

About 300 Ma
About 250 Ma

Q9. According to this phylogeny, when did mammals diverge from the other living tetrapods?

About 400 Ma
About 150 Ma
About 320 Ma
About 250 Ma

Q10. How much unique evolutionary history would be lost to the world if the tuatara were to go extinct?

About 400 Ma
About 320 Ma
About 220 Ma
About 150 Ma
About 50 Ma

Q11: If a scientist says, "phylogenetically speaking, tetrapods are just a subgroup of fishes", what do they mean?

They are trying to trick you on an exam question, because obviously tetrapods live on land and are not fishes

Because some tetrapods returned to the ocean (e.g. whales), the term "fishes" can include tetrapods.

The "tetrapods" are not a valid evolutionary group, because "tetra-pod" means "four feet", and some groups have lost their feet (snakes, whales, etc.).

Tetrapods are phylogenetically nested within the paraphyletic "fishes" (water-breathing vertebrates) group

Transitional fossils, and crown groups vs. stem groups

As scientists' ability to infer phylogenies has been improved, it has become useful to distinguish between "crown" and "stem" groups. These terms are most useful for fossils, which often are related to, but fall outside of, a living clade ("the crown").

(For an example of how extinct fossil groups can be added to a phylogeny of living species, see Figure 4, which is identical to Figure 3, except that fossils have been added. You are not responsible for knowing all of those dinosaur names, but you should understand the phylogenetic position of dinosaurs with respect to living birds.)

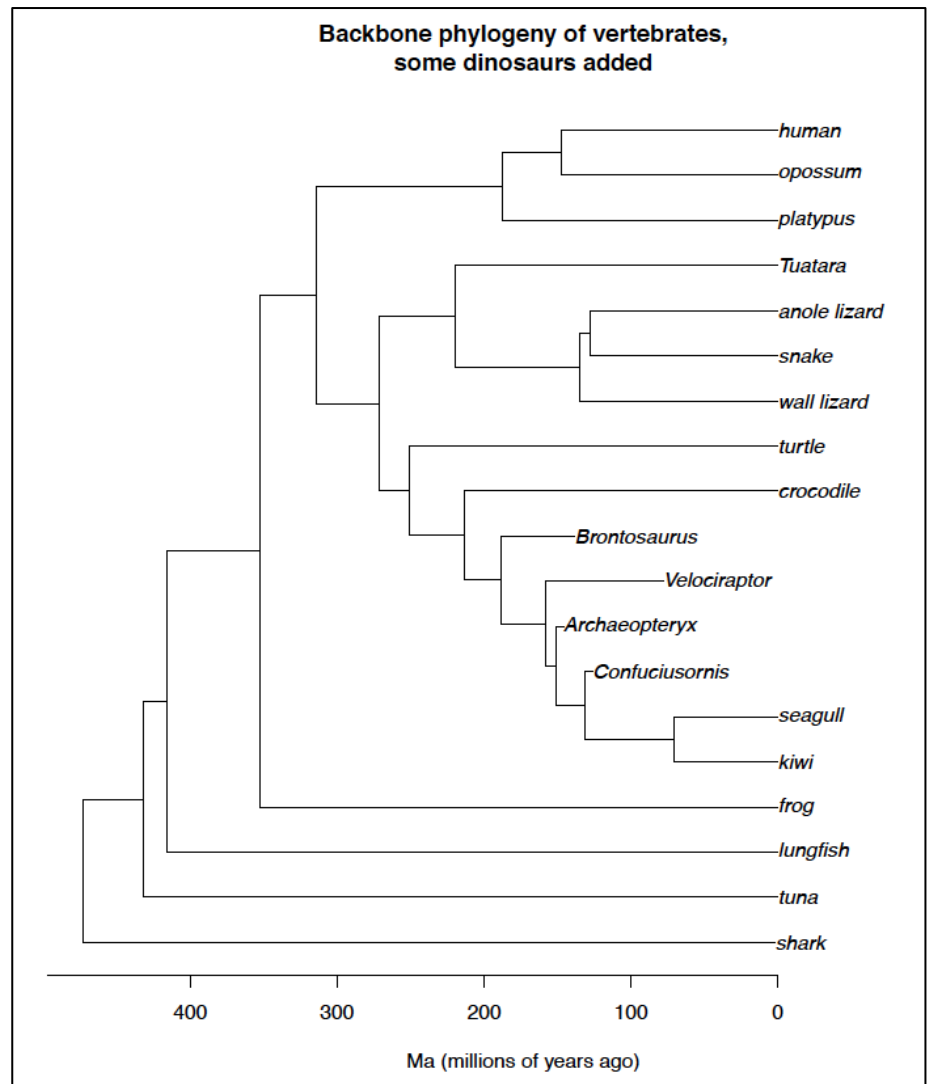


Figure 4. Phylogeny of vertebrates, with some fossils added.

Definitions:

To define a "**crown group**", pick 2 living taxa, and go back to their common ancestral node. Anything descending from this node is in the crown group.

A "**stem group**" is any group that falls outside of this crown, but is closer to that crown group than to any others.

The crown/stem distinction is useful because it avoids a problem commonly encountered with transitional fossils. For example, how "mammal-like" does a fossil have to be before it gets called "a mammal"? Transitional fossils, almost by definition, have combinations of characters that make them difficult to place clearly in present-day living groups.

Crown group birds can be defined by the common ancestor of paleognath birds (kiwis, moa, ostriches, and relatives) and neognath birds (all other living birds). The dinosaur fossils *Archaeopteryx* and *Confuciusornis* had feathers and could fly. However, while the dinosaur *Velociraptor* probably had feathers, and the dinosaur *Brontosaurus* might have had feathers, neither of them could fly.

Q12: Which fossils are stem groups for the bird crown group?

Confuciusornis
Archaeopteryx
Velociraptor
Brontosaurus
All of them

Q13. The common ancestor of crocodylians and living birds defines the crown group named “archosaurs”. Which of the fossils in Figure 4 fall within crown group archosaurs?

Confuciusornis
Archaeopteryx
Velociraptor
Brontosaurus
All of them

Tree-thinking: avoiding notions of "progress" and "higher" versus "lower"

Going back to the ancient Greeks, it has been common to think of life as a "**Great Chain of Being**", or a ladder. It looks something like this:

gods
angels
humans
apes
mammals
reptiles
amphibians
fishes
other squishy things ("lower animals")
plants
rocks

This way of thinking is so deeply embedded that it often creeps into both popular and scientific discussions of evolution and phylogeny. I even did it by accident in our vertebrate phylogeny.

Let's display a basic vertebrate phylogeny in the way it is often shown in textbooks:

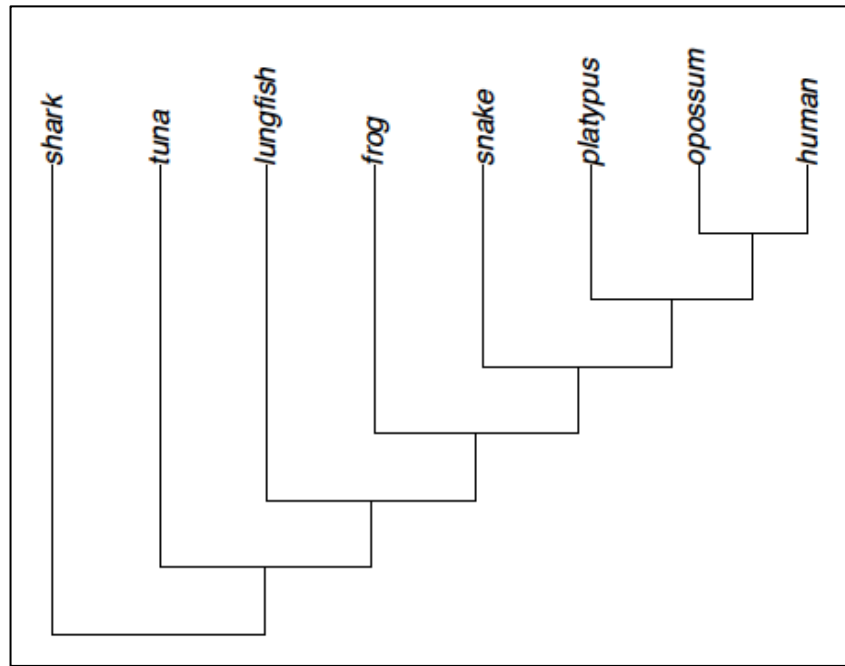


Figure 5. Simplified vertebrate phylogeny.

Here, because we read left-to-right, the display tends to accidentally reinforce the ladder-like, "Great-Chain-of-Being" misunderstanding of evolution.

To understand that this "linear view of evolution" is a misconception, one has to understand that:

IN VIEWING PHYLOGENIES, NODE-ROTATION IS ARBITRARY

...meaning, that any of the branches may be rotated around the nodes, and EXACT SAME INFORMATION IS ENCODED. A researcher might choose to arrange a tree a certain way in order to emphasise a particular point, or a particular clade of interest, but these are basically subjective decisions.

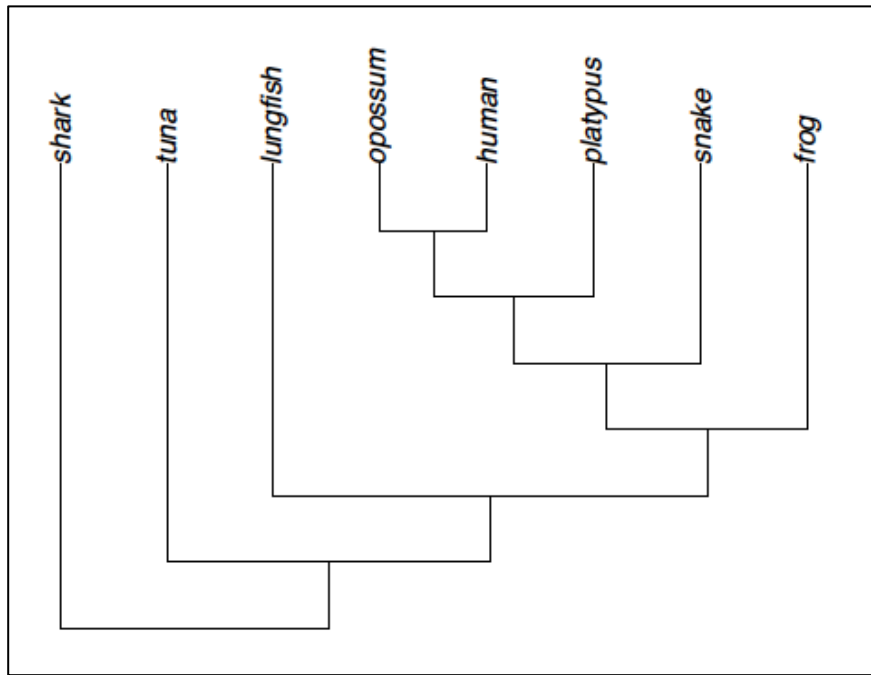


Figure 6. Simplified phylogeny of vertebrates.

Q14. Are mammals actually any more "advanced" in Figure 5 versus Figure 6? Why?

- Yes, mammals are more advanced in Figure 5, and more primitive in Figure 6, because primitive groups are traditionally displayed on the left, and the most advanced groups are displayed on the right.
- Yes, mammals are more advanced in Figure 5, and more primitive in Figure 6, not because of the arrangement of the figure, but because we know mammals, and especially humans, are the peak outcome of the ladder of evolution.
- No, mammals are not any more "advanced" or "primitive" in Figure 5 or Figure 6, because node rotation is arbitrary in phylogenies. Both figures show identical information.
- No, mammals are not any more "advanced" or "primitive" in Figure 5 or Figure 6, because node rotation is arbitrary in phylogenies. However, because we know evolution is ladder-like, we should prefer Figure 5.

Phylogeny and biogeography of kiwi, moa, and relatives

Several of the birds we looked at in Lab 4 were **paleognaths**. As we had only a few specimens, we did not show a full phylogeny of the paleognaths. As we will see below, recent discoveries about paleognath phylogeny have overturned some old ideas about the biogeography of this group, and about the loss of flight.

Scientists know that New Zealand and other continental blocks used to be connected in the ancient supercontinent of Gondwanaland. The major continental blocks split at approximately these times:

Gondwanaland breakup times (all approximate; Gibbs 2016, Yonezawa et al. 2017)

- 130 mya - Africa splits from South America (beginning of Atlantic Ocean)
- 130 mya - India + Madagascar break off from western Australia
- 80 mya - Zealandia splits off from eastern Australia; South America-Antarctica-Australia remain connected
- ~35 mya - Australia separates from Antarctica
- ~30 mya - Drake passage opens, separating Antarctica & South America

Vicariance

Speciation caused by geographic separation is known as "**allopatric**" speciation, and allopatric speciation caused by the formation of a barrier due to external factors (e.g., continental breakup) is known as "**vicariance**".

For many years, the geographic distribution of the flightless ratites has been claimed as a likely example of vicariance caused by continental break-up.

Paleognaths and Neognaths

Living birds are divided into two clades: **paleognaths** and **neognaths**. The paleognaths include many famous flightless birds, including the kiwi, the extinct moas, the Australian emu and cassowary, the South American rhea, the ostrich, and the extinct elephant birds of Madagascar. The tinamous of South America, which can fly, are also in the paleognath clade.

The neognath clade contains all other living birds.

For many years, the flightless paleognaths were thought to form a clade, named the **ratites**, with the flying tinamous as an outgroup.

For example, a 1997 source (Dingus & Rowe 1997) gives this cladogram of the ratites, based on an analysis of morphological characters:

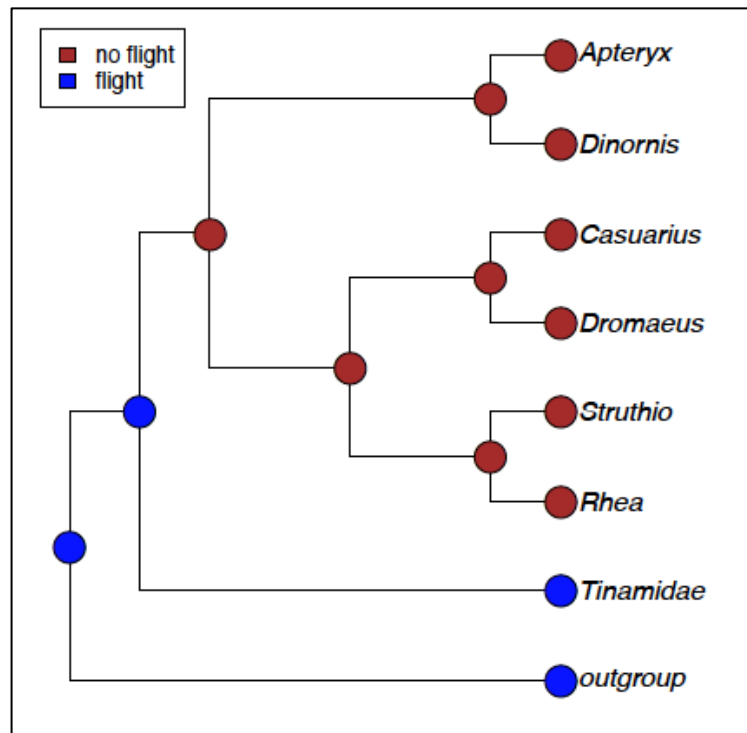


Figure 7. Cladogram of the ratites, from Dingus & Rowe 1997

The tinamous (Tinamidae) are a group of South American birds that are related to the ratites. They can fly.

The other genera are the classic ratites: *Apteryx* (kiwi), *Dinornis* (moa), *Casuaris* (cassowary), *Dromaeus* (emu), *Struthio* (ostrich), *Rhea* (South American rhea). None of these can fly.

Q15. According to the Figure 7 phylogeny, and the distribution of the "feathered flight" character, how many times was flight lost?

- Zero times
Once
Twice
Can't tell

Q16. If ratites lost flight only once, how could they have gotten distributed around the southern continents?

They would have to be ancient groups, ancient enough to have ridden the continental plates as Gondwanaland broke up through plate tectonics.

Maybe they could swim

Maybe they re-evolved flight and then lost it again

A 2017 paper by Yonezawa et al. conducted a comprehensive re-analysis of the phylogeny of paleognaths, combining morphological data with DNA from living species and ancient DNA from extinct subspecies of moa, and elephant birds (from Madagascar).

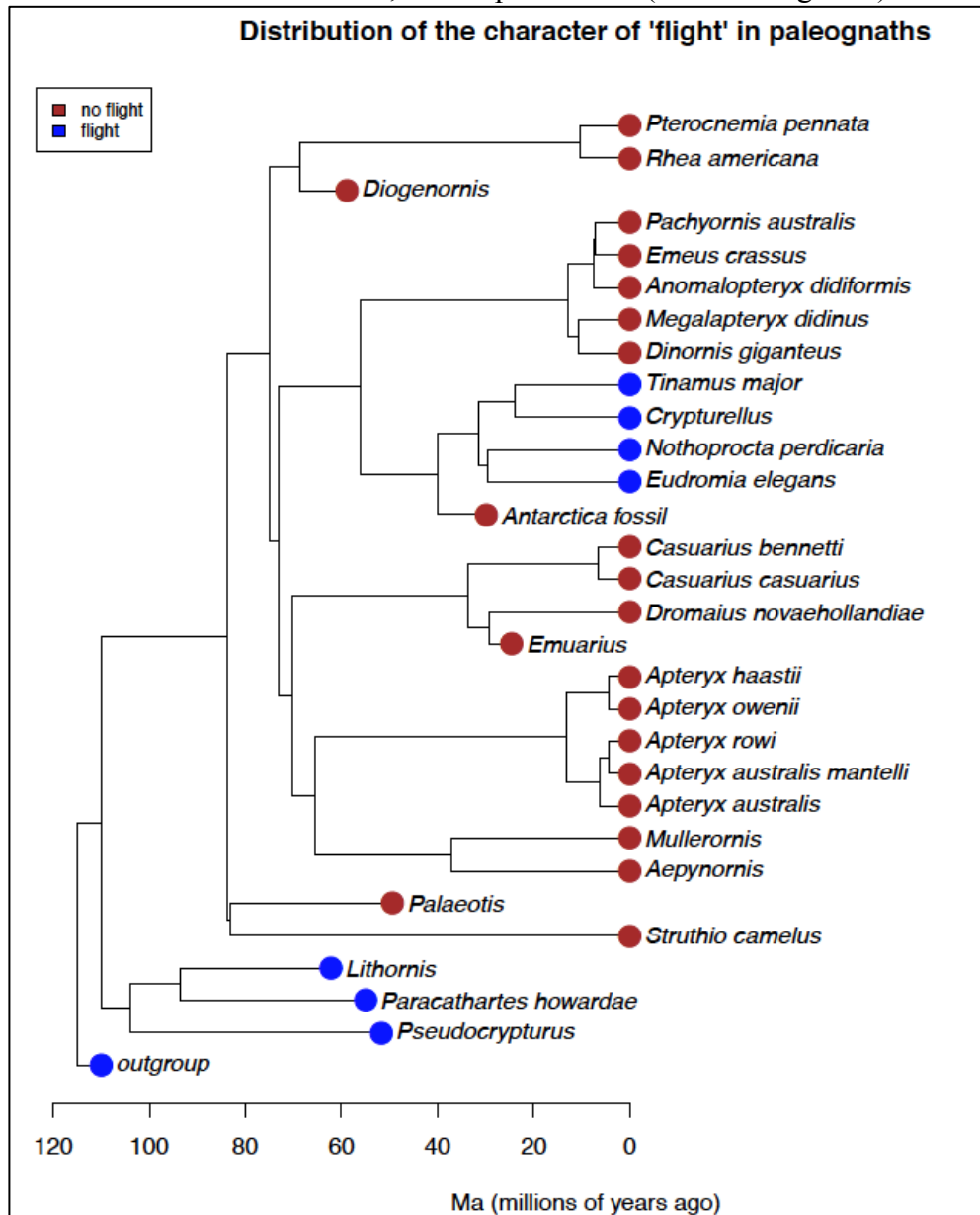


Figure 8. Phylogeny of paleognaths from Yonezawa et al. (2017).

This phylogeny (following on several other studies) suggested a different history of flight in the paleognath clade, which in turn impacts our ideas about its biogeographical history.

The tinamous (the crown group defined by the common ancestor of *Tinamus* and *Eudromia*) were found to be deeply nested within the “ratites” (previously defined in the Dingus & Rowe 1997 cladogram by the common ancestor of the ostrich and the kiwi). Several implications follow from this result.

Q17. What does the Yonezawa et al. phylogeny say about the validity of the traditional taxon name “ratites”?

It is invalid because it is monophyletic when it includes tinamous

It is valid because it is monophyletic as it includes tinamous
It is invalid because it is rendered polyphyletic by tinamous
It is invalid because it is rendered paraphyletic by tinamous

Q18. If we think that flight can be lost in birds, but then regained tens of millions of years later, how many transitions between flight/flightlessness are suggested by the Yonezawa et al. phylogeny?

- 1
- 2
- 3
- 4
- 5

Q19. If we think that it is basically impossible for flightless birds to re-evolve flight, how many loss-of-flight events are suggested by the Yonezawa et al. phylogeny?

- 1
- 2
- 3
- 4
- 5

Q20. What would repeated loss of flight in the paleognaths change about our understanding of their biogeographic history?

Nothing much, they probably are an ancient group that was broken up by vicariance as Gondwanaland rifted apart

Paleognath biogeography may have been produced primarily by flight, dispersing across water barriers, followed by repeated loss of flight and gigantism

Q21. According to Yonezawa et al. (2017), what is the closest sister group to the kiwi genus *Apteryx*?

the extinct moa of New Zealand
the Australian emu and cassowary
the South American rhea
the African ostrich
the extinct elephant birds of Madagascar

Q22. Deep thought question. In Lab 4, and in Q18, we looked for character state reconstructions that were “most parsimonious” – that is, they explained the observed character states by postulating the fewest number of character state changes. The argument for parsimony is that the simplest explanations are most likely to be correct. However, most scientists think the multiple-loss-of-flight scenario in Q19 is more likely to be correct. What

does this say about parsimony as a principle of inferring evolutionary history? Please think about the question, and choose the most correct answer.

- Parsimony is worthless, and we never should have taken it seriously as a principle of inference
- Parsimony is valuable, and likely to give correct inference of character state histories much of the time, but we can disregard it whenever we want to.
- Parsimony is justified by the idea that changes in a character state are evolutionarily rare, so we should use the minimum number of changes required. This may be as good as we can do without additional knowledge. However, in the case of loss-of-flight in birds, we have hundreds of examples where bird species isolated on islands etc. have lost flight, and a good understanding of why this might happen (flight is much less necessary if there are no predators). We also know that re-evolving flight in large, flightless ground birds would be very unlikely, because flight seems to evolve in small-tree dwelling organisms that can use gliding or fluttering as intermediate steps. Therefore, we are justified in overruling parsimony when we have a sufficiently good argument.
- We cannot resolve these questions without a video camera operating over hundreds of millions of years of geological history; the events that occurred so long ago are totally lost to us.

References

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Dingus, Lowell; Rowe, Timothy (1998). *The Mistaken Extinction & CD-Rom: Dinosaur Evolution and the Origin of Birds* (Academic Version), 1st Edition. W. H. Freeman, pp. 1-332 + CD-ROM. (ratite cladogram on CD-ROM)

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Yonezawa, Takahiro, et al. (2017). Phylogenomics and Morphology of Extinct Paleognaths Reveal the Origin and Evolution of the Ratites. *Current Biology*, 27, 68–77. [https://www.cell.com/current-biology/fulltext/S0960-9822\(16\)31214-3](https://www.cell.com/current-biology/fulltext/S0960-9822(16)31214-3)