



# Evolutionary norm-breaking and extinction in the marine tropics

Geerat J. Vermeij<sup>a,1</sup>

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Evolutionary innovations, defined as character states that transcend clade norms, are often studied in an exclusively phylogenetic context, but their distribution in time and space indicates that geography also influences the evolution of new ecological, morphological, and physiological traits. In an analysis of 99 fossilizable, norm-breaking innovations in tropical marine Neogene molluscan clades that arose uniquely in either (but not in both) the Indo-West Pacific (IWP) or Atlantic-East Pacific (AEP) realms, I show that there are far more innovations in the IWP (79%) than those in the AEP (21%). Most of the innovations are interpretable as defensive or competitive adaptations or as indicators of extreme habitat specialization. Although the innovations arose in taxonomically rich biotas, only 9% are associated with subclades comprising 10 or more species each, indicating that they contributed little to overall taxonomic richness. Compilations of extant species in 30 pantropical molluscan clades show that the IWP accounts for 71% of tropical shallow-water species, implying that the per-species incidence of norm-breaking innovations is higher there than in the AEP. Only 5% of innovations became extinct in the IWP as compared with 38% in the AEP, mirroring a similar difference in the magnitudes of Late Miocene and later taxonomic extinction in the two realms. These data imply that large-scale disruption strongly limits norm-breaking innovation. Opportunities for adaptive innovation are therefore likely to be few in today's heavily overexploited and disturbed biosphere.

innovation | biogeography | extinction | mollusca

An important question in evolutionary biology is under which ecological circumstances potentially adaptive innovations arise. Such innovations might include ecological expansions, morphological breakthroughs, and new physiological states. Typically, they have been explored in a primarily phylogenetic context in order to determine when and in which clades they evolve. Important as these approaches are, the ecological context in which the evolution of novel traits takes place also matters. Here, I explore the aspects of this context by documenting the geographic distributions and fates of fossilizable innovations in the tropical shallow oceans over the last 23 My, from the Miocene to the present day, and comparing these to the pattern of diversity and extinction in the tropical marine biota.

The extant shallow-water marine biota comprises two great geographic realms, the Indo-West Pacific (IWP), extending from the Red Sea and East Africa to eastern Polynesia and from southern Japan to northern Australia; and the Atlantic-East Pacific (AEP), including West Africa from Senegal to Angola, the western Atlantic from North Carolina and the Gulf of Mexico to southern Brazil, and the eastern Pacific from northern Mexico to northern Peru (1). Although these realms are each subdivided into geographic provinces, they underwent contrasting histories following their definitive separation during the Early to Middle Miocene (20 to 13.8 Ma) by the stepwise closure of the Mesopotamian Seaway (2). The IWP witnessed extensive lineage diversification beginning in the Late Miocene and suffered relatively little extinction, whereas the AEP experienced high rates of diversification followed by high magnitudes of Pliocene and Pleistocene extinction (1, 3).

Contrasts in diversity are not the only ways in which the IWP and AEP realms differ. Preliminary findings indicated that the incidence of traits representing realm-specific departures from clade norms is greater among IWP molluscs than that in the AEP. Of the 66 innovations that evolved during the Neogene in only one (but not in both) of the two realms in pantropical clades, 53 arose in the IWP and 13 did so in the AEP (1). The difference in the incidence of outlier traits exceeded the difference in realm-wide species diversity, implying that species richness and its history account for only part of the difference in evolutionary trajectory between the IWP and AEP (1).

Here, I substantially expand data on morphological outliers in IWP and AEP shell-bearing molluscs to confirm that innovations are disproportionately frequent in the IWP. Moreover, I suggest that the greater evolutionary conservatism in the AEP fauna is in part the consequence of the higher magnitude of extinction there. The evidence also has bearing

## Significance

How and under which circumstances evolutionary novelties arise is an important question, especially in the light of diminishing adaptive opportunities in the human-dominated biosphere. In an analysis of norm-breaking innovations in shell form in tropical shallow-water marine molluscs of the last 23 My, I show that high magnitudes of species extinction in the Atlantic-East Pacific realm accompanied a much lower incidence of innovations than that in the Indo-West Pacific realm, where few extinctions occurred. These data imply that large-scale ecological disruption is inimical to evolutionary innovation and that adaptive responses to changing circumstances are constrained when that change is too fast or too large on a geographic scale.

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<sup>1</sup>Email: gvermeij@ucdavis.edu.

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on how and when the IWP biota achieved its current status as the world's most competitive, biogeographically dominant marine evolutionary theater.

## Results

I identified 99 Neogene morphological states that represent unique, realm-specific departures from prevailing norms in tropical family- or subfamily-level molluscan clades (Tables 1–3). Compared with the earlier study (1), this work rejected 6 morphological and 12 ecological feeding- or habitat-related traits, the former because they are not unique to only one realm and the latter because they cannot be inferred from shell morphology. I therefore added 52 other character states.

Of the 99 morphological outliers, 78 (79%) are unique to the IWP and 21 (21%) are known only from the AEP. Twelve of the innovations belong to exclusively extinct lineages: four in the IWP and eight in the AEP. The ratio of AEP to total innovations (the innovation ratio) is therefore 0.21 for all innovations, but it drops to 0.15 when only innovations that are still extant are considered. These results are almost identical to the estimates in ref. 1.

All the 78 IWP innovations are embedded in exclusively IWP clades or subclades, but no fewer than 41 (53%) are known only in species for which a fossil record is unavailable (Tables 1 and 2). The 21 AEP innovations are likewise found in lineages with AEP origins, but only four of these (19%) are unknown in fossil representatives (Table 3). I attribute this difference to a much less adequately studied or preserved IWP fossil record. Most of the IWP innovations without a fossil record occur in geographically widely distributed lineages, particularly in taxa from the upper shore and reef environments where preservation in the IWP is spotty. They can therefore be expected to have existed for a considerable time during the Neogene.

Environments unlikely to be preserved in the fossil record host no fewer than 57 IWP innovations (73%) and 14 AEP innovations (66%). In the IWP, these environments include the upper seashore (9 innovations), hard reef-associated substrates (19 innovations), and habitats on or beneath the surface of shallow-water sand (29 innovations). For the AEP, 3 innovations are found in rock-dwelling lineages and 11 occur on or in sand. Except for the refugial upper shore, these environments host diverse predators and expose occupants to intense antipredatory selection.

Among the innovations that can be functionally interpreted, most confer defensive, locomotor, and predation-enhancing benefits. These include external spines, a shell enveloped by the mantle or foot, a closed siphonal canal, shell windows permitting transmission of light for photosymbionts, valve cementation, a lirate aperture, narrow aperture, rigid calcareous operculum, burrowing-enhancing ratchet sculpture, a broad ventral callus reflecting a large foot for locomotion, a strongly crenulated or toothed edge of the outer apertural lip, and a labral tooth enabling rapid subjugation of shell-bearing prey. These adaptive innovations account for at least 54 of the 78 IWP states (69%) and 16 of 21 AEP states (76%). At least seven of the IWP innovations are associated with life in refuges from predation, including intimate partnerships with corals and hermit crabs and specialization to the upper reaches of the intertidal zone. None of the AEP innovations belong to this category. Some traits, such as a decollate spire in gastropods, the absence of columellar folds in gastropod clades that typically have them, and imbricate sculpture, are difficult to interpret functionally given currently available evidence.

In the living fauna, most innovations are geographically limited to areas where diversity is high, but they have generally not contributed to that high taxonomic richness. Of the 43 IWP

innovations that are confined to only part of that large realm, 41 (95%) are or were limited to the most diverse provinces, that is, the western Indian Ocean and the Indo-Malayan region (or Coral Triangle) comprising coasts from southeast Asia to Indonesia, the Philippines, northern Australia, and Melanesia. Two innovations occur in single-species lineages endemic to oceanic islands (the southern Marianas and Marquesas). All extinct innovations are known only from Southeast Asia. Only one geographically restricted innovation occurs in a subclade (of Nassariinae) comprising more than ten extant species. By contrast, of the 35 innovations that occur in both continental and oceanic settings throughout the IWP, 8 (23%) characterize subclades with 10 or more species each, and none is extinct. In sum, innovation is associated with lineage diversification in only 9 of the 78 cases (11.5%). They are therefore not the so-called key innovations, that is, novel states that promote species formation.

At least seven lineages with innovations that evolved uniquely in the IWP have crossed the wide ocean barrier to the eastern Pacific, where they have often established viable populations. These include *Drupa albolabris*, *D. morum*, *Casmaria*, *Gibberulus*, *Mitra*, *Phyllocoma*, and *Streptopinna*. The strombid *Conomurex* is to my knowledge the only lineage with an IWP-unique innovation that has colonized the Mediterranean through the Suez Canal.

In the AEP, only 8 of the 21 innovations (38%) are or were distributed on both sides of the Central American Isthmus, but four of these have become restricted to the eastern Pacific side and one has become globally extinct. Of the remaining 13 innovations, 1 is known only from the eastern Atlantic, 1 is unique to the eastern Pacific, 7 are known only from the Caribbean region and Brazil (3 now extinct), 3 are known exclusively from the southeastern United States (all now extinct), and 1 (also extinct) occurred on both sides of the Atlantic. None of these innovations occurs in subclades of six or more species each. In short, regional or global extinction has affected a slight majority (12 of 21, 57%) of AEP innovations.

In an expanded survey of realm-wide extant species richness in 30 well-studied molluscan family- or subfamily-level clades (Table 4), the mean per-clade ratio of AEP to total tropical diversity (the diversity ratio) with SD is  $0.34 \pm 0.16$ , with a median of 0.33. The diversity ratio across all clades is 0.29. These ratios substantially exceed the innovation ratio of 0.21 for all innovations and 0.15 for extant innovations. Expressed alternatively, there is one innovation for every 38.8 species sampled in the IWP, but only one innovation per 57.6 species sampled in the AEP. The results of these analyses confirm and expand earlier work (1) showing that the per-species incidence of novel states is higher in the IWP than that in the AEP and that the higher magnitude of extinction of novelties in the AEP has magnified this difference.

This contrast between realms remains evident when gastropods and bivalves are treated separately. For gastropods, there are 13 AEP and 63 IWP innovations, giving an innovation ratio of 0.17. Of 21 innovations identified in bivalves, 7 evolved in the AEP and 14 did so in the IWP, giving an innovation ratio of 0.33. These ratios are well below the species ratios of 0.26 (gastropods) and 0.43 (bivalves). It is notable and unexplained that the innovation and diversity ratios are markedly higher for bivalves than those for gastropods.

## Discussion

The present work confirms and extends the conclusion that the IWP realm supports shell innovation, as defined by a departure from clade norms, more than the other great tropical realm, the AEP. Although the IWP is much richer in species than the AEP,

**Table 1. Unique molluscan innovations evolving in the Neogene IWP marine realm: Gastropoda**

Family (subfamily)	Taxon	Character	Range	Reference
Haliotidae	<i>Haliotis asinina</i> *	Mantle-enveloped shell	r	(1)
Neritidae	Some <i>Amphinerita</i> *	Mantle-enveloped spire	r	(1)
Neritidae	<i>Linnerita</i> and some <i>Cymostyla</i>	Polished adult outer lip	w	(1)
Cerithiidae s.l.	<i>Colina</i>	Decollate spire	r	(4)
Cerithiidae (Bittiinae)	<i>Limatium</i> *	Polished surface	r	(4)
Cerithiidae (Cerithiinae)	<i>Clypeomorus pellucida</i>	Dorsal varix	r	(5)
Cerithiidae (Cerithiinae)	<i>Cerithium</i>	Crenulated adult outer lip	mw	(6)
Cerithiidae	<i>Rhinoclavis</i> group	Terraced spiral sculpture	mw	(7)
Cerithiidae	<i>Longicerithium</i> *	Extended adapical channel	r	(7)
Potamididae	<i>Cerithidea</i>	Decollate spire	r	(8)
Potamididae	<i>Vicarya</i>	Expanded callus	er	(9)
Assimineidae	<i>Metassimineia</i> *	Calcareous operculum	r	(10)
Littorinidae	<i>Tectarius pagodus</i> group*	Lirate aperture	r	(6)
Littorinidae	<i>Tectarius viviparus</i> *	Calcareous operculum	r	(11)
Strombidae (Strombinae)	<i>Euprotomus bulla</i>	Mantle-enveloped spire	r	(1)
Strombidae (Strombinae)	<i>Conomurex</i>	Narrow parallel-sided aperture	w	(1)
Strombidae (Strombinae)	<i>Gibberulus</i>	Narrow parallel-sided aperture	w	(1)
Strombidae (Strombinae)	<i>Lambis</i> group	Laterally directed adult lip spines	mw	(1)
Strombidae (Strombinae)	<i>Tridentarius</i>	Anterior tooth-like lip serrations	w	(1)
Strombidae (Strombinae)	<i>Ministrombus</i> and <i>Tricornis</i>	Expanded callus	w	(9)
Ampullinidae	<i>Warakia</i>	Expanded callus	er	(9)
Naticidae	<i>Polinices mammilla</i> group	Expanded callus	w	(9)
Cassidae	<i>Phalium</i> and <i>Casmaria</i>	Spine-like lip serrations	mw	(1)
Bursidae	<i>Bursa</i> *	Extended adapical channel	w	(1)
Cymatiidae	<i>Gyrineum</i>	Dorsoventrally flattened shell	w	(1)
Ovulidae	<i>Crenavolva</i> *	Serrated lip	r	(6)
Colubrariidae	<i>Colubraria muricata</i> *	Expanded callus	r	(9)
Eosiphonidae	<i>Perangeria</i>	Labral tooth	r	(1)
Fascioliariidae (Fascioliariinae)	<i>Pleuroploca</i>	Keel-like entrance fold to siphonal canal	r	(1)
Fascioliariidae (Fusiniinae)	<i>Cyrtulus serotinus</i> *	Smooth barrel-shaped last whorl	r	(12)
Melongenidae	<i>Volegalea erecta</i>	Erect inner lip	er	(1)
Melongenidae	<i>Melongena murifactor</i> group	Apertural septum	er	(1)
Nassariidae	<i>Nassarius horridus</i> group	Labral tooth	r	(1)
Nassariidae	<i>Nassarius papillosus</i> group	Spine-like lip serrations	w	(6)
Nassariidae	<i>Nassarius coronatus</i> group	Spine-like lip serrations	w	(6)
Nassariidae	<i>Nassarius pullus</i> group	Dorsal varix	mr	(5)
Nassariidae	<i>Nassarius quadrasi</i> group*	Spiny sculpture	r	Herein
Nassariidae	<i>Nassarius granifer</i> group*	Mantle-enveloped spire	w	(13)
Nassariidae	many <i>Nassarius</i>	Terraced sculpture	mw	(7)
Muricidae (Coralliophilinae)	<i>Magilus</i>	Tubular last whorl	r	(1)
Muricidae (Ergalataxinae)	<i>Daphennopsis lamellosa</i>	Imbricate sculpture	r	Herein
Muricidae (Ergalataxinae)	<i>Muricodrupa</i> *	Labral tooth	w	(1)
Muricidae (Ergalataxinae)	<i>Lataxiena blosvillei</i>	Deep adapical apertural notch	r	Herein
Muricidae (Ergalataxinae)	<i>Phrygiomurex</i> *	Decollate spire	w	(8)
Muricidae (Rapaninae)	<i>Drupa morum</i> group*	Expanded callus	w	(9)
Muricidae (Rapaninae)	<i>Drupina</i> * and <i>Drupa ricinus</i> groups*	Adult lateral outer-lip spines	w	(14)
Muricidae (Rapaninae)	<i>Nassa</i> *	Polished convex adult lip	w	(14)
Vasidae	<i>Vasum rhinoceros</i> group	Expanded callus	r	(9)
Turbinellidae	<i>Syrinx</i> *	Absence of columellar folds	r	(1)

**Table 1.** (Continued)

Family (subfamily)	Taxon	Character	Range	Reference
Costellariidae	<i>Vexillum plicarium</i> group	Serrated lip	w	(6)
Costellariidae	<i>Ceratoxancus</i> *	Labral tooth	r	(1)
Mitridae	<i>Mitra</i> and <i>Quasimitra</i>	Spiny lip serrations	mw	(15)
Mitridae	<i>Mitra papalis</i> *	Adapically oriented shoulder spines	w	Herein
Mitridae	many species	Terraced spiral sculpture	mw	(7)
Olividae	<i>Carmione bulbosa</i> *	Ventral extension of inner-lip folds	r	(1)
Olividae	<i>Parvoliva</i> *	Decollate spire	r	(8)
Marginellidae	<i>Cryptospira</i>	Extension of inner lip fold	r	(1)
Conidae	<i>Conus</i> and <i>Puncticulus</i>	Serrated anterior outer lip	w	(6)
Conidae	<i>Elisaconus</i> *	Absence of anterior notch	w	(1)
Conidae	<i>Virroconus chaldaeus</i> *	Axial ribs	w	(1)
Conidae	<i>Gastrium</i> *	Broad aperture	w	Herein
Drillidae	<i>Clavus canalicularis</i> group*	Long shoulder spines	r	(16)
Terebridae	<i>Oxymeris crenulata</i> *	Shoulder tubercles	w	(17)
Ellobiidae	<i>Cassidula</i>	Ventral shield	r	(9)
Haminoeidae	<i>Smaragdinella</i> *	Limpet form	w	(18)

Key: globally extinct (e), multiple species, restricted distribution (mr), multiple species, widespread (mw), restricted distribution (r), widespread (w). Asterisks (\*) denote the taxon has no fossil occurrences.

the difference is not as dramatic as the difference in per-species frequency of innovation as documented here for shell-bearing molluscs. In other words, the likelihood of achieving a novel condition in a clade is not determined by standing diversity alone.

This pattern is part of a larger evolutionary contrast between the two present-day tropical marine realms. Compared with the AEP, the shallow-water IWP fauna shows higher frequencies and greater morphological specializations in molluscan antipredatory shell defense, aggressive resistance of shells to predators, sand-burrowing in molluscs, and life in or on specific well-defended hosts (7, 9, 35–37). Together with the findings on innovations, these adaptive contrasts between tropical biogeographic realms raise interesting questions about the causal relationships among diversity, innovation, specialization, and the status of biotas as sources of species that colonize other regions.

The norm-breaking innovations discussed here arose under conditions in which diversity was already high and increasing. By themselves, however, the new traits did little to stimulate diversification in either the IWP or AEP. In fact, high diversity is not necessary, and certainly not sufficient, as a factor favoring the origin and establishment of innovations, including adaptive ones. Early Miocene molluscan faunas in the tropical western Atlantic (Florida and Venezuela, about 600 and 700 species each, respectively) and the Late Oligocene and Early Miocene of southwestern Europe (then in the tropical eastern Atlantic part of the AEP with about 1,800 species; see ref. (38)), exceed in diversity all known Neogene faunas in East Africa, India, Indonesia, the Philippines, the insular Pacific, and tropical southwestern Japan; yet these AEP species-rich faunas spawned fewer shell-based molluscan innovations than the Neogene faunas of the IWP.

**Table 2. Unique molluscan innovations evolving in the Neogene IWP marine realm: Polyplacophora and Bivalvia**

Family (subfamily)	Taxon	Character	Range	Reference
Chitonidae	<i>Acanthopleura spinosa</i> *	Long girdle spines	r	(19)
Mytilidae	<i>Fungiacava</i> *	Mantle-enveloped shell	r	(20)
Mytilidae	<i>Modiolus auriculatus</i>	Twisted valves	w	Herein
Pectinidae	<i>Pedum</i> *	Strong valve overlap	w	Herein
Pinnidae	<i>Streptopinna</i> *	Twisted valves	w	(21)
Malleidae	<i>Malleus</i>	Greatly extended hinge	r	Herein
Lucinidae	<i>Rasta</i> *	Periostracal pipes	r	(1)
Galeommatidae	<i>Curvemysella</i> *	Strongly curved commissure	r	(22)
Cardiidae	<i>Corculum</i> * and some <i>Fragum</i> *	Shell windows	w	(1)
Cardiidae	<i>Chametrachea</i>	large byssal gape	mw	(23)
Veneridae	<i>Claudiconcha</i> *	Symmetrical cemented valves	r	(1)
Veneridae	<i>Smarangia</i> * and <i>Granocorium</i> *	Cement-like periostracum	r	(1)
Donacidae	<i>Hecuba</i> * and <i>Deltachion spiniferus</i> group*	Spiny keel	r	Herein
Donacidae	<i>Tridonax</i> *	Plicate shell	r	(23)
Solenidae	<i>Orbicularia</i>	Circular valve shape	r	(24)

For key, see Table 1.



**Table 3. Unique molluscan innovations evolving in the Neogene AEP marine realm**

Family (subfamily)	Taxon	Character	Range	Reference
Modulidae	<i>Psammmodulus</i>	Sand agglutinated	e	(1)
Turritellidae	<i>Springvaleia</i>	Sand agglutinated	e	(1)
Hipponicidae	<i>Rothpletzia</i>	Rudist-like shell	e	(25)
Cypraeidae	<i>Siphocypraea</i>	Spiral adapical channel	e	Herein
Ovulidae	<i>Jenneria</i>	Pustulose sculpture	r	Herein
Triviidae	some <i>Dolichopus</i> and <i>Pusula</i>	Expanded base	r	(9)
Columbellidae	<i>Dorsina</i>	Dorsal varix	r	(5)
Bulliidae	<i>Gordanops</i>	Extended adapical channel	e	Herein
Tomliniidae	<i>Trajana</i>	Closed siphonal canal	r	(1)
Fasciolaridae	<i>Liochlamys</i>	Mantle-enveloped shell	e	(1)
Olividae (Olivellidae)	<i>Dactylidia</i>	Lirate aperture	r	(1)
Volutidae	<i>Lyria gabbi</i> group	Spiny lip serrations	e	(26)
Marginellidae	some <i>Dentimargo</i> *	Labral tooth	r	(1)
Vasidae	<i>Siphovasum</i> *	Closed siphonal canal	r	(1)
Arcidae	<i>Caloosarca</i>	Imbricate sculpture	e	(27)
Arcidae	<i>Cunearca</i>	Anterior terraced concentric sculpture	w	(27)
Mytilidae	<i>Mytella</i> *	Concetric ridges	w	Herein
Lucinidae	<i>Lucina</i>	Long flexible periostracum	r	(28)
Cardiidae	<i>Cardium</i>	Hollow radial ribs	r	Herein
Veneridae	<i>Hysteroconcha lupanaria</i> group	Long posterior spines	w	Herein
Donacidae	<i>Assimilidonax</i> *	Posterior valve overlap	r	(29)

For key, see Table 1.

The IWP realm, and especially the Coral Triangle part of it, has long been recognized as a marine diversity hot spot in the extant biota (3, 39–43). A hot spot is defined as a region where diversity peaks relative to the surrounding regions as the result of species accumulation. What sets the modern IWP apart from the secondary tropical diversity hot spot in marine tropical America is that many of its lineages have colonized other tropical and warm-temperate regions (39, 40, 44). Lineages in the AEP have expanded from one province to another but have not colonized realms outside the AEP. The status of the IWP as the dominant tropical biota was achieved in part by a tenfold increase in shallow-water carbonate habitats suitable for reef development beginning in the Late Oligocene (45–47). Even as late as the Middle Miocene, however, the local diversity of molluscs and bryozoans in the Coral Triangle remained far below than that in the tropical western Atlantic (3).

It is possible that this deficit, and other aspects of the differences between the IWP and AEP realms, represents biases in the preservation of and knowledge about the fossil record. Highly diverse molluscan clades on rocky bottoms are largely absent from Neogene assemblages in the IWP, whereas in the AEP, they occur as fossils in Venezuela, the Dominican Republic, and southeastern Florida. The nearly complete absence of Late Neogene fossils in West Africa and the relative scarcity of deposits from the eastern Pacific compared with those in the western Atlantic could suppress the number of AEP innovations, although the eastern Atlantic record in southern Spain, where many clades that are currently confined to West Africa are known as Pliocene fossils, compensates for this deficit.

Regardless, the IWP biota changed to a donor biota in the Neogene from a recipient biogeographic entity during the Paleogene, when it received many of its founding Oligocene and Early Miocene lineages from the West (48–52). The definition of a diversity hot spot may have to be modified as a biota

or region that contains species capable of colonizing other biotas.

The IWP also differs from the AEP by much lower magnitudes of extinction (3). Analyses in progress indicate that at least four times as many subgenus-level molluscan lineages became globally extinct in the AEP (mainly in the eastern and western Atlantic) than that in the IWP. Within the AEP, moreover, hundreds of additional lineages became regionally extinct in the Atlantic and survived either in the eastern Pacific or the IWP (38, 53). Data on corals likewise demonstrate very low levels of extinction during the Pliocene in the IWP and very high magnitudes in the western Atlantic (54, 55). These patterns of taxonomic extinction are mirrored by the loss of Neogene realm-specific molluscan innovations. Like the extinction of taxa, the loss of innovations was greatest in the tropical Atlantic, less in the eastern Pacific, and least in the IWP.

These results indicate that the per-taxon incidence of realm-specific innovation is higher when widespread disturbance, as chronicled by extinction, is less severe. A similar pattern was documented for temperate Neogene marine faunas, where innovation was most frequent and extinction least frequent in the North Pacific compared with other regions in the North Atlantic and southern hemisphere (56, 57). Disruption and extinction appear to be inimical to the evolution and retention of novel morphological and ecological states.

**Conclusions**

The breaking or relaxation of clade norms has a strong geographic component throughout the marine biosphere. Norms are most likely to be breached in biotas that have witnessed a low incidence of widespread disruption, as indicated by extinction. It is only loosely tied to taxonomic richness. During the Neogene, an interval without global mass extinction, the most important disruptions

**Table 4. Estimates of extant species richness in the AEP and IWP marine realms**

Clade	Number of species		Species ratio	Reference
	AEP	IWP		
Haliotidae	7	23	0.23	(30)
Turbininae	20	86	0.19	(1)
Nertinae	12	65	0.15	(31)
Littorinidae	47	71	0.39	(1)
Cerithiinae	26	78	0.25	Herein
Planaxidae	7	12	0.37	Herein
Modulidae	12	2	0.86	(32)
Strombidae	12	110	0.1	Herein
Sininae	16	33	0.33	(1)
Cypraeidae	33	256	0.11	(1)
Cassidae	21	29	0.42	(1)
Bursidae	14	29	0.33	(1)
Melongenidae	10	20	0.33	Herein
Nassariinae	75	242	0.24	Herein
Fascioliariinae-Peristerniinae	71	110	0.39	Herein
Pisaniidae-Prodotiidae	76	94	0.45	Herein
Personidae	8	9	0.44	(1)
Rapaninae	32	62	0.34	(14)
Harpidae	13	19	0.41	Herein
Dolicholatiridae	5	15	0.15	Herein
Vasidae-Turbinellidae	10	23	0.3	Herein
Conidae	202	560	0.22	(33)
Terebridae	93	320	0.21	(17)
Mitridae	68	315	0.17	(15)
Bullidae	8	6	0.57	(1)
Arcidae	66	94	0.41	Herein
Cardiidae	54	139	0.28	Herein
Donacidae	36	35	0.51	Herein
Tellinidae	137	117	0.54	(34)
Solenidae	23	45	0.34	Herein
Total	1,212	3,027	0.29	

1. G. J. Vermeij, Crucibles of creativity: The geographical origins of tropical molluscan innovations. *Evol. Ecol.* **26**, 357–373 (2012).

2. O. M. Bialik, M. Frank, C. Betzler, R. Zammit, N. E. Waldmann, Two-step closure of the Miocene Indian Ocean gateway to the Mediterranean. *Sci. Rep.* **9**, 8842 (2019).

3. E. Di Martino, J. B. C. Jackson, P. D. Taylor, K. G. Johnson, Differences in extinction rates drove modern biogeographic patterns of tropical marine biodiversity. *Sci. Adv.* **4**, aaq1508 (2018).

4. E. E. Strong, P. Bouchet, A rare and unusual new bittine genus with two new species from the South Pacific (Cerithiidae, Gastropoda). *Zookeys* **758**, 1–18 (2018).

5. N. B. Webster, G. J. Vermeij, The varix: Evolution, distribution, and phylogenetic clumping of a repeated gastropod innovation. *Zool. J. Linn. Soc.* **180**, 732–754 (2017).

6. G. J. Vermeij, Molluscan marginalia: Serration at the lip edge in gastropods. *J. Molluscan Stud.* **80**, 326–336 (2014).

7. G. J. Vermeij, Shell features associated with the sand-burrowing habit in gastropods. *J. Molluscan Stud.* **83**, 153–160 (2017).

8. G. J. Vermeij, Overcoming the constraints of spiral growth: The case of shell remodelling. *Palaeontology* **63**, 1035–1047 (2020).

9. G. J. Vermeij, The balanced life: Evolution of ventral shell weighting in gastropods. *Zool. J. Linn. Soc.* **194**, 256–275 (2022).

10. H. Fukuda, W. F. Ponder, Australian freshwater assimineids, with a synopsis of the recent genus-group taxa of the Assimineidae (Mollusca: Caenogastropoda: Rissooidea). *J. Nat. Hist.* **37**, 1977–2032 (2003).

were likely large-scale reductions in either or both benthic and planktic primary productivity, as occurred in large parts of the western Atlantic following the shoaling and emergence of the Central American Isthmus (58); and major decreases in the extent of shallow-water habitats, as occurred with climatic cooling in the Late Pliocene and Pleistocene in the eastern Atlantic and Mediterranean (53). These conclusions are relevant in the light of rapid warming, global overexploitation and extinction of species in the wild, and the continuing effects on productivity caused by these factors (59).

**Methods**

Traits taken under consideration as realm-specific departures from molluscan clade norms were first identified by inspection of the shells of thousands of fossil and extant shell-bearing shallow-water species in museums and my collection. Many of these were documented in previous studies, but others were recognized in this study (Tables 1–3). I then examined these traits in the context of published phylogenies and geographic distributions. The following two criteria were employed to identify realm-specific innovations in tropical Neogene to Recent marine shallow-water shell-bearing molluscan clades at family or subfamily level that are distributed throughout the tropics: 1) the trait is a departure from clade norms and is known only from one (but not both) of the two tropical realms, the IWP and AEP; and 2) the trait evolved during or after the Late Oligocene. Traits that arose independently in the two realms were excluded. For the purposes of the present study, I included faunas of the Miocene and Pliocene in southwestern Europe as belonging to the AEP; their present-day equivalents, however, lie well outside the tropics and were therefore not included.

To assess whether the incidence of innovation tracks realm-wide species diversity, I compiled the number of extant species in the IWP and AEP in 30 well-studied family- or subfamily-level clades of molluscs (25 gastropod and 5 bivalve clades). Data were drawn from hundreds of published taxonomic sources; only the principal sources are cited in Table 4.

Deep-water taxa found at depths of 100 m or more were excluded. The data reported are estimates; taxa are being added to almost all the groups considered, but the ratio of AEP to total tropical diversity in each clade is not expected to change by more than two to three percentage points as taxonomic knowledge accumulates.

**Data, Materials, and Software Availability.** All study data are included in the article.

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Author affiliations: <sup>a</sup>Department of Earth and Planetary Sciences, University of California, Davis, CA 95616

11. D. G. Reid, J. B. Geller, A new ovoviviparous species of *Tectarius* (Gastropoda: Littorinidae) from Niue, South Pacific, with a molecular phylogeny of the genus. *J. Molluscan Stud.* **63**, 207–233 (1997).

12. G. J. Vermeij, M. A. Snyder, Proposed genus-level classification of large species of Fusininae (Gastropoda, Fascioliariidae). *Basteria* **82**, 57–82 (2018).

13. G. J. Vermeij, "Shells inside out: The architecture, evolution and function of shell envelopment in molluscs" in *Evolving Form and Function: Fossils and Development*, D. E. G. Briggs, Ed. (Peabody Museum of Natural History, Yale University, New Haven, 2005), pp. 197–221.

14. M. Claremont, G. J. Vermeij, S. T. Williams, D. G. Reid, Global phylogeny and new classification of the Rapaninae (Gastropoda: Muricidae), dominant molluscan predators on tropical rocky seashores. *Mol. Phylogenet. Evol.* **66**, 91–102 (2013).

15. A. E. Fedosov *et al.*, The collapse of *Mitra*: Molecular systematics and morphology of the Mitridae (Gastropoda: Neogastropoda). *Zool. J. Linn. Soc.* **183**, 253–337 (2018).

16. A. E. Fedosov, N. Puillandre, Integrative taxonomy of the *Clavus canalicularis* species complex (Drillidae, Conoidea, Gastropoda) with description of four new species. *Molluscan Res.* **40**, 251–266 (2020).

17. A. E. Fedosov *et al.*, Phylogenetic classification of the family Terebridae (Neogastropoda: Conoidea). *J. Molluscan Stud.* **85**, 359–388 (2019).

18. T. R. Oskars *et al.*, A molecular phylogeny of the gastropod family Haminoeidae sensu lato (Heterobranchia: Cephalaspidea): A generic revision. *Invertebr. Syst.* **33**, 426–472 (2019).

19. M. Sasaki, N. Hamaguchi, S. Nishihama, Distribution of *Acanthopleura spinosa* (Polyplacophora: Chitonidae) on Miyako and Irabu Islands, Okinawa. *Venus* **65**, 165–168 (2006).

20. M. Owada, B. W. Hoeksema, Molecular phylogeny and shell microstructure of *Fungiacava eilatensis* Goreau et al. 1968, boring into mushroom corals (Scleractinia: Fungiidae), in relation to other mussels (Bivalvia: Mytilidae). *Contrib. Zool.* **80**, 169–178 (2011).
21. J. Rosewater, The family Pinnidae in the Indo-Pacific. *Indo-Pac. Mollusca* **1**, 175–226 (1961).
22. B. Morton, The biology and functional morphology of *Curvemysella paula* (A. Adams, 1856) (Bivalvia: Galeommatroidea: Montacutidae) comme Ba1 with diogenes goniochirus forest, 1956 (Crustacea: Paguridea) on China Beach, Danang, Vietnam. *Am. Malacol. Bull.* **15**, 15–30, (2017).
23. M. Huber, Compendium of Bivalves (ConchBooks, Hackenheim, 2010).
24. R. von Cosel, "An introduction to the razor shells (Bivalvia: Solenacea)" in *The Bivalvia—Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge, Edinburgh, 1986* (Hong Kong University Press, Hong Kong, 1990), pp. 283–311.
25. H. E. Vokes, Notes on the fauna of the Chipola Formation—XXV: On the occurrence of the genus *Rothpletzia* Simonelli (Mollusca: Gastropoda). *Tulane Stud. Geol. Paleontol.* **17**, 51–54 (1982).
26. B. Landau, G. J. Vermeij, New Lyriinae (Mollusca: Volutidae) from the Lower Miocene Cantaure Formation of Venezuela. *Novapex* **12**, 119–123 (2011).
27. G. J. Vermeij, Asymmetrical sculpture in Arcidae (Bivalvia), with comments on the genera *Caloosarca* and *Cunearca* (Bivalvia: Arcidae). *Nautilus* **135**, 46–52 (2021).
28. J. D. Taylor, E. Glover, M. Peharda, G. Blattl, A. Ball, Extraordinary flexible shell sculpture: The structure and formation of calcified periostracal lamellae in *Lucina pensylvanica* (Bivalvia: Lucinidae). *Malacologia* **46**, 277–296 (2004).
29. G. J. Vermeij, Molluscan marginalia: Hidden morphological diversity at the bivalve shell edge. *J. Molluscan Stud.* **79**, 283–295 (2013).
30. D. L. Geiger, B. Owen, Abalone: World-Wide Haliotidae (ConchBooks, Hackenheim, 2012).
31. T. E. Elchhorst, *Neritidae of the World* (ConchBooks, Harxhelm, 2016).
32. B. Landau, G. J. Vermeij, S. Reich, 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 (2014).
33. N. Puillandre, T. F. Duda, C. Meyer, B. M. Olivera, P. Bouchet, One, four or 100 genera? A new classification of the cone snails. *J. Molluscan Stud.* **81**, 1–23 (2015).
34. M. Huber, A. Langleit, K. Kreipl, "Tellinidae" in *Compendium of Bivalves*, M. Huber, Ed. (ConchBooks, Hackenheim, 2015), vol. 2, pp. 564–746.
35. G. J. Vermeij, Marine faunal dominance and molluscan shell form. *Evolution* **28**, 656–664 (1974).
36. G. J. Vermeij, "Intimate associations and coevolution in the sea" in *Coevolution*, D. J. Futuyma, M. Slatkin, Eds. (Sinauer, Sunderland, 1983), pp. 311–327.
37. G. J. Vermeij, Interoceanic differences in adaptation: Effects of history and productivity. *Mar. Ecol. Prog. Ser.* **57**, 293–305 (1989).
38. P. Lozouet, Temporal and latitudinal trends in the biodiversity of European Atlantic Cenozoic gastropod (Mollusca) faunas. A base for the history of biogeographic provinces. *Carnets de Geologie* **14**, 273–314 (2014).
39. J. C. Briggs, Zoogeography and evolution. *Evolution* **20**, 282–289 (1966).
40. J. C. Briggs, Relationship of the tropical shelf regions. *Stud. Trop. Oceanogr.* **5**, 569–578 (1967).
41. W. Renema et al., Hopping hotspots: Global shifts in marine biodiversity. *Science* **321**, 654–657 (2008).
42. D. Huang, E. E. Goldberg, L. M. Chou, K. Roy, The origin and evolution of coral species richness in a marine diversity hotspot. *Evolution* **72**, 288–302 (2018).
43. M. Förderer, D. Rögger, C. R. Langer, Patterns of species richness and the center of diversity in modern Indo-Pacific larger Foraminifera. *Sci. Rep.* **8**, 8189 (2018).
44. G. J. Vermeij, The dispersal barrier in the tropical Pacific: Implications for molluscan speciation and extinction. *Evolution* **41**, 1046–1058 (1987).
45. M. E. J. Wilson, B. R. Rosen, "Implications of paucity of corals in the Paleogene of SE Asia: Plate tectonics or centre of origin?" in *Biogeography and Geological Evaluation of SE Asia*, R. Hall, J. D. Holloway, Eds. (Backhuys, Leiden, 1998), pp. 165–195.
46. K. Bromfield, J. M. Pandolfi, Regional patterns of evolutionary turnover in Neogene coral reefs from the central Indo-West Pacific Ocean. *Evol. Ecol.* **26**, 375–393 (2012).
47. L. B. McMonagle et al., A re-assessment of age dating of fossiliferous limestones in eastern Sabah, Borneo: Implications for understanding the origins of the Indo-Pacific marine biodiversity hotspot. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **305**, 28–42 (2011).
48. M. Harzhauser, W. E. Piller, F. F. Steltinger, Circum-Mediterranean Oligo-Miocene biogeographic evolution—The gastropods' point of view. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **183**, 103–133 (2002).
49. M. Harzhauser, O. Mandic, W. E. Piller, M. Reuter, A. Kroh, Tracing back the origin of the Indo-Pacific mollusc fauna: Basal Tridacninae from the Oligocene and Miocene of the Sultanate of Oman. *Palaeontology* **51**, 199–213 (2008).
50. M. Harzhauser et al., Oligocene and early Miocene gastropods in Kutch (NW India) document an early biogeographic switch from Western Tethys to Indo-Pacific. *Paläontol. Z.* **83**, 333–342 (2009).
51. G. J. Vermeij, "Community assembly in the sea: Geologic history of the living shore biota" in *Marine Community Ecology*, M. D. Bertness, S. D. Gaines, M. E. Hay, Eds. (Sinauer, Sunderland, 2001), pp. 39–60.
52. D. O. Obura, An Indian Ocean centre of origin revisited: Palaeogene and Neogene influences defining a biogeographic realm. *J. Biogeogr.* **43**, 229–242 (2016).
53. G. J. Vermeij, The tropical history and future of the Mediterranean biota and the West African enigma. *J. Biogeogr.* **39**, 31–41 (2012).
54. K. G. Johnson, J. B. C. Jackson, A. F. Budd, Caribbean reef development was independent of coral diversity over 28 million years. *Science* **319**, 1521–1523 (2008).
55. J. V. M. Saw, A. W. Hunter, K. G. Johnson, A. H. B. Abdul Rahman, Pliocene corals from the Togopi Formation of the Dent Peninsula, Sabah, northeastern Borneo, Malaysia. *Alcheringa* **43**, 291–319 (2019).
56. G. J. Vermeij, Comparative biogeography: Innovations and the rise to dominance of the North Pacific biota. *Proc. Biol. Sci.* **285**, 20182027 (2018).
57. G. J. Vermeij et al., The coastal North Pacific: Origins and history of a dominant marine biota. *J. Biogeogr.* **46**, 1–18 (2019).
58. A. O'Dea et al., Formation of the Isthmus of Panama. *Sci. Adv.* **2**, e1600883 (2016).
59. J. A. Estes, G. J. Vermeij, History's legacy: Why future progress in ecology demands a view of the past. *Ecology* **103**, e3788 (2022).
60. E. Y. W. Tan, Q. Z. B. Randolph, M. L. Neo, C. Fauvelot, D. Huang, Genome skimming resolves the giant clam (Bivalvia: Cardiidae: Tridacninae) tree of life. *Coral Reefs* **41**, 497–510 (2022).