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Comparative biogeography: innovations and the rise to dominance of the North Pacific biota

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The North Pacific is the largest cold-water source of lineages spreading to other modern marine temperate biotas. How this status was achieved remains unclear. One hypothesis is that functional innovations of large effect, defined as departures from the norm in temperate clades and which confer competitive or defensive benefits, increase resource availability, and raise performance standards in the biota as a whole, evolved earlier and more frequently in the North Pacific than elsewhere in the temperate zone. In support of this hypothesis, phylogenetic and fossil evidence reveals 47 temperate marine innovations beginning in the latest Eocene, of which half arose in the North Pacific. Of the 22 innovations of large effect, 13 (39%) evolved in the North Pacific, including basal growth in kelps and bottom-feeding herbivory and durophagy in mammals. Temperate innovations in the Southern Hemisphere and the North Atlantic appeared later and were less consequential. Most other innovations arose in refuges where the risks of predation and competition are low. Among temperate marine biotas, the North Pacific has the highest incidence of unique innovations and the earliest origins of major breakthroughs, five of which spread elsewhere.

1. Background

The question of where and when evolutionary innovations arise and spread has occupied scientists for many years. The answers are important because such innovations, which represent departures from the norm in a clade, can in some cases act as breakthroughs that lead to new or more intense patterns of natural selection and to lineage diversification.

It has become clear that isolated, island-like habitats permit many new forms and functions to evolve, but their isolation ensures that the novelties rarely spread and, in any case, do not often meet the performance standards in larger settings where diversity is higher [1].

If high-performance innovations contribute to the overall competitive vigour in a region with a large species pool, their number should be higher per species than in a more isolated setting. This expectation is borne out in the modern marine tropics, where molluscan innovations are more frequent per species in the Indo-West Pacific than in the less diverse, more extinction-prone Atlantic-East Pacific realm [1].

Here I extend this line of enquiry into the world's temperate marine regions. Among modern shallow-water temperate marine biotas, that of the North Pacific is the largest, most diverse and most biogeographically dominant [2]. This biota has exported more lineages to other temperate regions than have the biotas in the Southern Hemisphere and the North Atlantic [2]. Given its dominant status, the North Pacific should have spawned a larger number of functional and ecological innovations than other marine regions outside the tropics.

I distinguish two classes of innovation based on how they contribute to the ecosystems in which they arise. The first comprises innovations of large effect, which either facilitate evolution in other species by stimulating productivity or by making resources more accessible, or which increase the competitive or defensive capacities of their bearers. The effect of these innovations is therefore to raise performance standards in the system as a whole. The second category comprises innovations promoting specialization to a refugial mode of life, where risks from predators and competitors are reduced. Refugial innovations would therefore be favoured in regions where innovations of large effect increase the overall risk of predation and competition: they enable lineages that do not occupy top competitive positions in the ecosystem to make a living in relative safety. High-performance innovations might be expected to spread beyond the region in which they arose, whereas refugial innovations might be less likely to expand geographically.

2. Material and methods

I surveyed the taxonomic, phylogenetic, palaeontological and biogeographic literature on temperate marine multicellular organisms to identify traits representing innovations, defined for the purposes of this paper as morphological or ecological features that are departures from prevailing temperate norms in clades in which these new states evolved. Every effort was made to ensure that the search for innovations was exhaustive and representative. I accepted only those innovations for which the region of origin could be inferred from the fossil record or from phylogenetic relationships. Only innovations that arose during and after the Late Eocene, when the first substantial cooling occurred at high latitudes, were considered. Innovations that originated in the tropics or in a temperate area other than the focal temperate region were excluded. In other words, departures from the phenotypic norm were accepted if they evolved *in situ* in a given marine temperate region. If an innovation arose independently in more than one temperate region, it was counted for each region in which it arose. Although large size confers obvious benefits and often exceeds previously established size limits in a clade, I did not consider size increase beyond this limit as an innovation, because it does not by itself represent a morphological or ecological novelty.

3. Results and discussion

Innovations in the temperate marine realm are rare. I uncovered only 47 innovations distributed among 60 clades: 10 mammals, six birds, three teleost fishes, two echinoderms, one decapod, three Polyplacophora, 29 gastropods, five bivalves and two brown algae. No innovations were found in sponges, cnidarians, nematodes and related ecdysozoan phyla, annelids, nemerteans, brachiopods, bryozoans, scaphopods and cephalopods. These findings reflect real underlying patterns as well as limited phylogenetic and fossil evidence for some groups, but there is no geographical bias in what is known and what is not known.

I identified 24 innovations in 32 clades that evolved *in situ* in the North Pacific (table 1). At least 13 (59%) are innovations of large effect, five of which spread beyond the North Pacific. At least three innovations, all involving endotherms, evolved earlier in the North Pacific than in other temperate regions, where similar innovations evolved independently later.

In situ innovations are less frequent and evolved later in other temperate marine regions. There are ten in 13 clades in southern South America, five (50%) of which are of large effect; four innovations in four clades in southern Africa, one of large effect; four innovations in four clades in Australasia, one of large effect; and five innovations in six clades in the North Atlantic, two of large effect. Of a total of 23 innovations in these regions, only three evolved nowhere else in the temperate zone, a number significantly lower than the 15 unique North Pacific innovations (chi-square test, $p < 0.01$). Only two innovations, both from South America, including one of large effect, spread to other temperate regions. The North Pacific thus stands out as the region with the highest proportion and earliest origins of innovations of large effect and of unique innovations.

(a) North Pacific innovations

The most consequential North Pacific innovations are basal growth and a vascular system in laminarialean brown kelps, interpreted as adaptations to intense grazing [3]; and the related Early Oligocene colonization of desmostylians, the earliest large marine herbivorous mammals outside the tropics [4]. Kelps spread to all other temperate marine regions around the Miocene–Pliocene boundary [5] and became highly productive on temperate coasts. Neither the desmostylians, which became extinct in the Late Miocene, nor the later hydrodamaline sea cows that replaced them as herbivores, expanded beyond the North Pacific. Among kelps, an additional uniquely North Pacific innovation of uncertain function is perforation of the blades in members of the Arthrothamnaceae [5], several of which spread to the Arctic and Atlantic Oceans.

Another North Pacific innovation with large ripple effects was the *in situ* evolution of durophagy, defined as the predation of hard-shelled animals by means of breakage or other extractive techniques. The most important durophages in the North Pacific are large mammals, beginning with *Kolponomos* in the Late Oligocene [6] and followed successively by walruses (Odobenidae) and the extinct sea-lion genus *Gomphotaria* [7,8] during the Late Miocene, and the sea otter *Enhydra* during the Pliocene [9,10]. In each of these lineages, durophagy is a derived condition evolving from more raptorial modes of predation on more active prey. Suction-feeding walruses and shell-breaking sea otters expanded into the North Atlantic [11], although *Enhydra* became extinct there in the Pleistocene [9].

Besides limiting the abundance of small herbivores and therefore indirectly favouring the growth of algae including kelps, durophages probably became potent selective agents for benthic molluscs, echinoderms and crustaceans. At least six innovations are interpretable as anti-predatory or competition-enhancing adaptations: cementation by the scallop *Crassadoma* [12,13], plicate valves in the Miocene mussel *Plicatomytilus* [14], carcinization (adoption of a crab-like form in which the abdomen is held beneath the body in lithodid crustaceans from a hermit-crab ancestor) [15,16], coverage of the valves by the girdle in the chitons *Cryptochiton* and *Amicula* [17], territoriality and aggression in the limpet *Lottia gigantea* [18], and rock excavation by the limpet *L. scabra* [19]. Two of these innovations (carcinization and chiton valve coverage) spread to other temperate regions, the Southern Hemisphere and North Atlantic respectively.

Additional innovations enhancing competitive ability or enabled by high productivity remained confined to the North Pacific. These include photosymbiosis in the cockle *Clinocardium nuttalli* [20], excavation of bivalve prey from deep sediments by the sea star *Pisaster brevispinus* [21,22],

Table 1. Innovations in the coastal temperate marine realm. LE, Innovations of large effect; R, Refugial innovations; S, Innovations that spread beyond the region of origin; U, Unique innovations in the temperate realm.

Biota, innovation and clade	Type
North Pacific	
Herbivory by large endotherms, Desmostylia	LE
Durophagy by large endotherms, *Kolponomos*, Odobenidae, *Gomphotaria*, *Enhydra*	LE, S
Excavation of deep-burrowing prey by sea stars, *Pisaster*	LE, U
Filter-feeding by salmonids, *Oncorhyncus*	LE, U
Suspension feeding by sand dollars, *Dendraster*	LE, U
Territoriality in limpets, *Lottia gigantea*	LE
Rock excavation by limpets, *Lottia scabra*	LE
Valve encasement in chitons, *Cryptochiton*, *Amicula*	LE, S, U
Photosymbiosis in bivalves, *Clinocardium nuttalli*	LE, U
Basal growth and vascular system in algae, Laminariales	LE, S, U
Perforated blades in algae, Arthrothamnaceae	—
Carcinization in hermit crabs, *Pagurus* to Lithodidae	LE, S, U
Algal-stipe excavation by limpets, *Lottia instabilis*	R
Flightlessness in birds, Plotopteridae, Mancallinae, *Chendytes*	—
Life on algal blades by chitons, *Juvenichiton*	R, U
Life on shells by limpets, *Garnotia norrissiarum*, *Lottia asmi*	—
Limpet form in gastropods, *Piliscus*	—
Slug form in gastropods, Onchidiopsinae	—
Cementation in bivalves, *Crassadoma*	LE, U
Rock-boring in bivalves, *Platyodon*	R
Bivalve living in ascidians, *Mytilimeria nuttalli*	R, U
Plicate valves in mussels, *Plicatomytilus*	LE, U
Sinistral coiling in gastropods, *Neptunea*, *Pyrulofusus*	R
Southern South America	
Herbivory by large endotherms, *Thalassocnus*	LE
Durophagy by large endotherms, *Kadrokirus*, *Odobenocetops*, *Lontra*	LE
Labral tooth in gastropods, *Acanthina* clade, *Concholepas*	LE, S
Flightlessness in birds, *Tachyeres*	—
Intertidal algal grazing by fishes, *Sicyases*	LE
Slug habit in gastropods, *Buchanania*	—
Limpet form in gastropods, *Concholepas*	—
Algal-stipe excavation by limpets, *Scurria scurria*	R
Rock excavation by limpets, *Scurria*	LE
Sinistral coiling in gastropods, *Antistreptus*	R
Southern Africa	
Gardening on shell, *Bullia*	U
Algal-stipe excavation by limpets, *Cymbula*	R
Algal gardening by limpets, *Scutellastra*	LE
Labral tooth in gastropods, *"Thais" squamosa*	—
Australasia	
Algal grazing by fishes, Odacinae	LE
Labral tooth in gastropods, *Iosepha*	—
Envelopment of shell by mantle, *Tylospira*	—
Slug habit in gastropods, *Smeagol*	—
North Atlantic	
Flightlessness in birds, Pinguinus	—
Durophagy by large endoderms, *Mustela macrodon*	LE
Suction-feeding in birds, *Alle alle*	LE, U
Algal-stipe excavation by limpets, *Patella pellucida*	R
Sinistral coiling in gastropods, *Neptunea*, *"Terebra" inversa*	R

and suspension-feeding by the sand dollar *Dendraster* [23,24] and some Miocene salmon of the genus *Oncorhynchus* [25].

At least 12 of 13 innovations of large effect (92%) led to increases in body size [3]. Uniquely gigantic size, enabled by high productivity, distinguishes the North Pacific from other temperate biotas [3] and also occurs in many lineages without obvious morphological innovations.

Apart from the Palaeocene origin of penguins in the Southern Hemisphere, flightlessness in Late Eocene and later fish-eating birds evolved earlier and more often in the North Pacific than elsewhere, perhaps in response to reduced predation. The earliest to become flightless were penguin-like plotopterids [26], followed by Middle Miocene mancalline auks [27,28] and the Pleistocene duck *Chendytes* [29]. The recently extinct cormorant *Phalacrocorax perspicillatus* had strongly reduced wings and was at best a poor flier [30]. Increases in body size mark the history of flightlessness in all these lineages [28–30].

A North Pacific innovation that is unique among Polyplacophora is the presence of a ligament-like feature in the centre of each intermediate valve in *Schizoplax brandtii*. This feature has never been studied and its function is unknown.

Refugial innovations in the North Pacific include rock-boring in the bivalve *Platyodon* [31,32], life on algal blades by *Juvenichiton* and related chitons [33], stipe excavation by the limpet *Lottia instabilis* [34], occupation of outer shell surfaces of living gastropods by the limpet *Lottia asmi* and the calyptraeid slipper limpet *Garnotia norrisiarum* [35], and life of the bivalve *Mytilimeria nuttalli* inside ascidians [36]. The transition from right-handed (dextral) to left-handed (sinistral) coiling in marine gastropods is rare, but occurs in three North Pacific lineages: *Neptunea leva* in the Okhotsk Sea, the buccinid *Pyrulofusus* in the far North Pacific, and the pseudomelatomid *Antiplanes* with origins in the northwestern Pacific [37]. This minor innovation occurs most commonly in environments where predation on eggs and egg masses on the seafloor is reduced [37]. A transition from coiled ancestors to a limpet-like form and to a slug without a shell occurred separately in the North Pacific velutinid *Piliscus* [38] and the velutinid subfamily Onchidiopsinae [39], respectively. Among these innovations, left-handedness in *Pyrulofusus* spread to the Arctic Ocean (but not the Atlantic) and the limpet and slug expanded to the North Atlantic.

(b) Other temperate regions

Far fewer innovations originated in other temperate biotas. In South America, innovations of large effect arose later: algal grazing by the intertidal clingfish *Sicyases sanguineus* [40], herbivory by the Late Miocene to Early Pliocene marine sloth *Thalassocnus* [41], durophagy in three mammalian lineages, the Late Miocene to Early Pliocene seal *Hadrokirus* [42] and cetacean *Odobenocetops* [43] and the Pleistocene to Recent otter genus *Lontra* [4], and the predation-enhancing labral tooth in two gastropod lineages, the Acanthina clade and *Concholepas* [44]. Rock excavation evolved *in situ* by a lineage of scurriine limpets [45].

Innovations to a refugial life include the limpet form in *Concholepas* during the Middle Miocene [46], shell envelopment and the slug habit in the keyhole limpet *Buchanania* [47], algal-stipe excavation in *Scurria scurra* [45], and sinistral coiling in the buccinid *Antistreptus* [37].

Flightlessness evolved in the steamer duck *Tachyeres* during the Early Pleistocene [48].

Three of the four southern African innovations involve relationships between animals and algae: algal gardening on the shell by the nassariid gastropod *Bullia* [49] and by the territorial limpet genus *Scutellastra* [18,50]. The fourth innovation, a small labral tooth in '*Thais*' *squamosa* [42], is at best a minor predation-enhancing feature.

In temperate Australasia, and early (Oligocene) and important innovation was specialized herbivory by odacine wrasses [51]. Other novelties are minor: a small labral tooth in the buccinid *Iosepha* [44], shell envelopment in the struthiolariid *Tylospira* [52], and the slug habit in the pulmonate *Smeagol* [53].

Large-effect innovations in the North Atlantic appeared in the Pliocene or later: durophagy by the sea mink (*Mustela macrodon*) in eastern North America during the Late Pleistocene [4], suction-feeding in the planktovorous auk *Alle alle* from fish-eating ancestors during the Pliocene [54,55], and flightlessness in the great auk *Pinguinus* [27]. Two refugial innovations evolved during the Pliocene: stipe excavation by the limpet *Patella pellucida* [33] and sinistral coiling in the buccinid *Neptunea* and the extinct North Sea '*Terebra*' *inversa* [37].

4. General discussion

Cairns and colleagues [56] pointed out that endothermic vertebrates (mammals and birds) are generally the top predators in high-latitude oceans, whereas ectothermic fishes occupy that role in tropical seas. They noted that burst swimming speeds of ectotherms are temperature-dependent whereas those of endotherms are not, so that cold-water endotherms have a locomotor advantage in catching ectothermic prey, whereas warm-water endotherms do not. Temperature also affects muscle-generated forces applied in subduing prey. For bottom-dwelling marine animals and algae, therefore, the primary selective agents in temperate waters are usually endotherms (especially mammals), whereas on tropical coasts they tend to be ectothermic fishes, reptiles, crustaceans, and even molluscs and echinoderms. Herbivorous sirenian mammals are exceptions in that they have been important consumers of tropical seagrasses since the Eocene.

Flying birds are ecologically important on all coasts, including tropical shores, but they are likely to be secondary as selective agents to tropical crustaceans [57] and to temperate marine mammals because of their relatively small body sizes. It is notable that flightless marine birds, which tend to be larger than their flying counterparts, occur only in temperate and polar seas and are absent from more tropical mainland coasts. Tool use (by otters in the North Pacific) and shell-dropping (by gulls and crows) are also restricted to tropical coasts. Limits at low temperatures on calcification and force production constrain the adaptive responses of many temperate marine animals to intense selection from durophages, tilting the advantage toward endotherms even further.

Habitat specialization to refuges, however, should be little affected by temperature.

In short, the presence and early evolution of large endothermic marine mammals and birds in the North Pacific could go a long way toward accounting for the rise of the North Pacific biota to its current position as the dominant marine donor biota in the temperate realm. Through their strong ecological and evolutionary effects, these early endotherms and their successors raised the performance standards in the North Pacific biota as a whole to· high levels allowed by thermal conditions. In addition, durophagy by late-appearing South American otters and western Atlantic sea mink is much less specialized than that of North Pacific mammals.

An additional indication of the outsized role of the North Pacific in temperate biogeography, is that stipe-excavating limpets in South America, southern Africa and the North Atlantic evolved in response to the arrival of North Pacific kelps. European and South American kelps are derived directly from North Pacific ancestors, whereas those in southern Africa came from the North Atlantic by trans-equatorial dispersal [5,58]. In other words, without the North Pacific as the ultimate source of ecologically dominant lineages, temperate regions elsewhere would have witnessed even fewer innovations than they did.

In striking contrast to North Pacific innovations, many of which spread to other temperate regions, the innovations originating in temperate regions outside the North Pacific almost never spread beyond their areas of origin. The only two exceptions are South American: the labral tooth in the Acanthina clade, originating during the Oligocene and spreading to the northeastern Pacific and perhaps to southern Africa soon thereafter [44]; and the labral tooth in *Concholepas concholepas*, a lineage that spread briefly to southern Africa but not known to be living there today [59].

It may simply be an accident of geographical proximity to continents with large mammal faunas that the North Pacific was colonized early and often by mammalian lineages that subsequently became important marine herbivores and durophages. What is less clear is why such mammals were so late in appearing in southern South America or the North Atlantic. The North Atlantic biota lacking mammalian durophages until the Pliocene, when two walrus lineages, *Ontocetus* and later *Odobenus*, arrived from the North Pacific [8,11], followed in the Pleistocene by the sea otter [9].

Durophagous mammals never colonized or evolved in southern Africa or Australasia despite the presence of diverse pinnipeds and cetaceans there.

5. Conclusion

This investigation of the rise of the North Pacific biota to biogeographic supremacy through the evolution of innovations illustrates the value of placing such novelties in a comparative geographical context. Innovations of large effect, such as durophagy by animals with high metabolic rates, affect the distribution and evolution not only of the species directly targeted by these consumers, but of many other species as well, with important consequences for the biota as a whole. Biogeography and evolution are inextricably linked through feedbacks among enabling factors like the distribution of temperature, nutrients, and geographical features; and selective agents, the organisms that impose and respond to competition and consumption [60].

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References

1. Vermeij GJ. 2012 Crucibles of creativity: the geographical origins of tropical molluscan innovations. *Evol. Ecol.* **26**, 357–373. (doi:10.1007/s10682-010-9458-2)
2. Vermeij GJ, Banker R, Capece ER, Hernandez ES, Salmon SO, Vriesman VP, Wortham BE. In press. The coastal North Pacific: origins and history of a dominant marine biota. *J. Biogeogr.*
3. Vermeij GJ. 2012 The evolution of gigantism on temperate seashores. *Biol. J. Linn. Soc.* **106**, 776–793. (doi:10.1111/j.1095-8312.2012.01897.x)
4. Vermeij GJ, Motani R. 2018 Land to sea transitions in vertebrates: the dynamics of colonization. *Paleobiology* **44**, 237–250. (doi:10.1017/pab.2017.37)
5. Jackson C, Salomaki ED, Lane CE, Saunders GW. 2017 Kelp transcriptomes provide robust support for interfamilial relationships and revision of the little known Arthrothamnaceae (Laminariales). *J. Phycol.* **53**, 1–6. (doi:10.1111/jpy.12465)
6. Tseng ZJ, Grohé C, Flynn JJ. 2016 A unique feeding strategy of the extinct marine mammal *Kolponomos*: convergence on sabertooths and sea otters. *Proc. R. Soc. B* **283**, 20160044. (doi:10.1098/rspb.2016.0044)
7. Barnes LG, Raschke RE. 1991 *Gomphotaria pugnax*, a new genus and species of Late Miocene dusignathine otariid pinniped (Mammalia: Carnivora) from California. *Contrib. Sci. Nat. Hist. Mus. Los Angeles County* **426**, 1–16.
8. Boessenecker RW, Churchill M. 2013 A reevaluation of the morphology, paleoecology, and phylogenetic relationships of the enigmatic walrus *Pelagiarctos*. *PLoS ONE* **8**, e54311. (doi:10.1371/journal.pone.0054311)
9. Willemsen GF. 1992 A revision of the Pliocene and Quaternary Lutrinae from Europe. *Scr. Geol.* **101**, 1–115.
10. Timm-Davis LL, Davis RW, Marshall CD. 2017 Durophagous biting in sea otters (*Enhydra lutris*) differs kinematically from raptorial biting of other marine mammals. *J. Exp. Biol.* **220**, 4703–4710. (doi:10.1242/jeb.162966)
11. Boessenecker SJ, Boessenecker RW, Geisler JH. 2018 Youngest record of the extinct walrus. Ontocetus emmonsi from the Early Pleistocene of South Carolina and a review of North Atlantic walrus biochronology. *Acta Palaeontol. Pol.* **63**, 279–286. (doi:10.4202/app.00454.2018)
12. Yonge CM. 1951 Studies on Pacific coast mollusks. III. Observations on *Hinnites multirugosus* (Gale). *Univ. Calif. Publ. Zool.* **55**, 409–420.
13. Saavedra C, Peña JB. 2006 Phylogenetics of American scallops (Bivalvia: Pectinidae) based on partial 16S and 12S ribosomal RNA gene sequences. *Mar. Biol.* **150**, 111–119. (doi:10.1007/s00227-006-0335-z)
14. Yoshida K. 1998 Formation of plications in the Miocene bivalve *Mytilus* (*Plicatomytilus*) *sakurai* as a consequence of architectural constraint. *Paleontol. Res.* **2**, 224–238.
15. Tsang LM, Chan T-Y, Ahyong ST, Chu KH. 2011 Hermit to king, or hermit to all: multiple transitions to crab-like forms from hermit crab ancestors. *Syst. Biol.* **60**, 616–629. (doi:10.1093/sysbio/syr063)
16. Noever C, Glenner H. 2018 The origin of king crabs: hermit crab ancestry under the magnifying glass. *Zool. J. Linn. Soc.* **182**, 300–318. (doi:10.1093/zoolinnean/zlx033)
17. Sigwart JD, Stoeger I, Knebelsberger T, Schwabe E. 2013 Chiton phylogeny (Mollusca: Polyplacophora) and the placement of the enigmatic species *Choriplax grayi* (A. Adams and Angas). *Invertebr. Syst.* **27**, 603–621. (doi:10.1071/IS13013)
18. Lindberg DR. 2007 Reproduction, ecology and evolution of the Indo-Pacific limpet *Scutellastra flexuosa*. *Bull. Mar. Sci.* **81**, 219–234.
19. Lindberg DR, Dwyer KR. 1983 The topography, formation and role of the home depression of *Collisella scabra* (Gould) (Gastropoda: Acmaeidae). *Veliger* **25**, 229–234.
20. Jones DS, Jacobs DK. 1992 Photosymbiosis in *Clinocardium nuttalli*: implications for tests of photosymbiosis in fossil molluscs. *Palaios* **7**, 86–95. (doi:10.2307/3514798)
21. Van Veldhuizen RD, Phillips DW. 1978 Prey capture by *Pisaster brevispinus* (Asteroidea: Echinodermata) on soft substrate. *Mar. Biol.* **48**, 89–97. (doi:10.1007/BF00390534)
22. Sloan NA, Robinson SMC. 1983 Winter feeding by asteroids on a subtidal sandbed in British Columbia. *Ophelia* **22**, 125–140. (doi:10.1080/00785326.1983.10426591)
23. Highsmith RC. 1982 Induced settlement and metamorphosis of sand dollar (*Dendraster excentricus*) larvae in predator-free sites: adult sand dollar beds. *Ecology* **63**, 329–337. (doi:10.2307/1938950)
24. Beadle SC. 1991 The biogeography or origin and radiation: dendrasterid sand dollars in the northeastern Pacific. *Paleobiology* **17**, 325–339. (doi:10.1017/S009483730001068X)
25. Eiting TP, Smith GR. 2007 Miocene salmon (*Oncorhynchus*) from western North America: gill raker evolution correlated with plankton productivity in the eastern Pacific. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **249**, 412–424. (doi:10.1016/j.palaeo.2007.02.011)
26. Mayr G, Goedert JL. 2016 New Late Eocene and Oligocene remains of the flightless, penguin-like plotopterids (Aves, Plotopteridae) from western Washington State, *U.S.A. J. Vertebr. Paleontol.* **36**, e163573.
27. Smith NA. 2011 Taxonomic revision and phylogenetic analysis of the flightless *Mancallinae* (Aves, Pan-Alcidae). *Zookeys* **91**, 1–116. (doi:10.3897/zookeys.91.709)
28. Smith NA. 2016 Evolution of body mass in the Pan-Alcidae (Aves, Charadriiformes): the effects of combining neontological and paleontological data. *Paleobiology* **42**, 8–26. (doi:10.1017/pab.2015.24)
29. Livezey BC. 1993 Morphology of flightlessness in *Chendytes*, fossil seaducks (Anatidae: Mergini) of coastal California. *J. Vertebr. Paleontol.* **13**, 185–199.
30. Livezey BC. 1992 Flightlessness in the Galápagos cormorant (*Compsohalieus* (*Nannopterum*) *harrisi*): heterochrony, giantism and specialization. *Zool. J. Linn. Soc.* **105**, 155–224. (doi:10.1111/j.1096-3642.1992.tb01229.x)
31. Yonge CM. 1951 Studies on Pacific coast mollusks. II. Structure and adaptations of rock boring in *Platyodon cancellatus* (Conrad). *Univ. Calif. Publ. Zool.* **55**, 401–407.
32. Adegoke OS. 1967 Earliest Tertiary West American species of *Platyodon* and *Penitella*. *Proc. Calif. Acad. Sci.* **35**, 1–22.
33. Vermeij GJ. 1992 Time of origin and biogeographical history of specialized relationships

between northern marine plants and herbivorous molluscs. *Evolution* **46**, 657–664. (doi:10.1111/j.1558-5646.1992.tb02073.x)

34. Lindberg DR. 1990 Movement patterns of the limpet *Lottia asmi* (Middendorff): networking in California rocky intertidal communities. *Veliger* **33**, 375–383.
35. Vermeij GJ, Lowell RB, Walters LJ, Marks JA. 1987 Good hosts and their guests: relations between trochid gastropods and the epizoic limpet *Crepidula adunca*. *Nautilus* **101**, 69–74.
36. Yonge CM. 1952 Studies on Pacific coast mollusks. V. Structure and adaptation in *Entodesma saxicola* (Baird) and *Mytilimeria nuttallii* Conrad, with a discussion on evolution within the family Lyonsiidae (Lamellibranchia). *Univ. Calif. Publ. Zool.* **55**, 439–450.
37. Vermeij GJ. 2003 The geography of evolutionary opportunity: hypothesis and two cases in gastropods. *Integr. Comp. Biol.* **42**, 935–940. (doi:10.1093/icb/42.5.935)
38. Gulbin VV, Golikov AN. 1997 A review of the prosobranch family Velutinidae in cold and temperate waters of the northern hemisphere. I. Capulacmaeinae. *Ophelia* **47**, 43–54. (doi:10.1080/00785326.1997.10433389)
39. Gulbin VV, Golikov AN. 2001 A review of the prosobranch family Velutinidae of cold and temperate waters of northern hemisphere. V. Onchidiopsinae. *Ophelia* **54**, 119–132. (doi:10.1080/00785236.2001.10409460)
40. Paine RT, Palmer AR. 1978 *Sicyases sanguineus*: a unique trophic generalist from the Chilean intertidal zone. *Copeia* **1978**, 75–80. (doi:10.2307/1443824)
41. Amson E, de Muizon C, Laurin M, Argot C, de Buffrénil V. 2014 Gradual adaptation of bone structure to aquatic lifestyle in extinct sloths from Peru. *Proc. R. Soc. B* **281**, 20140192. (doi:10.1098/rspb.2014.0192)
42. Amson E, de Muizon C. 2014 A new durophagous phocid (Mammalia: Carnivora) from the Late Neogene of Peru and considerations on monachine seals phylogeny. *J. Syst. Palaeontol.* **12**, 523–548. (doi:10.1080/14772019.2013.799610)
43. de Muizon C, Domning DP. 2002 The anatomy of *Odobenocetops* (Delphinoidea, Mammalia), the walrus-like dolphin from the Pliocene of Peru and its palaeobiological implications. *Zool. J. Linn. Soc.* **134**, 423–452. (doi:10.1046/j.1096-3642.2002.00015.x)
44. Vermeij GJ. 2001 Innovation and evolution at the edge: origins and fates of gastropods with a labral tooth. *Biol. J. Linn. Soc.* **72**, 461–508. (doi:10.1111/j.1095-8312.2001.tb01333.x)
45. Espoz C, Lindberg DR, Simison WB. 2004 Intertidal limpets of Chile and Peru. *Rev. Chil. Hist. Nat.* **77**, 257–283. (doi:10.4067/S0716-078X2004000200006)
46. Vermeij GJ. 2017 The limpet form in gastropods: evolution, distribution, and implications for the comparative study of history. *Biol. J. Linn. Soc.* **120**, 22–37.
47. McLean JR. 1984 Shell reduction and loss in fissurellids: a review of genera and species in the Fissurellidea group. *Am. Malacol. Bull.* **2**, 21–34.
48. Fulton PTL, Letts B, Shapiro B. 2012 Multiple losses of flight and recent speciation in steamer ducks. *Proc. R. Soc. B* **279**, 2339–2346. (doi:10.1098/rspb.2011.2599)
49. Harris SA, da Silva FM, Bolton JJ, Brown AC. 1986 Algal gardens and herbivory in a scavenging sandy-beach nassariid whelk. *Malacologia* **27**, 299–305.
50. Mmonwa KL, Teske PR, McQuaid CD, Barker NP. 2017 Evolution of foraging behaviour: deep intra-generic genetic divergence between territorial and non-territorial southern African patellid limpets. *Mol. Phylogenet. Evol.* **117**, 95–101. (doi:10.1016/j.ympev.2017.05.024)
51. Clements KD, Alfaro ME, Fessler JL, Westneat MW. 2004 Relationships of the temperate Australasian labrid fish tribe Odacini (Perciformes; Teleostei). *Mol. Phylogenet. Evol.* **32**, 575–587. (doi:10.1016/j.ympev.2004.02.003)
52. Darragh TA. 1991 A revision of the Australian genus *Tylospira* Harris, 1897 (Gastropoda: Struthiolariidae). *Alcheringa* **15**, 151–175. (doi:10.1080/03115519108619015)
53. Tillier S, Ponder WF. 1992 New species of *Smeagol* from Australia and New Zealand, with a discussion of the affinities of the genus (Gastropoda: Pulmonata). *J. Molluscan Stud.* **58**, 135–155. (doi:10.1093/mollus/58.2.135)
54. Enstipp R, Descamps S, Fort J, Grémillet D. 2018 Almost like a whale—first evidence of suction feeding in a seabird. *J. Exp. Biol.* **221**, jeb182170. (doi:10.1242/jeb.182170)
55. Smith NA, Clarke JA. 2015 Systematics and evolution of the Pan-Alcidae (Aves, *Charadriiformes)*. *J. Avian Biol.* **46**, 125–140. (doi:10.1111/jav.00487)
56. Cairns DK, Gaston AJ, Huettmann F. 2008 Endothermy, ectothermy and the global structure of marine vertebrate communities. *Mar. Ecol. Prog. Ser.* **356**, 239–250. (doi:10.3354/meps07286)
57. Bom RA, de Fouw J, Klaassen RHG, Piersma T, Lavaleye MSS, Ens BJ, Oudman T, van Gils JA. 2018 Food web consequences of an evolutionary arms race: molluscs subject to crab predation on intertidal mudflats in Oman are unavailable to shorebirds. *J. Biogeogr.* **45**, 342–354. (doi:10.1111/jbi.13123)
58. Rothman MC, Mattio L, Person RJ, Bolton JJ. 2017 A phylogeographic investigation of the kelp genus *Laminaria* (Laminariales, Phaeophyceae), with emphasis on the South Atlantic Ocean. *J. Phycol.* **53**, 778–789. (doi:10.1111/jpy.12544)
59. Kensley BF. 1985 The faunal deposits of a Late Pleistocene raised beach at Milnerton, Cape Province, South Africa. *Ann. S. Afr. Mus.* **95**, 111–122.
60. Vermeij GJ. 2013 On escalation. *Annu. Rev. Earth Planet. Sci.* **41**, 1–19. (doi:10.1146/annurev-earth-050212-124123)