wonders about the fine print of such a small-worlds metaphysics: should one think of them as bridgeable islands, hamstrung monads, layered cakes, braided ropes, flow vortices, musical symphonies? If we are "enclosed within" them, are we locked in? Can we escape or at least expand them? Or are we doomed to at best approach the surface of those other worlds casting our human blankets over them? Too many questions to answer; too tragic to refuse to entertain.

At the end of the day, even if we fail, we must try. Scientific imagination is underrated and shriveled. We need to restore its proper place amongst reason and intuition[7]. Our attempts to conceive such extraordinary worlds are a healthy break from the hype and hope for artificially simulated realities that plague current academe and saturate laypeople's attention. Digital prophets postulate the imminent arrival of the multiverse. Many are already trapped and lost in conversation with chatbots. Some physicists continue to rejoice at untestable parallel universes. Biologists, however, have at their disposal a key to plebeian uncanny worlds, not as wild speculations or technocratic delusions, but as the concrete enacting of embodied life in the natural world.

DECLARATION OF INTERESTS

The author declares no competing interests.

REFERENCES

1. von Uexküll, J. (2010). A Foray into the Worlds of Animals and Humans: With a Theory of Meaning (Minneapolis: University of Minnesota Press).
2. Grimm, D. (2023). Suffering in silence. Science *379*, 974–977.
3. Hadot, P. (2008). The Veil of Isis: An Essay on the History of the Idea of Nature (Cambridge, MA: Harvard University Press).
4. Bacon, F. (1858). *De Augmentis Scientiarum*. The Works of Francis Bacon (London: Spottiswoode and Co).
5. Despret, V. (2016). What Would Animals Say If We Asked the Right Questions? (Minneapolis: University of Minnesota Press).
6. Feiten, T.E. (2020). Mind after Uexküll: A foray into the worlds of ecological psychologists and enactivists. Front. Psychol. *11*, 480.
7. McGilchrist, I. (2021). The Matter with Things: Our Brains, Our Delusions, and the Unmaking of the World (London: Perspectiva Press).

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Primer
Plesiosaurs

P. Martin Sander[1,2]

In the early 19th century, long before the discovery of the dinosaurs, scientists and the public alike were faced with the realization that strange beasts, wholly extinct, were once populating Earth's ancient oceans. In no small part, this realization was through the discovery of the first plesiosaurs (and ichthyosaurs) along the Dorset coast of England in the seaside town of Lyme Regis. There was this large marine reptile resembling a large sea turtle, but with four evenly shaped flippers and looking as though a large snake had been pulled through its carapace. It was soon to be named scientifically *Plesiosaurus*, in reference to its greater similarity to living reptiles than the *Ichthyosaurus* (Figure 1). While the *Ichthyosaurus* was relatively easily understood as a fish-shaped reptile descended from land-living ancestors, the *Plesiosaurus* was beyond comprehension, even though incomplete skeletons had been unearthed already in the early 18th century. Plesiosaurs seemed so alien that the first complete skeleton, discovered by the famed Mary Anning a little more than 200 years ago (Figure 1A), was considered a fake by the leading anatomist of the day, the Baron Georges Cuvier in Paris. Only study of the original specimen convinced him of the authenticity of this animal but reinforced his seminal insight that there is extinction.

What intrigued Cuvier most, and still offers a challenge to evolutionary developmental biologists today, was the incredibly long neck (Figure 1A), consisting of over 40 (or more) vertebrae, almost twice as many as any other tetrapod. The tail, by contrast, was short, unlike in most other reptiles. This combination of a short tail and an unreasonably long neck precipitated another famous episode in the history of paleontology some decades later. Reconstructing the most long-necked of plesiosaurs, an elasmosaur, American paleontologist and zoologist Edward Drinker Cope had mounted its

skull on the tip of its tail (Figure 1C). Apparently, he too could not cope with the notion of an animal having over 70 neck vertebrae. When this error was repeatedly noted in public by his competitor Othniel Charles Marsh, the 'bone wars' ensued, which later played out in the race over dinosaur discoveries in the Wild West.

Returning to the first plesiosaur skeleton, the flippers presented a puzzle as well. Their anatomy is not very different from the front limbs of whales and sea turtles, but the hind flippers, which are absent in whales and small in sea turtles, look very much like the front flippers (Figure 2). In fact, on occasion, front flippers have been mixed up with hind flippers in mounted skeletons in museums, in the tradition of Cope. The similarity in shape of fore- and hindlimbs is also a unique feature among tetrapods, suggesting that all limbs served exactly the same function.

Popular interest in the sea monsters from Lyme Regis was such that, in 1830, it led to an artistic visualization of plesiosaurs as living animals, the beginnings of paleoart. The genre started with a bang, as a loose-leaf lithograph entitled *Duria Antiquior* (a more ancient Dorset; Figure 1B). This iconic depiction of a plesiosaur attacked by an ichthyosaur surrounded by a marine menagerie in an Early Jurassic sea is the archetype of many such illustrations, immortalized by Jules Verne in his *Journey to the Center of the Earth* from 1864 (Figure 1D). Paleoart, even in its earliest version, derives its scientific relevance by visualizing paleobiological hypotheses, albeit more or less well supported and often only implicitly. However, such visualizations sometimes inspire real-life scientific questions such as: How exactly did plesiosaurs use their four equally shaped flippers in locomotion, or why was the plesiosaur neck so incredibly long, and how flexible was it? These questions are at the center of much modern plesiosaur research and lend importance to the study of unique but extinct *Bauplans* such as that of plesiosaurs for our understanding of evolution.

A tale of three extinctions
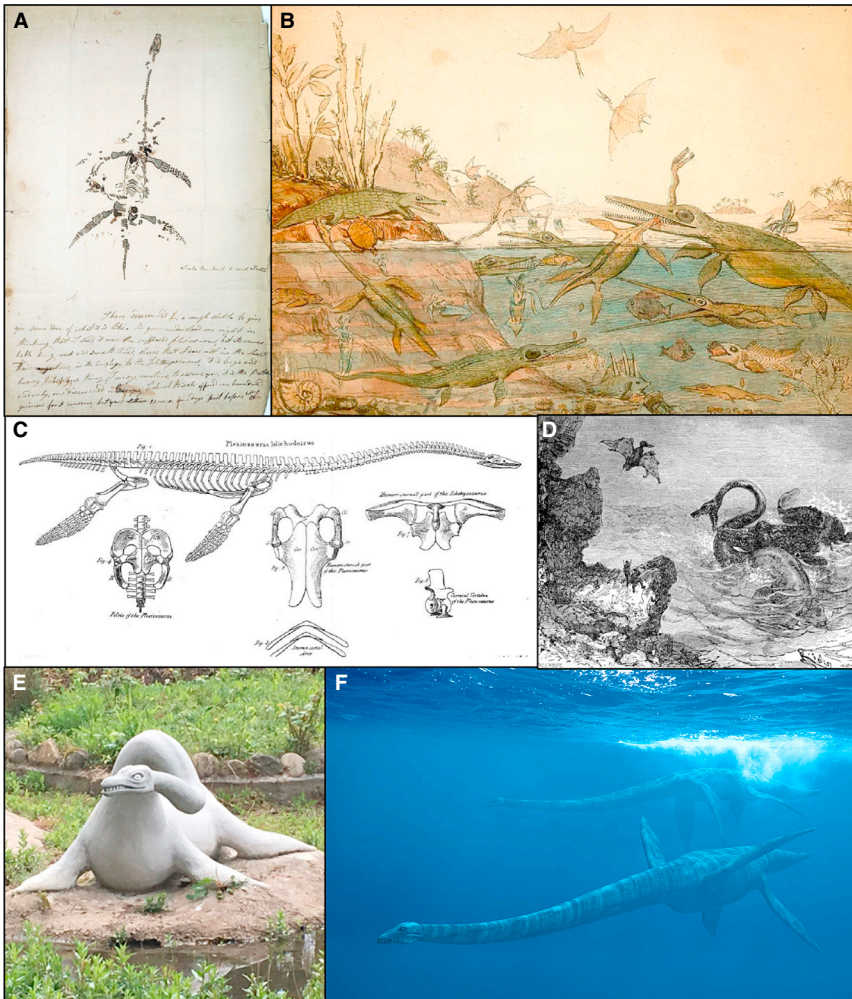Often called 'the mother of all extinctions', the end-Permian mass

Figure 1. 190 years of plesiosaur life restorations.
(A) Letter and sketch by Mary Anning reporting the discovery of her second plesiosaur skeleton in 1823. (B) Watercolor illustration entitled *Duria Antiquior* by Henry De la Beche from 1830. (C) Illustration of the skeletal anatomy of a *Plesiosaurus dolichodeirus* from Conybeare's 1824 publication that described the almost complete plesiosaur skeleton found by Mary Anning. (D) Illustration by Édouard Rioux from Jules Verne's 1864 novel *Journey to the Center of the Earth*, echoing *Duria Antiquior*. (E) Plesiosaur sculpture by Benjamin Waterhouse Hawkins in the Crystal Palace grounds in south London from around 1854 (Image used with permission from Friends of Crystal Palace Dinosaurs). (F) Modern plesiosaur life restoration researched, modeled and composited by Frank DeNota.

extinction 251.9 million years ago virtually emptied the oceans of life. A major pattern in the recovery is the colonization of the sea by different kinds of land-living, air-breathing amniotes. Prominent examples are the ichthyosaurs and the sauropterygians, of which the plesiosaurs are a subgroup. These lineages, collectively known as 'Mesozoic marine reptiles', are the geologically earliest examples of life transitioning from land back to the ocean. It is increasingly becoming clear that recovery from the catastrophe was extremely fast, and marine reptiles diversified within the first few million years of the Mesozoic. In fact, ever older finds dating to the earliest Triassic hint at a pre-Triassic origin of at least the ichthyosaurs but possibly also the sauropterygians.

Ichthyosaurs dispersed over the world's ocean (Panthalassa), whereas sauropterygians were restricted to the precursor of the Mediterranean, the Tethys ocean; except for one lineage, the pistosaurs, of which plesiosaurs are a subgroup (Figure 3).

In the Triassic, non-plesiosaur pistosaurs left scanty records not only in the Tethys but also in Siberia and in eastern Panthalassa. Like other sauropterygians, non-plesiosaur pistosaurs were propelled by their tail. However, they already show many similarities with plesiosaurs, including the skull architecture and the long neck. This is why non-plesiosaur pistosaurs have long been suspected to have given rise to the plesiosaurs in the Late Triassic, but good intermediate forms are missing to this day, due to the poor fossil record of marine reptiles in the last 25 million years of the Triassic. Only recently, evidence of the Triassic origin of plesiosaurs came to light in a clay pit in Germany in the form of *Rhaeticosaurus*. This skeleton of a small plesiosaur is the only one from the Triassic.

The second mass extinction, at the end of the Triassic, 201.4 million years ago, played an important role in plesiosaur evolution. It seemingly wiped out (or nearly so) most of the competition, including all other sauropterygians (Figure 3), thalattosaurs and giant ichthyosaurs. Then, in the earliest Jurassic, there is an abundance of small (<100 kg body mass) plesiosaurs from places like Lyme Regis (Figure 1A). This had suggested that plesiosaurs evolved very rapidly in the aftermath of the extinction event in the earliest Jurassic, just as their ancestors had done in the earliest Triassic. However, phylogenetic inference, corroborated by the relatively derived position of *Rhaeticosaurus*, reveals that plesiosaurs diversified before the end of the Triassic (Figure 3). In addition, isolated large plesiosaur bones from the Late Triassic represent animals that must have weighed several hundred kilograms and suggest that plesiosaur body size took a dip across the boundary.

Based on a largely European record from the first 20 million years of the Jurassic, plesiosaur diversification continued, and maximum body size gradually evolved to pre-extinction levels. Larger body size correlates with an increasingly macropredatory lifestyle (feeding on other marine reptiles) in some plesiosaurs: the iconic long neck became shorter, and the skull very large (Figures 2 and 3). This macropredatory body plan is

exemplified by Jurassic pliosaurs, such as *Pliosaurus* and *Liopleurodon* (Figure 2C) and the giant *Kronosaurus* from the Early Cretaceous of Australia (Figure 3), but evolved repeatedly during plesiosaur history, both in the Jurassic and the Cretaceous. Some pliosaur skulls approach 2.4 meters in length, and their teeth are among the largest marine amniote teeth to evolve. Pliosaurs continued into the Late Cretaceous with smaller heads adapted to feeding on large fish, a diet also inferred for the polycotylids. In general, plesiosaurs show little evolutionary change across the Jurassic–Cretaceous boundary and continued to thrive, both the short-necked macropredators and the long-necked fish-eaters (piscivores) (Figure 3). The Late Cretaceous also saw their further specialization, an ever-increasing neck length in the elasmosaurs (Figure 4A). Neck lengthening evolved by addition of vertebrae, not by elongation of the neck vertebrae (as in giraffes and sauropod dinosaurs). As a result, some elasmosaurs have more than 75 neck vertebrae, and the neck of the eponymous *Elasmosaurus* from the Late Cretaceous Western Interior Seaway of North America is seven meters long! While mainly being piscivores, some elasmosaurs appear to have been filter-feeding. Plesiosaurs still thrived in the latest Cretaceous (Figure 3), as documented in Antarctica, but all fell victim to the Cretaceous–Paleogene mass extinction event 66 million years ago, bringing their illustrious history to an end.

Plesiosaur biology

Plesiosaurs were medium-sized to very large marine reptiles, ranging in total length from under two meters to over 12 meters (Figure 2). Small plesiosaurs may not have exceeded 100 kilograms in body mass and medium-sized ones a few to several hundred kilograms. Among the largest plesiosaurs, such as elasmosaurs, in which half of the length was taken up by the neck, body mass calculations yielded up to six metric tons (Figure 4C), whereas the largest pliosaurs over 10 meters long must have exceeded 15 metric tons. Unlike for dinosaurs, body mass has been little studied in plesiosaurs, and estimates are only based on volumetric calculations from life models, drawings

Figure 2. Plesiosaur fossils.
(A) Mounted skeleton of *Cryptoclidus* from the Middle Jurassic of England. (B) Front flipper of *Hauffiosaurus* from the Early Jurassic of Germany. (C) Mounted skeleton of *Liopleurodon* from the Middle Jurassic of England (Image by Ghedoghedo/Wikimedia Commons (CC BY-SA 3.0). (D) Mounted skeleton of the elasmosaur *Morenosaurus* from the Late Cretaceous of California, USA. (E) *Polycotylus* fetal vertebrae among phalanges and a rib of the mother from the Late Cretaceous of Kansas, USA. (F) Skull of *Hauffiosaurus* in ventral view from the Early Jurassic of Germany. (G) Middle neck region of *Plesiopterys* from the Early Jurassic of Germany. Note the tight intervertebral joints.

and three-dimensional capture of mounted skeletons. No empirical relationships between any skeletal measurement, such as skull length or humerus length, and body mass have been established.

The plesiosaur skeleton (Figures 1 and 2) is well known because of many finds from sedimentary rocks laid down

in poorly oxygenated quiet waters (such as the Early Jurassic deposits from the Dorset coast) preserving the entire skeleton (albeit the small head of the long-necked forms is often missing). Skull architecture is relatively uniform with a single temporal opening and little variation in suture patterns. The small-headed piscivores had short
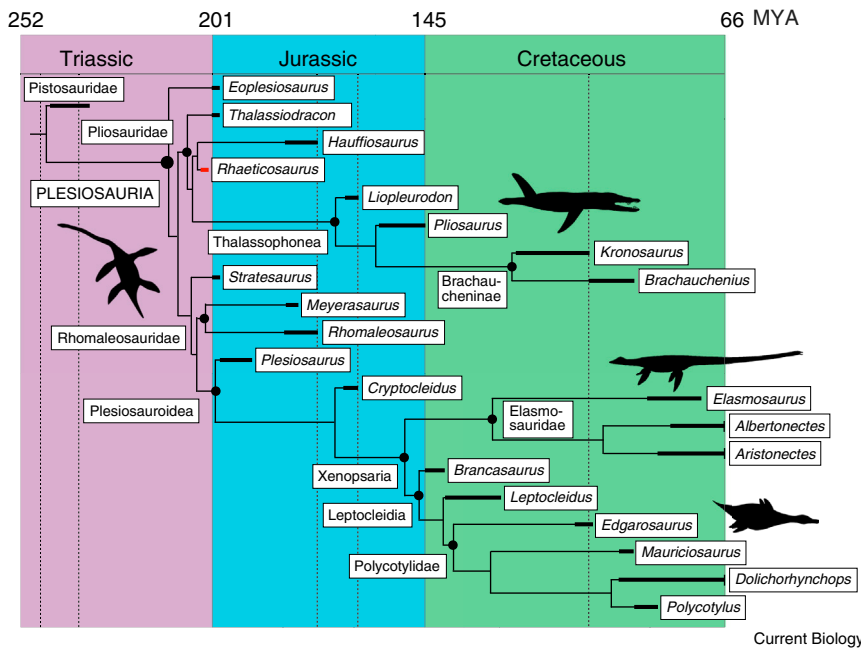
Figure 3. Calibrated plesiosaur phylogeny.
Phylogenetic relationships and occurrence ages are mainly based on Fischer *et al*. (2018). Plesiosauria and Pistosauridae together constitute Pistosauria (silhouettes from phylopic.org, credits (from left to right): The basal plesiosauroid *Microcleidus* by Gareth Monger, *Liopleurodon* by JF-studios, *Albertonectes* by Frank DeNota, *Edgarosaurus* by Bruno Maggia).

snouts (Figure 2A,D), often armed with slender recurving and interlocking teeth. Whereas their long neck intuitively looks very flexible, modern research indicates a surprisingly stiff structure based on the tight articulation of the vertebrae with each other (Figures 1 and 2). The function of the long, stiff neck probably was for visual and hydrodynamic concealment of the large body from the prey, allowing efficient harvesting of small, schooling fish from a distance.

Larger-headed forms, including the giant macropredatory ones, had a rather crocodile-like snout with large fangs and a constriction behind the anterior 'crown' of fangs (Figure 2C,F). Their teeth are more robust but mostly retain the basic conical shape with distinct, sometimes sharp, ridges formed by the tooth enamel. *Pliosaurus* had trenchant teeth with a triangular cross section and two sharp cutting edges for dismembering large prey items, including ichthyosaurs and other plesiosaurs but also sea turtles. Predation of this kind is documented by fossilized plesiosaur stomach contents.

The plesiosaur trunk was short and rigid, with roughly 20 dorsal vertebrae.

The single-headed ribs together with the very well developed 'basket' of belly ribs define a streamlined, but wide body (Figures 2 and 4). The connection between the shoulder girdle and the vertebral column appears weak, because the scapula is small and does not overlie the rib cage (Figure 2). This is puzzling with regard to flipper function and swimming style. The ventral parts of both the shoulder girdle and pelvic girdle are large, flat plates of bone (Figures 2 and 4D) that appear mechanically linked to the gastral basket. The pelvic girdle is weakly attached to the vertebral column by a single sacral rib. The tail is short, not exceeding the length of the trunk, and rapidly tapering to a point. Whether plesiosaurs had a small tail fin is controversial.

Plesiosaur limbs were modified into stiff flippers with simplified, flattened upper and lower limb bones (Figures 2 and 4). However, unlike in ichthyosaurs, the uniformly five digits remained discrete and had a greatly increased number of phalanges. Muscle reconstruction in conjunction with functional finite element analysis indicates that the discrete fingers

effected torsion of the flippers around their long axis during underwater flight (Figure 4D,E). Historical skeletal mounts and paleoart generally depict a rowing (drag-based) style of underwater locomotion, but modern consensus is four-winged underwater flight (lift-based locomotion). Clear morphological evidence for lift-based over drag-based locomotion is the shape of the flippers, long and slender and tapering to a point (Figures 2 and 4). The upstroke of the plesiosaur flipper appears to have been weaker than its downstroke because of the relatively small attachment areas available for the muscles lifting the flippers.

Such four-winged underwater flight does not exist in living animals (sea turtles, penguins, and sea lions only use their front flippers in various kinds of underwater flight). Thus, understanding how it works in plesiosaurs has been challenging — but also inspiring from a biomimetic perspective. One issue has been the coordination of the front flippers with the hind flippers, because the latter had to cope with the vortices generated by the former. Analog hydrodynamic models (Figure 4F) show that proper coordination, flipper spacing and geometry result in greatly improved thrust and efficiency of the system compared to two independent sets of flippers. In addition to the four flippers allowing faster acceleration for effective ambushing, they may have also provided greater maneuverability than two flippers. This has inspired a biomimetic four-winged underwater robot, but further analog and digital modelling of the plesiosaur four-winged underwater flight will be rewarding. In particular, one is left to wonder why marine turtles and mammals did not evolve a plesiosaur-like system of propulsion.

Preciously little is known about the plesiosaur integument despite their fossils occurring in *Lagerstätten* famous for their soft part preservation. Plesiosaur skin presumably lacked scales but was smooth and was underlain by a thick layer of blubber, serving both insulation and hydrodynamics. Likewise, little is known about plesiosaur sense organs. They neither have particularly large nor small eyes, and their inner ear

labyrinth shows similarities with that of other pelagic amniotes. However, the snout may have harbored a special sense organ based on its rich internal vascularization. No direct evidence is available for the respiratory system, but any long-necked plesiosaur must have had a very large lung volume to compensate for dead space in their long trachea.

Several lines of recent evidence indicate that plesiosaurs were fully endothermic, hence the inferred existence of blubber as an insulating material. For one, their unique fossilized bone histology indicates extremely fast growth, and bone histomorphometry infers metabolic rates comparable to those of birds (Figure 5). Preserved molecular metabolic markers point in the same direction. Bone histology and a singular find of a gravid female (Figure 2E) inform plesiosaur life history strategies. They apparently were extreme K strategists, as a single fetus was born at 60% of the mother's size, growing to full size within a few years (Figure 5). For comparison, this is much faster than similar-sized cetaceans and pinnipeds. Nothing is known about parental care, sexual dimorphism, social behavior or migration. There is limited evidence, again from bone histology, for deep diving. As any large pelagic animal, plesiosaurs must have been capable divers in order to harvest enough food for supporting their large size and fast metabolism. The somewhat regular occurrence of gastroliths (stomach stones) within plesiosaur skeletons was once viewed in the context of deep diving but the gastroliths more likely helped stabilize the body.

Global dispersal and habitat

Analysis of plesiosaur biogeography based on their recently solidified phylogenetic tree is lacking, but similarities in plesiosaur faunas around the world suggest that these animals had a high dispersal capability, colonizing the entire globe. Dispersal was facilitated by their low-energy cruising style combined with endothermy. Plesiosaur skeletons from the Jurassic and the Cretaceous (Figure 2) are mostly found in deposits of the open sea, often together with other large marine reptiles such as ichthyosaurs and mosasaurs (in the Late
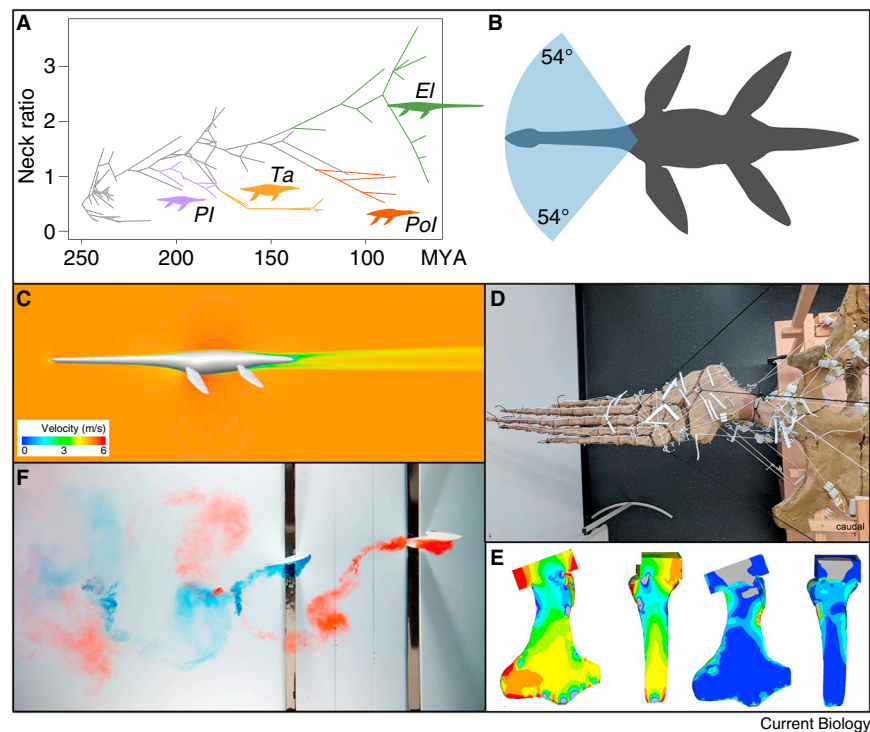

Figure 4. Plesiosaur biology.
(A) Evolution of neck length in different plesiosaur groups through time. Neck ratio is relative length of the neck compared to the trunk. Abbreviations: El, Elasmosauridae; Pl, basal Plesiosauria; Po, Polycotylidae; Ta, Thalassophonea (reprinted from Gutarra *et al*. (2022) with permission from Communications Biology (CC BY 4.0)). (B) Limited lateral neck mobility in *Cryptoclidus* (reprinted from Wintrich *et al*. (2019) with permission from PeerJ (CC BY 4.0)). (C) Computational model of fluid flow around an elasmosaur. This model also served in body mass calculation (reprinted from Gutarra *et al*. (2022) with permission from Communications Biology (CC BY 4.0)). (D) Analog reconstruction of the muscles (white strings) in the forelimb of *Cryptoclidus*. (E) Finite element structural synthesis of forelimb downstroke, compressive stresses on left, tensile stresses on right ((D,E) reprinted from Krahl *et al*. (2022) with permission from PeerJ (CC BY 4.0)). (F) Experimental visualization in a flume tank of flow during plesiosaur four-winged underwater flight (with permission of Royal Society from Muscutt *et al*. (2017)).

Cretaceous). Commonly, such deposits also contain pterosaur fossils. A 2017 compilation recognized nearly 120 plesiosaur species.

Classical plesiosaur *Lagerstätten* are the lowermost Jurassic of the Dorset coast of the UK, the Jurassic Posidonia Shale of Germany, the Oxford and Kimmeridge Clays and similar deposits of the UK, France and the Arctic archipelago of Svalbard, and the Late Cretaceous Niobrara Chalk and similar deposits of the Western Interior Seaway of North America. However, plesiosaur fossils are found around the globe, often in remote places. A non-comprehensive listing includes the latest Cretaceous finds from Seymour and Vega islands, Antarctica, South American finds from Chile, Argentina and Columbia, African plesiosaurs from Angola and Morocco, plesiosaur fossils from New Zealand

and Australia (sometimes preserved as precious opal), and finally Asian ones from Japan and Russia. These finds are mostly from Cretaceous rocks, primarily reflecting the much wider distribution of these younger deposits compared to the older Jurassic ones. The sedimentology and faunal composition of these *Lagerstätten* listed above would suggest that plesiosaurs were less pelagic than ichthyosaurs, but a test of this hypothesis is lacking. However, unlike ichthyosaurs, but like smaller cetaceans, plesiosaurs also invaded freshwater habitats, for instance in the Late Cretaceous Dinosaur Park Formation of Alberta, Canada.

The relevance of plesiosaurs

Plesiosaurs have much to offer to our understanding of the process of evolution and the history of life.
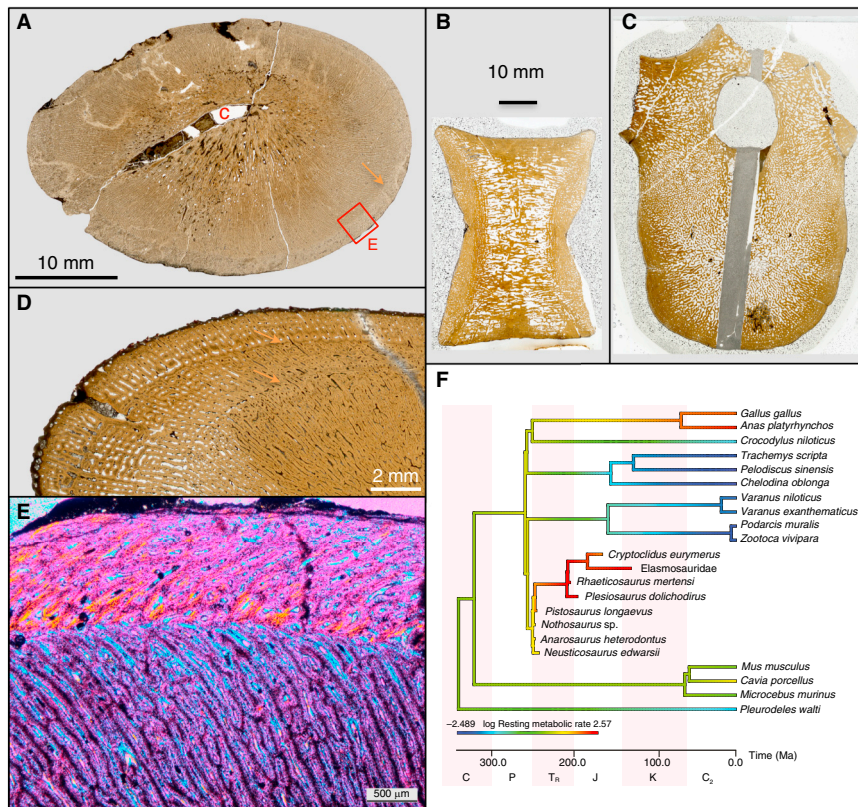
Figure 5. Microanatomy and histology of plesiosaur bones in thin section.
(A) Mid-shaft cross-section of the femur of *Rhaeticosaurus* intersecting the large nutrient canal (marked by 'C'). Note the dense but highly vascularized bone tissue. There is a single growth mark (arrow) in the outermost cortex, indicating that the individual died during its second year. (B) Sagittal and (C) transverse section of trunk vertebra of *Cryptoclidus* showing cancellous bone. (D) Partial mid-shaft cross-section of the humerus of Plesiosaurus showing two growth marks (arrows). (E) Close-up covering the growth mark of the red box in (A) in cross-polarized light and lambda filter. Note the radial canals and generally pink appearance. Both features indicate very fast growth. All photomicrographs by P. Martin Sander. (F) Histomorphometric inference model for resting metabolic rate in selected amniotes (from Fleischle *et al.* (2018) with permission from PeerJ (CC BY 4.0)).

This was already understood by the early geologists, paleontologists and zoologists. Cuvier had posited that the changes in life forms through time were caused by a series of catastrophes, while Darwin, inspired by Lyell's gradualism, had emphasized the gradual transformation of species; our modern understanding of the plesiosaur reveals the truth in both views. Plesiosaurs gradually evolved their unique *Bauplan*, which then remained essentially unchanged for 140 million years. It went extinct not because of poor adaptation, but through catastrophic geological and cosmological processes.

Secondary marine adaptation is one of the big trends in tetrapod evolution, and one that makes convergent evolution particularly obvious. The standard model of the marine amniote, that of the tail-propelled swimmer, first arose in ichthyosaurs (Figure 1B) and early sauropterygians but then many times again during the entire Mesozoic (e.g., marine crocodiles and mosasaurs) and Cenozoic (e.g., cetaceans and sirenians). Plesiosaurs, on the other hand, remain unique, adding a novel evolutionary solution to living in the sea as an amniote (Figure 1F). Nevertheless, plesiosaurs share certain nearly universal adaptations, such as endothermy and vivipary, with other fully marine amniotes, extinct and extant. Because plesiosaurs are extinct, we have to understand them with the methods of paleontology but have to explain them with the knowledge of modern biology. Plesiosaurs are thus model organisms for evolution, and many

more fundamental insights are to be expected from their continued study.

DECLARATION OF INTERESTS

The author declares no competing interests.

FURTHER READING

Benson, R.B.J., Evans, M., Smith, A.S., Sassoon, J., Moore-Faye, S., Ketchum, H.F., and Forrest, R. (2013). A giant pliosaurid skull from the Late Jurassic of England. PLoS One *8*, e65989.

Benson, R.B.J., and Druckenmiller, P.S. (2014). Faunal turnover of marine tetrapods during the Jurassic–Cretaceous transition. Biol. Rev. Camb. Philos. Soc. *89*, 1–23.

Conybeare, W.D. (1824). XXI.—On the discovery of an almost perfect skeleton of the *Plesiosaurus*. Trans. Geo. Soc. Lon. *2*, 381–389.

Fischer, V., Benson, R.B.J., Zverkov, N.G., Soul, L.C., Arkhangelsky, M.S., Lambert, O., Stenshin, I.M., Uspensky, G.N., and Druckenmiller, P.S. (2017). Plasticity and convergence in the evolution of short-necked plesiosaurs. Curr. Biol. *27*, 1667–1676.e3.

Fischer, V., Benson, R.B.J., Druckenmiller, P.S., Ketchum, H.F., and Bardet, N. (2018). The evolutionary history of polycotylid plesiosaurians. R. Soc. Open. Sci. *5*, 172177.

Fleischle, C.V., Wintrich, T., and Sander, P.M. (2018). Quantitative histological models suggest endothermy in plesiosaurs. PeerJ *6*, e4955.

Frey, E., Mulder, E.W.A., Stinnesbeck, W., Rivera-Sylva, H.E., Padilla-Gutiérrez, J.M., and González-González, A.H. (2017). A new polycotylid plesiosaur with extensive soft tissue preservation from the early Late Cretaceous of northeast Mexico. Boletín de la Sociedad Geológica Mexicana *69*, 87–134.

Gutarra, S., and Rahman, I.A. (2022). The locomotion of extinct secondarily aquatic tetrapods. Biol. Rev. Camb. Philos. Soc. *97*, 67–98.

Gutarra, S., Stubbs, T.L., Moon, B.C., Palmer, C., and Benton, M.J. (2022). Large size in aquatic tetrapods compensates for high drag caused by extreme body proportions. Commun. Biol. *5*, 380.

Krahl, A., Lipphaus, A., Sander, P.M., and Witzel, U. (2022). Determination of muscle strength and function in plesiosaur limbs: finite element structural analyses of *Cryptoclidus eurymerus* humerus and femur. PeerJ *10*, e13342.

Muscutt, L.E., Dyke, G., Weymouth, G.D., Naish, D., Palmer, C., and Ganapathisubramani, B. (2017). The four-flipper swimming method of plesiosaurs enabled efficient and effective locomotion. Proc. R. Soc. Lond. B. Biol. Sci. *284*, 20170951.

O'Keefe, F.R.O., and Chiappe, L.M. (2011). Viviparity and K-selected life history in a Mesozoic marine plesiosaur (Reptilia, Sauropterygia). Science *333*, 870–873.

Sander, P.M., and Wintrich, T. (2021). Histology of Plesiosauria. In Vertebrate Skeletal Histology and Paleohistology, V. de Buffrénil, A. de Ricqlès, L. Zylberberg and K. Padian, eds. (Boca Raton: CRC Press), pp. 444–457.

Wintrich, T., Hayashi, S., Houssaye, A., Nakajima, Y., and Sander, P.M. (2017). A Triassic plesiosaurian skeleton and bone histology inform on evolution of a unique body plan. Sci. Adv. *3*, e1701144.

Wintrich, T., Jonas, R., Wilke, H.-J., and Sander, P.M. (2019). Neck mobility in the Jurassic plesiosaur *Cryptoclidus eurymerus*: finite element analysis as a new approach to understanding the cervical skeleton in fossil vertebrates. PeerJ *7*, e7658.

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