELER, M. & SYMONDSON, W.O.C., 2001. Spiders and harvestmen as gastropod predators. — Ecological Entomology 26: 617-628.

OKAJIMA, R. & CHIBA, S., 2011. How does life adapt to a gravitational environment? The outline of the terrestrial gastropod shell. — American Naturalist 178: 801-809.

OKAJ IMA, R. & CHIBA, S., 2013. Adaptation from restricted geometries: the shell inclination of terrestrial gastropods. — Evolution 67: 429-437.

OLIVERIO, M., BARCO, A., RICHTER, A. & MODICA, M.V., 2009. The Coralliophiline (Gastropoda: Muricidae) radiation: repeated colonization of the deep sea? — Nautilus 123: 113-120.

O'SULLIVAN, J.B., MCCONNAUGHEY, R.R. & HUBER, M.E., 1987. A blood-sucking snail: the Cooper's nutmeg, *Cancellaria cooperi* Gabb, parasitizes the California electric ray, *Torpedo californica* Ayres. — Biological Bulletin 172: 362-366.

PAINE, R.T., 1966. Function of labial spines, composition of diet, and size of certain marine gastropods. — Veliger 9: 17-24.

PAKARINEN, E., 1994. The importance of mucus as a defence against carabid beetles by the slugs *Arion fasciatus* and *Deroceras reticulatum*. — Journal of Molluscan Studies 60: 149-155.

PALMER, A.R., 1979. Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. — Evolution 33: 697-713.

PALMER, A.R., 1985. Adaptive value of shell variation in *Thais lamellosa*: effect of thick shells on vulnerability to and preference by crabs. — Veliger 27: 349-356.

PASTORINO, G., 1993. The association between the gastropod *Buccinanops cochlidium* (Dillwyn, 1817) and the sea anemone *Phlycteanthus australis* Carlgren, 1949 in Patagonian shallow waters. — Nautilus 106: 152-154.

PATEK, S.N. & CALDWELL, R.L., 2005. Extreme impact and cavitation forces of a biological hammer: strike forces of the peacock mantis shrimp *Odontodactylus scyllaris*. — Journal of Experimental Biology 208: 3655-3664.

PATEK, S.N., KORFF, W.L., & CALDWELL, R.L., 2004. Deadly strike mechanism of a mantis shrimp. — Nature 428: 819.

PEDRIALI, L. & ROBBA, E., 2008. A revision of the Pliocene naticids of northern and central Italy. I. The subfamily Naticinae except *Tectonatica*. — Rivista Italiana di Paleontologia e Stratigrafia 111: 109-179.

PERRY, D.M., 1985. Function of the shell spine in the predaceous rocky intertidal snail *Acanthina spirata* (Prosobranchia: Muricacea). — Marine Biology 88: 51-58.

PREECE, R.C., & WHITE, D., 2008. Incidence and persistence of reversed-coiling in Quaternary land snails. — Basteria 72: 267-279.

QUENSEN, J.F. & WOODRUFF, D.S., 1997. Associations between shell morphology and land crab predation in the land snail *Cerion*. — Functional Ecology 11: 474-479.

RASSER, M.W. & COVICH, A.P., 2014. Predation on freshwater snails in Miocene Lake Steinheim: a trigger for intralacustrine Evolution? — Lethaia 47: 524-532.

REAKA, M.L., 1978. The effect of an ectoparasitic gastropod, *Caledoniella montrouzieri*, upon molting and reproduction of a stomatopod crustacean, *Gonodactylus viridis*. — Veliger 21: 251-254.

REICHARDT, A., RABOUD, C., BURLA, H. & BAUR, B., 1985. Causes of death and possible regulatory processes in *Arianta arbustorum* (L., 1758) (Pulmonata, Helicidae). — Basteria 49: 36-46.

REID, D.G., 1992. Predation by crabs on *Littoraria* species (Littorinidae) in a Queensland mangrove forest. — Proceedings of the Third International Symposium on Littorinid Biology: 141-151.

REID, D.G. & GELLER, J.B., 1997. A new ovoviviparous species of *Tectarius* (Gastropoda: Littorinidae) from Niue, South Pacific, with a molecular phylogeny of the genus. — Journal of Molluscan Studies 63: 207-233.

REID, D.G., ARAVIND, R.A. & MADHYASTHA, N.A., 2013. A unique radiation of marine littorinid snails in the freshwater streams of the western Ghats of India: the genus *Cremnoconchus* W. T. Blanford, 1869 (Gastropoda: Littorinidae). — Zoological Journal of the Linnean Society 167: 93-135.

REIJNEN, B.T., HOEKSEMA, B.W. & GITTENBERGER, E., 2010. Host specificity and phylogenetic relationships among Atlantic Ovulidae (Mollusca: Gastropoda). — Contributions to Zoology 79: 69-78.

REIMCHEN, T.E., 1979. Substratum heterogeneity, crypsis, and colour polymorphism in an intertidal snail (*Littorina mariae*). — Canadian Journal of Zoology 57: 1070-1085.

RINTELEN, T. VON, WILSON, A.B., MEYER, A. & GLAUBRECHT, M., 2004. Escalation and trophic specialization drive adaptive radiation of freshwater gastropods in ancient lakes on Sulawesi, Indonesia. — Proceedings of the Royal Society B 271: 2541-2549.

ROBERTSON, R., 1970. Review of the predators and parasites of stony corals, with special reference to symbiotic prosobranch gastropods. — Pacific Science 24: 43-54.

ROHR, D.M., 1991. Borings in the shell of an Ordovician (Whiterockian) gastropod. — Journal of Paleontology 65: 687-688.

ROHR, D.M. & BOUCOT, A.J., 1985. Observations on the operculum of *Oriostoma* (Silurian Gastropoda). — Canadian Journal of Earth Sciences 22: 294-296.

ROHR, D.M. & GUBANOV, A.P., 1997. Macluritid opercula (Gastropoda) from the Middle Ordovician of Siberia and Alaska. — Journal of Paleontology 71: 394-400.

ROHR, D.M. & PACKARD, J.J., 1982. Spine-bearing gastropods from the Silurian of Canada. — Journal of Paleontology 56: 324-334.

ROHR, D.M. & YOCHELSON, E.L., 1999. Life association of shell and operculum of Middle Ordovician gastropod *Maclurites*. — Journal of Paleontology 73: 1078-1080.

ROSIN, Z.M., KOBAK, T., LESICKI, A. & TRYJANOWSKI, P., 2013. Differential shell strength of *Cepaea nemoralis* colour polymorphs – implications for their antipredatory defence. — Naturwissenschaften 100: 843-851.

RUPERT, S.D. & PETERS, W.S., 2011. Autotomy of the posterior foot of *Agaronia* (Caenogastropoda: Olividae) occurs in animals that are fully withdrawn into their shells.

— Journal of Molluscan Studies 77: 437-440.

RUST, J., 1997. Evolution, Systematik, Paläoökologie und stratigraphischer Nutzen Neogener Süß- und Brackwasser-Gastropoden in Nord-Ägäis-Raum. — Palaeontographica Abt. A 243: 37-189.

SAVAZZI, E., 1989. Burrowing mechanisms and sculptures in Recent gastropods. — Lethaia 22: 31-47.

SAVAZZI, E., 1998. The colour patterns of cypraeid cowries. — Lethaia 31: 15-27.

SAVAZZI, E. & PAN, H., 1994. Experiments on the frictional properties of terrace sculptures. — Lethaia 27: 325-336.

SAVAZZI, E. & SASAKI, T., 2013. Observations on land-snail shells in near-ultraviolet, visible and near-infrared radiation. — Journal of Molluscan Studies 79: 95-111.

SCHEJTER, L., ESCOLAR, M. & BREMEC, C., 2011. Variability in epibiont colonization of shells of *Fusitriton magellanicus* (Gastropoda) on the Argentinian shelf. — Journal of the Marine Biological Association of the United Kingdom 91: 897-906.

SCHIAPARELLI, S., OLIVERO, M., TAVIANI, M., GRIFFITHS, H., LORZ, A.-N. & ALBERTELLI, G., 2008. Circumpolar distribution of the pycnogonid-ectoparasitic gastropod *Dickdellia labioflecta* (Dell, 1990) (Mollusca: Zerotulidae). — Antarctic Science 20: 497-498.

SCHILTHUIZEN, M., VAN TIL, A., SALVERDA, M., LIEW, T.-S., JAMES, S.S., BIN ELAHAN, B. & VERMEULEN, J.J., 2006. Microgeographic evolution of snail shell shape and predator behavior. — Evolution 60: 1851-1858.

SCHILTHUIZEN, M., CRAZE, P.G., CABANBAN, A.S., DAVISON, A., STONE, J., GITTENBERGER, E. & SCOTT, B.J., 2007. Sexual selection maintains whole-body chiral polymorphism in snails. — Journal of Evolutionary Biology 20: 1941-1949.

SHIGEMIYA, Y., 2003. Does the handedness of the pebble crab *Eriphia smithii* influence its attack success on two dextral snail species? — Journal of Zoology 269: 259-265.

SIGNOR, P.W. III, 1982a. Constructional morphology of gastropod ratchet sculpture. — Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 163: 349-368.

SIGNOR, P.W., 1982b. Resolution of life habits using multiple morphologic criteria: shell form and life-mode in turritelliform gastropods. — Paleobiology 8: 378-388.

SIGNOR, P.W. III, 1982c. Influence of shell shape on burrowing rates in turritelliform snails. — Third North American Paleontological Convention Proceedings 2: 483-487.

SIGNOR, P.W. III, 1983. Burrowing and the functional significance of ratchet sculpture in turritelliform gastropods. — Malacologia 23: 313-320.

SIGNOR, P.W. III, 1985. The role of shell geometry as a deterrent to predation in terebrid gastropods. — Veliger 28: 179-185.

SIRENKO, B.I., 2000. Symbiosis of an Antarctic gastropod and pantopod. — Ruthenica 10: 159-162.

SKOVSTED, C.B., BROCK, G.A., LINDSTRÖM, A., PEEL, J.S., PATERSON, J.R. & FULLER, M.K., 2007. Early Cambrian record of failed durophagy and shell repair in an epibenthic mollusc. — Biology Letters 3: 314-317.

SMITH, T.B. & TEMPLE, S.A., 1982. Feeding habits and bill polymorphism in hook-billed kites. — Auk 99: 197-207.

SMYTH, M.J., 1990. Incidence of boring organisms in gastropod shells on reefs around Guam. — Bulletin of Marine Science 46: 432-449.

SNYDER, N.F.R. & KALE, H.W., 1983. Mollusk predation by snail kites in Colombia. — Auk 100: 93-97.

SNYDER, N.F.R. & SNYDER, H.A., 1969. A comparative study of mollusc predation by limpkins, Everglade kites, and boat-tailed grackles. — The Living Bird 8: 177-223.

SOLEM, A., 1972. Microarmature and barriers in the aperture of land snails. — Veliger 15: 81-87.

SOLEM, A., TILLIER, S. & MORDAN, P., 1984. Pseudo-operculate pulmonate land snails from New Caledonia. — Veliger 27: 193-199.

STASEK, C.R., 1967. Autotomy in the Mollusca. — Occasional Papers of the California Academy of Sciences 61: 1-44.

STIMSON, J., 1970. Territorial behavior of the owl limpet, *Lottia gigantea*. — Ecology 51: 113-118.

STIMSON, J., 1973. The role of the territory in the ecology of the intertidal limpet *Lottia gigantea* (Gray). — Ecology 54: 1020-1030.

STWORZEWICZ, E., SZULC, J. & POKRYSZKO, B.M., 2009. Late Paleozoic continental gastropods from Poland: systematics, evolutionary and paleoecological approach. — Journal of Paleontology 83: 938-945.

TAKANO, T. & KANO, Y., 2014. Molecular phylogenetic investigations of the relationships of the echinoderm-parasite family Eulimidae within Hypsogastropoda (Mollusca). — Molecular Phylogenetics and Evolution 79: 258-269.

TAYLOR, D.W., 1966a. Summary of North American Blancan nonmarine mollusks. — Malacologia 4: 1-172.

TAYLOR, D.W., 1966b. A remarkable snail fauna from Coahuila, Mexico. — Veliger 9: 152-228.

TAYLOR, J.D. & MORTON, B., 1996. The diets of predatory gastropods in the Cape D'Aguilar Marine Reserve, Hong Kong. — Asian Marine Biology 13: 141-166.

TODD, J.A. & HARPER, E.A., 2011. Stereotypic boring behaviour inferred from the earliest known octopod feeding traces: Early Eocene, southern England. — Lethaia 44: 214-222.

TSENG, R. & DAYRAT, B., 2014. Anatomical redescription of the limpet-like marine pulmonate *Trimusculus reticulatus* (Sowerby, 1835). — Veliger 51: 194-207.

TUCKER, J.K. & MCLEAN, J.H., 1993. The rediscovery, morphology, and identity of *Conus emersoni* Hanna, 1963. — Nautilus 107: 29-32.

VAN MOL, J.J., 1978. Étude de la morphologie et des affinités systématiques de *Aillya camerunensis* Odhner (gastéropodes: pulmonés, Aillyidae). — Revue de Zoologie Africaine 92: 1003-1021.

VAN OSSELAER, C., BOUILLON, R. OUIN, J.M. & TURSCH, B., 2004. Studies on Olividae. XVIII. The distribution of *Oliva* species and the variation of their colour patterns in Hansa Bay (Papua New Guinea). — Apex 9: 29-46.

VERMEIJ, G.J., 1969. Observations on the shells of some fresh-water neritid gastropods from Hawaii and Guam. — Micronesica 5: 155-162.

VERMEIJ, G.J., 1973. West Indian molluscan communities in the rocky intertidal zone: a morphological approach. — Bulletin of Marine Science 23: 351-386.

VERMEIJ, G.J., 1975. Evolution and distribution of left-handed and planispiral coiling in snails. — Nature 254: 419-420.

VERMEIJ, G.J., 1982. Unsuccessful predation and evolution. — American Naturalist 120: 701-720.

VERMEIJ, G.J., 1987. Evolution and escalation: an ecological history of Life. Princeton University Press, Princeton.

VERMEIJ, G.J., 1989a. Habitat and form of *Crepidula grandis* in Japan, with comments on habitat specialization in calyptraeid gastropods. — Nautilus 103: 89-91.

VERMEIJ, G.J., 1989b. Interoceanic differences in adaptation: effects of history and productivity. — Marine Ecology Progress Series 57: 293-305.

VERMEIJ, G.J., 1992. Time of origin and biogeographical history of specialized relationships between northern marine plants and herbivorous molluscs. — Evolution 46: 657-664.

VERMEIJ, G.J., 1993. A natural history of shells. Princeton Univerity Press, Princeton.

VERMEIJ, G.J., 1998. *Sabia* on shells: a specialized Pacific-type commensalism in the Caribbean Neogene. — Journal of Paleontology 72: 465-472.

VERMEIJ, G.J., 2001. Innovation and evolution at the edge: origins and fates of gastropods with a labral tooth. — Biological Journal of the Linnean Society 72: 461-508.

VERMEIJ, G.J., 2002. The geography of evolutionary opportunity: hypothesis and two cases in gastropods. — Integrative and Comparative Biology 42: 935-940.

VERMEIJ, G.J., 2004. Nature: an economic history. Princeton University Press, Princeton.

VERMEIJ, G.J., 2005a. Shells inside out: the architecture, evolution and function of shell envelopment in molluscs. — [In] Evolving form and function: fossils and development, ed. BRIGGS, D. E. G., Pp. 197-221. Peabody Museum of Natural History, Yale University, New Haven.

VERMEIJ, G.J., 2005b. Invasion and evolution: why do herbivorous and carnivorous snails invade but do not originate on islands? — American Malacological Bulletin 20: 143-146.

VERMEIJ, G.J., 2007. The ecology of invasion: acquisition and loss of the siphonal canal in gastropods. — Paleobiology 33: 469-493.

VERMEIJ, G.J., 2011. Shifting sources of productivity in the coastal marine tropics during the Cenozoic era. — Proceedings of the Royal Society B 278: 2362-2368.

VERMEIJ, G.J., 2012a. The limits of adaptation: humans and the predator-prey arms race. — Evolution 66: 2007-2014.

VERMEIJ, G.J., 2014a. The oyster enigma variations: a hypothesis of microbial calcification. — Paleobiology 40: 1-13.

VERMEIJ, G.J., 2014b. Molluscan marginalia: serration at the lip edge in gastropods. — Journal of Molluscan Studies 80: 326-336.

VERMEIJ, G.J. & COVICH, A.P., 1978. Coevolution of freshwater gastropods and their predators. — American Naturalist 112: 833-843.

VERMEIJ, G.J. & FREY, M.A., 2008. Almost terrestrial: small supratidal species of *Nerita* (Gastropoda, Neritidae) in the western Pacific. — Basteria 72: 253-261.

VERMEIJ, G.J. & GROSBERG, R.K., 2010. The great divergence: when did diversity on land exceed that in the sea? — Integrative and Comparative Biology 50: 675-682.

VERMEIJ, G.J. & SIGNOR, P.W. III, 1992. The geographic, taxonomic and temporal distribution of determinate growth in marine gastropods. — Biological Journal of the Linnean Society 47: 233-247.

VERMEIJ, G.J. & WILLIAMS, S.T., 2007. Predation and the geography of opercular thickness in turbinid gastropods. — Journal of Molluscan Studies 73: 67-73.

VERMEIJ, G.J. & ZIPSER, E., 1986a. A short-term study of growth and death in a population of the gastropod *Strombus gibberulus* in Guam. — Veliger 28: 314-317.

VERMEIJ, G.J. & ZIPSER, E., 1986b. Burrowing performance of some tropical Pacific gastropods. — Veliger 29: 200-206.

VERMEIJ, G.J. & ZIPSER, E., 2015. The diet of *Diodon hystrix* (Teleostei: Tetraodontiformes): shell-crushing on Guam's reefs. — Bishop Museum Bulletin in Zoology 9: 169-175.

VERMEIJ, G.J., SCHINDEL, D.E. & ZIPSER, E., 1981. Predation through geological time: evidence from gastropod shell repair. — Science 214: 1024-1026.

VERMEIJ, G.J., LOWELL, R.B., WALTERS, L.J. & MARKS, J.A., 1987. Good hosts and their guests: relations between trochid gastropods and the epizoic limpet *Crepidula adunca*. — Nautilus 101: 69-74.

WARÉN, A., 1984. A generic revision of the family Eulimidae (Gastropoda, Prosobranchia). — Journal of Molluscan Studies, Supplement 13: 1-96.

WARÉN, A., 1992. New and little-known “skeneimorph” gastropods from the Mediterranean Sea and the adjacent Atlantic Ocean. — Bollettino Malacologico 27: 149-248.

WARÉN, A. & GOFAS, S., 1996. *Kaiparapelta askewi* McLean & Harasewych, 1995 (Gastropoda: Pseudococculinidae): a spongivorous cocculiniform limpet and a case of remarkable convergence in radular morphology. — Haliotis 25: 107-116.

WARREN, S., 1916. The feeding habits of *Busycon*. — Nautilus 30: 66-68.

WEAVER, J.C., MILLIRON, G.W., MISEREZ, A., EVANS-LUTTERODT, K., HERRERA, S., GALLANA, I., MERSHON, W.J., SWANSON, B., ZAVATTIERI, P., DIMASI, E. & KISAILUS, D., 2012. The stomatopod dactyl club: a formidable damage-tolerant biological hammer. — Science 336: 1275-1280.

WEBSTER, N.B., VAN DOOREN, T.J.M. & SCHILTHUIZEN, M., 2012. Phylogenetic reconstruction and shell evolution of the Diplommatinidae (Gastropoda:

Caenogastropoda). — Molecular Phylogenetics and Evolution 63: 625-638.

WELLS, H.W., 1958. Feeding habits of *Murex fulvescens*. — Ecology 39: 556-558.

WELLS, H.W., 1969. Hydroid and sponge commensals of *Cantharus cancellarius* with a “false shell.” — Nautilus 82: 93-102.

WESSELINGH, F.P. & GITTENBERGER, E., 1999. The giant Amazonian snail (Pulmonata: Acavidae) beats them all. — Veliger 42: 67-71.

WEST, K. & COHEN, A., 1996. Shell microstructure of gastropods from Lake Tanganyika, Africa: adaptation, convergent evolution, and escalation. — Evolution 50: 672-681.

WEST, K., COHEN, A. & BARON, M., 1991. Morphology and behavior of crabs and gastropods from Lake Tanganyika, Africa: implications for lacustrine predator-prey coevolution. — Evolution 45: 589-606.

WHITENACK, L.B. & HERBERT, G.S., 2015. Did shell-crushing crabs trigger an escalatory arms race in the aftermath of a Late Neogene regional mass extinction event? — Palaeogeography, Palaeoclimatology, Palaeoecology 417: 57-65.

WILLIAMS, J.D. & MCDERMOTT, J.D., 2004. Hermit crab biocoenoses: a worldwide review of the diversity and natural history of hermit crab associations. — Journal of Experimental Marine Biology and Ecology 305: 1-128.

WILLIAMS, S.T., 2008. The calcareous operculum as a character defining subgenera in the marine gastropod genus *Turbo*. — Vita Malacologica 7: 1-13.

WILLIAMS, S.T. & OZAWA, T., 2006. Molecular phylogeny suggests polyphyly for both the turban shells (family Turbinidae) and the superfamily Trochoidea (Mollusca: Vetigastropoda). — Molecular Phylogenetics and Evolution 39: 33-51.

WISE, S. W. Jr., 1970. Microarchitecture and deposition of gastropod nacre. — Science 167: 1486-1487.

WOOD, J.B., MAYNARD, A.E., LAWLOR, A.G., SAWYER, E.K., SIMMONS, D.M., PENNOYER, K.E. & DERBY, C.D., 2010. Caribbean reef squid, *Semioteuthis sepioidea*, use ink as a defense against predatory French grunts, *Haemulon flavolineatum*. — Journal of Experimental Marine Biology and Ecology 388: 20-27.

YANES, Y., MARTÍN, J., DELGADO, J.D., ALONSO, M. R. & IBÁÑEZ, M., 2010. Active disguise in land snails: *Napius badiosus* (Gastropoda, Pulmonata, Enidae) from the Canary Islands. — Journal of Conchology 40: 143-148.

YOCHELSON, E.L., 1979. Gastropod opercula as objects of paleobiogeographic study. — [In] Plate tectonics, historical biogeography, and the changing environment, ed. GRAY, J. & BOUCOT, A.J., Pp. 37-43. Oregon State University Press, Corvallis.

ZABALA, S., BIGATTI, G., BOTTO, F., IRIBARNE, O.O. & GALVÁN, D.E., 2013. Trophic relationships between a Patagonian gastropod and its epibiotic anemone revealed by using stable isotopes and direct observations. — Marine Biology 160: 909-919.

ZHANG, Z.F., HOLMER, L.E., ROBSON, S.P., HU, S.X., WANG, X.R. & WANG, H.Z., 2011. First record of repaired durophagous shell damages in Early Cambrian lingulate brachiopods with preserved pedicles. — Palaeogeography, Palaeoclimatology, Palaeoecology 302: 206-212.

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