REVIEW SUMMARY

VERTEBRATE EVOLUTION

Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene

Neil P. Kelley^{1,2*} and Nicholas D. Pyenson^{1,3}

BACKGROUND: More than 30 different lineages of amphibians, reptiles, birds, and mammals have independently invaded oceans ecosystems. Prominent examples include ichthyosaurs and mosasaurs during the Mesozoic (252 to 66 million years ago) and penguins and sea otters during the Cenozoic (66 million years ago to the present). In today's oceans, marine tetrapods are ecologically important consumers with trophic influence disproportionate to their abundance. They have occupied apex roles in ocean food webs for more than 250 million years, through major changes in ocean and climate, and through mass ex-

tinctions. Major paleontological discoveries in the past 40 years have clarified the early landsea transitions for some marine tetrapods (e.g., whales, sea cows), although the terrestrial origins of many lineages remain obscure. Incipient invasions appear frequently in marine tetrapod history, but such early transitions account for only a small proportion of the total fossil record of successful marine lineages, which in some cases persist for hundreds of millions of years.

ADVANCES: Marine tetrapods provide ideal models for testing macroevolutionary hypotheses because the repeated transitions between



CREDIT: SILHOUETTES FROM PHYLOPIC.ORG



land and sea have driven innovation, convergence, and diversification against a backdrop of changing marine ecosystems and mass extinctions. Recent investigations across a broad range of scales-from molecules to food webshave clarified the phylogenetic scope, timing, and ecological consequences of these repeated innovations. Studies of the physiology and functional morphology of living species have illuminated the constraints and tradeoffs that

ON OUR WEB SITE

Read the full article at http://dx.doi. org/10.1126/ science.aaa3716

shape the pathway of initial marine invasions. Comparative studies on muscle myoglobin concentration or the evolution of sex determination mechanisms. for example, have revealed

rampant convergence for these adaptive traits in the marine realm. Exceptionally preserved fossils have also revealed insights into reproductive biology, soft tissue structures, and trophic interactions. Fossils provide critical baselines for understanding historical changes in marine communities and diversity through time, and these baselines remain vital for evaluating the ongoing and severe anthropogenic disturbance to marine tetrapod populations and marine ecosystems as a whole.

OUTLOOK: Technological advances in remote sensing and biologging will continue to provide crucial insights into the macroecology of marine tetrapods below the water's edge. Field data, when combined with extensive vouchers represented in museum collections, provide the basis for integrative models of the function and ecology of these logistically challenging organisms. Placed in a phylogenetic comparative framework, these data can enable tests of hypotheses about macroevolutionary patterns. Although perpetually incomplete, new fossil discoveries continue to improve our understanding of the early land-sea transitions in lineages and reveal past ecologies that could not have otherwise been predicted. Emerging imaging, molecular, and isotopic techniques provide an opportunity to expand the investigational scope for studying extinct taxa and to inform our understanding of how living species evolved. Lastly, resolving the full evolutionary scope of marine tetrapod history provides context for the origins of modern ecological patterns and interactions, which are fundamentally being altered by human activities.

¹Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA. ²Department of Earth and Environmental Sciences. Vanderbilt University, Nashville, TN 37240, USA ³Departments of Mammalogy and Paleontology, Burke Museum of Natural History and Culture, Seattle, WA 98195, USA.*Corresponding author. E-mail: kelleynp@si.edu Cite this article as N. P. Kelley, N. D. Pyenson, Science 348, aaa3716 (2015). DOI:10.1126/science.aaa3716

REVIEW

VERTEBRATE EVOLUTION

Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene

Neil P. Kelley^{1,2*} and Nicholas D. Pyenson^{1,3}

Many top consumers in today's oceans are marine tetrapods, a collection of lineages independently derived from terrestrial ancestors. The fossil record illuminates their transitions from land to sea, yet these initial invasions account for a small proportion of their evolutionary history. We review the history of marine invasions that drove major changes in anatomy, physiology, and ecology over more than 250 million years. Many innovations evolved convergently in multiple clades, whereas others are unique to individual lineages. The evolutionary arcs of these ecologically important clades are framed against the backdrop of mass extinctions and regime shifts in ocean ecosystems. Past and present human disruptions to marine tetrapods, with cascading impacts on marine ecosystems, underscore the need to link macroecology with evolutionary change.

ore than 30 lineages of tetrapods (amphibians, reptiles, birds, and mammals) independently invaded marine ecosystems during the Phanerozoic (Fig. 1). Such repeated transitions from terrestrial or freshwater to marine habitats are generally uncommon in other clades (1). Reconfigurations in morphology, physiology, life history, and sensory systems characterize each transition. For example, differential constraints on movement between these realms—gravity on land versus drag in water—led to similar locomotory adaptations in marine tetrapods (2) (Fig. 2).

Sequences of fossil cetaceans (3) and sirenians (4) from Eocene rocks provide the best examples of major morphological transformations following marine invasions. Both groups show pelvic decoupling from the vertebral column and subsequent reduction of the pelvis and hindlimbs; later specializations included forelimb streamlining, tail propulsion, and posterior migration of the nostrils. Unfortunately, the early histories of most other marine tetrapod lineages remain obscure. For example, the freshwater carnivoran Puijila darwini provides clues about the origins of pinnipeds (5), but it is geologically younger than other marine stem pinnipeds (6) and is thus not likely a direct ancestor of modern pinnipeds. Likewise, semi-aquatic Permian reptiles, initially proposed to represent plesiosaur ancestors (7), are not closely related to plesiosaurs in recent analyses (8); the Early Cretaceous turtle Santanachelys (9) was once viewed as a stem predecessor to modern sea turtles, but this position is no longer supported (10). Thus, origins of several important marine tetrapod groups remain essentially unknown, with the oldest known fossil representatives exhibiting derived morphologies without obvious terrestrial antecedents. Prominent examples include penguins (11) and ichthyosaurs (12), although the recently described basal ichthyosauriform *Cartorhynchus* may clarify the origins of the latter (13).

The history of terrestrial-marine transitions reveals links between Earth system changes and marine tetrapod invasions, modulated by ecology and physiology. Marine transgressions and warming episodes coincided with Mesozoic and Early Cenozoic marine tetrapod invasions (3, 4, 14-18). Modern marginal marine tetrapods are concentrated in low-latitude mangroves, estuaries, and archipelagos (19). The paleoenvironmental context of marginal marine tetrapod fossils (7, 20) likewise indicates that warm, shallow marginal marine habitats provide favorable settings for terrestrial-marine transitions, especially in ectotherms. Conversely, mid-Cenozoic cooling and increases in marine productivity-particularly in the North Pacific and Southern Ocean-coincided with bird and mammal invasions (21, 22), and these regions remain hotspots of marine mammal diversity (23). However, such relationships are not always rigid throughout the history of a clade: Cetaceans evolved in shallow equatorial seas (18) but now thrive in high-latitude oceans; the origin of penguins preceded Southern Hemisphere cooling by several million years (24).

Studies of living marginal marine species illuminate ecological (25, 26), functional (2, 27–29), and physiological (30–32) pathways that facilitate transitions. A common theme is the high degree of plasticity in ecologically marginal taxa (26, 28, 31). Isotopic investigations of fossils suggest similar patterns, demonstrating mixed habitat and resource use (*33*). Repeated independent invasions among some clades suggest that certain ecologies and/or body plans may predispose groups to marine transitions. Independent adaptation to marine lifestyles among close relatives simultaneously or in close succession would complicate efforts to decipher and enumerate transitions in the fossil record (*34, 35*).

Convergent evolution from molecules to morphology

Marine tetrapods provide canonical illustrations of evolutionary convergence (Fig. 2) (36), widely regarded as repeated solutions to problems imposed by physical contrasts between land and water. Simple visual comparisons, however, cannot fully decipher the processes that shape evolutionary convergence. Apparent similarities can mask differences in functional performance (37), and mechanical convergence can be achieved with alternative morphological solutions, often constrained by phylogeny (38). Thus, the dorsoventral caudal propulsion of cetaceans derives from the bounding locomotory mode of terrestrial mammalian ancestors (2), while the lateral caudal propulsion of ichthyosaurs evolved from the locomotion of lizard-like predecessors (39).

Quantitative functional morphology provides a means to quantify and compare performance and functional trade-offs, particularly in species that spend time both on land and in the water, such as snakes (29) and pinnipeds (40). Functional trade-offs can ultimately drive specialization and steer evolutionary convergence, as with repeated loss of flight among seabirds specialized for aquatic locomotion (41). In vivo studies of feeding performance provide similar insight into functional trade-offs and specialization (42–44), which shaped convergence in marine tetrapod feeding systems (45).

Increased bone density evolved repeatedly in coastal marine tetrapods for stability and buoyancy regulation (46-51). Conversely, decreased bone density has evolved among many pelagic groups, reducing the costs of sustained swimming, or as a consequence of increased growth rates (50). Some lineages, such as cetaceans (48, 49), ichthyosaurs (13, 49), and sauropterygians (51), transitioned through these contrasting phases sequentially, with increased bone density during early evolution followed by reduced bone density after open marine adaptation. The evolution of insulating structures in marine mammals follows a similar progression, with thick fur in coastal invaders replaced by thick insulating fat for energy storage and streamlining in more oceanic marine mammals (52). Fossil anatomy reveals the evolution of countercurrent heat exchange in penguins (53), convergent with similar systems in marine mammals.

The scope of recent studies of convergent evolution extends beyond morphology to include molecular physiology (54), metabolism and thermoregulation (55, 56), and life history (56, 57). Genomic investigations have revealed convergent genetic origins of important innovations, such as

¹Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA. ²Department of Earth and Environmental Sciences, Vanderbilt University, Nashville, TN 37240, USA. ³Departments of Mammalogy and Paleontology, Burke Museum of Natural History and Culture, Seattle, WA 98195, USA. *Corresponding author. E-mail: kelleynp@si.edu



Fig. 1. Temporal and phylogenetic distribution of marine tetrapod groups. Circles indicate first appearance datum (FAD) for each lineage based on fossils, or divergence estimates for groups lacking a fossil record (136); daggers denote extinctions. Marine tetrapod taxa are numbered in order of appearance in the fossil record: (1) Mesosauria, (2) Trematosauria, (3) Ichthyosauromorpha, (4) Sauropterygia, (5) Thalattosauriformes, (6) Tanystropheidae, (7) Thalattosuchia, (8) Pleurosauridae, (9) Plesiochelyidae, (10) Pholidosauridae, (11) Simiolophiidae, (12) Mosasauroidea, (13) Protostegidae, (14) Hesperornithiformes, (15) Chelonioidea, (16) Dyrosauridae, (17) Acrochordoidea, (18) Sphenisciformes, (19) Cetacea, (20) Sirenia, (21) Gryposuchinae, (22) Plotopteridae, (23) Alcidae, (24) Pinnipedimorpha, (25) Desmostylia, (26) Laticaudini, (27) Hydrophiini, (28) *Thalassocnus*, (29) *Pelecanoides*, (30) *Tachyeres*, (31) *Enhydra*, (32) *Ursus maritimus*, (33) *Amblyrhynchus*. Colored boxes match convergent taxa shown in Fig. 2, A to D. Ma, millions of years ago. (Silhouettes from phylopic.org; see supplementary materials for usage and attribution details.)

sex determination mechanisms (58), myoglobin adaptations facilitating deep diving (54), and echolocation (59). Stable isotopes from fossils elucidate parallel histories of habitat shift in early cetaceans and sirenians (33) and convergent evolution of endothermy in Mesozoic marine reptiles (53). Recent breakthroughs in fossil pigment reconstruction have resolved structural and pigment adaptations in fossil seabird feathers (60) and have revealed widespread dark coloration in fossil marine reptiles, possibly for temperature regulation or ultraviolet light protection (55).

Exceptionally preserved fossils (57, 61, 62) document convergent reproductive adaptations in marine reptiles. Recently discovered early ichthyosaur fossils (62) extend the history of viviparity in this group back to the Early Triassic and indicate that viviparity evolved in terrestrial forerunners as an enabling factor for, rather than an adaptive response to, aquatic life. Fossils suggest that some marine reptiles converged upon K-selected life histories observed among marine mammals (57). Aquatic birth evolved early in cetacean and sirenian evolution, but these transitions are so far only partly constrained by fossils (63).

Causes and consequences of convergence, innovation, and radiation

In addition to external drivers, convergent evolution is shaped by the underlying genetic and developmental pathways that give rise to convergent structures. Thus, repeated evolution of hydrodynamic limbs (Fig. 2E) (64) and axial modifications (65) likely exploited parallel developmental mechanisms. Such shared pathways may extend to the level of gene regulation linking genomic and phenotypic convergence and innovation. Recent work on marine mammal genomic convergence has questioned the prevalence of such linkages (66); however, more work is needed to evaluate potential scaling of convergence from gene to phenotype.

Innovations facilitate and constrain downstream evolution, as illustrated in the discrete pathways from drag-based to lift-based swimming in limband tail-propelled aquatic mammals (2). Likewise, independent innovation of aquatic birth in multiple marine reptile and marine mammal lineages removed the constraints of terrestrial locomotion, enabling limb and skeletal modification to increase swimming performance, as well as gigantism in some clades. Convergent evolutionary pathways [e.g., the emergence of taildriven locomotion in ichthyosaurs, mosasaurs, and whales (Fig. 2A)] might follow similar tempos across groups (67), but this hypothesis awaits further testing.

Particularly diverse clades have frequently been characterized as adaptive radiations facilitated by new ecological opportunities after marine invasions (*68*). However, external factors may be equally important in shaping and pacing these radiations (*69*). Although diverse clades are often ecologically and morphologically disparate, as predicted under adaptive radiation models (*70*), diversity and disparity are not tightly coupled in other radiations (*71*).

Diversification can be triggered by innovations that occur well after initial invasions. For example, echolocation and baleen-two key innovations that evolved tens of millions of years after whales first entered the oceans-mark the emergence of crown cetaceans (72), the most speciesrich marine tetrapod clade. Hydrophiine sea snakes, which entered marine environments in the last 6 million years and now comprise at least 60 species (71, 73), provide a key example of a marine tetrapod group in the midst of major radiation. Even within this group, diversity is heterogeneously distributed within subclades and linked to specific intraclade innovations, rather than simply reflecting rapid niche expansion after initial marine invasion (71).

Iterative evolution and ecological turnover

Marine tetrapods first diversified during the restructuring of marine ecosystems that followed



Fig. 2. Convergent morphology in marine tetrapods. Similar anatomy evolved among lineages that independently adopted marine lifestyles. From top to bottom: (**A**) early whale *Dorudon*, mosasaur *Platecarpus*, ichthyosaur *Cymbospondylus* (scale bars, 1 m); (**B**) ichthyosaur *Stenopterygius*, dolphin *Stenella*; (**C**) early seal *Acrophoca*, sauropterygian *Nothosaurus* (scale bars, 50 cm); (**D**) penguin *Pygoscelis* (left), great auk *Pinguinus* (right). (**E**) Forelimbs of select marine tetrapods (from left to right: ichthyosaur, mosasaur, whale, sea turtle, sea lion, penguin) showing anatomical convergence reflecting limb streamlining [adapted from (*36*, *64*)]. Colors identify homologous elements labeled on ichthyosaur: H, humerus (pink); R, radius (yellow); U, ulna (orange); c, carpals (blue); m, metacarpals (green); p, phalanges (white). Phylogeny and contrasting locomotory patterns account for finer scale differences, such as proportionally longer humeri in forelimb-driven swimmers (sea turtle, sea lion, penguin) relative to tail-driven swimmers (ichthyosaur, mosasaur, whale). See supplementary materials for image sources.

the end-Permian mass extinction, and the rise of the so-called "Modern Fauna" (74). Their appearance has been characterized as a final step in the bottom-up reassembly of marine ecosystems after a delayed recovery (75, 76). However, the early appearance of predatory marine tetrapods in the Triassic has recently been cited as evidence that recovery was not delayed after all (77). Although later Mesozoic and Cenozoic invasions replaced these early groups, marine tetrapods have remained a persistent fixture of marine ecosystems since the Triassic. Some replacements coincided with mass extinctions (Fig. 1) (78); others were staggered across intervals of gradual faunal change (78, 79).

Persistent biological processes such as competition ("Red Queen") and stochastic environmental factors ("Court Jester") (*80*) may regulate marine tetrapod community structure and diversity at different time scales (*81*). Pelagic habitats are typically dominated by one or two cosmopolitan marine tetrapod clades with long histories [e.g., ichthyosaurs from the Triassic to Cretaceous (*78*), plesiosaurs from the Jurassic to the Cretaceous-Paleogene (K-Pg) boundary (*78*), cetaceans since the Eocene (*3*)]. Near-shore communities often host more lineages with higher endemism and frequent turnover (16, 82–84). Specific spatial and temporal successions hint at competitive interactions, as among flightless seabirds and marine mammals competing for shore space (22), replacement of herbivorous desmostylians by sirenians in the North Pacific (82), and replacement of phocids by otariids in South America (83).

These episodes of replacement between lineages are mirrored by iterative patterns within lineages. For example, evolution of herbivory and durophagy (feeding on hard-shelled prey) drove repeated convergent feeding morphologies in living and fossil sea turtles (85). Similarly, independent invasions of freshwater ecosystems by different odontocete lineages gave rise to a convergent "river dolphin" morphotype (86). Ecological interactions among sympatric relatives also drive iterative evolution. Multispecies fossil sirenian assemblages show parallel patterns of ecomorphological partitioning (82), contrasting with the relictual and disjunct distribution of living species. Sympatric or parapatric ecomorphs observed in widely distributed odontocetes (87, 88) have arisen through niche differentiation and onshore-offshore partitioning. Cryptic speciation and iteration is common among sea snakes, with repeated parallel evolution of morphotypes (71). Iterative evolution and resource partitioning may account for contrasting morphotypes in co-occurring fossil taxa (82, 89) and repeated evolution of certain morphotypes, such as polyphyletic "pliosaurs" (90).

Marine tetrapods themselves constituted an important trophic resource for other species in Mesozoic ecosystems beginning in the Triassic (76). Intriguingly, although hypercarnivory evolved repeatedly among Cenozoic marine mammals (91, 92), many lineages later specialized on resources at lower trophic levels. Hypercarnivorous species that regularly consume other tetrapods are comparatively rare in modern oceans, represented only by killer whales, leopard seals, and marginal marine crocodiles, all generalist predators that also feed regularly at lower trophic levels (42, 88). The comparative rarity of hypercarnivorous marine tetrapods in modern oceans may reflect different structuring of Mesozoic, Early Cenozoic, and modern marine food webs.

Contrasting Mesozoic and Cenozoic patterns of fossil richness

Patterns in raw marine tetrapod fossil species richness (Fig. 3) resemble those observed in the marine invertebrate record (*93–95*). Fluctuating Mesozoic diversity reflects repeated extinctions of incumbent clades (Fig. 1) followed by diversification of new groups (*78*) as well as geologic biases on the marine tetrapod fossil record (*14*). Contrasting patterns between coastal and pelagic Mesozoic marine tetrapod groups (*14*, *15*) point to "common-cause" dynamics, whereby geologic processes that affect marine diversity also control sedimentary rock accumulation (*95*). The pronounced drop in richness at the K-Pg boundary corresponds to the simultaneous extinction of mosasaurs, plesiosaurs, and other lineages (Figs. 1 and 3).



Fig. 3. Marine tetrapod fossil richness. Raw marine tetrapod fossil occurrence binned at intervals of ~10 million years [from (*81*)] and marine invertebrate genera [from (*94*)]. Both groups show episodic variation in fossil richness during the Mesozoic ending with abrupt drop at the K-Pg mass extinction, followed by continually increasing richness during the Cenozoic. Partial correspondence with marine transgression/regression [second order, cycles of ~10 to 100 million years, from (*134*)] suggests influence of sea level on shallow marine diversity and/or rock record bias, particularly in the Mesozoic.

After the K-Pg mass extinction, Early Cenozoic diversification of cetaceans (3), sirenians (96), and penguins (24, 97) brought Paleogene marine tetrapod richness back to peak Mesozoic levels. The emergence of crown cetaceans (72) and the invasion of pinnipeds (21), along with other groups, coincide with a marked increase in fossil richness to even higher levels. The apparent Cenozoic marine tetrapod diversity increase, like marine invertebrate richness (94), may be inflated by preservation biases (e.g., "pull of the recent"). However, recent investigations of fossil invertebrates (93) and marine mammals (98, 99) propose that increasing Cenozoic richness largely reflects a real biological signal. Fossil bias has been evaluated for some marine tetrapod groups (14, 98), but integrated comparisons of biases across the Mesozoic and Cenozoic are still needed.

Changes in ocean productivity regimes (100) and ecological escalation (101) may help to explain the differing trajectories of Cenozoic and Mesozoic marine tetrapod diversification. Exceptional diversification rates of eutherian mammals (102) might also account for increasing Cenozoic diversity, given the repeated marine invasions of placental mammals during the Cenozoic. However, other groups with elevated diversification rates, including Neoaves and squamates, also invaded marine ecosystems with varying degrees of success, indicating that phylogenetic differences alone cannot account for these differences.

Increasing marine tetrapod diversity since the Mesozoic also tracks increasing marine resources and expanding niches. Clear evidence of herbivory is unknown among marine reptiles until herbivorous sea turtles evolved, coincident with the first seagrasses in the Cretaceous (85), which is consistent with "delayed herbivory" in other marine clades (103). Likewise, there is no evidence for pelagic suspension-feeding marine tetrapods in the Mesozoic (104) and little evidence for deepdiving mesopelagic feeders until the Jurassic (37). These absent ecologies suggest that Early Mesozoic marine food webs were less complex than modern equivalents.

Shifted baselines and marine tetrapod macroecology since the Pleistocene

Marine tetrapod and hominid ecological interactions began at least by the Late Pleistocene, with evidence for Neandertal (*Homo neanderthalensis*) exploitation of marine mammals in Gibraltar, Spain (105). Humans have continued to directly and indirectly interact with marine ecosystems ever since this time (106). Although these impacts have lagged behind profound human perturbations to terrestrial ecosystems, technological innovation has escalated their rate and magnitude in recent centuries (107).

The extinction of Steller's sea cow (*Hydro-damalis gigas*) marks the first well-documented marine mammal species extinction in historic times (*108*). Hunting brought some cetacean species perilously close to extinction (*109*) and exterminated at least two pinniped species (*110, 111*). Historically, several marine mammal species were thought extinct until refugial populations were rediscovered (*112, 113*). Seabirds have been similarly vulnerable to human hunting, with historic and prehistoric extinctions of large flightless

seabirds (114–116) and others critically endangered (117). Many living marine reptiles also risk extinction—including six of seven sea turtle species—largely because of human exploitation and habitat alteration (117). The conservation status of many marine tetrapod species is poorly known because of the difficulties of studying wild marine populations.

The only cetacean extinction at human hands, the Yangtze River dolphin (*Lipotes*), was largely caused by habitat degradation (*118*). Before the end of this decade, another cetacean, the vaquita (*Phocoena sinus*), may be driven extinct through by-catch in small-scale fisheries in the Gulf of California (*119*). Such indirect impacts are a growing concern, with recent attention turning to ship collisions (*120*), shipping noise (*121*), military sonar (*122*), microplastics (*123*), and humanborne pathogens (*124*), among other emerging threats (*107*).

Anthropogenic climate change is already driving changes in marine tetrapod populations, particularly in polar ecosystems (125). Shrinking sea ice and changing ocean thermal gradients are also driving range shifts, most strikingly documented by repeated recent dispersal from the Pacific into the Atlantic by gray whales (Eschrichtius) via an ice-free northwest passage (126), potentially anticipating a recolonization of the Atlantic following extirpation four centuries ago (127). Global warming may have major impacts on ectothermic marine reptiles, potentially altering range limits, activity levels (128), and even the sex ratio in species with temperature-dependent reproduction (129). Potential feedbacks between anthropogenic warming and complex climate dynamics such as El Niño-known to trigger marine tetrapod population collapses (130)-suggest that impacts of climate change on marine tetrapods may be abrupt, episodic, and difficult to predict (100).

Anthropogenic declines in marine mammal populations also have downstream effects on marine food webs (131) via trophic cascades, for example, with killer whale-sea otter-mysticete interactions off southeast Alaska (132) and mysticete-sealpenguin interactions in the Southern Ocean (133). Emerging technologies such as animal-borne recording devices (used in biologging) promise to reveal new details about marine tetrapod ecology (134) and the state of the oceans themselves, such as information about ocean currents provided by biologged data (135).

Conclusions

Despite their status as conservation icons, major questions remain concerning marine tetrapod macroecology, morphology, and even alpha taxonomy. New discoveries and new techniques are helping to frame and test hypotheses about marine tetrapod evolution. Realizing the full potential of these advances requires integrating data sets from disparate disciplines to address unifying questions in ecology, evolutionary biology, and Earth systems history. Marine tetrapods have been ecologically influential members of ocean food webs since the end-Permian mass extinction, persisting through later mass extinctions, anoxic events, and ocean restructuring. The ecological importance of marine tetrapods in modern food webs raises questions about their role during major episodes of change and their sensitivity to bottom-up perturbations in the past. Evaluating the place of tetrapods in contemporary ocean ecosystems also requires accounting for shifts from baseline abundances driven by human activities. Understanding the full history of marine tetrapods provides necessary context for constraining the scope of potential future shifts in marine ecosystems.

REFERENCES AND NOTES

- G. J. Vermeij, R. Dudley, Why are there so few evolutionary transitions between aquatic and terrestrial ecosystems? *Biol. J. Linn. Soc. London* **70**, 541–554 (2000). doi: 10.1111/ j.1095-8312.2000.tb00216.x
- 2. F. E. Fish, Transitions from drag-based to lift-based propulsion in mammalian swimming. *Am. Zool.* **36**, 628–641 (1996).
- M. D. Uhen, The origin(s) of whales. Annu. Rev. Earth Sci. 38, 189–219 (2010). doi: 10.1146/annurev-earth-040809-152453
- D. P. Domning, The earliest known fully quadrupedal sirenian. Nature 413, 625–627 (2001). doi: 10.1038/35098072; pmid: 11675784
- N. Rybczynski, M. R. Dawson, R. H. Tedford, A semi-aquatic Arctic mammalian carnivore from the Miocene epoch and origin of Pinnipedia. *Nature* 458, 1021–1024 (2009). doi: 10.1038/nature07985; pmid: 19396145
- A. Berta, C. E. Ray, A. R. Wyss, Skeleton of the oldest known pinniped, *Enaliarctos mealsi. Science* 244, 60–62 (1989). doi: 10.1126/science.244.4900.60; pmid: 17818847
- R. L. Carroll, Plesiosaur ancestors from the Upper Permian of Madagascar. *Philos. Trans. R. Soc. London Ser. B* 293, 315–383 (1981). doi: 10.1098/rstb.1981.0079
- J. M. Neenan, N. Klein, T. M. Scheyer, European origin of placodont marine reptiles and the evolution of crushing dentition in Placodontia. *Nat. Commun.* 4, 1621 (2013). doi: 10.1038/ncomms2633
- R. Hirayama, Oldest known sea turtle. *Nature* **392**, 705–708 (1998). doi: 10.1038/33669
- W. G. Joyce, J. F. Parham, T. R. Lyson, R. C. Warnock, P. C. Donoghue, A divergence dating analysis of turtles using fossil calibrations: An example of best practices. *J. Paleontol.* 87, 612–634 (2013). doi: 10.1666/12-149
- D. T. Ksepka, S. Bertelli, N. P. Giannini, The phylogeny of the living and fossil Sphenisciformes (penguins). *Cladistics* 22, 412–441 (2006). doi: 10.1111/j.1096-0031.2006.00116.x
- M. W. Maisch, Phylogeny, systematics, and origin of the lchthyosauria—the state of the art. *Palaeodiversity* 3, 151–214 (2010).
- R. Motani et al., A basal ichthyosauriform with a short snout from the Lower Triassic of China. Nature 517, 485–488 (2015). doi: 10.1038/nature13866
- R. B. Benson, R. J. Butler, Uncovering the diversification history of marine tetrapods: Ecology influences the effect of geological sampling biases. *Geol. Soc. London Spec. Publ.* 358, 191–208 (2011). doi: 10.1144/SP358.13
- N. P. Kelley, R. Motani, D. Y. Jiang, O. Rieppel, L. Schmitz, Selective extinction of Triassic marine reptiles during long-term sea-level changes illuminated by seawater strontium isotopes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 400, 9–16 (2014). doi: 10.1016/j.palaeo.2012.07.026
- J. E. Martin, R. Amiot, C. Lécuyer, M. J. Benton, Sea surface temperature contributes to marine crocodylomorph evolution. *Nat. Commun.* 5, 4658 (2014). doi: 10.1038/ ncomms5658
- N. Bardet, A. Houssaye, J. C. Rage, X. Pereda Suberbiola, The Cenomanian-Turonian (Late Cretaceous) radiation of marine squamates (Reptilia): The role of the Mediterranean Tethys. *Bull. Soc. Geol. Fr.* **179**, 605–622 (2008). doi: 10.2113/ gssgfbull.179.6.605
- P. D. Gingerich, N. A. Wells, D. E. Russell, S. M. Shah, Origin of whales in epicontinental remnant seas: New evidence from the early Eocene of Pakistan. *Science* 220, 403–406 (1983). doi: 10.1126/science.220.4595.403; pmid: 17831411
- J. C. Murphy, Marine invasions by non-sea snakes, with thoughts on terrestrial-aquatic-marine transitions. *Integr. Comp. Biol.* 52, 217–226 (2012). doi: 10.1093/icb/ics060; pmid: 22576813

- G. Piñeiro, A. Ramos, C. Goso, F. Scarabino, M. Laurin, Unusual environmental conditions preserve a Permian mesosaur-bearing Konservat-Lagerstätte from Uruguay. *Acta Palaeontol. Pol.* 57, 299–318 (2011). doi: 10.4202/ app.2010.0113
- T. A. Deméré, A. Berta, P. J. Adam, Pinnipedimorph evolutionary biogeography. *Bull. Am. Mus. Nat. Hist.* **279**, 32–76 (2003). doi: 10.1206/0003-0090(2003)279<0032: C>2.0.C0;2
- T. Ando, R. E. Fordyce, Evolutionary drivers for flightless, wing-propelled divers in the Northern and Southern Hemispheres. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 400, 50–61 (2014). doi: 10.1016/j.palaeo.2013.08.002
- D. P. Tittensor *et al.*, Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**, 1098–1101 (2010). doi: 10.1038/nature09329; pmid: 20668450
- J. A. Clarke *et al.*, Paleogene equatorial penguins challenge the proposed relationship between biogeography, diversity, and Cenozoic climate change. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 11545–11550 (2007). doi: 10.1073/pnas.0611099104; pmid: 17601778
- W. A. Buttemer, W. R. Dawson, Temporal pattern of foraging and microhabitat use by Galapagos marine iguanas, *Amblyrhynchus cristatus. Oecologia* 96, 56–64 (1993). doi: 10.1007/BF00318031
- D. H. Monson, J. A. Estes, J. L. Bodkin, D. B. Siniff, Life history plasticity and population regulation in sea otters. *Oikos* **90**, 457–468 (2000). doi: 10.1034/j.1600-0706.2000.900304.x
- T. M. Williams, The evolution of cost efficient swimming in marine mammals: Limits to energetic optimization. *Philos. Trans. R. Soc. London Ser. B* **354**, 193–201 (1999). doi: 10.1098/rstb.1999.0371
- F. Aubret, X. Bonnet, R. Shine, The role of adaptive plasticity in a major evolutionary transition: Early aquatic experience affects locomotor performance of terrestrial snakes. *Funct. Ecol.* 21, 1154–1161 (2007). doi: 10.1111/j.1365-2435.2007.01310.x
- F. Aubret, R. Shine, The origin of evolutionary innovations: Locomotor consequences of tail shape in aquatic snakes. *Funct. Ecol.* 22, 317–322 (2008). doi: 10.1111/j.1365-2435.2007.01359.x
- D. P. Costa, G. L. Kooyman, Contribution of specific dynamic action to heat balance and thermoregulation in the sea otter *Enhydra lutris. Physiol. Zool.* 57, 199–203 (1984).
- R. L. Cramp, E. A. Meyer, N. Sparks, C. E. Franklin, Functional and morphological plasticity of crocodile (*Crocodylus porosus*) salt glands. *J. Exp. Biol.* **211**, 1482–1489 (2008). doi: 10.1242/jeb.015636; pmid: 18424682
- F. Brischoux, Y. V. Kornilev, Hypernatremia in dice snakes (*Natrix* tessellata) from a coastal population: Implications for osmoregulation in marine snake prototypes. *PLOS ONE* 9, e92617 (2014). doi: 10.1371/journal.pone.0092617
- M. T. Clementz, A. Goswami, P. D. Gingerich, P. L. Koch, Isotopic records from early whales and sea cows: Contrasting patterns of ecological transition. J. Vertebr. Paleontol. 26, 355–370 (2006). doi: 10.1671/0272-4634(2006)26[355: IRFEWA12.0.CO:2
- M. W. Caldwell, A challenge to categories: "What, if anything, is a mosasaur?" *Bull. Soc. Geol. Fr.* 183, 7–34 (2012). doi: 10.2113/gssgfbull.183.1.7
- X. H. Chen, R. Motani, L. Cheng, D. Y. Jiang, O. Rieppel, The enigmatic marine reptile Nanchangosaurus from the Lower Triassic of Hubei, China and the phylogenetic affinities of Hupehsuchia. *PLOS ONE* 9, e102361 (2014). doi: 10.1371/ iournal.oone.0102361
- A. B. Howell, Aquatic Mammals: Their Adaptations to Life in the Water (Charles C. Thomas, Baltimore, MD, 1930).
- R. Motani et al., Absence of suction feeding ichthyosaurs and its implications for Triassic mesopelagic paleoecology. PLOS ONE 8, e66075 (2013). doi: 10.1371/journal. pone.0066075
- P. C. Wainwright, M. E. Alfaro, D. I. Bolnick, C. D. Hulsey, Many-to-one mapping of form to function: A general principle in organismal design? *Integr. Comp. Biol.* 45, 256–262 (2005). doi: 10.1093/icb/45.2.256; printi: 21676769
- R. Motani, H. You, C. McGowan, Eel-like swimming in the earliest ichthyosaurs. *Nature* 382, 347–348 (1996). doi: 10.1038/382347a0
- J. N. Garrett, F. E. Fish, Kinematics of terrestrial locomotion in harbor seals and gray seals: Importance of spinal flexion by amphibious phocids. *Mar. Mamm. Sci.* 10.1111/mms.12170 (2014). doi: 10.1111/mms.12170

- K. H. Elliott *et al.*, High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 9380–9384 (2013). doi: 10.1073/pnas.1304838110; pmid: 23690614
- D. P. Hocking, A. R. Evans, E. M. Fitzgerald, Leopard seals (*Hydrurga leptonyx*) use suction and filter feeding when hunting small prey underwater. *Polar Biol.* **36**, 211–222 (2013). doi: 10.1007/s00300-012-1253-9
- E. A. Kane, C. D. Marshall, Comparative feeding kinematics and performance of odontocetes: Belugas, Pacific white-sided dolphins and long-finned pilot whales. *J. Exp. Biol.* **212**, 3939–3950 (2009). doi: 10.1242/jeb.034686; pmid: 19946072
- J. A. Goldbogen, N. D. Pyenson, R. E. Shadwick, Big gulps require high drag for fin whale lunge feeding. *Mar. Ecol. Prog. Ser.* 349, 289–301 (2007). doi: 10.3354/meps07066
- N. P. Kelley, R. Motani, Trophic convergence drives morphological convergence in marine tetrapods. *Biol. Lett.* **11**, 20140709 (2015). doi: 10.1098/rsbl.2014.0709; pmid: 25631228
- A. Houssaye, "Pachyostosis" in aquatic amniotes: A review. Integr. Zool 4, 325–340 (2009). doi: 10.1111/j.1749-4877.2009.00146.x; pmid: 21392306
- E. Amson, C. de Muizon, M. Laurin, C. Argot, V. de Buffrénil, Gradual adaptation of bone structure to aquatic lifestyle in extinct sloths from Peru. Proc. R. Soc. B 281, 20140192 (2014). doi: 10.1098/rspb.2014.0192; pmid: 24621950
- N. M. Gray, K. Kainec, S. Madar, L. Tomko, S. Wolfe, Sink or swim? Bone density as a mechanism for buoyancy control in early cetaceans. *Anat. Rec.* 290, 638–653 (2007). doi: 10.1002/ar.20533; pmid: 17516430
- A. Houssaye, P. Tafforeau, C. de Muizon, P. D. Gingerich, Transition of Eocene whales from land to sea: Evidence from bone microstructure. *PLOS ONE* **10**, e0118409 (2015). doi: 10.1371/journal.pone.0118409
- A. Houssaye, T. M. Scheyer, C. Kolb, V. Fischer, P. M. Sander, A new look at ichthyosaur long bone microanatomy and histology: Implications for their adaptation to an aquatic life. *PLOS ONE* 9, e95637 (2014). doi: 10.1371/journal. pone.0095637
- A. Krahl, N. Klein, P. M. Sander, Evolutionary implications of the divergent long bone histologies of *Nothosaurus* and *Pistosaurus* (Sauropterygia, Triassic). *BMC Evol. Biol.* 13, 123 (2013). doi: 10.1186/1471-2148-13-123; pmid: 23773234
- H. E. Liwanag, A. Berta, D. P. Costa, S. M. Budge, T. M. Williams, Morphological and thermal properties of mammalian insulation: The evolutionary transition to blubber in pinnipeds. *Biol. J. Linn. Soc.* **107**, 774–787 (2012). doi: 10.1111/j.1095-8312.2012.01992.x
- D. B. Thomas, D. T. Ksepka, R. E. Fordyce, Penguin heat-retention structures evolved in a greenhouse Earth. *Biol. Lett.* 7, 461–464 (2011). doi: 10.1098/rsbl.2010.0993; pmid: 21177693
- S. Mirceta *et al.*, Evolution of mammalian diving capacity traced by myoglobin net surface charge. *Science* **340**, 1234192 (2013). doi: 10.1126/science.1234192; pmid: 23766330
- A. Bernard et al., Regulation of body temperature by some Mesozoic marine reptiles. Science 328, 1379–1382 (2010). doi: 10.1126/science.1187443; pmid: 20538946
- J. Lindgren et al., Skin pigmentation provides evidence of convergent melanism in extinct marine reptiles. *Nature* 506, 484–488 (2014). doi: 10.1038/nature12899; pmid: 24402224
- F. R. O'Keefe, L. M. Chiappe, Viviparity and K-selected life history in a Mesozoic marine plesiosaur (Reptilia, Sauropterygia). *Science* 333, 870–873 (2011). doi: 10.1126/ science.1205689; pmid: 21836013
- C. L. Organ, D. E. Janes, A. Meade, M. Pagel, Genotypic sex determination enabled adaptive radiations of extinct marine reptiles. *Nature* 461, 389–392 (2009). doi: 10.1038/ nature08350; pmid: 19759619
- J. Parker *et al.*, Genome-wide signatures of convergent evolution in echolocating mammals. *Nature* **502**, 228–231 (2013). doi: 10.1038/nature12511; pmid: 24005325
- J. A. Clarke *et al.*, Fossil evidence for evolution of the shape and color of penguin feathers. *Science* **330**, 954–957 (2010). doi: 10.1126/science.1193604; pmid: 20929737
- P. M. Sander, Reproduction in early amniotes. Science 337, 806–808 (2012). doi: 10.1126/science.1224301; pmid: 22904001
- R. Motani, D. Y. Jiang, A. Tintori, O. Rieppel, G. B. Chen, Terrestrial origin of viviparity in Mesozoic marine reptiles indicated by early Triassic embryonic fossils. *PLOS ONE* 9, e88640 (2014). doi: 10.1371/journal.pone.0088640

- P. D. Gingerich, W. von Koenigswald, W. J. Sanders, B. H. Smith, I. S. Zalmout, New protocetid whale from the middle Eocene of Pakistan: Birth on land, precocial development, and sexual dimorphism. *PLOS ONE* 4, e4366 (2009). doi: 10.1371/journal.pone.0004366
- M. W. Caldwell, From fins to limbs to fins: Limb evolution in fossil marine reptiles. *Am. J. Med. Genet.* **112**, 236–249 (2002). doi: 10.1002/ajmg.10773; pmid: 12357467
- J. Müller et al., Homeotic effects, somitogenesis and the evolution of vertebral numbers in recent and fossil amniotes. Proc. Natl. Acad. Sci. U.S.A. 107, 2118–2123 (2010). doi: 10.1073/pnas.0912622107; pmid: 20080660
- A. D. Foote *et al.*, Convergent evolution of the genomes of marine mammals. *Nat. Genet.* **47**, 272–275 (2015). doi: 10.1038/ng.3198; pmid: 25621460
- J. Lindgren, M. W. Caldwell, T. Konishi, L. M. Chiappe, Convergent evolution in aquatic tetrapods: Insights from an exceptional fossil mosasaur. *PLOS ONE* 5, e11998 (2010). doi: 10.1371/journal.pone.0011998
- J. H. Lipps, E. Mitchell, Trophic model for the adaptive radiations and extinctions of pelagic marine mammals. *Paleobiology* 2, 147–155 (1976).
- M. E. Steeman *et al.*, Radiation of extant cetaceans driven by restructuring of the oceans. *Syst. Biol.* **58**, 573–585 (2009). doi: 10.1093/sysbio/syp060; pmid: 20525610
- G. J. Slater, S. A. Price, F. Santini, M. E. Alfaro, Diversity versus disparity and the radiation of modern cetaceans. *Proc. R. Soc. B* 277, 3097–3104 (2010). doi: 10.1098/ rspb.2010.0408; pmid: 20484243
- K. L. Sanders, M. S. Mumpuni, M. S. Y. Lee, Uncoupling ecological innovation and speciation in sea snakes (Elapidae, Hydrophiiniae, Hydrophiini). *J. Evol. Biol.* 23, 2685–2693 (2010). doi: 10.1111/j.1420-9101.2010.02131.x; pmid: 21077974
- J. Gatesy et al., A phylogenetic blueprint for a modern whale. Mol. Phylogenet. Evol. 66, 479–506 (2013). doi: 10.1016/j. ympev.2012.10.012; pmid: 23103570
- K. L. Sanders et al., Multilocus phylogeny and recent rapid radiation of the viviparous sea snakes (Elapidae: Hydrophiinae). Mol. Phylogenet. Evol. 66, 575–591 (2013). doi: 10.1016/j.ympev.2012.09.021; pmid: 23026811
- J. J. Sepkoski Jr., A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* 10, 246–267 (1984).
- Z. Q. Chen, M. J. Benton, The timing and pattern of biotic recovery following the end-Permian mass extinction. *Nat. Geosci.* 5, 375–383 (2012). doi: 10.1038/ngeo1475
- N. B. Fröbisch, J. Fröbisch, P. M. Sander, L. Schmitz, O. Rieppel, Macropredatory ichthyosaur from the Middle Triassic and the origin of modern trophic networks. *Proc. Natl. Acad. Sci. U.S.A.* 110, 1393–1397 (2013). doi: 10.1073/ pnas.1216750110; pmid: 23297200
- T. M. Scheyer, C. Romano, J. Jenks, H. Bucher, Early Triassic marine biotic recovery: the predators' perspective. *PLOS ONE* 9, e88987 (2014). doi: 10.1371/journal.pone.0088987
- N. Bardet, Extinction events among Mesozoic marine reptiles. Hist. Biol. 7, 313–324 (1994). doi: 10.1080/10292389409380462
- R. B. Benson, P. S. Druckenmiller, Faunal turnover of marine tetrapods during the Jurassic-Cretaceous transition. *Biol. Rev. Camb. Philos. Soc.* 89, 1–23 (2014). doi: 10.1111/ brv.12038; pmid: 23581455
- M. J. Benton, The Red Queen and the Court Jester: Species diversity and the role of biotic and abiotic factors through time. *Science* **323**, 728–732 (2009). doi: 10.1126/ science.1157719; pmid: 19197051
- N. D. Pyenson, N. P. Kelley, J. F. Parham, Marine tetrapod macroevolution: Physical and biological drivers on 250 Ma of invasions and evolution in ocean ecosystems. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 400, 1–8 (2014). doi: 10.1016/j. palaeo.2014.02.018
- J. Velez-Juarbe, D. P. Domning, N. D. Pyenson, Iterative evolution of sympatric seacow (Dugongidae, Sirenia) assemblages during the past ~26 million years. *PLOS ONE* 7, e31304 (2012). doi: 10.1371/journal. pone.0031304
- A. M. Valenzuela-Toro, C. S. Gutstein, R. M. Varas-Malca, M. E. Suarez, N. D. Pyenson, Pinniped turnover in the South Pacific Ocean: New evidence from the Plio-Pleistocene of the Atacama Desert, Chile. J. Vertebr. Paleontol. 33, 216–223 (2013). doi: 10.1080/02724634.2012.710282
- D. P. Domning, An ecological model for late Tertiary sirenian evolution in the North Pacific Ocean. Syst. Biol. 25, 352–362 (1976).

- J. F. Parham, N. D. Pyenson, New sea turtle from the Miocene of Peru and the iterative evolution of feeding ecomorphologies since the Cretaceous. J. Paleontol. 84, 231–247 (2010). doi: 10.1666/09-077R.1
- H. Hamilton, S. Caballero, A. G. Collins, R. L. Brownell Jr., Evolution of river dolphins. *Proc. R. Soc. B* 268, 549–556 (2001). doi: 10.1098/rspb.2000.1385; pmid: 11296868
- A. E. Moura *et al.*, Recent diversification of a marine genus (*Tursiops* spp.) tracks habitat preference and environmental change. Syst. *Biol.* **62**, 865–877 (2013). doi: 10.1093/sysbio/ syt051; pmid: 23929779
- P. J. de Bruyn, C. A. Tosh, A. Terauds, Killer whale ecotypes: Is there a global model? *Biol. Rev. Camb. Philos. Soc.* 88, 62–80 (2013). doi: 10.1111/j.1469-185X.2012.00239.x; pmid: 22882545
- J. E. Martin, V. Fischer, P. Vincent, G. Suan, A longirostrine Termodontosaurus (lchthyosauria) with comments on Early Jurassic ichthyosaur niche partitioning and disparity. Palaeontology 55, 995–1005 (2012). doi: 10.1111/j.1475-4983.2012.01159.x
- F. R. O'Keefe, The evolution of plesiosaur and pliosaur morphotypes in the Plesiosauria (Reptilia: Sauropterygia). *Paleobiology* 28, 101–112 (2002). doi: 10.1666/0094-8373 (2002)028<0101:TEOPAP>2.0.CO;2
- E. M. Fitzgerald, Archaeocete-like jaws in a baleen whale. *Biol.* Lett. 8, 94–96 (2012). doi: 10.1098/rsbl.2011.0690; pmid: 21849306
- O. Lambert *et al.*, The giant bite of a new raptorial sperm whale from the Miocene epoch of Peru. *Nature* 466, 105–108 (2010). doi: 10.1038/nature09067; pmid: 20596020
- D. Jablonski, K. Roy, J. W. Valentine, R. M. Price, P. S. Anderson, The impact of the pull of the recent on the history of marine diversity. *Science* **300**, 1133–1135 (2003). doi: 10.1126/science.1083246; pmid: 12750517
- J. Alroy et al., Phanerozoic trends in the global diversity of marine invertebrates. Science 321, 97–100 (2008). doi: 10.1126/science.1156963; pmid: 18599780
- A. B. Smith, G. T. Lloyd, A. J. McGowan, Phanerozoic marine diversity: Rock record modelling provides an independent test of large-scale trends. *Proc. R. Soc. B* 279, 4489–4495 (2012). doi: 10.1098/rspb.2012.1793; pmid: 22951734
- J. Vélez-Juarbe, Ghost of seagrasses past: Using sirenians as a proxy for historical distribution of seagrasses. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 400, 41–49 (2014). doi: 10.1016/j. palaeo.2013.05.012
- T. Ksepka, J. A. Clarke, The basal penguin (Aves: Sphenisciformes) *Perudyptes devriesi* and a phylogenetic evaluation of the penguin fossil record. *Bull. Am. Mus. Nat. Hist.* 337, 1–77 (2010). doi: 10.1206/653.1
- M. D. Uhen, N. D. Pyenson, Diversity estimates, biases, and historiographic effects: Resolving cetacean diversity in the Tertiary. *Palaeontol. Electronica* 10, 11–22 (2007).
- F. G. Marx, M. D. Uhen, Climate, critters, and cetaceans: Cenozoic drivers of the evolution of modern whales. *Science* 327, 993–996 (2010). doi:10.1126/science.1185581; pmid: 20167785
- R. D. Norris, S. K. Turner, P. M. Hull, A. Ridgwell, Marine ecosystem responses to Cenozoic global change. *Science* **341**, 492–498 (2013). doi: 10.1126/science.1240543; pmid: 23908226
- 101. G. J. Vermeij, On escalation. Annu. Rev. Earth Sci. 41, 1–19 (2013). doi: 10.1146/annurev-earth-050212-124123
- M. E. Alfaro *et al.*, Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 13410–13414 (2009). doi: 10.1073/pnas.0811087106; pmid: 19633192
- 103. G. J. Vermeij, D. R. Lindberg, Delayed herbivory and the assembly of marine benthic ecosystems. *Paleobiology* 26, 419–430 (2000). doi: 10.1666/0094-8373(2000)026<0419: DHATAO>2.0.CO;2
- R. Collin, C. M. Janis, in *Ancient Marine Reptiles*, J. M. Callaway, E. L. Nicholls, Eds. (Academic Press, San Diego, CA, 1997), pp. 451–466.
- C. B. Stringer et al., Neanderthal exploitation of marine mammals in Gibraltar. Proc. Natl. Acad. Sci. U.S.A. 105, 14319–14324 (2008). doi: 10.1073/pnas.0805474105; priidi: 18809913
- T. C. Rick, J. Erlandson, Eds., Human Impacts on Ancient Marine Ecosystems: A Global Perspective (Univ. of California Press, Berkeley, 2008).
- D. J. McCauley et al., Marine defaunation: Animal loss in the global ocean. Science 347, 1255641 (2015). doi: 10.1126/ science.1255641; pmid: 25593191

- S. T. Turvey, C. L. Risley, Modelling the extinction of Steller's sea cow. *Biol. Lett.* 2, 94–97 (2006). doi: 10.1098/ rsbl.2005.0415; pmid: 17148336
- R. R. Reeves, T. D. Smith, in *Whales, Whaling, and Ocean Ecosystems*, J. A. Estes *et al.*, Eds. (Univ. of California Press, Berkeley, 2006), pp. 82–101.
- L. R. Gerber, R. Hilborn, Catastrophic events and recovery from low densities in populations of otariids: Implications for risk of extinction. *Mammal Rev.* **31**, 131–150 (2001). doi: 10.1046/j.1365-2907.2001.00081.x
- D. M. Scheel *et al.*, Biogeography and taxonomy of extinct and endangered monk seals illuminated by ancient DNA and skull morphology. *ZooKeys* **409**, 1–33 (2014). doi: 10.3897/ zookeys.409.6244; pmid: 24899841
- C. L. Hubbs, K. S. Norris, in *Antarctic Pinnipedia*, W. H. Burt, Ed. (American Geophysical Union, Washington, DC, 1971), pp. 35–52.
- M. L. Bonnell, R. K. Selander, Elephant seals: Genetic variation and near extinction. *Science* **184**, 908–909 (1974). doi: 10.1126/science.184.4139.908; pmid: 4825892
- G. J. Vermeij, Biogeography of recently extinct marine species: Implications for conservation. *Conserv. Biol.* 7, 391–397 (1993). doi: 10.1046/j.1523-1739.1993.07020391.x
- 115. S. Boessenkool *et al.*, Relict or colonizer? Extinction and range expansion of penguins in southern New Zealand. *Proc. R. Soc. B* 276, 815–821 (2009). doi: 10.1098/ rspb.2008.1246; pmid: 19019791
- T. L. Jones et al., The protracted Holocene extinction of California's flightless sea duck (*Chendytes lawi*) and its implications for the Pleistocene overkill hypothesis. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 4105–4108 (2008). doi: 10.1073/ pnas.0711140105; pmid: 18334640
- 117. IUCN Red List of Species, version 2014.3; www.iucnredlist.org.
- N. D. Pyenson, Requiem for *Lipotes*: An evolutionary perspective on marine mammal extinction. *Mar. Mamm. Sci.* 25, 714–724 (2009). doi: 10.1111/j.1748-7692.2008.00266.x
- T. Gerrodette, L. Rojas-Bracho, Estimating the success of protected areas for the vaquita, *Phocoena sinus*. *Mar. Mamm. Sci.* 27, E101–E125 (2011). doi: 10.1111/j.1748-7692.2010.00449.x
- F. Ritter, Collisions of sailing vessels with cetaceans worldwide: First insights into a seemingly growing problem. *J. Cetacean Res. Manage.* 12, 119–128 (2012).
- R. M. Rolland *et al.*, Evidence that ship noise increases stress in right whales. *Proc. R. Soc. B* **279**, 2363–2368 (2012). doi: 10.1098/rspb.2011.2429; pmid: 22319129
- P. L. Tyack et al., Beaked whales respond to simulated and actual navy sonar. PLOS ONE 6, e17009 (2011). doi: 10.1371/ journal.pone.0017009
- 123. M. C. Fossi et al., Large filter feeding marine organisms as indicators of microplastic in the pelagic environment: The case studies of the Mediterranean basking shark (*Cetorhinus maximus*) and fin whale (*Balaenoptera physalus*). *Mar. Environ. Res.* **100**, 17–24 (2014). doi: 10.1016/j. marenvres.2014.02.002; pmid: 24612776
- 124. F. F. Mazzillo, K. Shapiro, M. W. Silver, A new pathogen transmission mechanism in the ocean: The case of sea otter exposure to the land-parasite *Toxoplasma gondii*. *PLOS ONE* 8, e82477 (2013). doi: 10.1371/journal.pone.0082477
- O. Schofield *et al.*, How do polar marine ecosystems respond to rapid climate change? Science **328**, 1520–1523 (2010). doi: 10.1126/science.1185779; pmid: 20558708
- S. E. Alter et al., Climate impacts on transocean dispersal and habitat in gray whales from the Pleistocene to 2100. *Molec. Ecol.* 24, 1510–1522 (2015). doi: 10.111/mec.13121
- S. E. Noakes, N. D. Pyenson, G. McFall, Late Pleistocene gray whales (*Eschrichtius robustus*) offshore Georgia, USA, and the antiquity of gray whale migration in the North Atlantic Ocean. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **392**, 502–509 (2013). doi: 10.1016/j.palaeo.2013.10.005
- H. Heatwole, A. Grech, J. F. Monahan, S. King, H. Marsh, Thermal biology of sea snakes and sea kraits. *Integr. Comp. Biol.* 52, 257–273 (2012). doi: 10.1093/icb/ics080; pmid: 22669175
- L. I. Wright *et al.*, Turtle mating patterns buffer against disruptive effects of climate change. *Proc. R. Soc. B* 279, 2122–2127 (2012). doi: 10.1098/rspb.2011.2285; pmid: 22279164
- P. C. Fiedler, Environmental change in the eastern tropical Pacific Ocean: Review of ENSO and decadal variability. *Mar. Ecol. Prog. Ser.* 244, 265–283 (2002). doi: 10.3354/ meps244265

- J. A. Estes *et al.*, Trophic downgrading of planet Earth. Science **333**, 301–306 (2011). doi: 10.1126/science.1205106; pmid: 21764740
- 132. J. A. Estes, M. T. Tinker, T. M. Williams, D. F. Doak, Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282**, 473–476 (1998). doi: 10.1126/science.282.5388.473; pmid: 9774274
- D. G. Ainley, G. Ballard, K. M. Dugger, Competition among penguins and cetaceans reveals trophic cascades in the western Ross Sea, Antarctica. *Ecology* 87, 2080–2093 (2006). doi: 10.1890/0012-9658(2006)87[2080:CAPACR] 2.0.C0:2; pmid: 16937647
- 134. B. A. Block et al., Tracking apex marine predator movements in a dynamic ocean. Nature 475, 86–90 (2011). doi: 10.1038/ nature10082; pmid: 21697831
- K. I. Ohshima *et al.*, Antarctic Bottom Water production by intense sea-ice formation in the Cape Darnley polynya. *Nat. Geosci.* 6, 235–240 (2013). doi: 10.1038/ ngeo1738
- 136. See supplementary materials on Science Online.
- TSCreator, version 6.4; https://engineering.purdue.edu/ Stratigraphy/tscreator/index/index.php.
- 138. J. Vélez-Juarbe, C. A. Brochu, H. Santos, A gharial from the Oligocene of Puerto Rico: Transoceanic dispersal in the history

of a non-marine reptile. *Proc. R. Soc. B* **274**, 1245–1254 (2007). doi: 10.1098/rspb.2006.0455; pmid: 17341454

- T. H. Worthy, A. J. D. Tennyson, C. Jones, J. A. McNamara, B. J. Douglas, Miocene waterfowl and other birds from Central Otago, New Zealand, J. Syst. Palaeontol. 5, 1–39 (2007). doi: 10.1017/S1477201906001957
- T. L. Fulton, B. Letts, B. Shapiro, Multiple losses of flight and recent speciation in steamer ducks. *Proc. R. Soc. B* 279, 2339–2346 (2012). doi: 10.1098/rspb.2011.2599; pmid: 22319122
- 141. T. L. Fulton, C. Strobeck, Multiple fossil calibrations, nuclear loci and mitochondrial genomes provide new insight into biogeography and divergence timing for true seals (Phocidae, Pinnipedia). J. Biogeogr. 37, 814–829 (2010). doi: 10.1111/ ij.1365-2699.2010.02271.x
- 142. F. Hailer et al., Nuclear genomic sequences reveal that polar bears are an old and distinct bear lineage. *Science* **336**, 344–347 (2012). doi: 10.1126/ science.1216424; pmid: 22517859
- 143. K. Rassmann, D. Tautz, F. C. Trillmich, C. Gliddon, The microevolution of the Galápagos marine iguana Amblyrhynchus cristatus assessed by nuclear and mitochondrial genetic analyses. *Mol. Ecol.* 6, 437–452 (1997). doi: 10.1046/j.1365-294X.1997.00209.x
- 144. TimeTree, www.timetree.org.

- 145. S. B. Hedges, J. Dudley, S. Kumar, TimeTree: A public knowledge-base of divergence times among organisms. *Bioinformatics* 22, 2971–2972 (2006). doi: 10.1093/ bioinformatics/btl505; pmid: 17021158
- Fossil Calibration Database, http://fossilcalibrations.org.
 F. Gradstein, J. Ogg, M. Schmitz, G. Ogg, *The Geologic Time*
- Scale 2012 (Elsevier, Amsterdam, 2012).

ACKNOWLEDGMENTS

We thank D. Erwin, J. Jackson, M. Carrano, J. Goldbogen, J. Parham, J. Velez-Juarbe, and J. Oster for helpful comments on previous versions of this paper, and three anonymous reviewers for helpful suggestions. D. Johnston provided the penguin photograph for Fig. 2. Supported by a Smithsonian Institution Peter Buck Postdoctoral Fellowship (N.P.K.), a Smithsonian Institution National Museum of Natural History Small Grant Award and the Remington Kellogg Fund (N.D.P.), and the Basis Foundation (N.D.P. and N.P.K.).

SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/348/6232/aaa3716/suppl/DC1 Materials and Methods References (137–147)

10.1126/science.aaa3716





Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene Neil P. Kelley and Nicholas D. Pyenson *Science* **348**, (2015); DOI: 10.1126/science.aaa3716

This copy is for your personal, non-commercial use only.

If you wish to distribute this article to others, you can order high-quality copies for your colleagues, clients, or customers by clicking here.

Permission to republish or repurpose articles or portions of articles can be obtained by following the guidelines here.

The following resources related to this article are available online at www.sciencemag.org (this information is current as of April 16, 2015):

Updated information and services, including high-resolution figures, can be found in the online version of this article at: http://www.sciencemag.org/content/348/6232/aaa3716.full.html

Supporting Online Material can be found at: http://www.sciencemag.org/content/suppl/2015/04/15/348.6232.aaa3716.DC1.html

This article **cites 135 articles**, 58 of which can be accessed free: http://www.sciencemag.org/content/348/6232/aaa3716.full.html#ref-list-1

This article appears in the following **subject collections:** Evolution http://www.sciencemag.org/cgi/collection/evolution

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published weekly, except the last week in December, by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. Copyright 2015 by the American Association for the Advancement of Science; all rights reserved. The title *Science* is a registered trademark of AAAS.