

# Ruffling the Feathers

Constructing Phylogenies to  
Understand the Evolutionary History  
of Ratites

James Morris  
Professor of Biology  
Brandeis University

# Ratites



Ostrich

# Ratites



Emu

# Ratites



Rhea

# Ratites



Kiwi

# Ratites



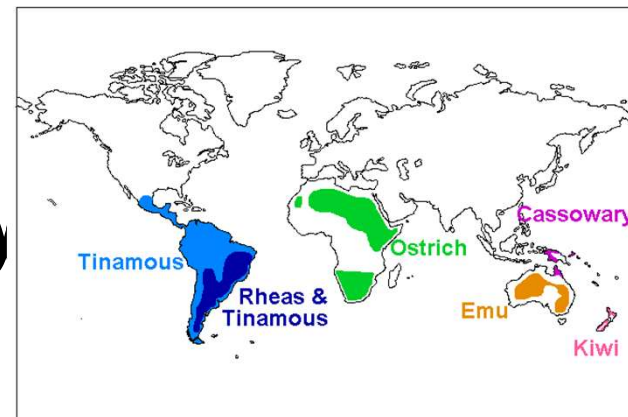
Cassowary

# Reconstructing the Past

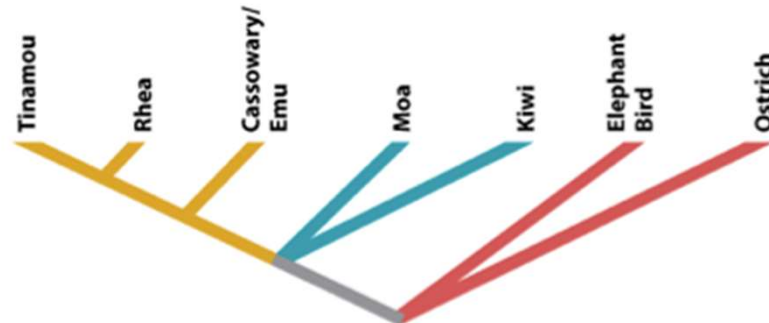
- Fossils



- Biogeography



- Phylogeny

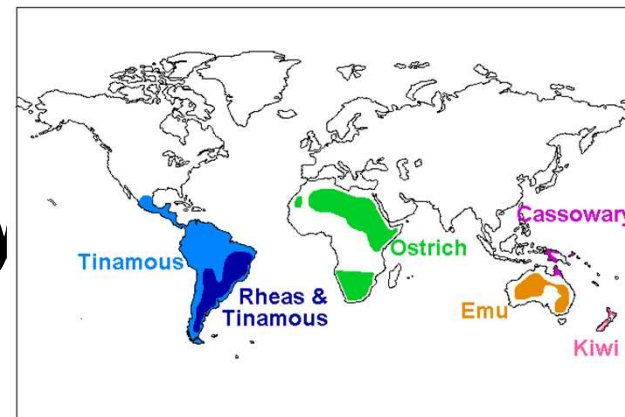


# Reconstructing the Past

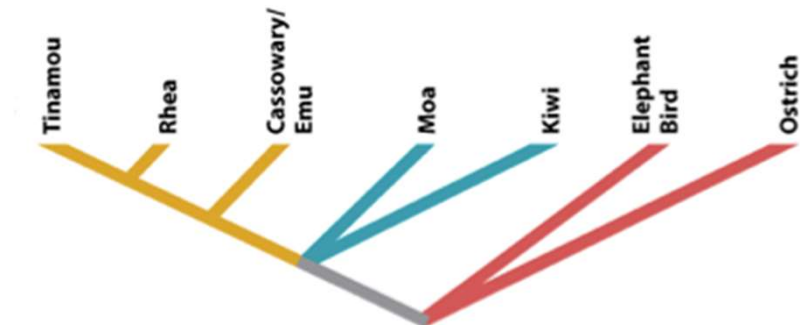
- Fossils



- Biogeography



- Phylogeny





# Fossils

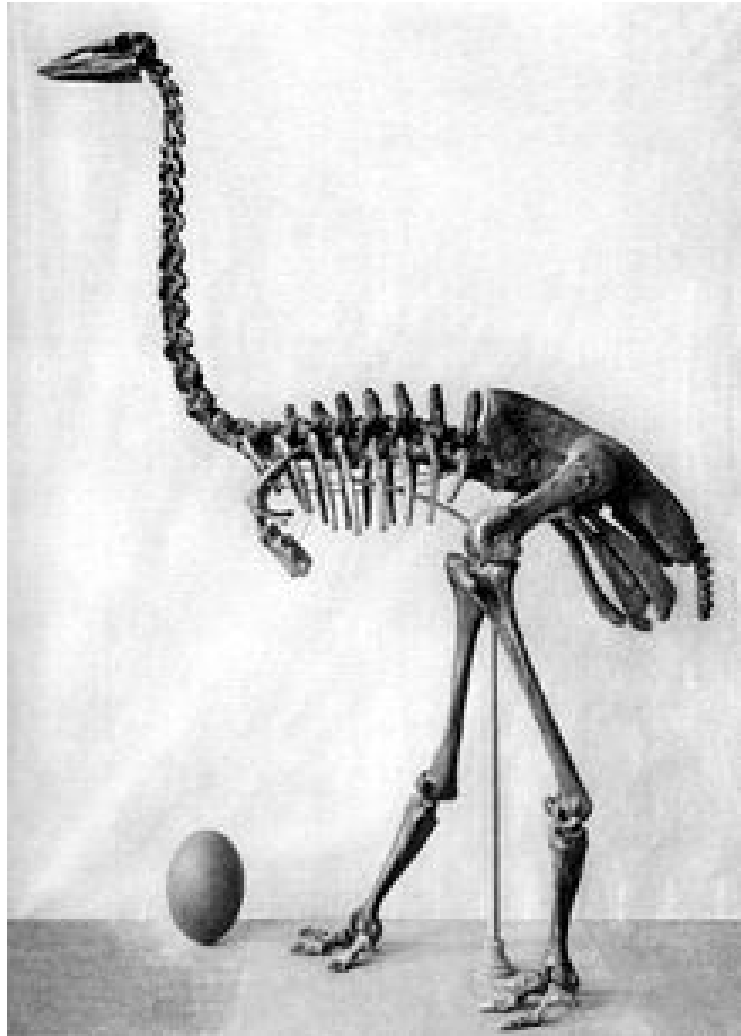
In an ideal world, we would be able to reconstruct the past by simply following the sequence of fossils through time.

# Fossils



Moa (Extinct)

# Fossils

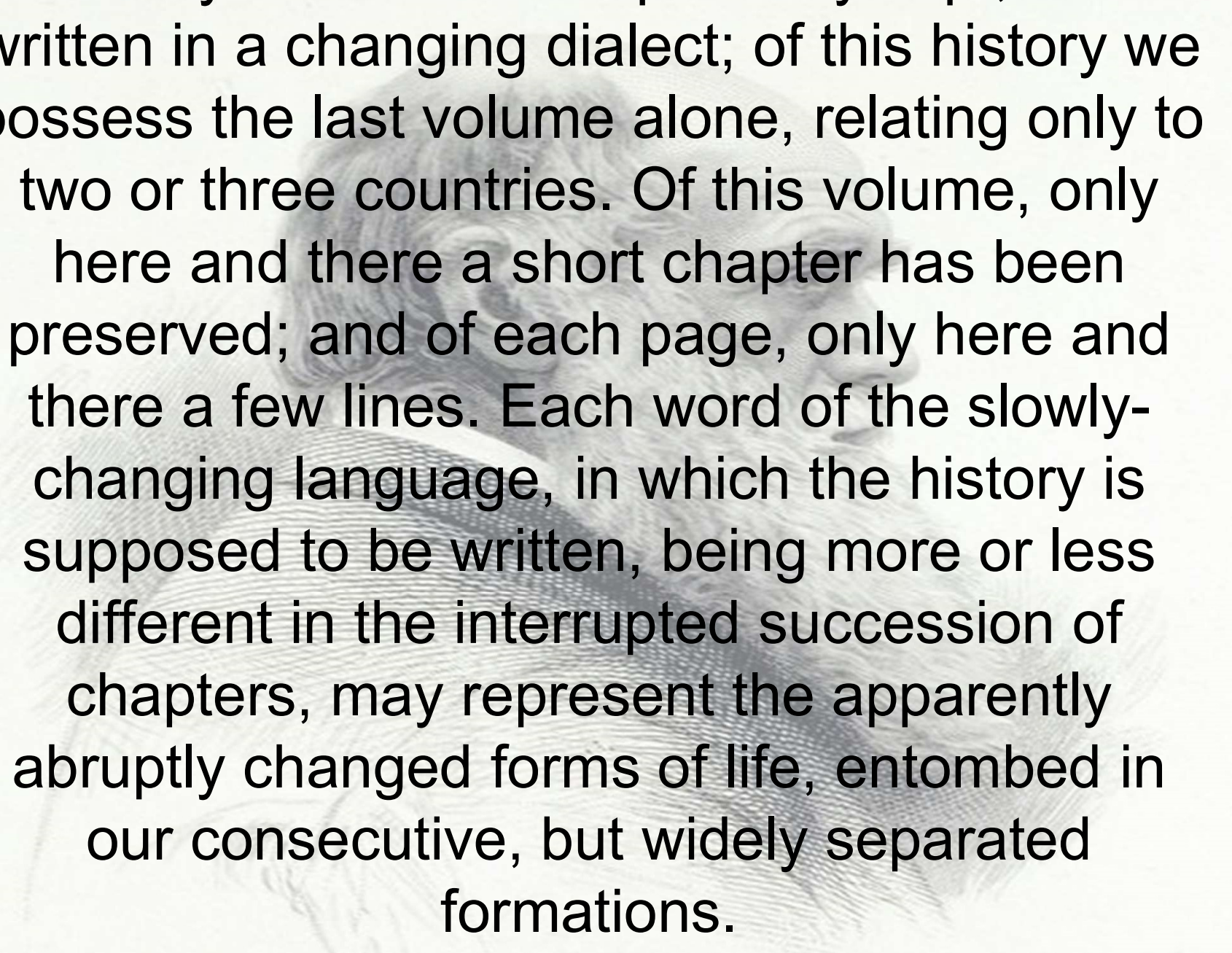


Elephant Bird (extinct)

# Fossils

Unfortunately, the real world  
is not ideal.

The fossil record is not nearly  
complete enough to permit this.

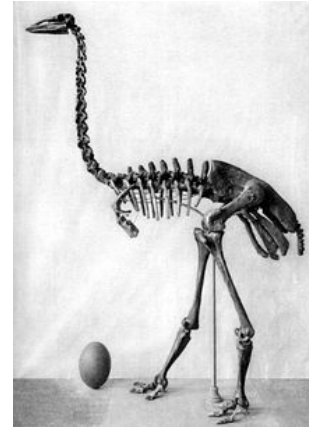


I look at the natural geological record as a history of the world imperfectly kept, and written in a changing dialect; of this history we possess the last volume alone, relating only to two or three countries. Of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines. Each word of the slowly-changing language, in which the history is supposed to be written, being more or less different in the interrupted succession of chapters, may represent the apparently abruptly changed forms of life, entombed in our consecutive, but widely separated formations.

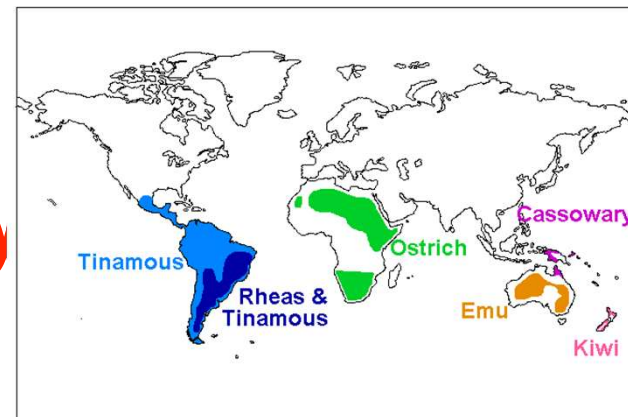
Charles Darwin. *On the the Oriain of Species* (1859)

# Reconstructing the Past

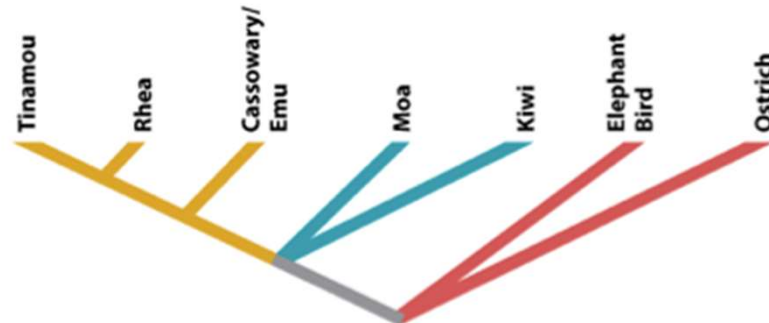
- Fossils



- Biogeography



- Phylogeny



# Biogeography

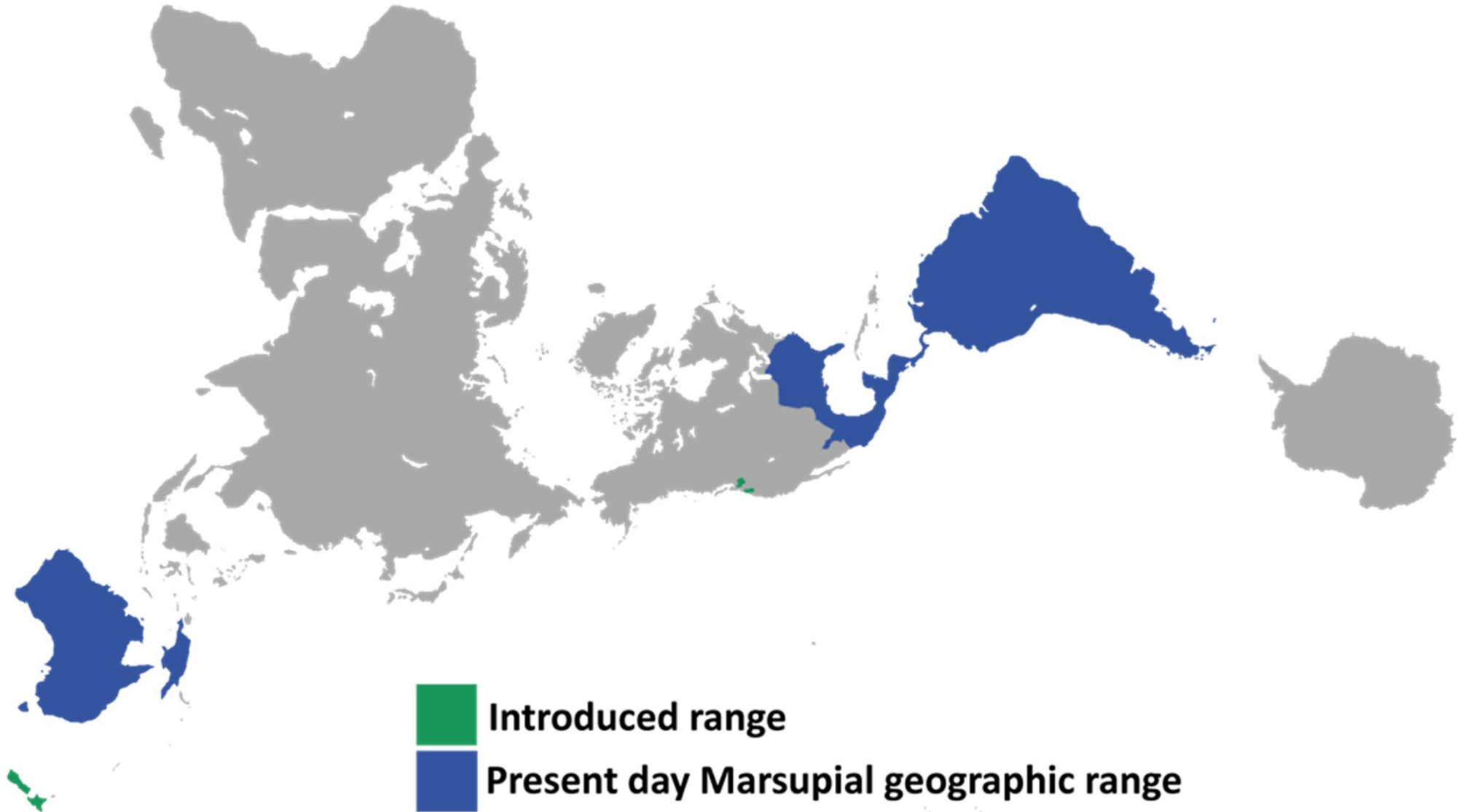


Why are penguins only found in the Southern Hemisphere?





Why are marsupials only found in Australia and the Americas?



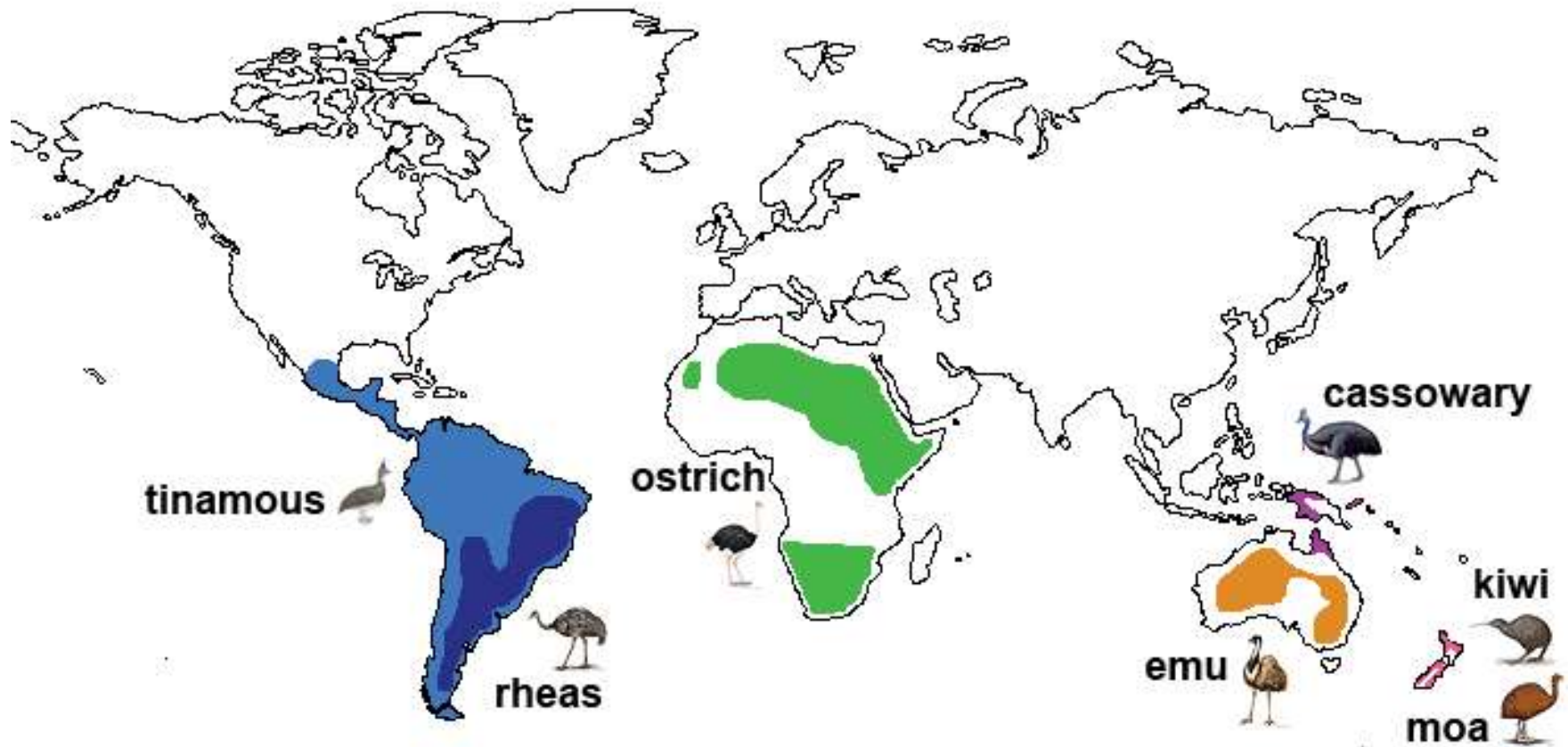
Why are Tasmanian devils only found  
in Tasmania?



Why are Darwin's finches only found in the Galápagos?

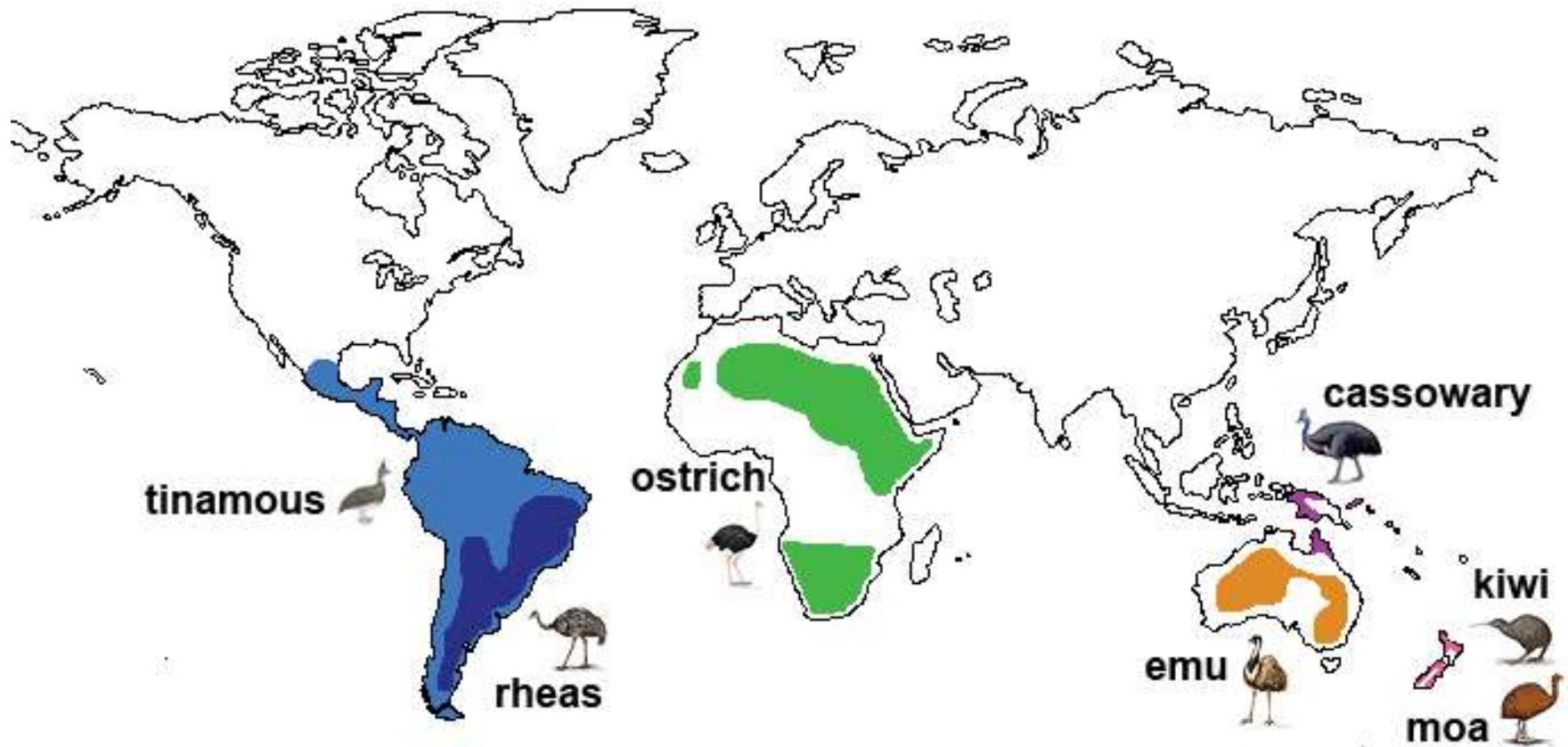


# Biogeography



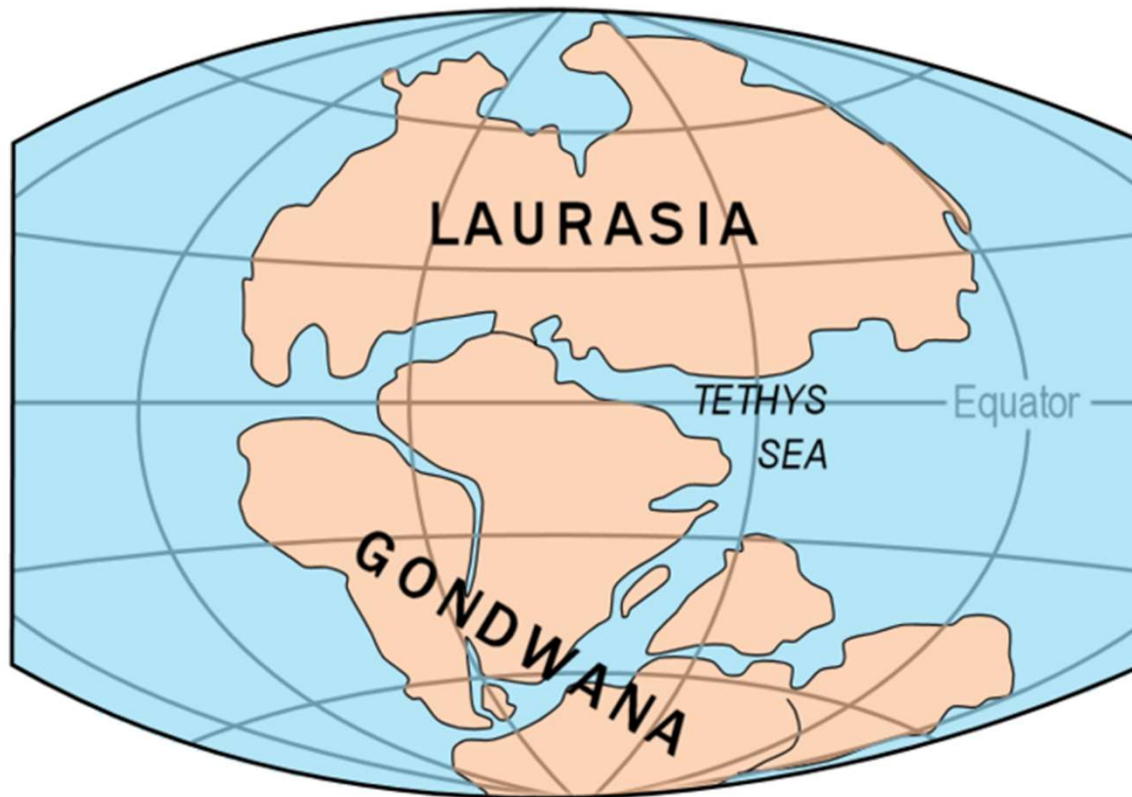
Southern Distribution

# Biogeography



Gondwanan Distribution

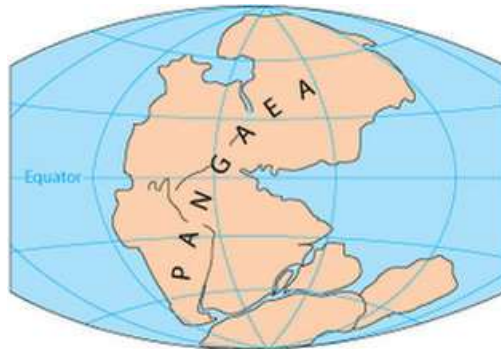
# Biogeography



TRIASSIC  
200 million years ago

## Gondwanan Distribution

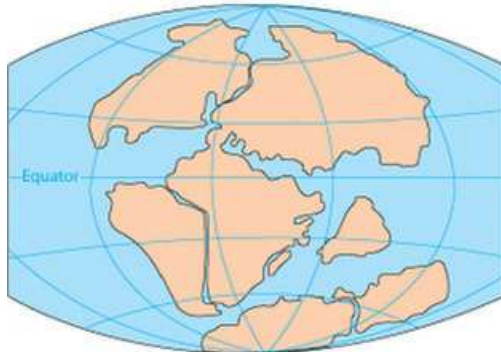
# Biogeography



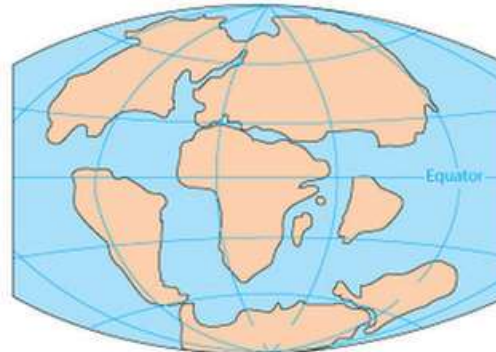
PERMIAN  
250 million years ago



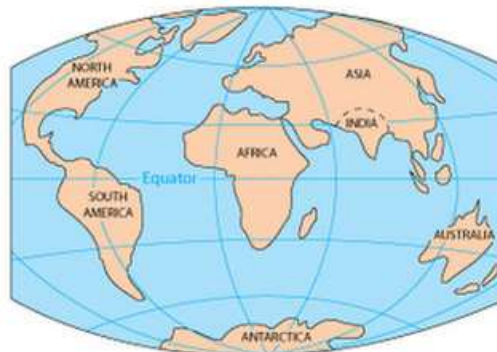
TRIASSIC  
200 million years ago



JURASSIC  
145 million years ago



CRETACEOUS  
65 million years ago



PRESENT DAY

# Biogeography

## Hypothesis:

Ratite ancestor originated in Gondwana and then descendant species dispersed and speciated as the continents broke up.



# Biogeography

## Prediction:

Oldest lineages should be found on land masses that broke off earlier, and newest lineages on land masses that broke off later.

# Biogeography

## Prediction:

Groups found on the same land mass or continent should be most closely related to each other (sister groups).

# Biogeography



These maps show the breakup of Gondwana. Based on these maps, ratites from \_\_\_\_\_ should have oldest lineages.

- A. South America
- B. Africa
- C. Australia
- D. New Zealand

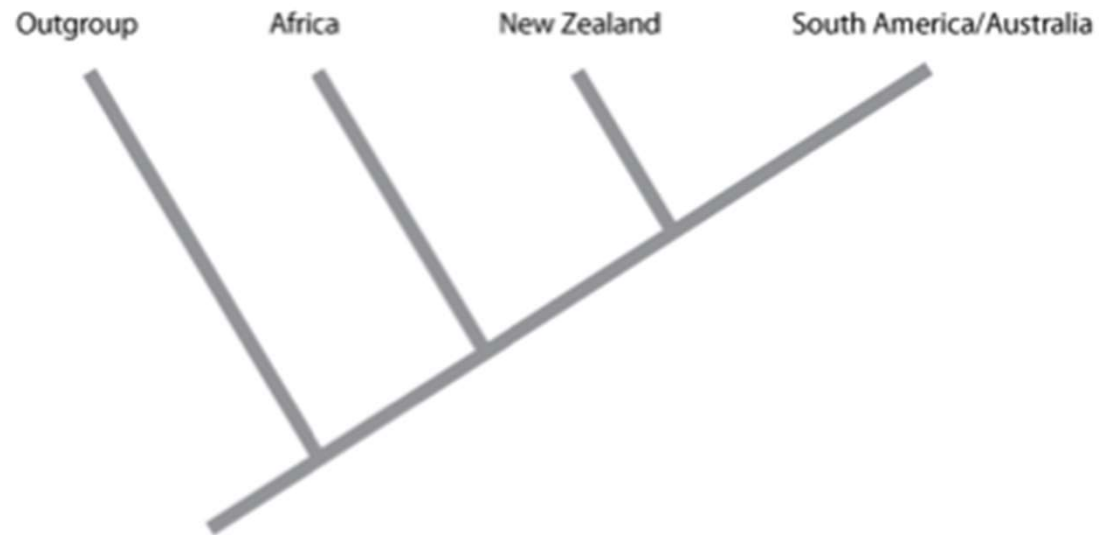
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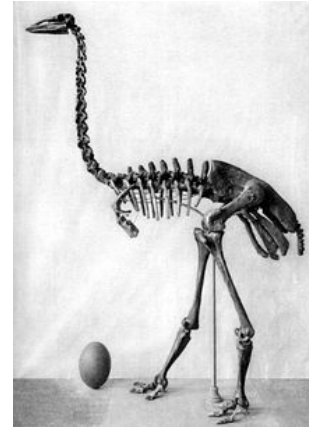
# Biogeography



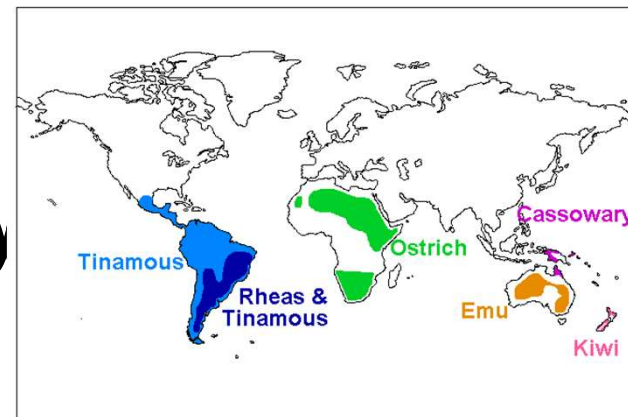
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# Reconstructing the Past

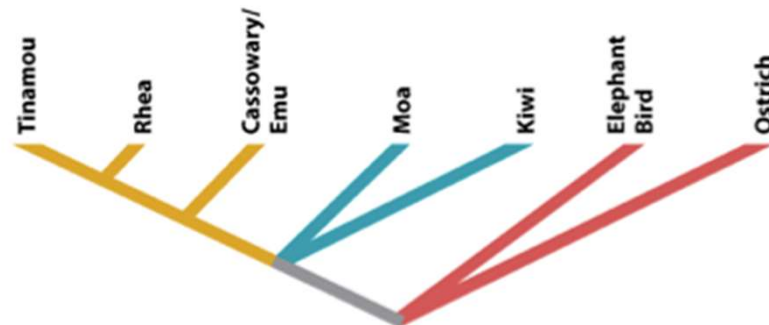
- Fossils



- Biogeography



- Phylogeny



The affinities of all the beings of the same class have sometimes been represented by a great tree. I believe this simile largely speaks the truth. The green and budding twigs may represent existing species; and those produced during former years may represent the long succession of extinct species.

Charles Darwin, *On the Origin of Species* (1859)

# Phylogeny

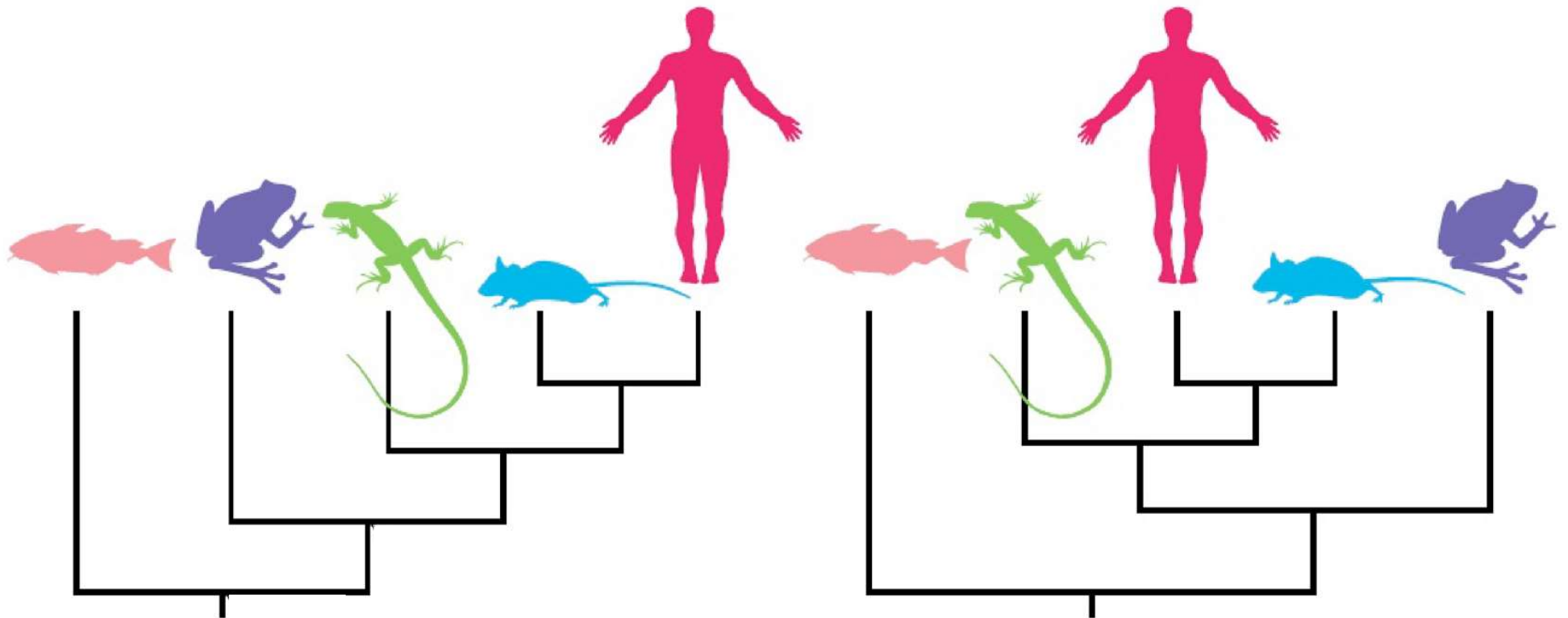


ter group





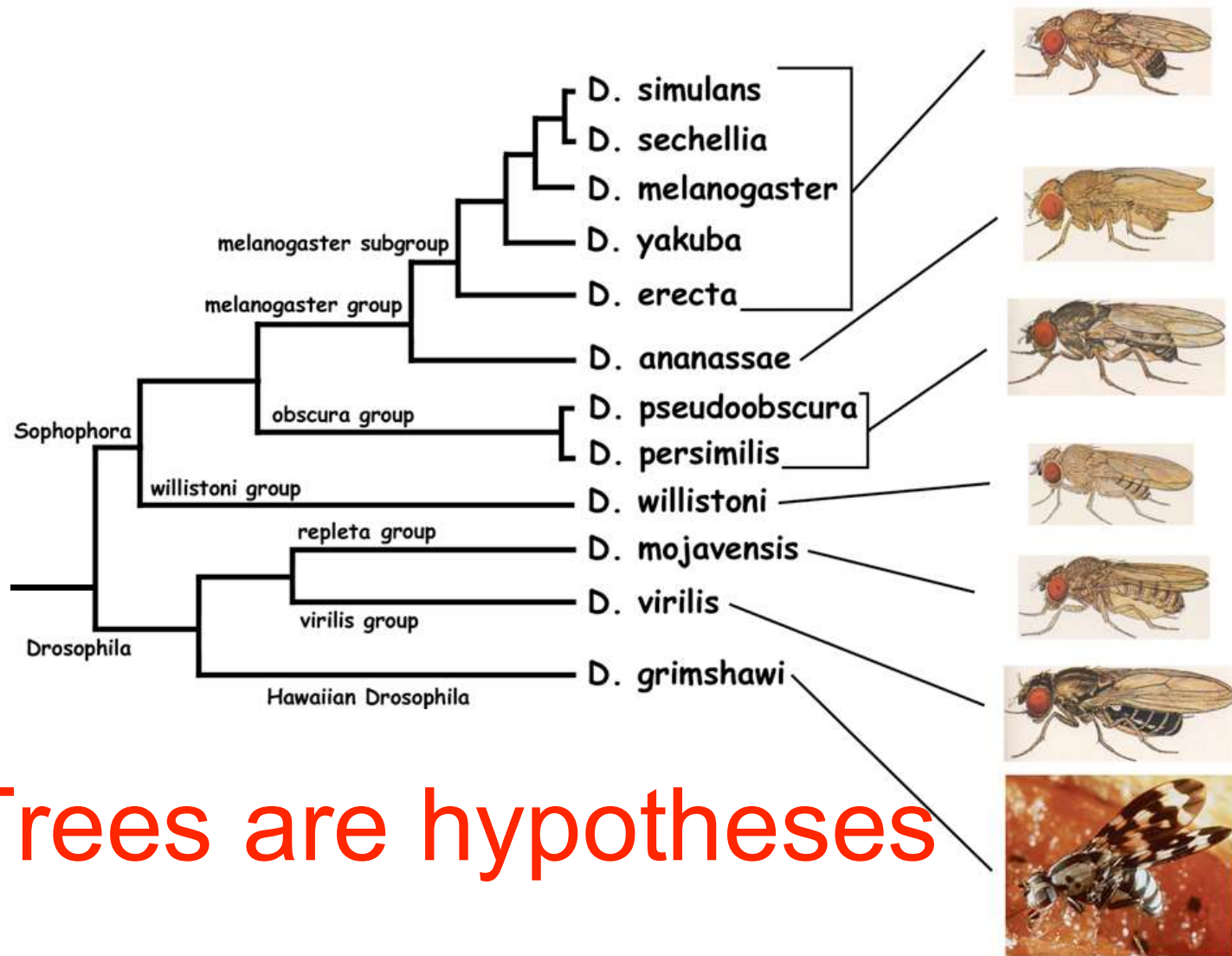
Which tree suggests a closer evolutionary relationship of frogs and lizards?



Neither

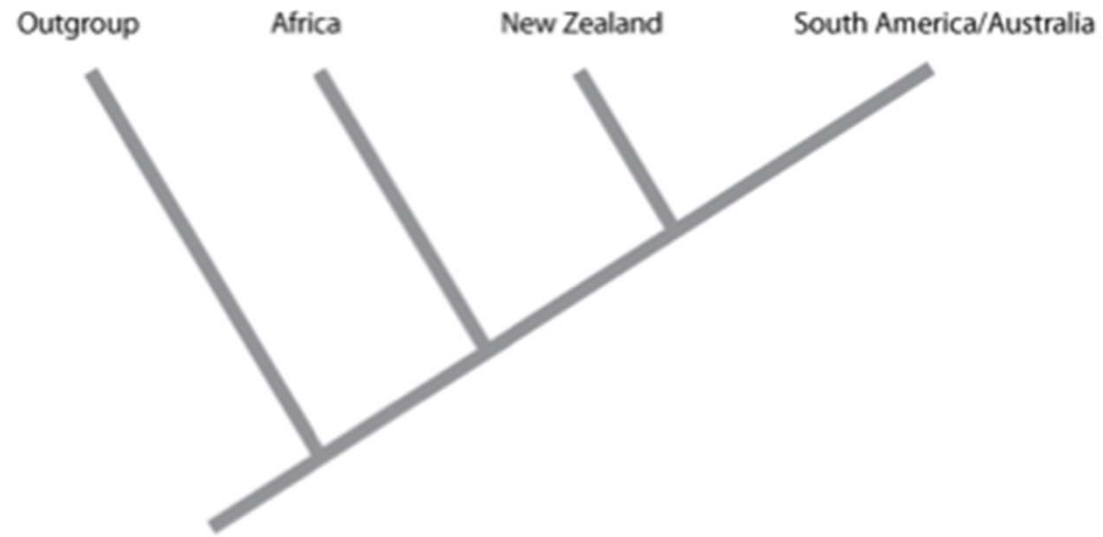
The two trees are equivalent.

# Phylogeny



Trees are hypotheses

# Phylogeny



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Trees are hypotheses

# Build Your Own Tree

In an ideal world, we would be able to reconstruct the past by looking at overall similarity between organisms.

Thus, the extent of difference between two groups would simply be a function of the time they have been evolutionarily separated.

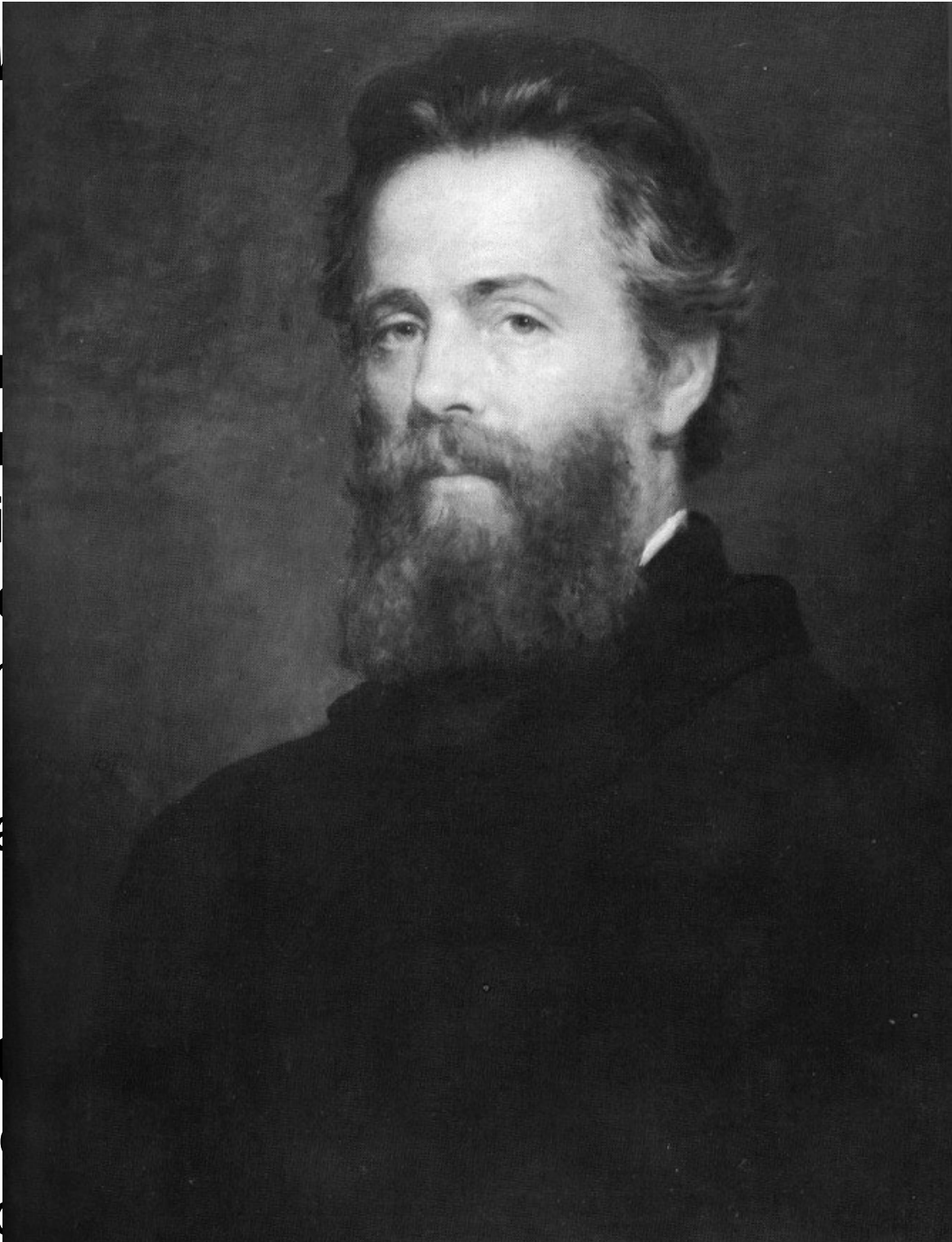
# Build Your Own Tree

Unfortunately, the real world is not ideal. Convergent evolution occurs when species that are only distantly related acquire similar traits under the influence of similar selection pressures.



M

y



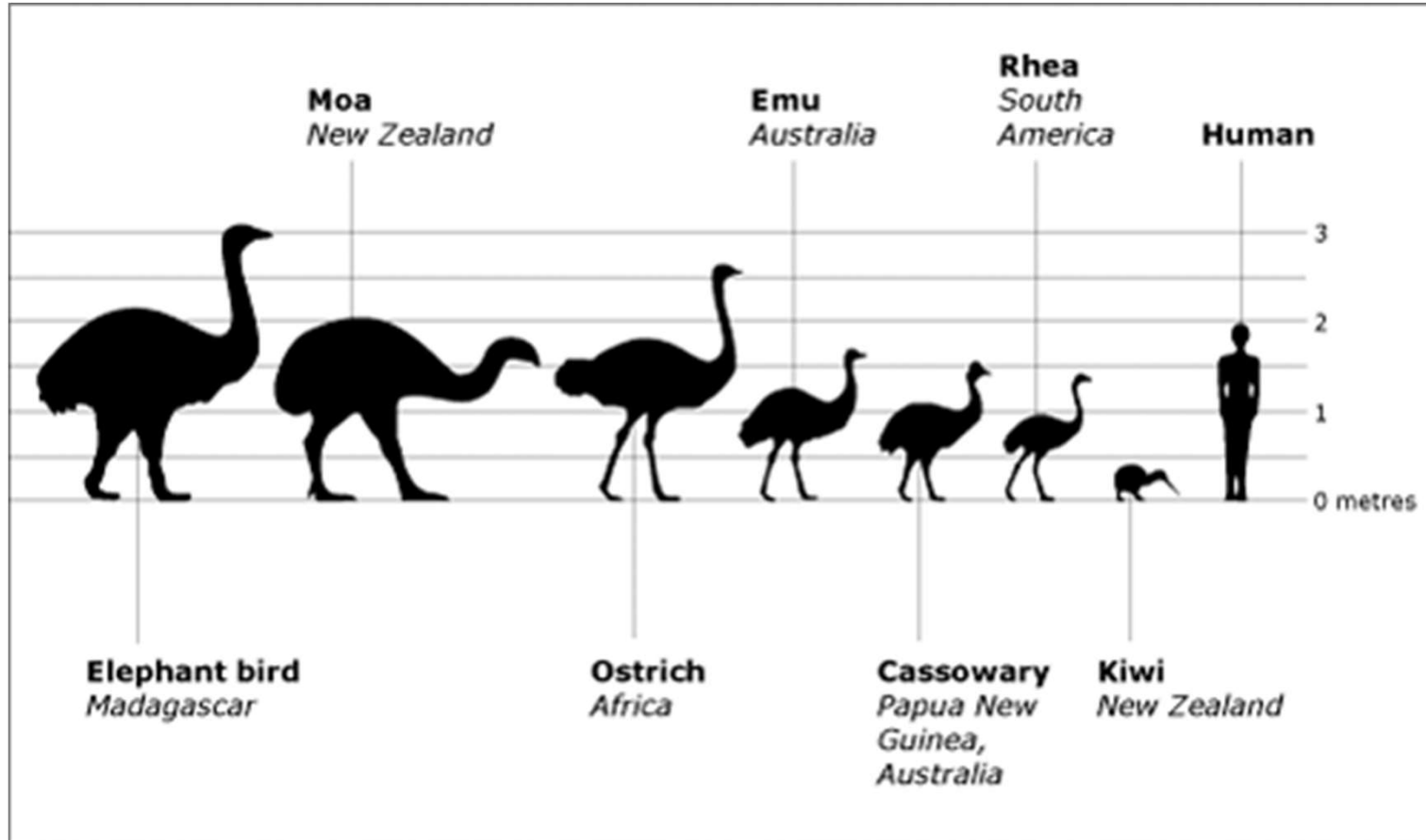
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# Build Your Own Tree



# Build Your Own Tree

## **Analogy**

- a similar trait in two groups that results from convergent evolution
- evolved more than once independently
- *e.g.*, the wing of a bird and the wing of an

insect

## **Homology**

- a similar trait in two groups that results from common ancestry
- evolved once
- *e.g.*, the pentadactyl (five-fingered) limb in humans and lizards



# Build Your Own Tree

## Analogy

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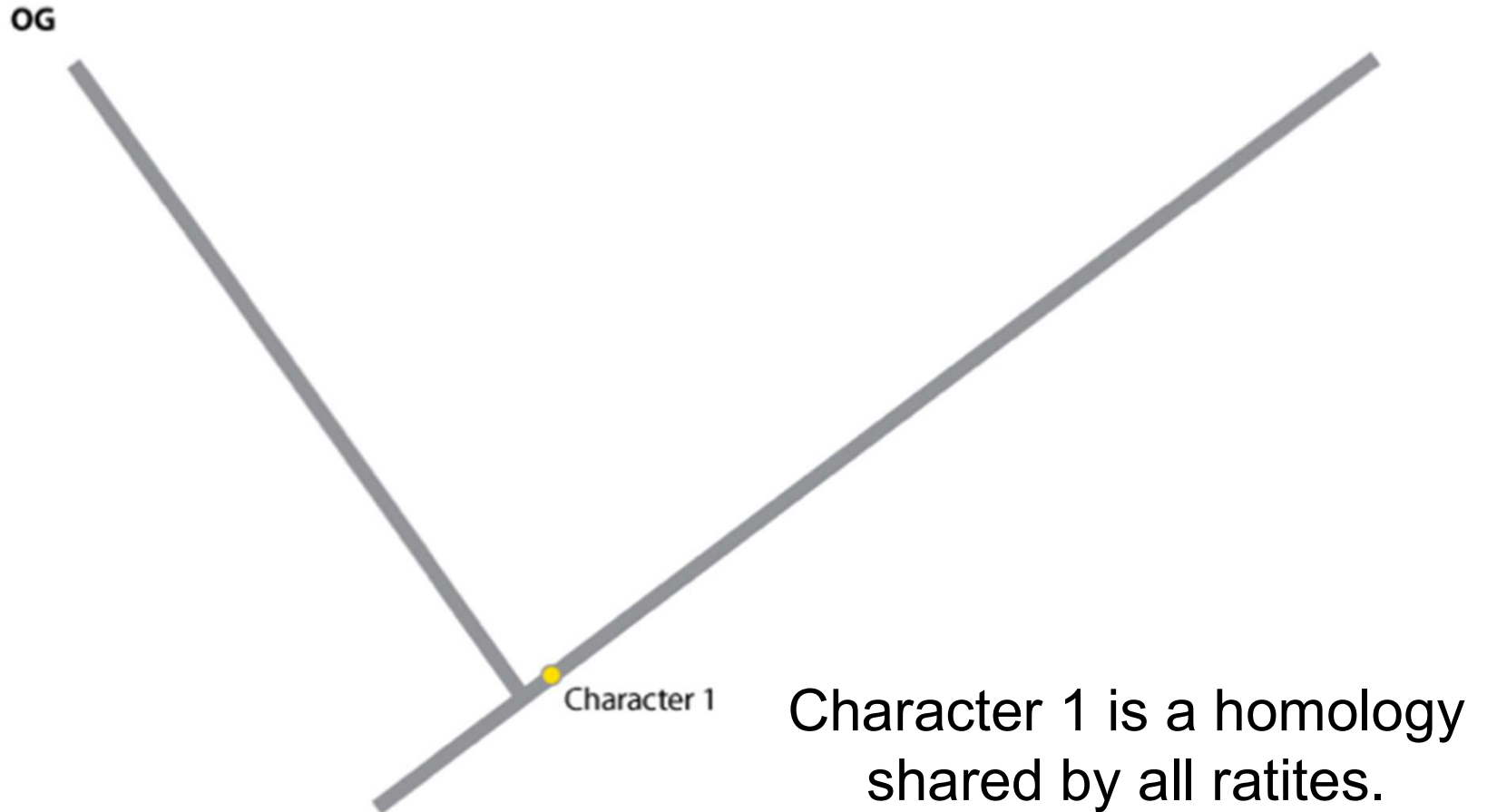
# Build Your Own Tree

		Characters														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Taxonomic group	OG															
	A	X	X	X								X				
	B	X	X											X		X
	C	X	X	X	X		X				X					
	D	X	X											X	X	
	E	X	X	X	X		X			X						
	F	X	X	X	X	X		X								
	G	X	X	X	X	X			X							
	H	X												X		

Taxonomic groups			
A	Elephant bird	E	Emu
B	Kiwi	F	Rhea
C	Cassowary	G	Ostrich
D	Moa	H	Tinamou

OG Outgroup

# Build Your Own Tree



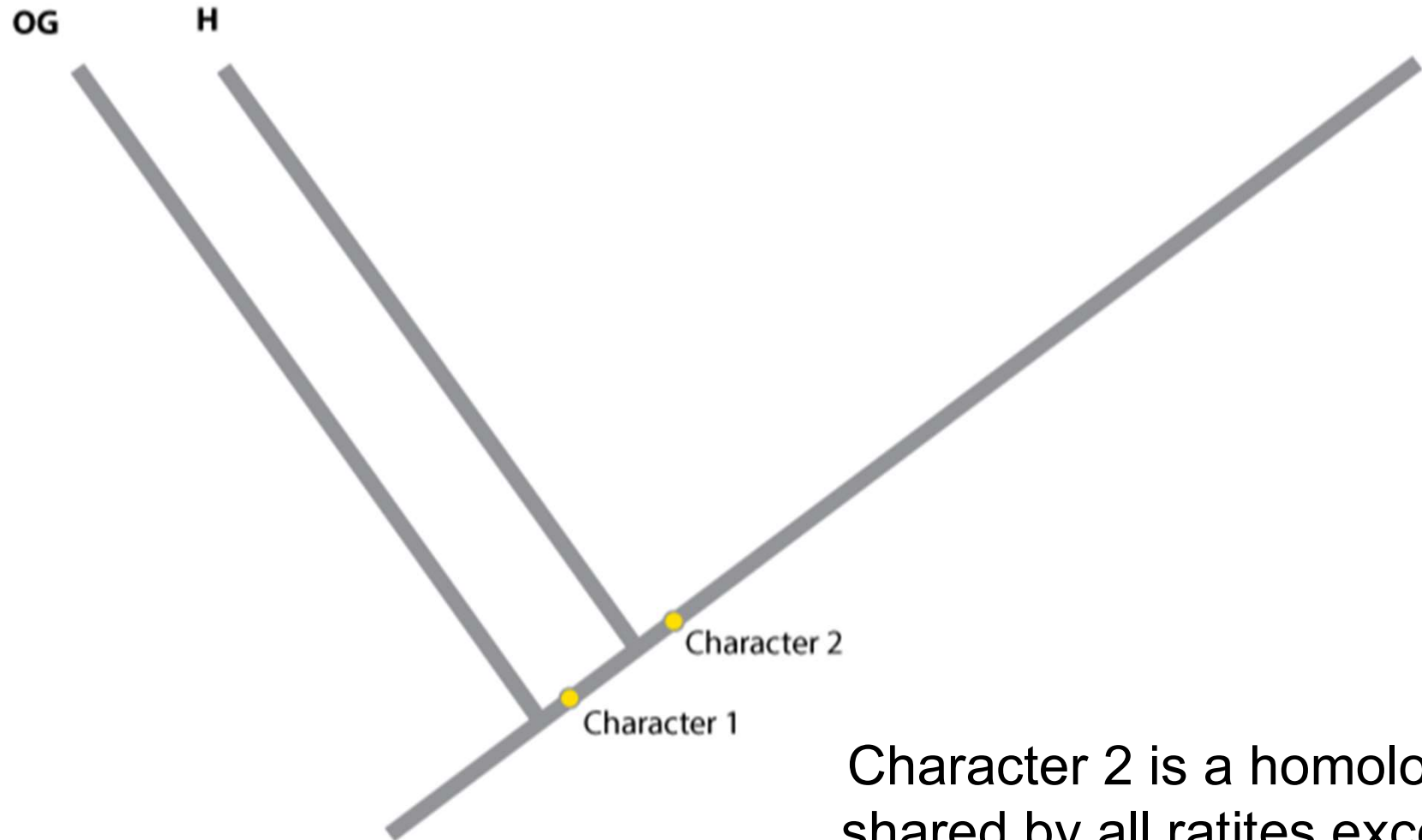
# Build Your Own Tree

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		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Taxonomic group	OG															
	A	X	X	X								X				
	B	X	X											X		X
	C	X	X	X	X		X				X					
	D	X	X											X	X	
	E	X	X	X	X		X			X						
	F	X	X	X	X	X		X								
	G	X	X	X	X	X			X							
	H	X												X		

Taxonomic groups			
A	Elephant bird	E	Emu
B	Kiwi	F	Rhea
C	Cassowary	G	Ostrich
D	Moa	H	Tinamou

OG Outgroup

# Build Your Own Tree



Character 2 is a homology shared by all ratites except Tinamous.

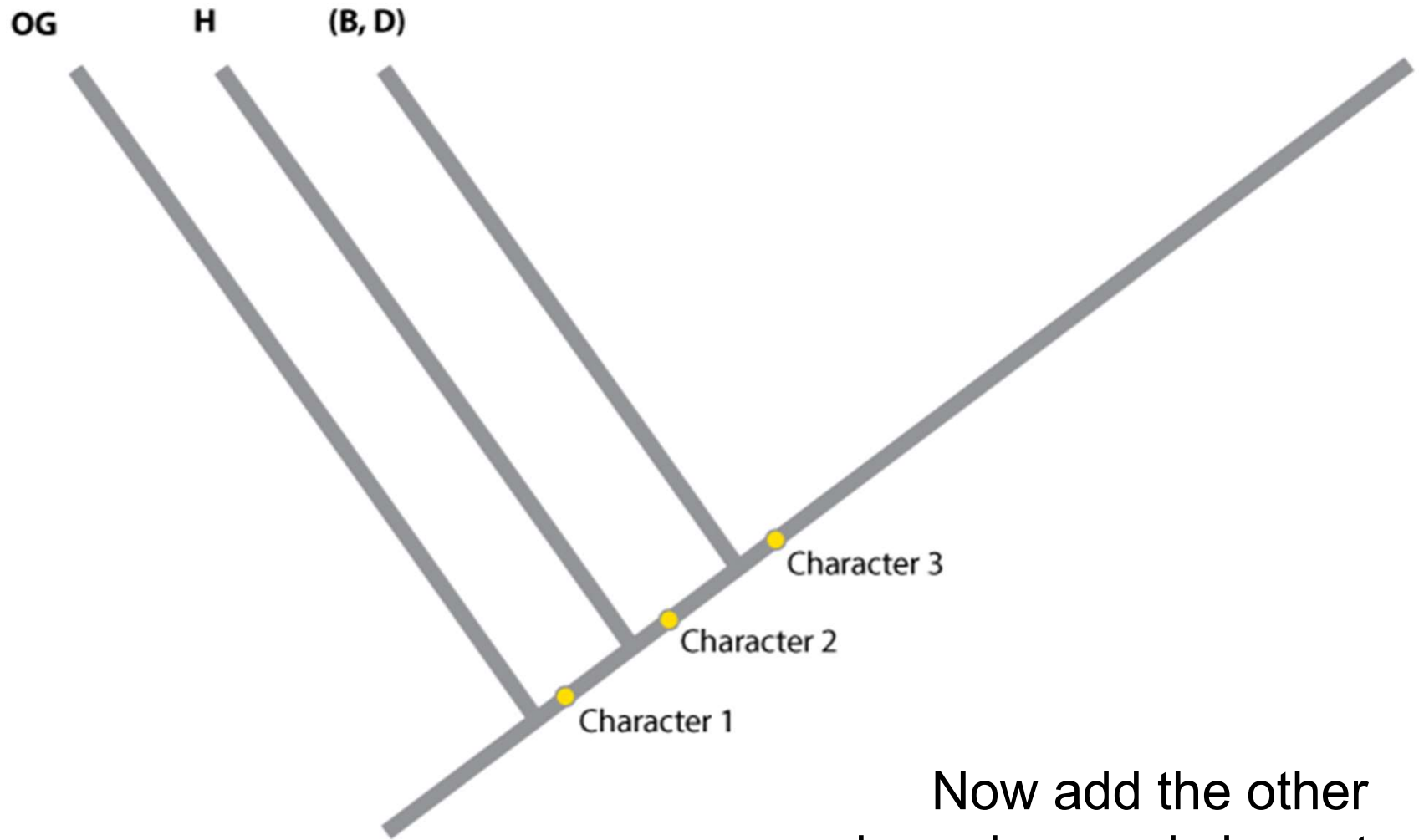
# Build Your Own Tree

		Characters														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Taxonomic group	OG															
	A	X	X	X								X				
	B	X	X											X		X
	C	X	X	X	X		X				X					
	D	X	X											X	X	
	E	X	X	X	X		X			X						
	F	X	X	X	X	X		X								
	G	X	X	X	X	X			X							
	H	X												X		

Taxonomic groups			
A	Elephant bird	E	Emu
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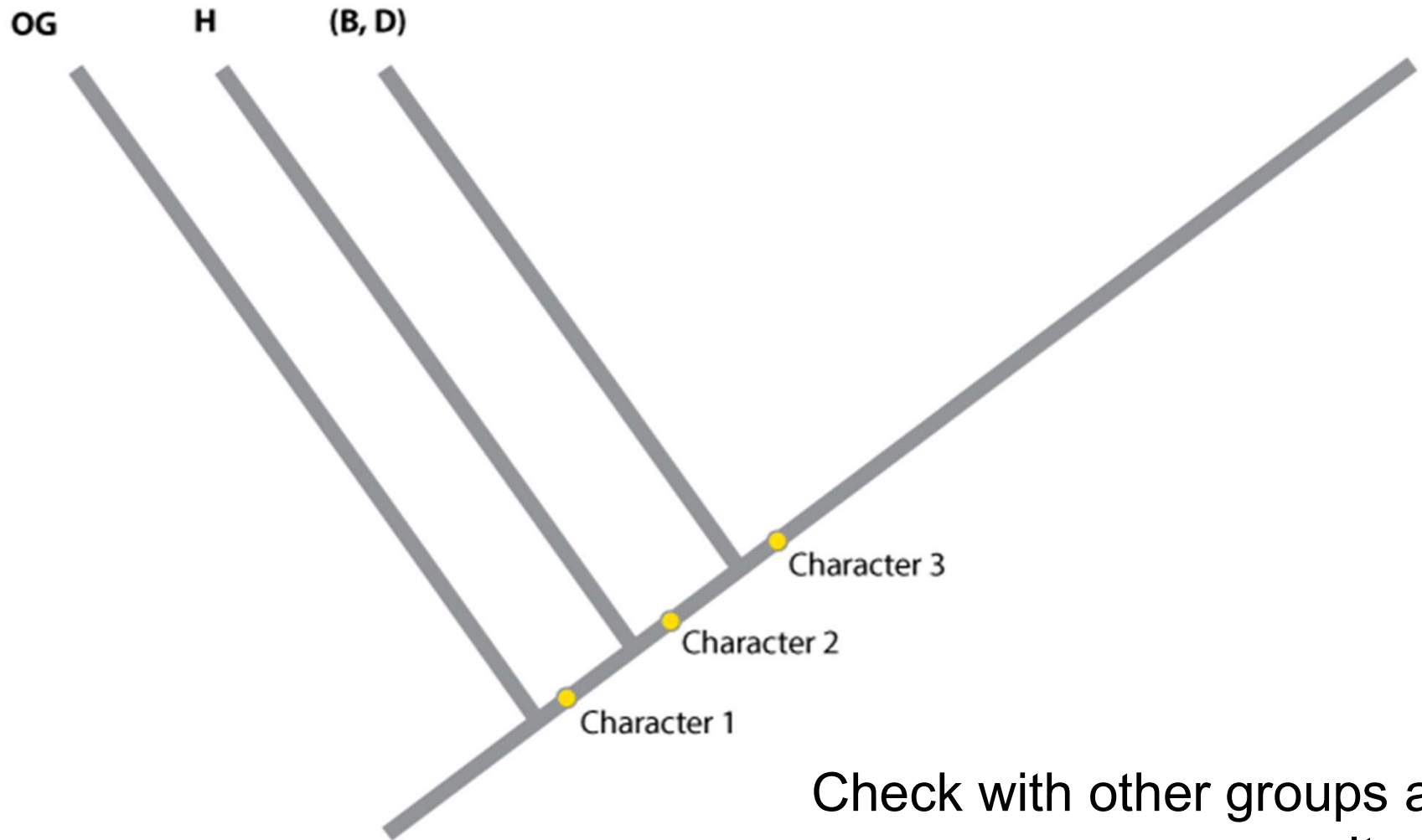
OG Outgroup

# Build Your Own Tree



Now add the other  
branches and characters

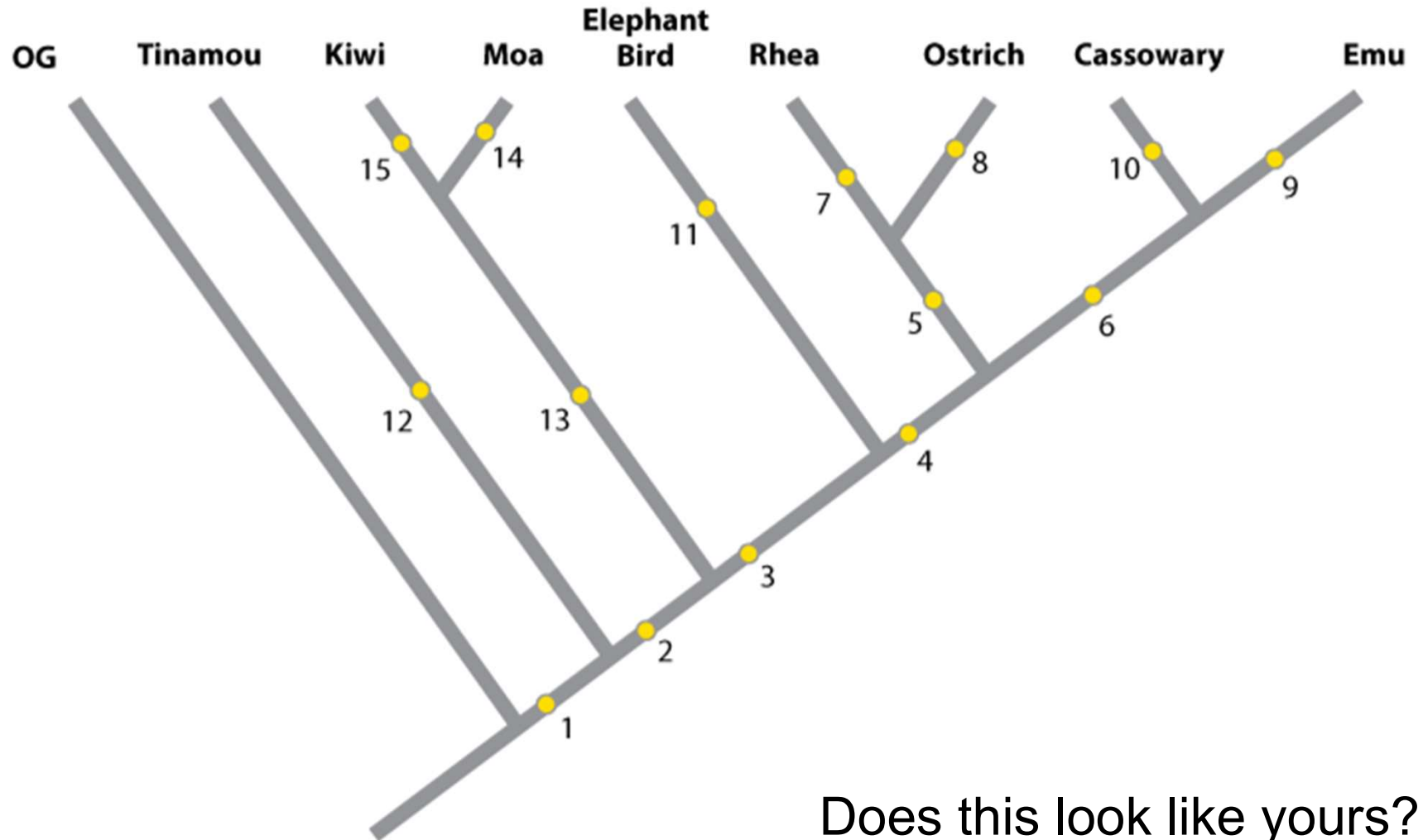
# Build Your Own Tree



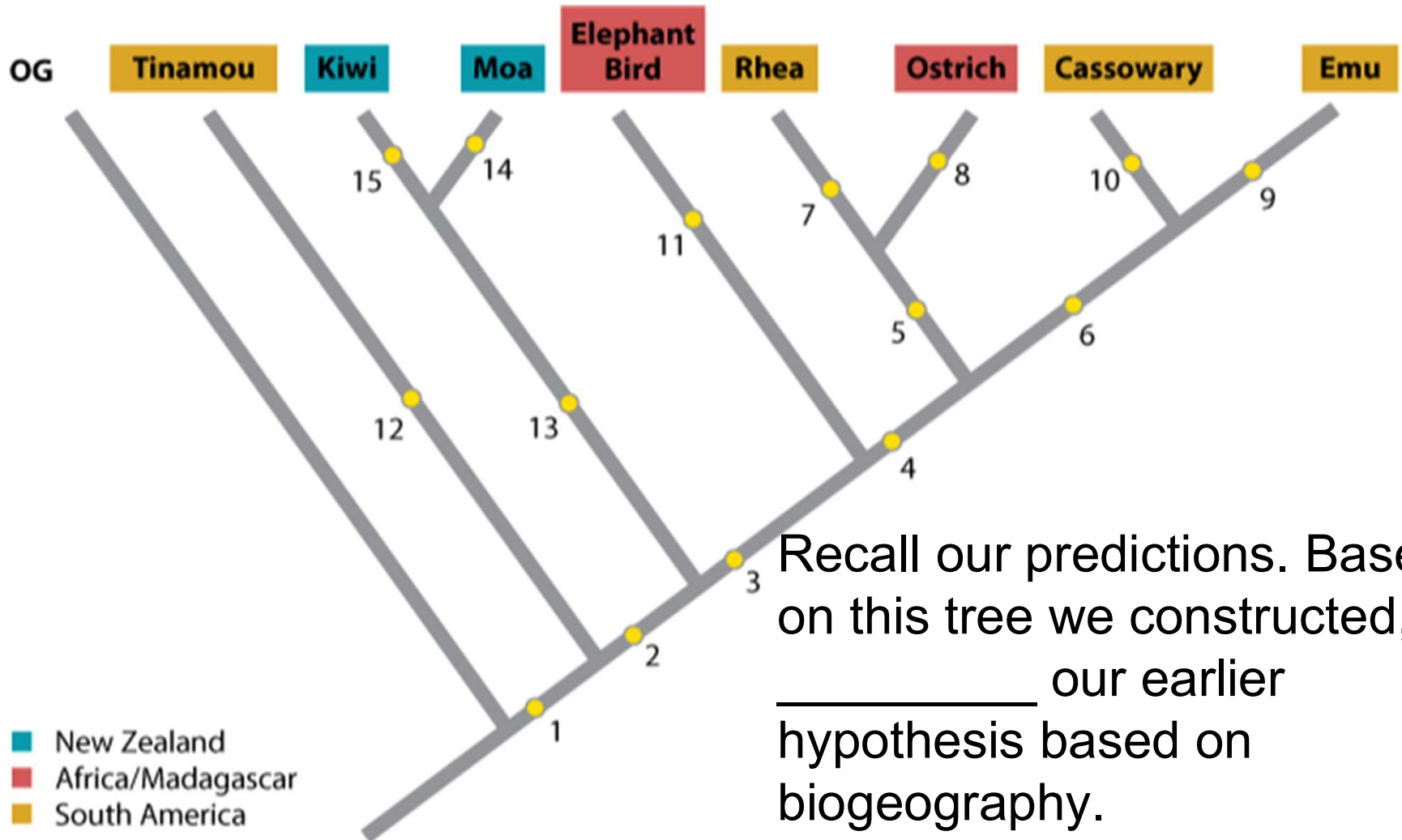
Check with other groups and  
compare your results



# Build Your Own Tree



# Build Your Own Tree



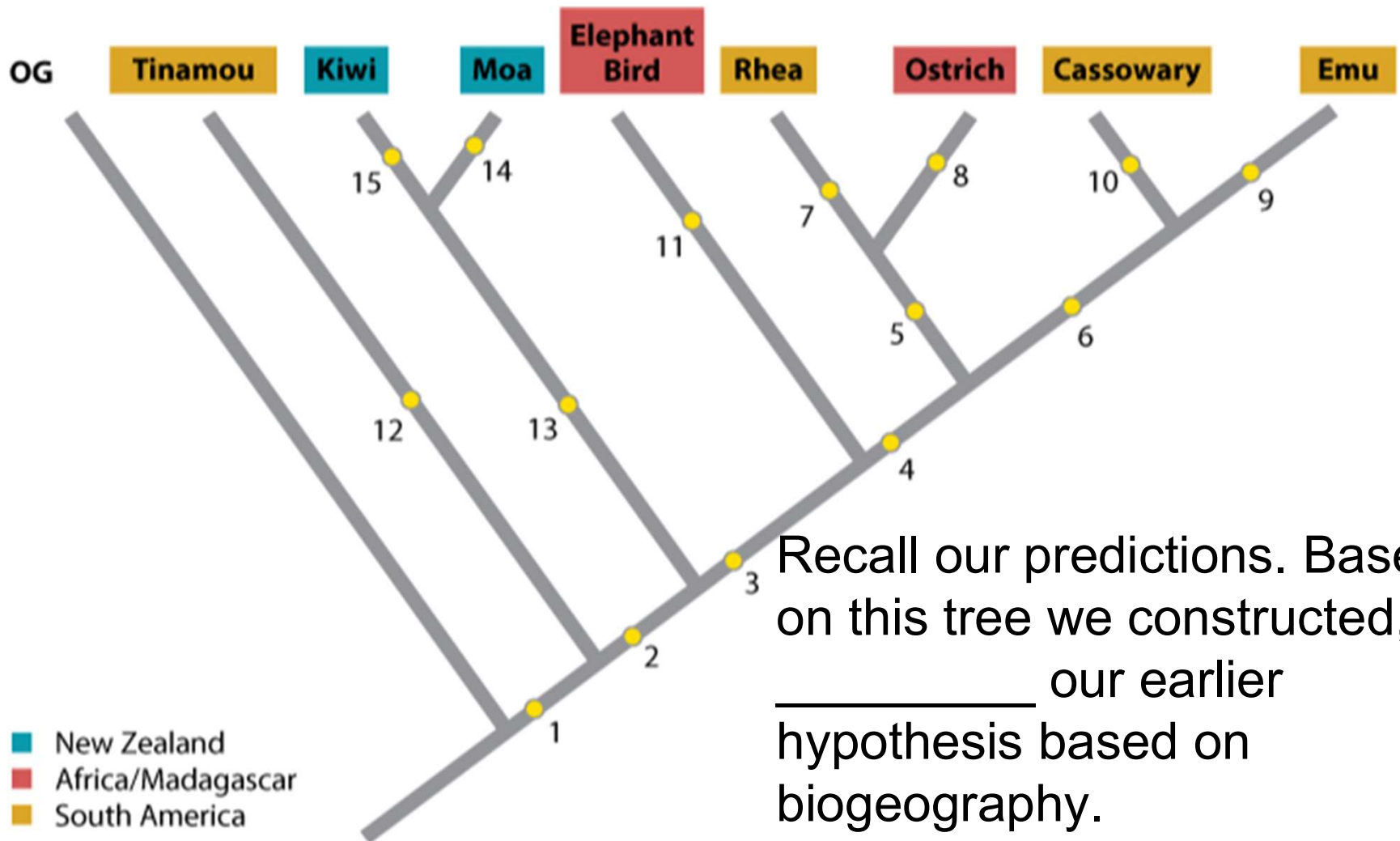
- New Zealand
- Africa/Madagascar
- South America

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Recall our predictions. Based on this tree we constructed, we \_\_\_\_\_ our earlier hypothesis based on biogeography.

- A. Accept
- B. Reject
- C. Need more data

# Build Your Own Tree



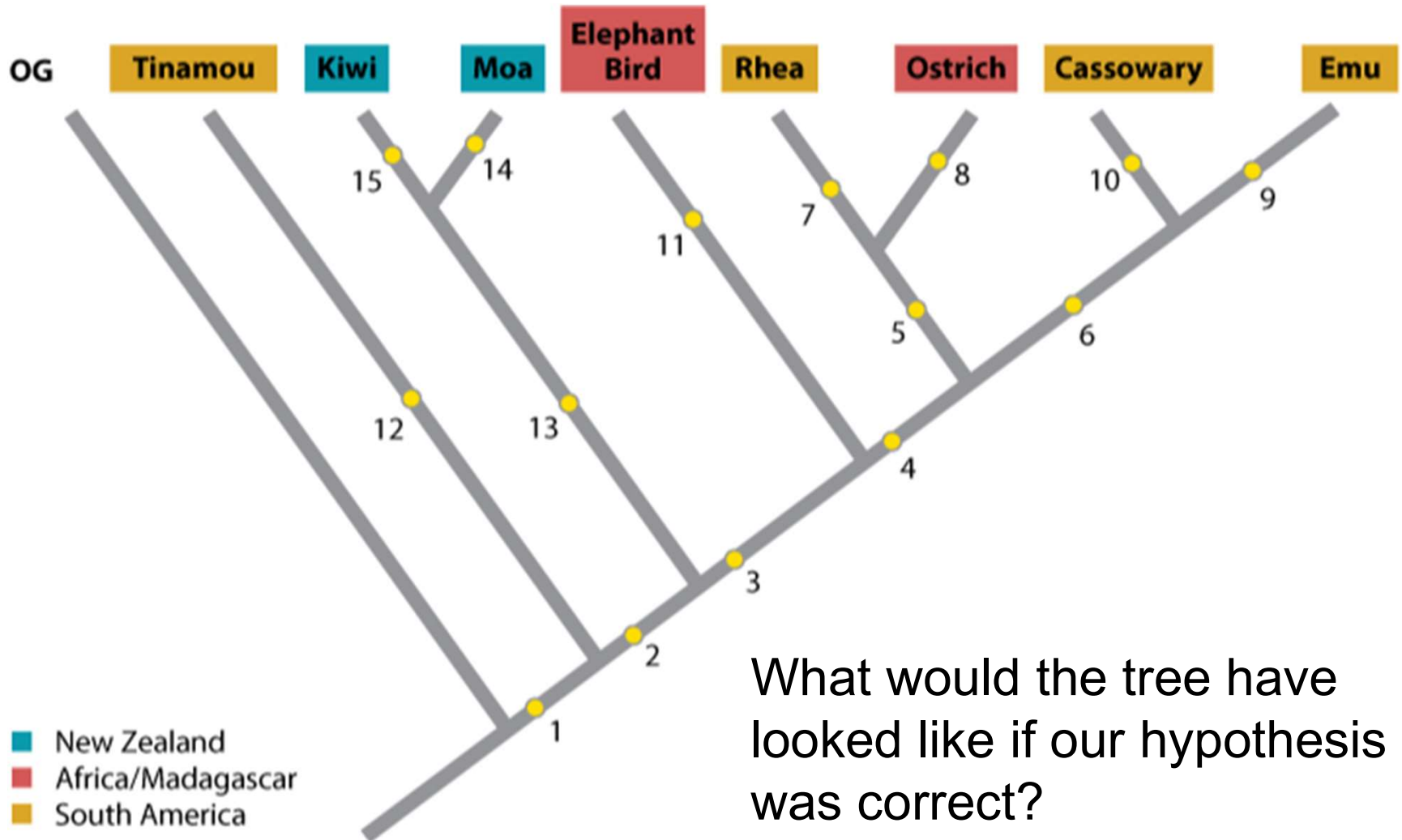
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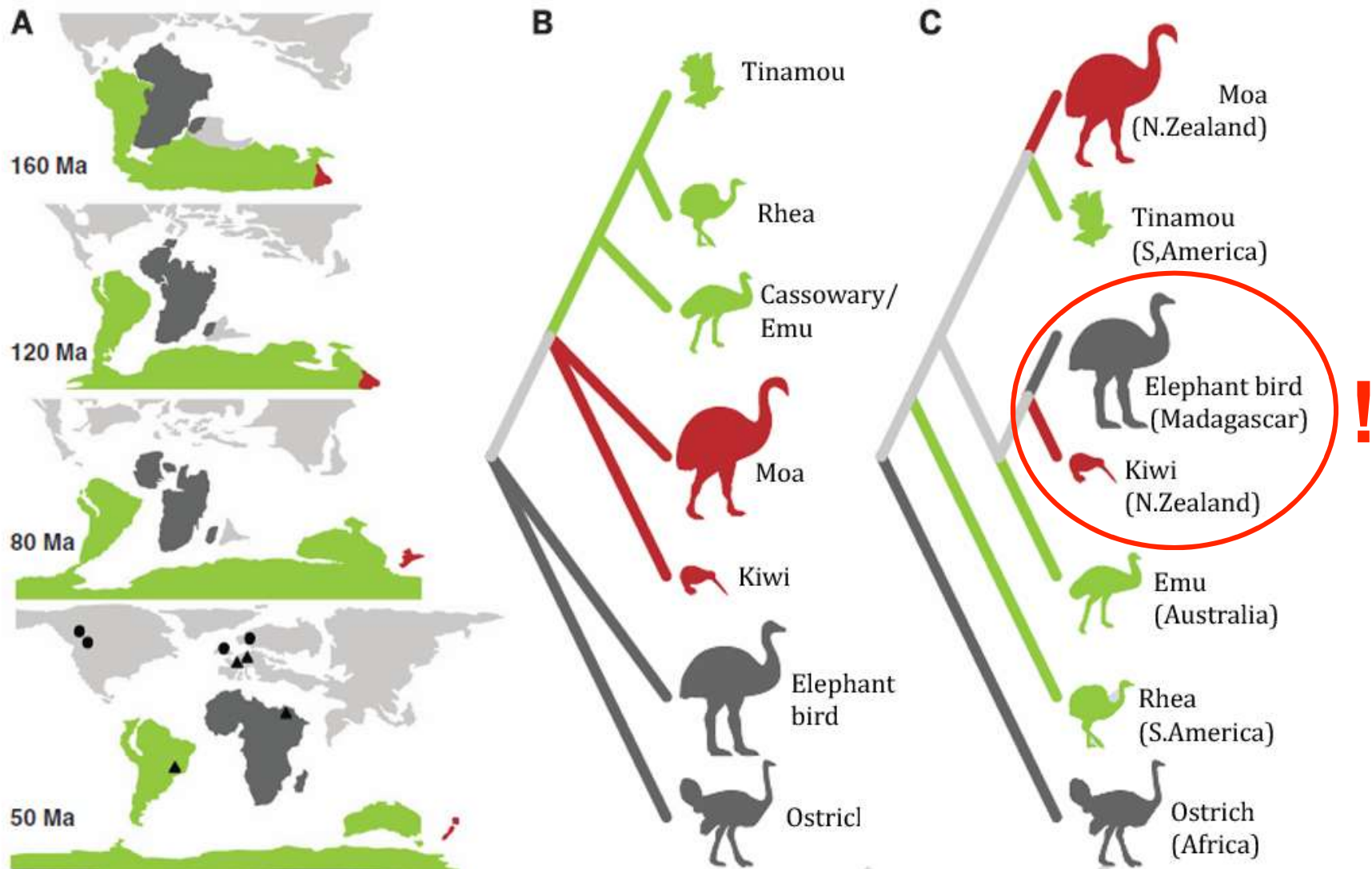
- A. Accept
- B. Reject
- C. Need more data

# Build Your Own Tree



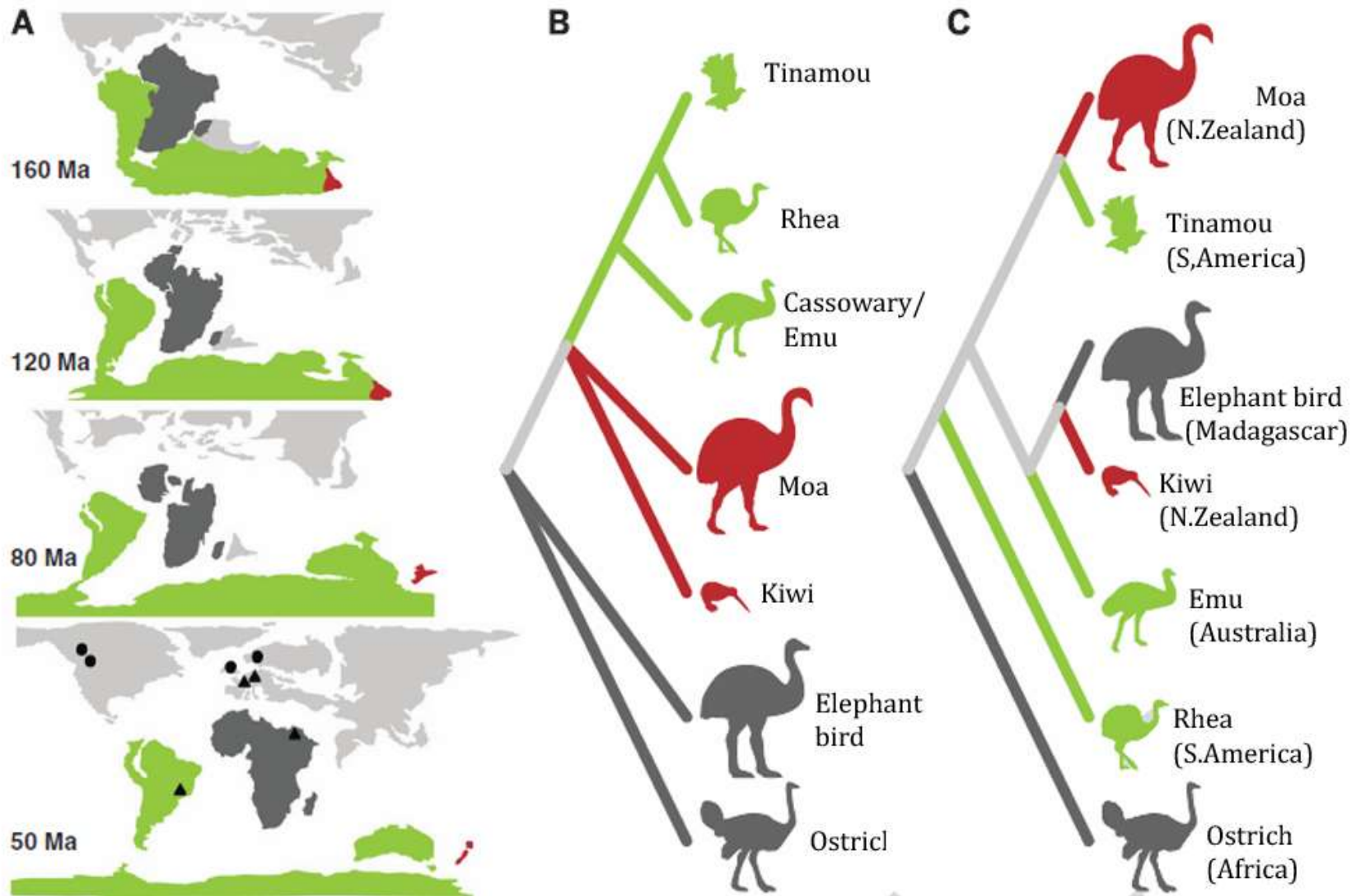
What would the tree have looked like if our hypothesis was correct?

# Build Your Own Tree



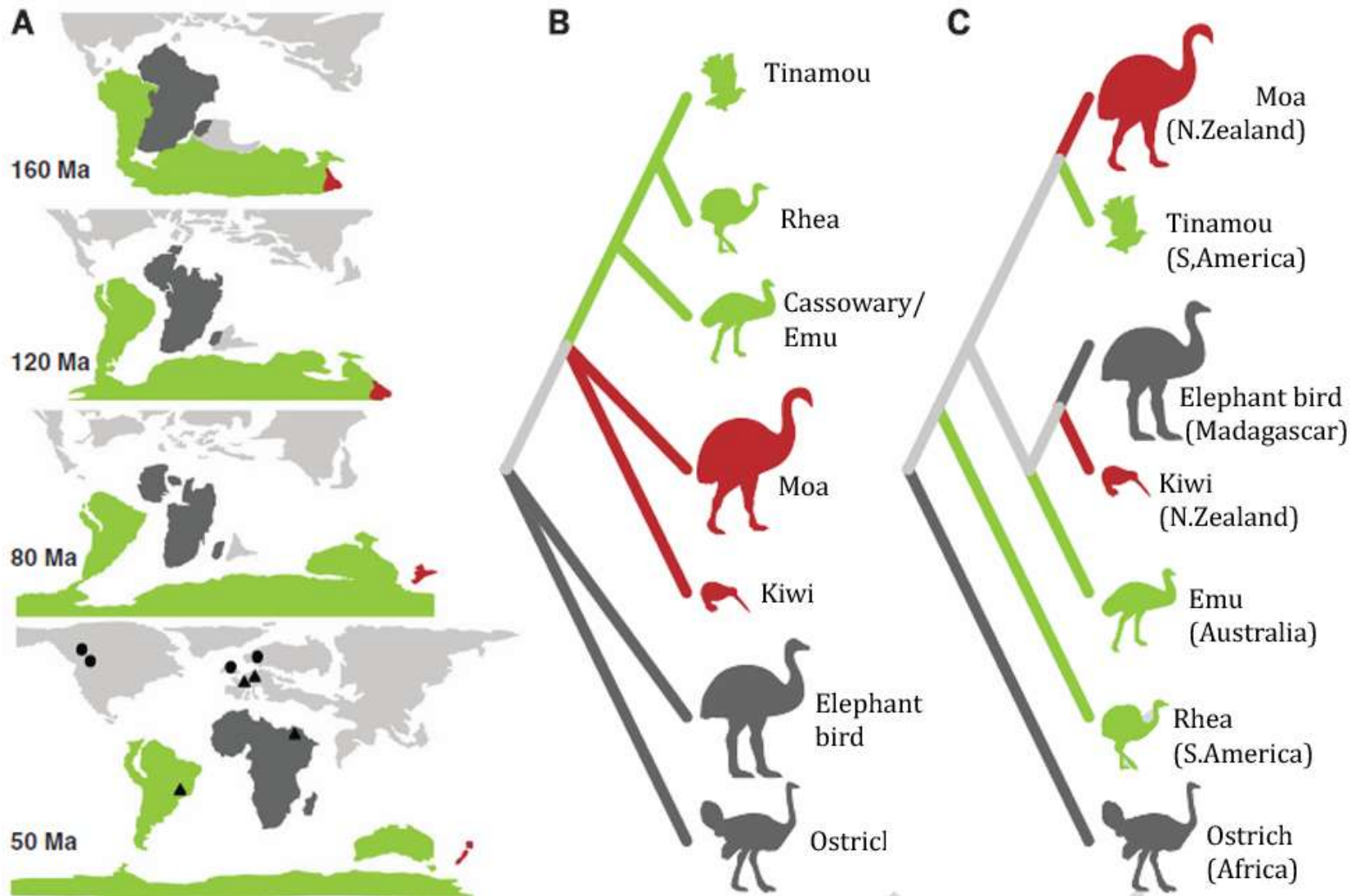
Identify a sister group in part c.

# Build Your Own Tree



How are the largest birds related to one another?

# Build Your Own Tree



Can you think of a new hypothesis to explain these relationships?

# New Hypothesis

How did they disperse to different land masses?

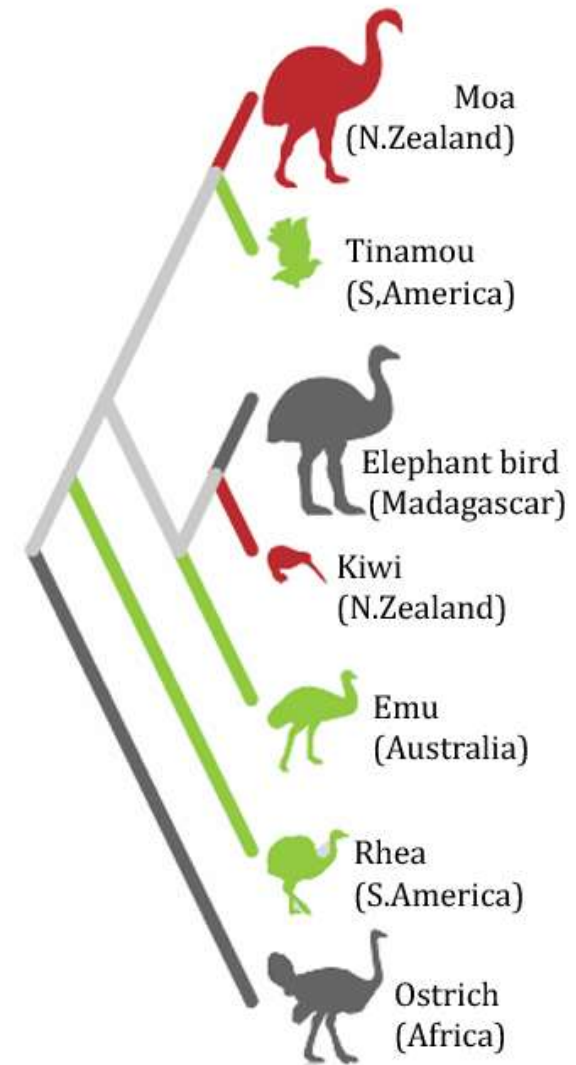
Flight

How did they become flightless?

Convergent evolution

How did they become so large (gigantism)?

Convergent evolution





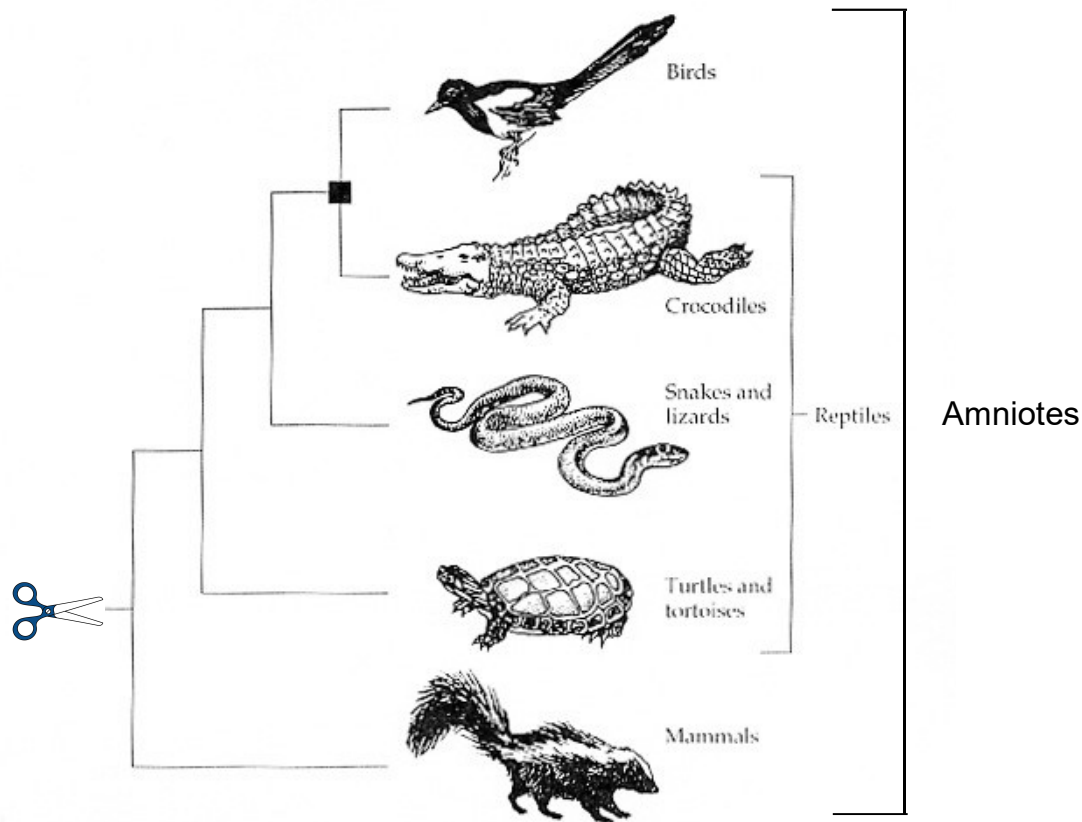
# Phylogenetic Patterns

A common ancestor and  
*all* of its  
descendants

A common ancestor and  
*some* of its  
descendants

Unrelated  
groups with  
no common  
ancestor

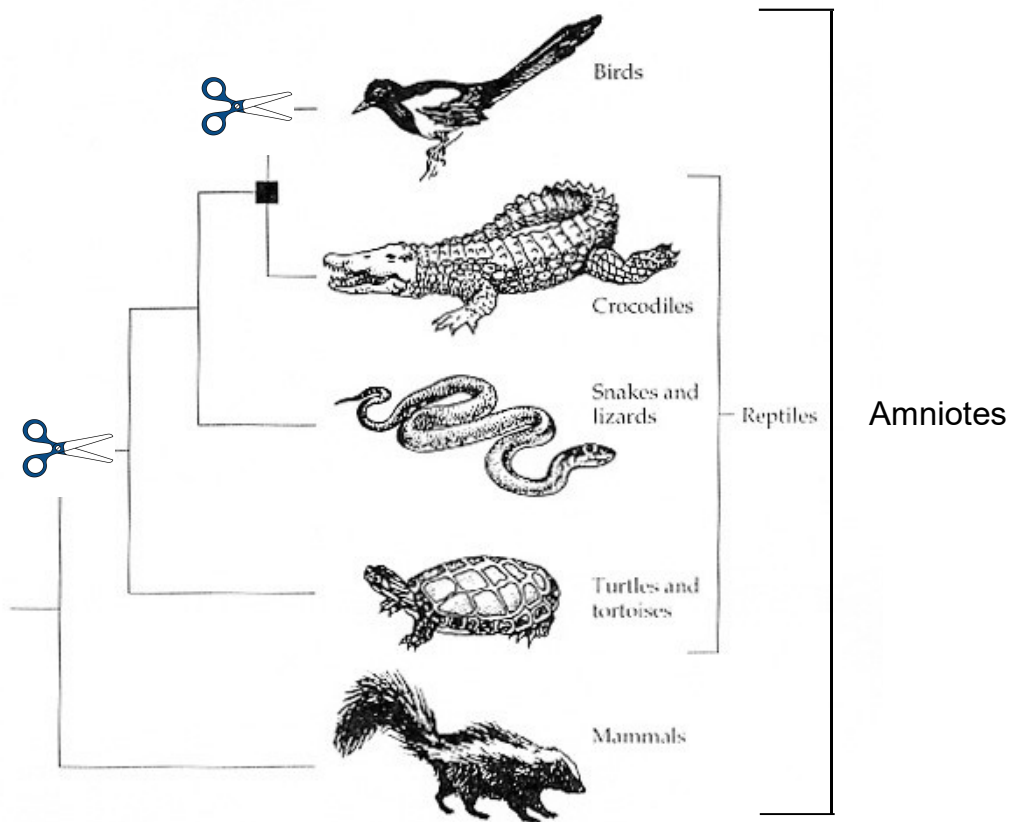
# Phylogenetic Patterns



- Amniotes are monophyletic

**Figure 5.5** Phylogenetic tree of birds, reptiles, and mammals. The reptiles do not constitute a natural clade since they share ancestors with the birds, which are not included in the Reptilia. Birds and crocodiles, on the other hand, constitute a natural clade (Archosauria) since they share a common ancestor (black box) not shared by any other organism. From Li and Graur (1991).

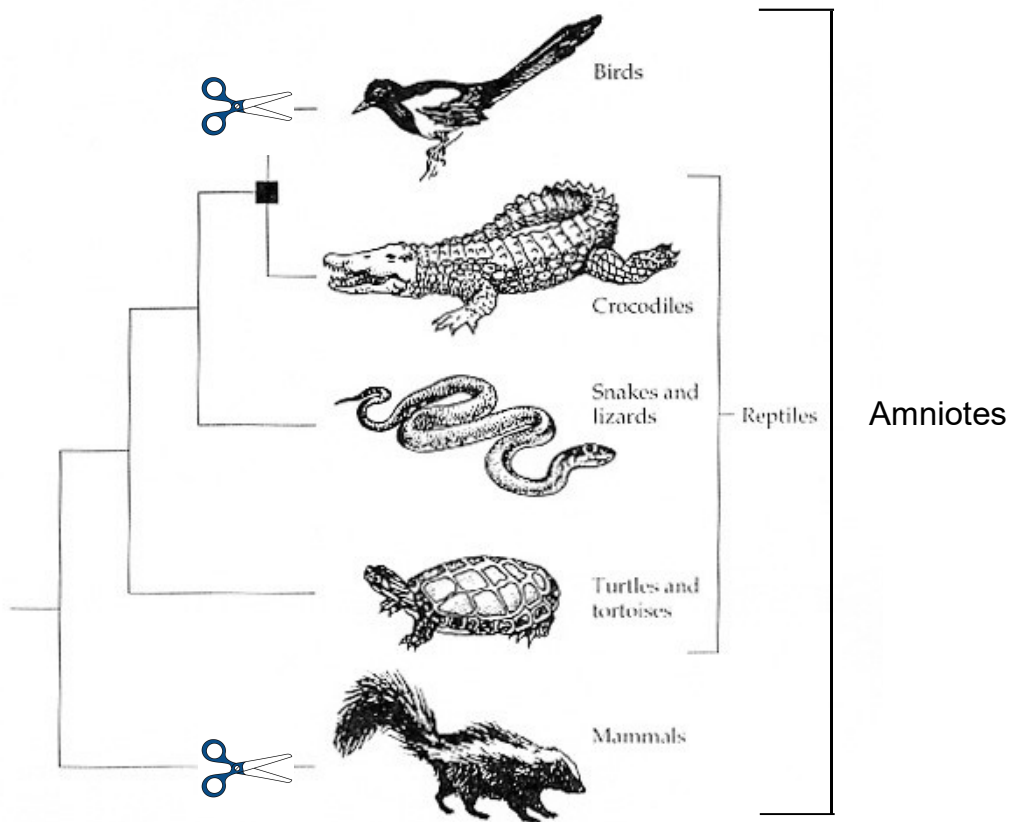
# Phylogenetic Patterns



- Reptiles are paraphyletic

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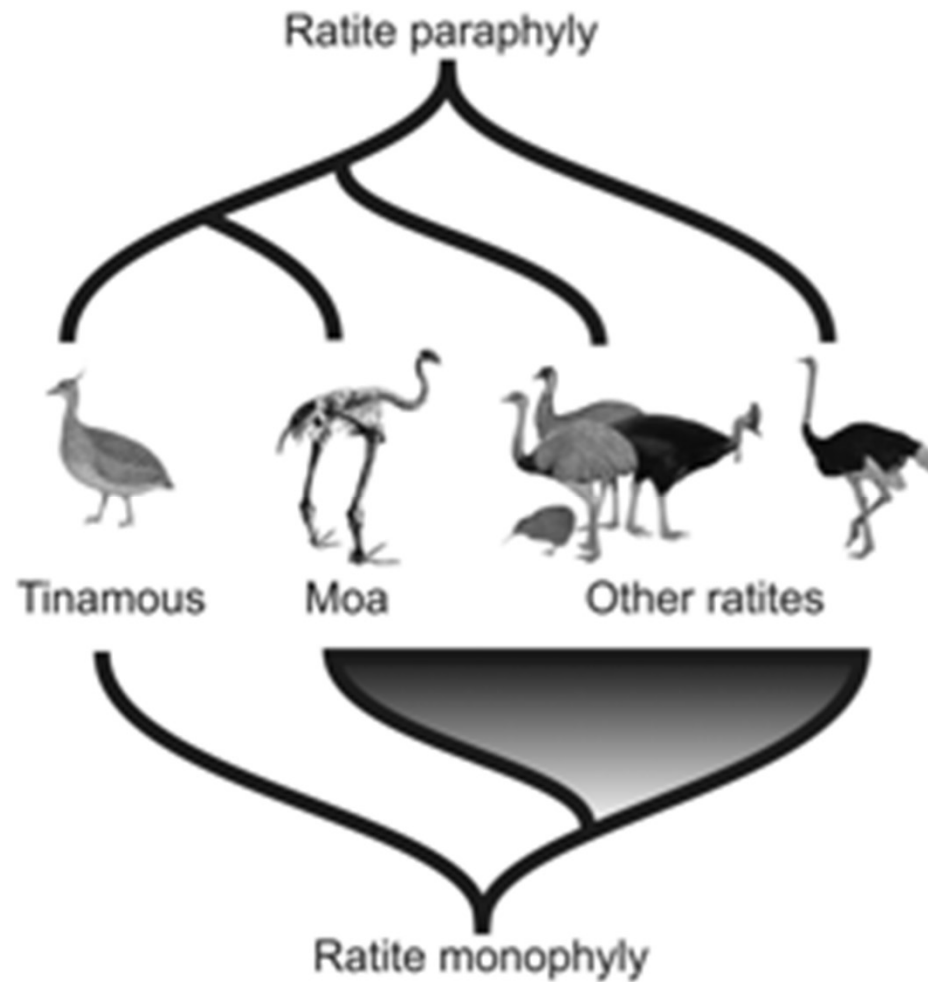
# Phylogenetic Patterns



- Warm-blooded animals are polyphyletic

**Figure 5.5** Phylogenetic tree of birds, reptiles, and mammals. The reptiles do not constitute a natural clade since they share ancestors with the birds, which are not included in the Reptilia. Birds and crocodiles, on the other hand, constitute a natural clade (Archosauria) since they share a common ancestor (black box) not shared by any other organism. From Li and Graur (1991).

# Phylogenetic Patterns



# Reference

## EVOLUTION

### **Ancient DNA reveals elephant birds and kiwi are sister taxa and clarifies ratite bird evolution**

Kieren J. Mitchell,<sup>1</sup> Bastien Llamas,<sup>1</sup> Julien Soubrier,<sup>1</sup> Nicolas J. Rawlence,<sup>1\*</sup>  
Trevor H. Worthy,<sup>2</sup> Jamie Wood,<sup>3</sup> Michael S. Y. Lee,<sup>1,4</sup> Alan Cooper<sup>1†</sup>

The evolution of the ratite birds has been widely attributed to vicariant speciation, driven by the Cretaceous breakup of the supercontinent Gondwana. The early isolation of Africa and Madagascar implies that the ostrich and extinct Madagascan elephant birds (Aepyornithidae) should be the oldest ratite lineages. We sequenced the mitochondrial genomes of two elephant birds and performed phylogenetic analyses, which revealed that these birds are the closest relatives of the New Zealand kiwi and are distant from the basal ratite lineage of ostriches. This unexpected result strongly contradicts continental vicariance and instead supports flighted dispersal in all major ratite lineages. We suggest that convergence toward gigantism and flightlessness was facilitated by early Tertiary expansion into the diurnal herbivory niche after the extinction of the dinosaurs.

*Science* 344: 898-900

# Reference

## Genomic Support for a Moa–Tinamou Clade and Adaptive Morphological Convergence in Flightless Ratites

Allan J. Baker,<sup>\*1,2</sup> Oliver Haddrath,<sup>1</sup> John D. McPherson,<sup>3</sup> and Alison Cloutier<sup>2</sup>

<sup>1</sup>Department of Natural History, Royal Ontario Museum, Toronto, Ontario, Canada

<sup>2</sup>Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada

<sup>3</sup>Ontario Institute for Cancer Research, Toronto, Ontario, Canada

**\*Corresponding author:** E-mail: allanb@rom.on.ca.

**Associate editor:** Nicolas Vidal

### Abstract

One of the most startling discoveries in avian molecular phylogenetics is that the volant tinamous are embedded in the flightless ratites, but this topology remains controversial because recent morphological phylogenies place tinamous as the closest relative of a monophyletic ratite clade. Here, we integrate new phylogenomic sequences from 1,448 nuclear DNA loci totaling almost 1 million bp from the extinct little bush moa, Chilean tinamou, and emu with available sequences from ostrich, elegant crested tinamou, four neognaths, and the green anole. Phylogenetic analysis using standard homogeneous models and heterogeneous models robust to common topological artifacts recovered compelling support for ratite paraphyly with the little bush moa closest to tinamous within ratites. Ratite paraphyly was further corroborated by eight independent CR1 retroposon insertions. Analysis of morphological characters reinterpreted on a 27-gene paleognath topology indicates that many characters are convergent in the ratites, probably as the result of adaptation to a cursorial life style.

*Mol. Biol. Evol.* 31:1686–1696

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**\*Corresponding author:** E-mail: allanb@rom.on.ca.

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# Reference

## **Phylogeny and Biogeography of Ratite Birds Inferred from DNA Sequences of the Mitochondrial Ribosomal Genes**

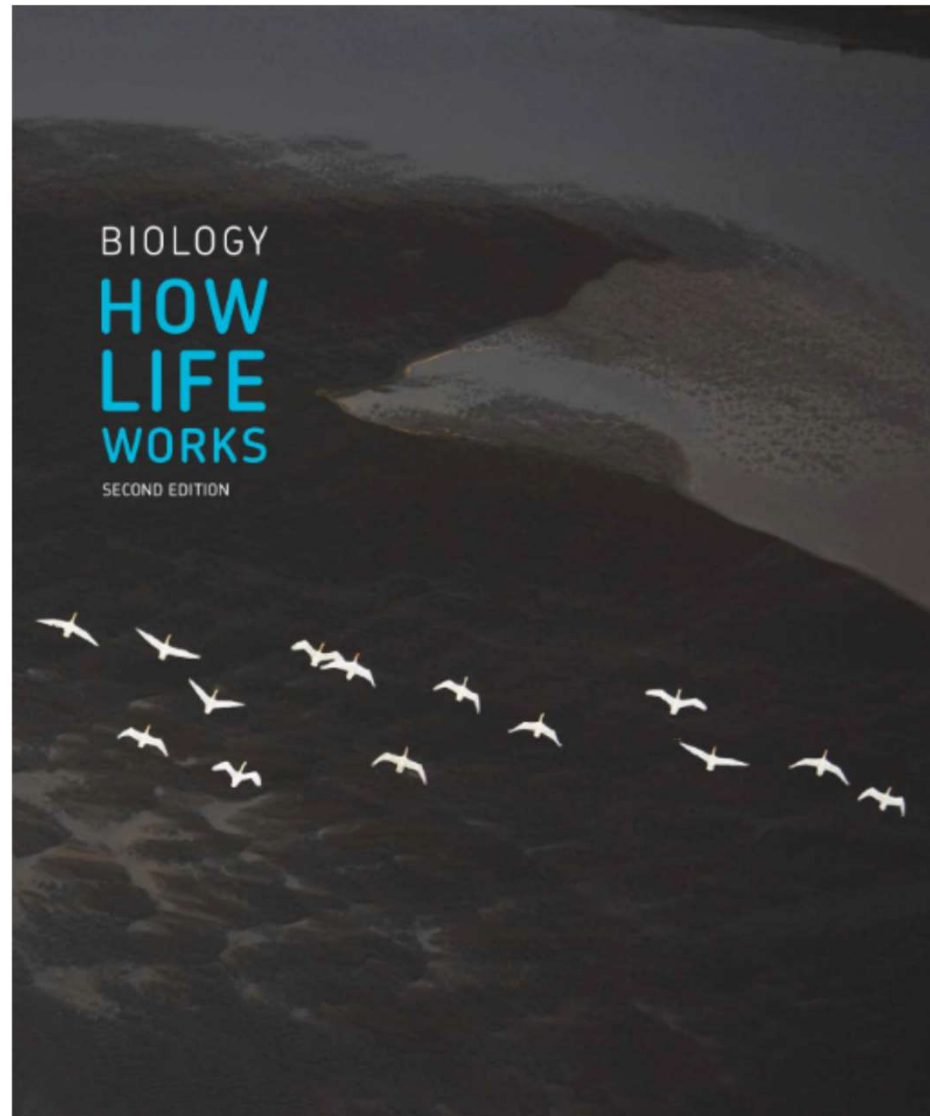
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The origin of the flightless ratite birds of the southern continents has been debated for over a century. Whether dispersal or vicariance (continental breakup) best explains their origin depends largely on their phylogenetic relationships. No consensus has been reached on this issue despite many morphological and molecular studies. To address this question further we sequenced a 2.8-kb region of mitochondrial DNA containing the ribosomal genes in representative ratites and a tinamou. Phylogenetic analyses indicate that *Struthio* (Africa) is basal and *Rhea* (South America) clusters with living Australasian ratites. This phylogeny agrees with transferrin and DNA hybridization studies but not with sequence analyses of some protein-coding genes. These results also require reevaluation of the phylogenetic position of the extinct moas of New Zealand. We propose a new hypothesis for the origin of ratites that combines elements of dispersal and vicariance.

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# Reference



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