Au1

Phylogeny and Evolution of Vertebrates

Susan E. Evans
Department of Anatomy & Developmental Biology,
University College London, London

Synonyms

Evolution of vertebrates; Phylogeny

Definition

The phylogeny of a group, in this case back-boned animals (vertebrates), represents the course of evolutionary change undergone by that group over time. It is typically represented in the form of a ►dichotomous branching tree in which the vertical axis represents time and the horizontal axis represents closeness of relationship (Fig. 1).

Characteristics

Underlying Methodology

The framework used here is cladistic. Groups must be monophyletic (including the common ancestor and all its descendents) and are diagnosed on the basis of shared ►derived characters. Only monophyletic groups are given formal scientific names. The primitive absence of a derived trait (e.g. the absence of jaws, absence of hair) cannot be used to group organisms. The use of paraphyletic, gradal, groups confuses the discussion of morphological evolution. For example, the old view that reptiles gave rise to mammals (instead of being their ►sister group) left many comparative anatomists trying to derive mammalian structures (e.g. the middle ear) directly from those of living reptiles, despite more than 300 million years of independent history.

Ages in millions of years before present (Ma BP) are based on the most recent geological timescale [1], but should be regarded as minimum estimates reflecting the earliest known occurrence of a fossil group or its phylogenetic sister taxon. Given that individual geological strata cannot always be dated with precision, such dates should also be understood to carry error bars.

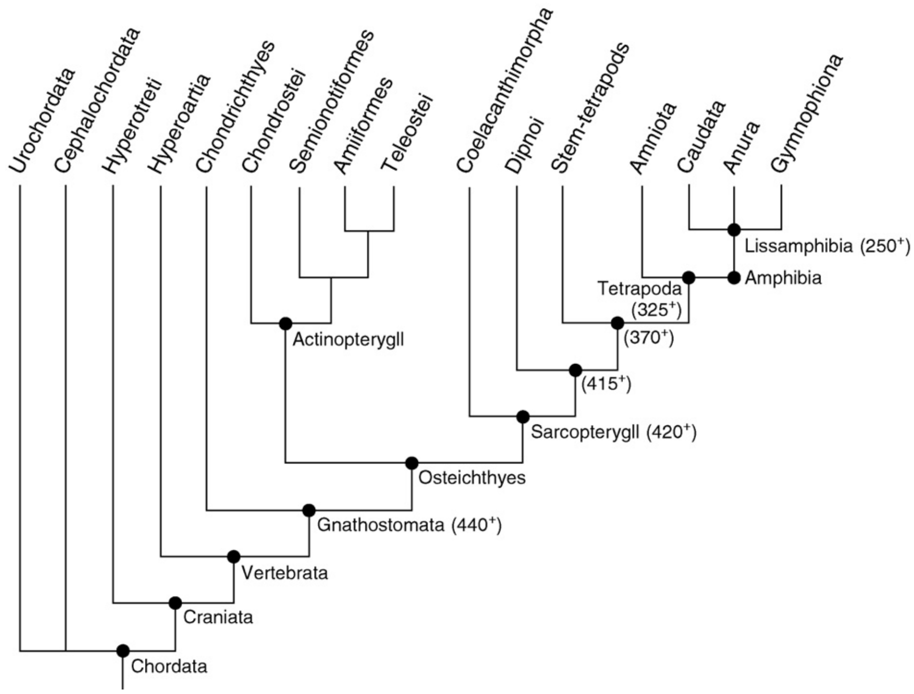
Vertebrates

Vertebrates (backboned animals) are part of the wider group Chordata (see ►Phylogeny and Evolution of Chordates), characterized by the possession of an axial stiffening rod (notochord), a perforated pharynx, a dorsal hollow nerve cord, and a post-anal tail. Chordata has a long fossil record, the earliest known representatives occurring some 570 Ma BP. Today, only two groups of basal chordates survive – the Urochordata (e.g. ►*Ciona*) and the Cephalochordata (e.g. the lancelet, ►*Branchiostoma*). All remaining chordates are craniates (Craniata). The name acknowledges the common possession of an organized head with a brain, well-developed sense organs, cranial nerves, and the beginning of a skull (all linked to the evolution of ectodermal placodes and migratory neural crest).

Craniates are divided informally into ►agnathans and ►Gnathostomata. Agnathans are a gradal concept rather than a valid monophyletic group since they include a range of primitive craniates (mostly now extinct) that lack jaws. Some agnathans (e.g. the extinct ►osteostracans) are more closely related to derived vertebrates (gnathostomes) than are others (e.g. lampreys). Today, only two agnathan lineages survive – the primitive hagfish (Hyperotreti) and the lampreys (Hyperoartia). However, researchers are divided as to whether lampreys are more closely related to hagfish (to form a monophyletic Cyclostomi [2,3]) or to gnathostomes [4]. Under the second hypothesis, lampreys and gnathostomes form the Vertebrata, while hagfish would be considered craniates but not vertebrates. Under the first, Craniata and Vertebrata are synonymous [2]. Fig. 1 illustrates the second hypothesis in order to clarify the conceptual distinction between craniate and vertebrate, but with the recognition that a monophyletic Cyclostomi is more widely accepted amongst neontologists.

Gnathostomes

The evolution of jaws from gill arch (branchial arch) cartilages occurred at least 440 Ma BP. Unlike their predecessors, early gnathostomes were adapted to an active predatory niche, with paired pectoral and pelvic fins and a streamlined body shape. Aquatic fusiform gill-breathing gnathostomes are traditionally, and colloquially, called fish (and were once grouped as Pisces), but "fish" do not form a monophyletic group. A zebrafish



Phylogeny and Evolution of Vertebrates. Figure 1 Tree showing relationships amongst major vertebrate groups. Clade names have been added to appropriate nodes. The numbers at some nodes represent the minimum age estimates (in millions of years) for the last common ancestor of the descendant lineages.

is more closely related to a human than either is to a shark. All living "fish" are grouped into one of two major clades – the Chondrichthyes (with a cartilaginous skeleton, like sharks, rays [Elasmobranchii] and parrotfish [Holocephali]), and Osteichthyes (with true bone). The monophyletic Osteichthyes includes ALL vertebrates with a bony endoskeleton, ranging from goldfish and lungfish through to dinosaurs, birds and monkeys.

Living osteichthyans are themselves subdivided, based on fin type, into Actinopterygii and Sarcopterygii that separated at least 420 Ma BP. Actinopterygii are the ray-finned fish. As the name suggests, this group encompasses fish in which the fins consist of a fan of delicate rays. The most derived actinopterygians are the teleosts (e.g. zebrafish, cod, tuna), but some members of more ancient stem clades have also survived, including Amiiformes (the bowfin, [illegible]ia), Semionotiformes (gars, e.g., *Lepisosteus*), and Chondrostei (paddlefish, e.g., ►*Polyodon*, and sturgeons, e.g., ►*Acipenser*).

Sarcopterygians

The Sarcopterygii, or lobe-fins, differ from actinopterygians in having a skeletal axis to the pectoral and pelvic appendages. The largest living group of sarcopterygians is comprised, of course, of the tetrapods, but two extant fish groups also fall into this clade – the Coelacanthimorpha or ►coelacanths (►*Latimeria*) and the Dipnoi or lungfish (►*Lepidosiren, Neoceratodus*, ►*Protopterus*). The freshwater lungfish, as the name suggests, have functional lungs, internal nostrils, and a pulmonary circulation. Both lineages (lungfish and coelacanths) go back more than 415 Ma, but of the two, lungfish are probably the more closely related to tetrapods [but see 5], although not on the tetrapod stem. Paleontological and molecular evidence suggests a rapid diversification of the major sarcopterygian lineages, including the immediate fossil ancestors of tetrapods, within a relatively short space of time around 420–400 Ma BP [5].

Tetrapods

In common parlance, a tetrapod is an animal with four limbs (tetra-pod), but Tetrapoda ►*sensu stricto* encompasses the last common ancestor of living amphibians and living amniotes, and all descendents of that ancestor. This definition omits some of the earliest truly limbed vertebrates and these are best termed ►stem-tetrapods. The earliest known stem-tetrapods date from the later part of the Devonian period, around 370 Ma (e.g. ►*Acanthostega, Ichthyostega*, [6]). They were still aquatic, using a combination of lung and gill breathing, like the living Australian lungfish, ►*Neoceratodus*.

The main vertebrate colonization of the land appears to have begun during the Carboniferous (c. 340–320 Ma

BP), perhaps coinciding with a sharp rise in atmospheric oxygen levels, and the fossil record documenting a gradual radiation of stem-tetrapods into available ►*niches*. The phylogenetic tree is rather "bushy" at this stage, but two major lineages emerged: amphibians and amniotes. The latter clade includes all truly terrestrial groups (e.g. birds, tortoises, lizards and snakes, mammals) that possess an ►amniote egg (or a derivative structure such as the placenta). This group is covered in more detail elsewhere (see ►The Phylogeny and Evolution of Amniota). Amphibia are rather more challenging. Under traditional usage, Amphibia is a paraphyletic group for tetrapods that are not amniotes, but under a cladistic definition, Amphibia encompasses those tetrapods that are more closely related to living amphibians (frogs, salamanders, caecilians) than to amniotes. Unlike amniotes, they still generally require water to reproduce, typically have an aquatic larva, and undergo ►metamorphosis. Paleontologists do not agree as to the ancestry of living forms. For neontologists, this is relatively unimportant except that it impacts on the timing of the divergence between the ancestors of Amphibia and of Amniota. Nonetheless, by any estimate, the last common ancestor of amniotes and amphibians lived more than 325 Ma BP [7].

Modern amphibians comprise of the Lissamphibia: frogs, salamanders and the limbless caecilians. The relationships of the three living clades are not fully resolved. Many workers place frogs (Salientia) and salamanders (Caudata) as close sister taxa but others argue for separate origins from distinct fossil lineages [7]. Caecilians are even more problematic: they may be the sister group of frogs plus salamanders (most morphological analyses and some molecular ones), they may be the sister group of salamanders alone, or they may be unrelated [7]. This affects estimated divergence times for the three major groups (325–200 Ma BP). The earliest known fossil stem-frogs are recorded from c. 245 Ma BP, while the equivalent dates for salamanders and caecilians are 170 Ma BP and 190 Ma BP respectively [7,8].

Amongst living frogs, the North American ►*Ascaphus* and New Zealand ►*Leiopelma* represent the oldest and most basal lineages, followed by discoglossids (e.g. ►*Alytes*, *Discoglossus*), and then pipids (e.g. ►*Xenopus*), pelobatids and rhinophrynids. The most diverse and derived frog clade is the Neobatrachia (e.g. ►*Bufo, Hyla, Rana*). Fossil ascaphids have not been identified with certainty, but discoglossids are recorded with confidence from around 145 Ma BP, basal pipids from 120 Ma BP, and early neobatrachians from at least 80 Ma BP, these dates giving the latest possible divergence times for each lineage [9]. Living salamanders fall into two major groups, Cryptobranchoidea (e.g. ►*Cryptobranchus*, *Hynobius*) and Salamandroidea (e.g. ►*Salamandra*, *Ambystoma*) and, judging from recent fossil finds in China and the USA, these groups had already separated by at least 145 Ma BP. Nonetheless, the position of sirenids (e.g. ►*Siren*) is still uncertain (basal or highly derived, [6]), as are the interrelationships of living families. The fossil record of caecilians is extremely poor and no certain representative of modern families has been recovered from Mesozoic deposits.

References

1. Gradstein FM, Ogg JG (2004) Geological time scale 2004 – why, how and where next. Lethaia 37:75–181
2. Furlong RF, Holland PWH (2002) Bayesian phylogenetic analysis supports monophyly of Ambulacraria and of cyclostomes. Zool Sci 19:593–599
3. Takezaki N, Figueroa F, Zaleska-Rutczynska Z, Klein J (2003) Molecular phylogenetics of early vertebrates: monophyly of the agnathans as revealed by sequences of 35 genes. Mol Biol Evol 20:287–292
4. Janvier P (1996) The dawn of vertebrates: characters versus common ascent in current vertebrate phylogenies. Palaeontology 39:259–287
5. Takezaki N, Figueroa F, Zaleska-Rutczynska Z, Takahata N, Klein J (2004) The phylogenetic relationship of tetrapod, coelacanth and lungfish revealed by the sequences of 44 nuclear genes. Mol Biol Evol 21:1512–1524
6. Clack JA (2002) Gaining ground: the origin and evolution of tetrapods. Indiana University Press, Bloomington, Indiana
7. Frost DR, Grant T, Faivovich J, Bain RH, Haas A, Haddad CFB, de Sá RO, Channing A, Wilkinson M, Donnelan SC, Raxworthy CJ, Campbell JA, Blotto BL, Moler P, Drewes RC, Nussbaum RA, Lynch JD, Green DM, Wheeler WC (2006) The amphibian tree of life. Bull Am Mus Nat Hist 297:370 pp
8. Zhang P, Chen Y-Q, Zhou H, Wang X-L, Qu LH (2003) The complete mitochondrial genome of a relic salamander, *Ranodon sibiricus* (Amphibia, Caudata) and implications for amphibian phylogeny. Mol Phylogenet Evol 28:620–626
9. Rocek Z (2000) Mesozoic anurans. In: Heatwole H, Carroll RL (eds) Amphibian biology, vol 4: Palaeontology. Surrey Beatty and Sons, Australia, pp 1295–1331

Comp. by: RPushparaj Date:28/1/08 Time:21:22:06 Stage:First Proof File Path://spiina1001z/womat/
production/PRODENV/0000000005/0000006643/0000000016/0000760055.3D Proof by: QC by:

Author Query Form

Title: Encyclopedia of Neuroscience
Alpha - P

Query Refs.	Details Required	Author's response
AU1	Kindly provide us with a list of key terms (glossay terms) within your essay that need further defining. Please explain them in a sentence or two and underline all respective terms in your manuscript.	