the TIMETREE of LIFE

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Vertebrates (Vertebrata)

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Abstract

The vertebrates (~58,000 sp.) comprise a phylum of mostly mobile, predatory animals. The evolution of jaws and limbs were key traits that led to subsequent diversification. Atmospheric oxygen change appears to have played a major role, with an initial rise in the late Precambrian (~580–542 million years ago, Ma) permitting larger body size, followed by two Paleozoic pulses affecting prey. The First Pulse (~430–390 Ma) brought fishes to brackish and freshwater environments where they diversified, with one lineage giving rise to tetrapods. The Second Pulse (~340–250 Ma) led to a Permo-Carboniferous explosion of tetrapods, adapting to diverse terrestrial niches.

The Phylum Vertebrata includes ~58,000 living species in seven evolutionary clades that diverged in the latest Precambrian and in the Paleozoic Era, ~600–360 Ma. Approximately one half of the species (28,183 sp.) are fishes—not an evolutionary group—and the other half (29,638 sp.) are tetrapods, which comprise a monophyletic group. Vertebrates (Fig. 1) are mobile animals that possess a cranium (skull) and, at least ancestrally, a backbone consisting of vertebrae protecting the nerve cord (*1–4*). The cyclostomes (~85 sp.) are jawless fishes (agnathans) and include lampreys and hagfishes. Chondrichthyans (~1200 sp.) are the cartilaginous fishes and include the sharks, rays, and chimaeras. Actinopterygians (26,890 sp.) are ray-finned fishes and include bichirs, sturgeons, paddlefishes, gars, bowfins, and teleosts, with the latter group comprising nearly all species of actinopterygians. Actinistia (two sp.), which is alternatively called Coelacanthimorpha, includes lobe-finned fishes (coelacanths). Dipnoans (six sp.) are the lungfishes. Lissamphibians (6200 sp.) are the living amphibians and include the frogs and toads, salamanders, and caecilians. Amniota (23,438 sp.) comprises the mammals, tuataras, squamates (lizards, snakes, and amphisbaenians), turtles, crocodilians, and birds). Here, the relationships and divergence times of these major lineages of vertebrates are reviewed.

Vertebrates are treated here as a separate phylum rather than a subphylum of Chordata. The morphological disparity among the chordates (urochordates, cepahalochordates, and vertebrates), and their deep time of separation based on molecular clocks (*5*) is as great as that among other groups of related animal phyla (e.g., arthropods, tardigrades, and onycophorans). The phylogeny of the lineages covered here is uncontroversial, for the most part. Evidence from nuclear genes and morphology (*1, 2, 6, 7*) agree in the backbone phylogeny of vertebrates represented by these nested groups: Tetrapoda (Lissamphibia, Amniota), Sarcopterygii (Actinistia, Dipnoi, Tetrapoda), Osteichthyes (Actinopterygii, Sarcopterygii), and Gnathostomata (Chondrichthyes, Osteichthyes).

Cyclostomata was originally considered a basal, monophyletic group based on morphology (*8*), but later morphological analyses placed lampreys as closest relatives of gnathostomes (*9–11*). However, molecular phylogenies from many genes since the early 1990s have consistently supported cyclostome monophyly (*6, 7, 12–17*) and therefore this basal branch is a classical example of

Fig. 1 Representative vertebrates. (A) A clownfish, *Amphiprion ocellaris*, from East Timor (upper left); (B) A lizard, *Anolis allisoni*, from Cuba (upper right); (C) a frog, *Eleutherodactylus portoricensis*, from Puerto Rico (lower left), and a white ibis, *Eudocimus albus*, from the Dominican Republic (lower right). Credits: N. Hobgood (upper left), E. Fernandez (upper right), and A. Sanchez (lower left and right).
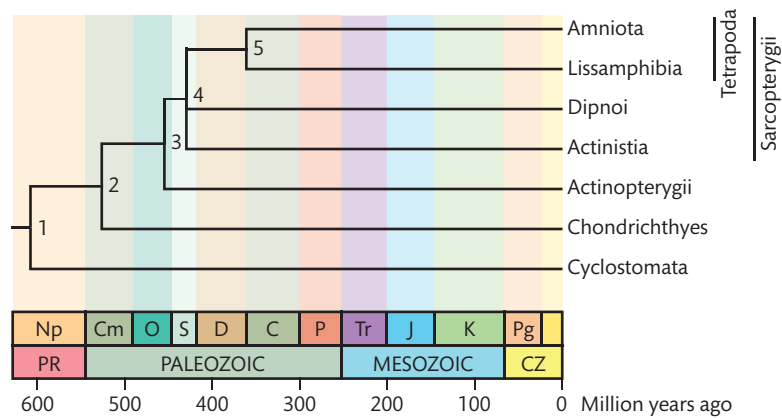
Fig. 2 A timetree of vertebrates. Times of divergence are averages of estimates from different studies listed in Table 1. *Abbreviations*: C (Carboniferous), Cm (Cambrian), CZ (Cenozoic), D (Devonian), J (Jurassic), K (Cretaceous), Np (Neoproterozoic), O (Ordovician), P (Permian), Pg (Paleogene), PR (Proterozoic), S (Silurian), and Tr (Triassic).

apparent conflict between morphological and molecular data. The only currently unresolved portion of the vertebrate backbone tree, from the molecular perspective, involves the relationships among coelacanths, lungfishes, and tetrapods. This question has been pursued vigorously in many morphological and molecular studies over the last several decades, without full resolution, although a close relationship between lungfishes and tetrapods is currently favored among paleontologists (*18*) and has been the most frequent and recent result in molecular studies (e.g., *8, 19–27*).

The fossil record of vertebrates is more complete than that of most organisms, primarily because of the durability of their bony endoskeleton (in most groups) which includes a mineral, hydroxyapetite. Fossil vertebrates were important for Darwin in development of his ideas on evolution (*28*) and even, before that, were used by Cuvier to establish the concept of extinction. Two large compendia (*29, 30*) provide an overview of the vertebrate fossil literature up to ~1990, and there are several more recent texts (*1–3*). The earliest vertebrate fossils are of agnathans, resembling cyclostomes, from the Lower Cambrian of China (~525 Ma) (*31*). The first jawed vertebrates (gnathostomes) to appear in the fossil record are—controversially—conodonts in the late Cambrian (~500 Ma), although probably not closest relatives of any living lineage (*11*). Alternatively, the earliest jawed vertebrates were acanthodians from the mid-Ordovician (~461 Ma) (*32*). However, vertebrate diversity was low until the late Silurian and early Devonian (~430–380 Ma), during which time all of the remaining living groups of fishes first appear including chondrichthyans,

actinopterygians, actinistians, and lungfishes (*1, 33, 34*). One of the best-documented evolutionary transitions is recorded in Devonian fossils (~390–360 Ma), linking one group of lobe-finned fish to tetrapods (*8, 24, 35–39*). Fossils from the Carboniferous (359–299 Ma) and Permian (~299–251) show a great diversification of land-dwelling vertebrates, including the first lissamphibians and amniotes (~330 Ma) (*32, 40*) as well as many extinct groups.

Only two molecular clock studies have been published that have estimated all, or nearly all, of the nodes in the backbone tree of major vertebrate groups. The first involved analyses of nuclear protein-coding genes, 13–107 genes depending on the node, screened for lineage-specific rate variation by relative rate tests, and used two calibration points (*41*). The resulting time estimates for the split of Lissamphibia and Amniota (360 Ma) and the split of Actinopterygii and Sarcopterygii (450 Ma) were only 20–35 million years older (5–8%) than fossil record estimates for those divergences (*32, 42–44*). Fewer fossil constraints have been available for the earlier divergences, between Chondrichthyes and Osteichthyes, and between Agnatha and Gnathostomata (*45*), and therefore the estimates for those splits—528 and 564 Ma—are older than the fossil record suggests. A more recent study used a Bayesian relaxed clock method and 48–325 genes depending on the node (*6*). Similar times for the Lissamphibia–Amniota (370 Ma), Actinopterygii–Sarcopterygii (476 Ma), and Chondrichthyes–Osteichthyes (525 Ma) divergences were obtained, but an older time (652 Ma) was estimated for the Agnatha–Gnathostomata divergence. Also, the

Table 1. Divergence times (Ma) among vertebrates.

Timetree		Estimates							
Node	Time	Ref. (*6*)		Ref. (*41*)		Ref. (*46*)		Ref. (*47*)	
		Time	CI	Time	CI	Time	CI	Time	CI
1	608	652	742–605	564	710–418	–	–	–	–
2	527	525	580–494	528	639–417	–	–	–	–
3	455	476	494–442	450	520–380	–	–	458	499–421
4	430	430	438–421	–	–	–	–	–	–
5	361	370	–	360	389–331	383	414–352	–	–

Node	Estimates (*continued*)							
	Ref. (*48*)		Ref. (*49*)		Ref. (*50*)(b)		Ref. (*50*)(a)	
	Time	CI	Time	CI	Time	CI	Time	CI
1	–	–	–	–	–	–	–	–
2	–	–	–	–	–	–	–	–
3	–	–	–	–	438	480–412	451	495–413
4	–	–	–	–	–	–	–	–
5	360	373–346	354	367–341	–	–	–	–

Node	Estimates (*continued*)					
	Ref. (*51*)		Ref. (*52*)(a)		Ref. (*52*)(b)	
	Time	CI	Time	CI	Time	CI
1	–	–	–	–	–	–
2	–	–	–	–	–	–
3	–	–	–	–	–	–
4	–	–	–	–	–	–
5	356	369–341	353	365–341	354	370–340

Note: See text for details. In the case of two studies (*50, 52*), each analyzed two different data sets (a) = nucleotides, (b) = amino acids and both estimates are shown here.

three-way Dipnoi–Actinistia–Tetrapoda split was estimated as 430 Ma. Six other studies have estimated single nodes in the timetree of vertebrates (*46–52*), all concerning the three latest divergences, among osteichthyians (Table 1). The timetree of vertebrates (Fig. 2) reflects the nodal averages for all of these molecular studies and, except for the early divergence of cyclostomes and gnathostomes, is more-or-less uncontroversial.

Continental reconstructions for the Paleozoic are not as well resolved as those for later time periods. In general, they show a gradual coalescence of land areas into a supercontinent Pangaea (*53, 54*). There is no evidence yet that breakup of land areas was responsible for any of the

major divergences under consideration here. Sea-level changes also can cause the separation of evolutionary lineages, but the pattern for the Paleozoic, which shows a high in the Ordovician (488–444 Ma) followed by generally falling levels (*55*), also does not map directly to the vertebrate timetree (Fig. 2). However, variation in oxygen levels has been invoked as a major driver of animal evolution (*56–63*). During a surprisingly short interval in the latest Precambrian, 580–542 Ma, oxygen levels increased from 1% to 10% of the present level (*64, 65*) to nearly 100% of the present level (*61, 66*). If correct, a spike in oxygen of that magnitude would explain the Cambrian Explosion in the fossil record, reflecting an increase in

animal body size and production of hard parts (57–59). Evidence from molecular clocks indicates that this was decoupled from evolutionary divergences among animal phyla which occurred much earlier (67, 68).

Atmospheric oxygen levels varied considerably during the Phanerozoic (542–0 Ma), presumably in response to changes in land floras and hence carbon burial, resulting in two major pulses (66). The First Pulse was in the late Silurian and early Devonian (~430–390 Ma), where the level reached a maximum of 25% at 410 Ma (the current level is 21%). This was followed by the Second Pulse in the Carboniferous and Permian (~340–250 Ma), reaching a maximum of 35% at ~270 Ma. Some effects of high oxygen levels are known, at least anecdotally, because insect gigantism is directly associated with the Second Pulse (56, 60). Also at a gross level, the timing of the two pulses coincides with periods diversification of vertebrates (1), suggesting a relationship. Otherwise it is difficult to link specific oxygen levels to favorable or unfavorable effects on vertebrates (62, 63). For example, the lowest level (~12%) during the entire Phanerozoic occurred in the Jurassic (200–146 Ma), yet this is the time when vertebrates were diversifying in body plans and increasing greatly in body size (e.g., dinosaurs), indicating that whatever limitations existed were overcome by the organisms. Nonetheless, the association of oxygen levels and Phanerozoic taxonomic diversity is still compelling and suggests some cause–effect relationship, even if mostly tied to invertebrate prey.

Against this backdrop of atmospheric change, the origin of the vertebrate lineage began deep in the Neoproterozoic (~800–700 Ma), according to molecular clocks (5). That the earliest divergence among vertebrates (Fig. 2) occurred in the Precambrian (Neoproterozoic) as well is supported by the presence of diverse lineages of agnathans in the early Cambrian (31), only 20 million years after the Precambrian–Cambrian boundary. Under the interpretation of cyclostome monophyly, the distinction of craniates and vertebrates disappears, and therefore the first vertebrates that existed before the divergence between cyclostomes and gnathostomes are inferred to have had both a cranium and a vertebral column. However, because oxygen levels were very low they were surely small in size and soft-bodied, lacking bone, and initially probably fed on microorganisms. Prediction of the environment of the earliest vertebrates based on kidney structure and function has been debated (69–71), with an estuarine habitat favored most recently (72).

In the latest Precambrian (e.g., Edicaran) when oxygen levels rose dramatically, there would have been already multiple lineages of early vertebrates. One led to the living cyclostomes and another—the gnathostomes—took on the role of a major predator. The interpretation of conodonts as being on the gnathostome lineage (11) helps to fill in the otherwise large gap in the fossil record of gnathostomes forced by the presence of agnathans in the early Cambrian. Still, the absence of vertebrates and many other phyla from the latest Precambrian fossil record remains a problem for this hypothesis. If they were much smaller in size and soft-bodied, their fossils may only be discoverable in the finest-grain sediments representing low-energy environments (e.g., 73).

In the Paleozoic, a good case can be made for oxygen as a driver of vertebrate evolution through prey abundance and diversity. The fossil record shows an explosion of fish lineages arising precisely during the First Pulse in the late Silurian and early Devonian. Presumably the pulse was from the land flora, known to be expanding at that time (74). A diversity of aquatic and terrestrial invertebrates also underwent diversification during the interval (63), making coastal and freshwater habitats a new resource niche for small fishes, which in turn were food for larger fishes.

The first tetrapods appear in the fossil record later in the Devonian (~360 Ma), between the first and second pulses, and most authors consider the Second Pulse as key for tetrapod evolution (60, 62, 63). This is almost certainly true for the diversification of tetrapods, including the origin of lissamphibians and amniotes. The timetree (Fig. 2) suggests that the phylogenetic divergence of lissamphibians and amniotes occurred at a time (~360 Ma) when the first tetrapods appear in the fossil record. This rapid diversification is supported by the fossil record as well, which shows evidence that those two major tetrapod groups split no more than 25 million years later (44), with subsequent splitting into the lineages leading to caecilians, frogs, and salamanders on the one hand and synapsids and sauropsids on the other (4, 32, 40, 42, 43, 52, 75, 76). The ecological and evolutionary details of this "Permo-Carboniferous Explosion" of tetrapods have yet to be fully understood.

However, most of the stage for the conquest of land by tetrapods was likely set during the First Pulse. Shallow-water habitats were teeming with life and the great number of lineages of fishes that appeared at that time, some having adaptations for living in shallow water (e.g., lungs, bony elements in fins) attests to the importance of that habitat. These included two major lineages of living fishes—coelacanths and lungfishes—and other extinct groups, one of which (osteolepiforms) led to tetrapods.

Species transitional between fishes and tetrapods first appear in the fossil record ~385 Ma (*37–39*), at the end of the First Pulse. Although these transitional forms lacked digits and were adapted to shallow water—not land—they had already started to evolve most of the major tetrapod body plan traits. Whether oxygen did or did not play a major role in the origin of tetrapods, the reason was still probably related to a new prey resource (*1*) rather than escape from drying ponds (*8*).

In summary, the early history of vertebrates may have extended 100–300 million years into the Precambrian but little is known about those organisms other than that they lived in very low oxygen levels and therefore were necessarily small and soft-bodied. Since the evolution of jaws in the latest Precambrian or Cambrian (according to the molecular timetree), vertebrates have dominated most environments on Earth as the top predators. Variation in oxygen levels during the Phanerozoic affected vertebrate prey and hence vertebrate diversity, and appears to have been responsible for bringing vertebrates onto land. The only remaining unsolved portion of the vertebrate backbone phylogeny, based on molecular data, is the relationships of tetrapods to lungfishes and coelacanths. In this case it is unclear whether resolving that node will answer any major questions not already addressed by fossils (*18*) and molecular clocks (Fig. 2), which place the divergences close in time. In the future, more sequences and fossils, and more reliable phylogenies incorporating fossil data, will allow for better calibration of molecular clocks and reduced variance of time estimates, and therefore a better resolution of the timescale of vertebrate evolution.

Acknowledgments

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