The Geometry of Growth and Form

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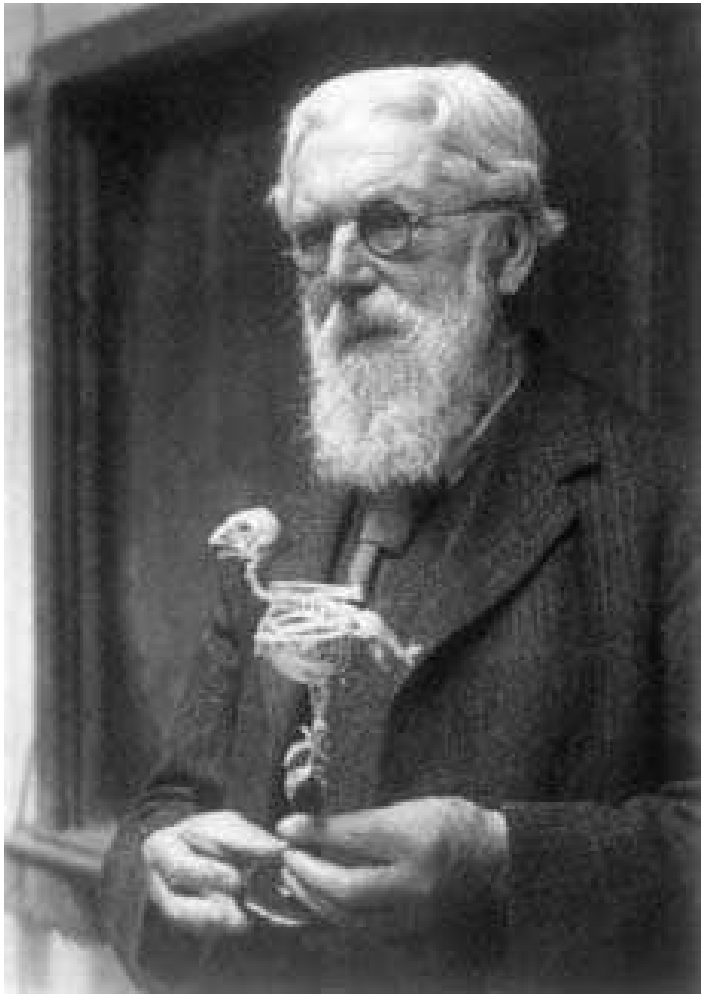
Part 1. “On Growth and Form”

This will be a commentary on a much loved book, first published in 1917.

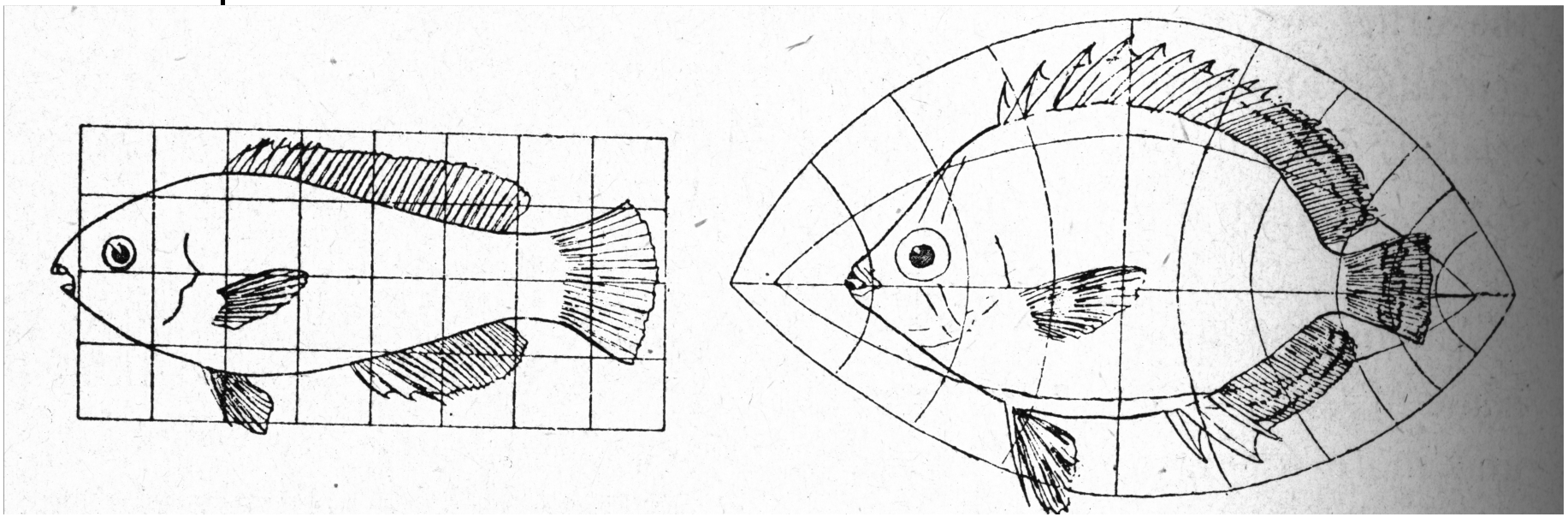


D’ARCY THOMPSON (1860-1948)

Comparison of Shapes

Thompson compared the shapes of related species.

For example:



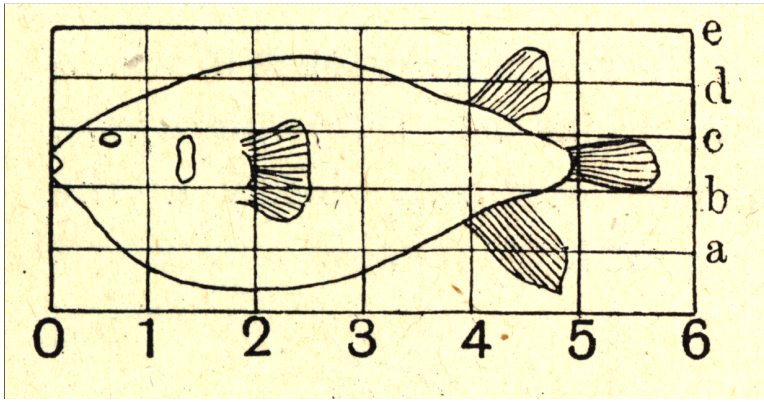
Left: Parrotfish (Scarus sp.); Right: Angelfish (Pomacanthus)

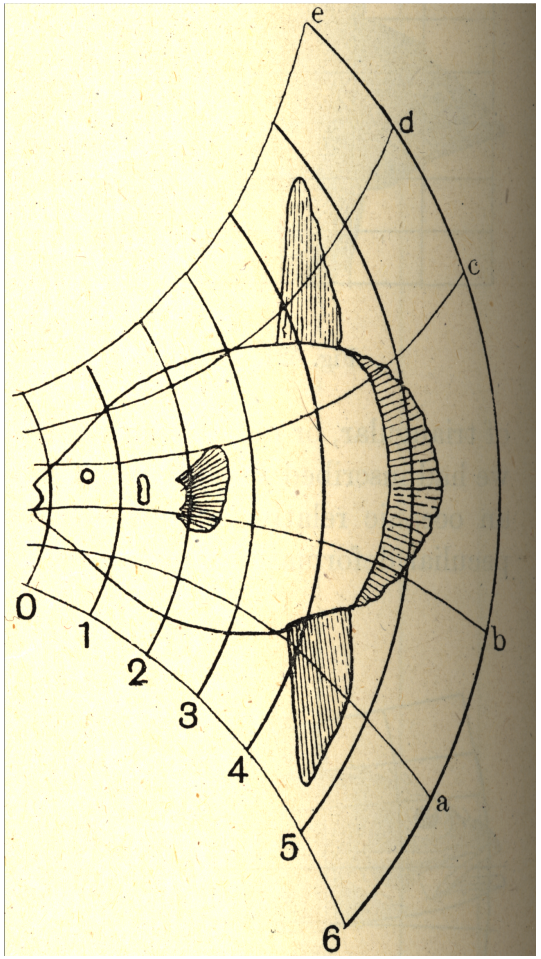
"Let us deform its rectilinear coordinates [for the Parrotfish] into a system of (approximately) coaxial circles, $\cdots$, then filling into the new system, $\cdots$ we obtain a very good outline of an allied fish $\cdots$ of the genus Pomacanthus."

Angelfish in color.

“This case is very interesting since upon the body of the Pomacanthus there are striking color bands, which correspond in direction very closely to the lines of our new coordinates.”

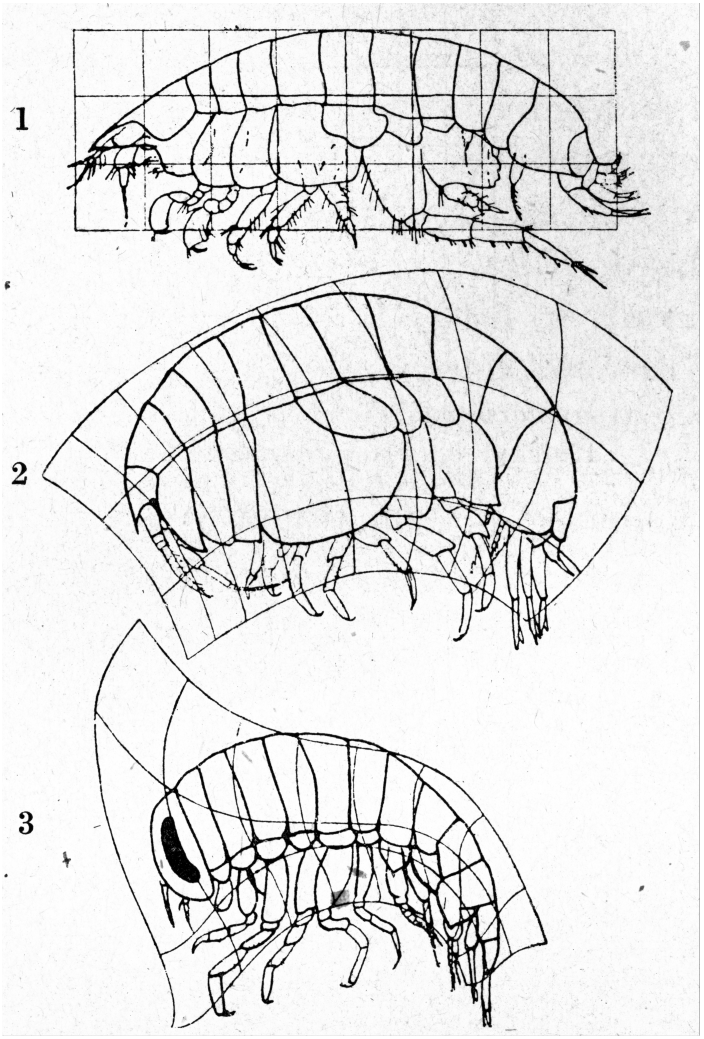
Porcupine-fish and Sunfish





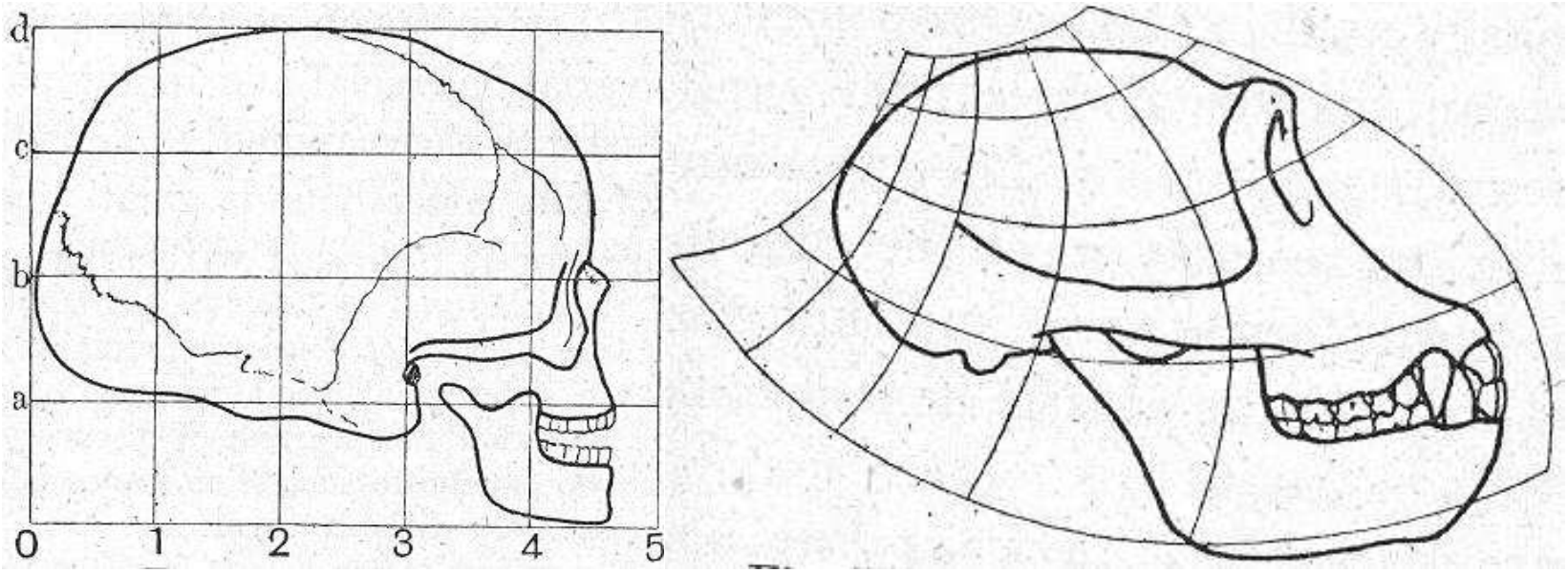
"· · · on the right I have deformed its vertical coordinates into a system of concentric circles, and its horizontal coordinates into a system of curves which, approximately and provisionally, are made to resemble a system of hyperbolas [to obtain] a representation of the closely allied **sunfish**."

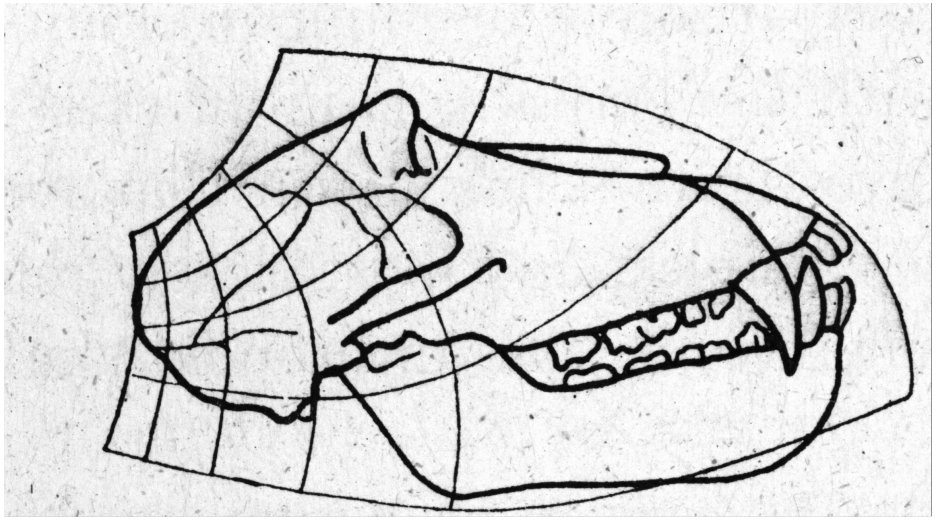
Three Marine Crustacea:



1. Harpinia plumosa Kr.; 2. Stegocephalus inflatus Kr.; 3. Hyperia galba. The last picture requires a greater deformation, so is less accurate but still a tolerable representation of Hyperia galba.

Comparison of skulls: human, chimpanzee,





and baboon.

Conformal Transformations?

"The empirical coordinates which I have sketched in for the chimpanzee as a conformal transformation of the Cartesian coordinates of the human skull look as if they might find their place in an equipotential elliptic field."

"I have shewn the similar deformation in the case of the baboon, and it is obvious that the transformation is of precisely the same order [as that for the chimpanzee], and differs only in an increased intensity or degree of deformation."

OUR QUESTION: *To what extent is it true that individuals of closely related species can be transformed, one into the other, by a*

conformal transformation

which carries every significant feature of one into the corresponding feature of the other?

The Mathematics of Conformal Transformations

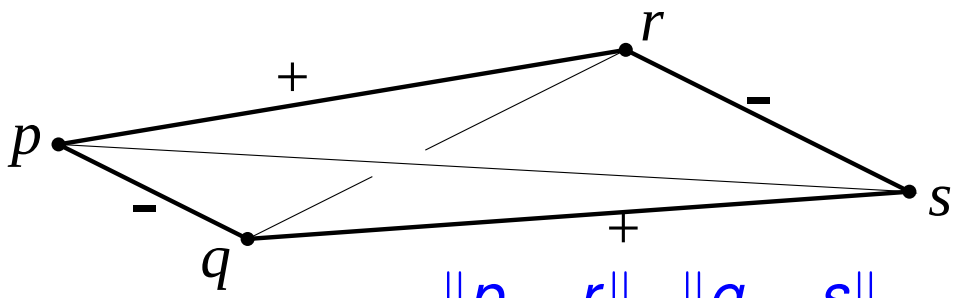
Although Thompson's diagrams are necessarily 2-dimensional, they represent 3-dimensional organisms.

Conformal transformations in 3-space are much more restricted than those in two dimensions—in fact they form a finite dimensional Lie group:

> **Theorem of Liouville.** *If a smooth transformation from one region in* $\mathbb{R}^3$ *to another preserves angles, then it extends uniquely to a smooth angle preserving transformation from* $\mathbb{R}^3 \cup \infty$ *onto itself.*

Distance Cross-Ratios

The most convenient invariant of a conformal transformation of $\mathbb{R}^n \cup \infty$ is the cross-ratio of Euclidean distances between four distinct points:



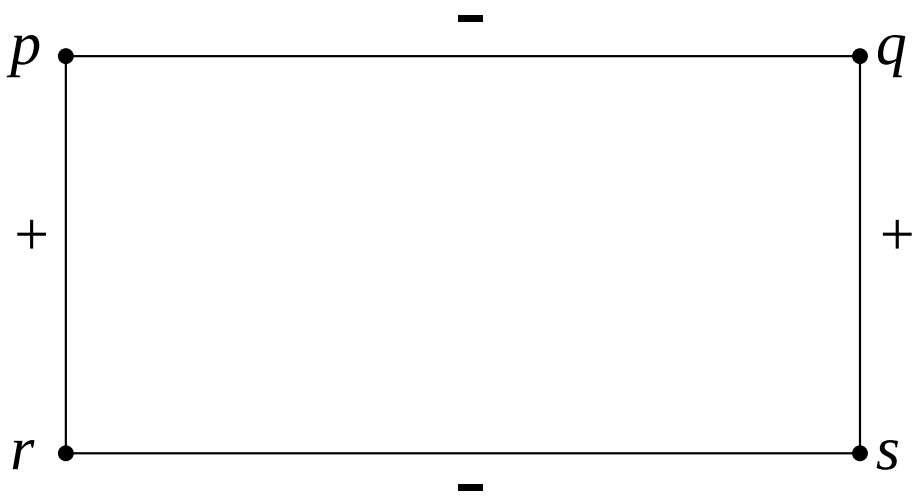
$$[p,\, q,\, r,\, s] \;=\; \frac{\|p-r\| \cdot \|q-s\|}{\|p-q\| \cdot \|r-s\|}\,.$$

This extends by continuity to the case $s = \infty$:

$$[p,\, q,\, r,\, \infty] \;=\; \frac{\|p-r\|}{\|p-q\|}\,.$$

Lemma 1. A transformation of $\mathbb{R}^n \cup \infty$ fixes the point at infinity, and preserves distance cross-ratios, if and only if it is a Euclidean similarity transformation, multiplying all distances by a fixed constant.

Example



For a rectangle, the cross-ratio is given by

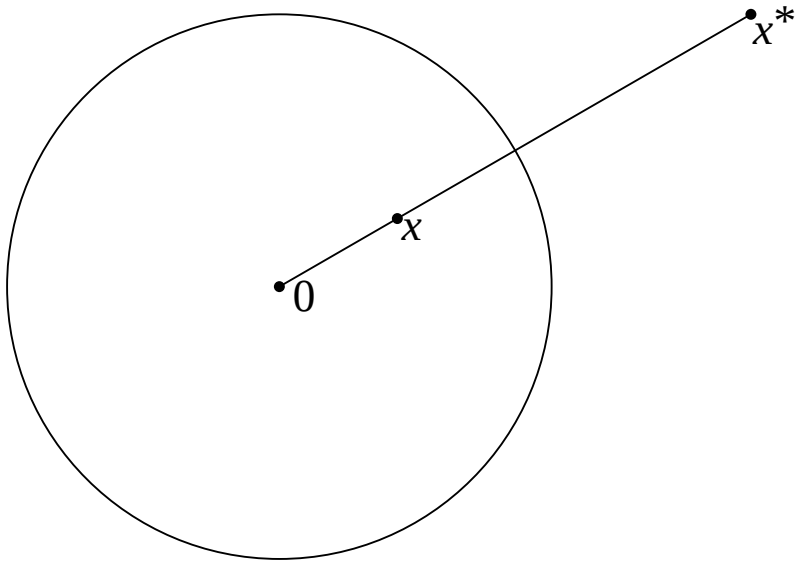
$$[p,\, q,\, r,\, s] \;=\; \left(\frac{\text{height}}{\text{width}}\right)^2 .$$

Inversion

Consider the **inversion map**

$$x \mapsto x^* = \frac{x}{\|x\|^2}$$

from $\mathbb{R}^n \cup \infty$ to itself.



Lemma 2: $[p^*, q^*, r^*, s^*] = [p, q, r, s]$.

Proof. Note the identity

$$\|x^* - y^*\| = \frac{\|x - y\|}{\|x\| \cdot \|y\|}. \tag{1}$$

In $\mathbb{R}^2$ this is a straightforward computation.
(Identify $\mathbb{R}^2$ with $\mathbb{C}$, so that $z^* = z/(z\overline{z}) = 1/\overline{z}$.)
Since any two vectors in $\mathbb{R}^n$ are contained in a copy of $\mathbb{R}^2$, this proves (1); and the Lemma follows immediately. $\square$

The Möbius Group (for $n \geq 1$)

For any $n \geq 1$, define the **Möbius group** $M(n)$ to be the group of all transformations of $\mathbb{R}^n \cup \infty$ which preserve the distance cross-ratio $[p, q, r, s]$.

Other descriptions:

- $M(n)$ is generated by inversion, together with all similarity transformations of $\mathbb{R}^n$, or together with all translations of $\mathbb{R}^n$.

- Locality: Any transformation from a region in $\mathbb{R}^n$ into $\mathbb{R}^n$ which preserves distance cross-ratios can be extended uniquely to a Möbius transformation of $\mathbb{R}^n \cup \infty$.

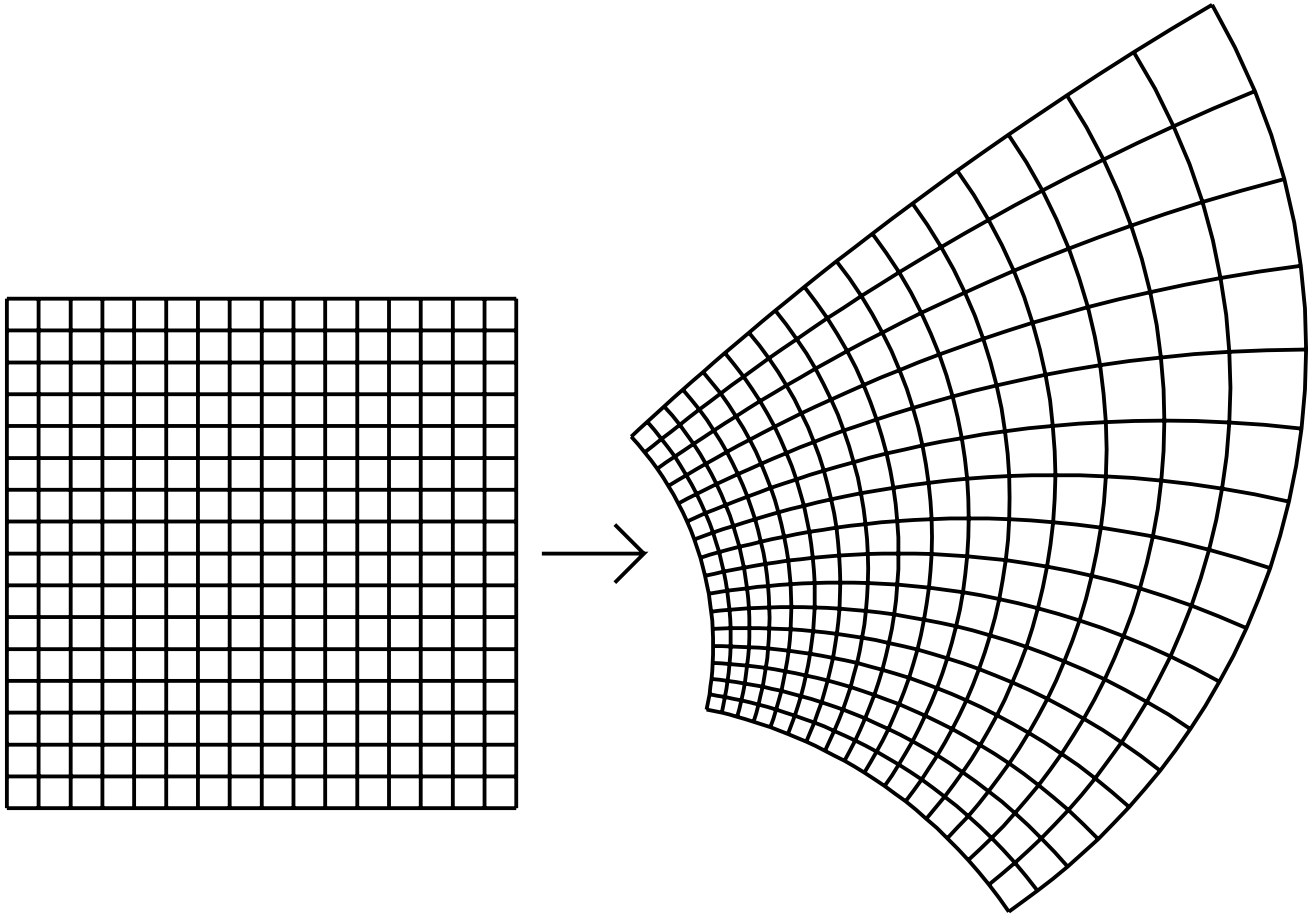
- $M(n)$ can be identified with the group of all transformations of the unit sphere $S^n \subset \mathbb{R}^{n+1}$ which preserve cross-ratios of Euclidean distances.

  - *For any $n \geq 1$, this Möbius group is isomorphic to the group of all isometries of hyperbolic $(n+1)$-space, or to the projective orthogonal group $PO(n+1, 1)$.*

The Möbius Group for $n \geq 2$.

- Conformality: For $n \geq 2$, a transformation of $\mathbb{R}^n \cup \infty$ (or of S^n) is Möbius if and only it preserves angles,

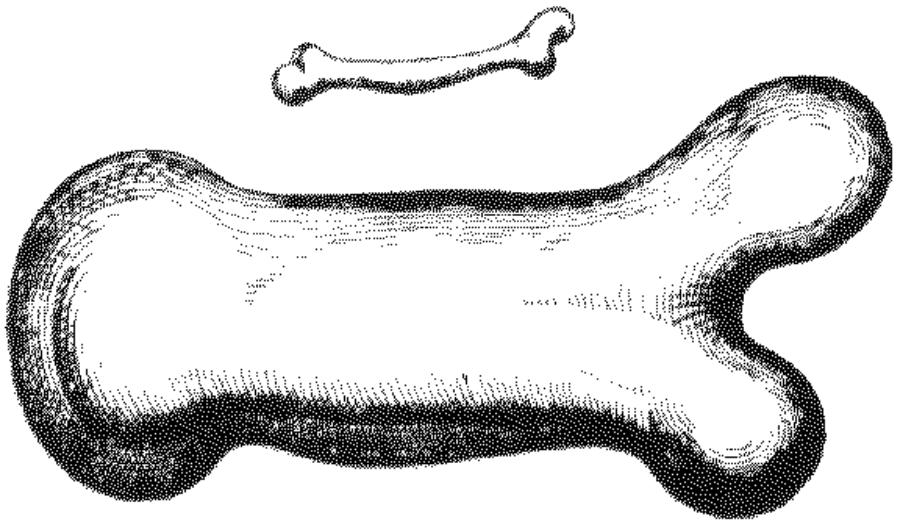
or if and only if it maps circle and lines to circles or lines.



Back to Biology

RECALL THE QUESTION: To what extent is it true that individuals of closely related species can be transformed, one into the other, by a **conformal transformation** *which carries every significant feature of one into the corresponding feature of the other?*

One difficulty was well known to Thompson:

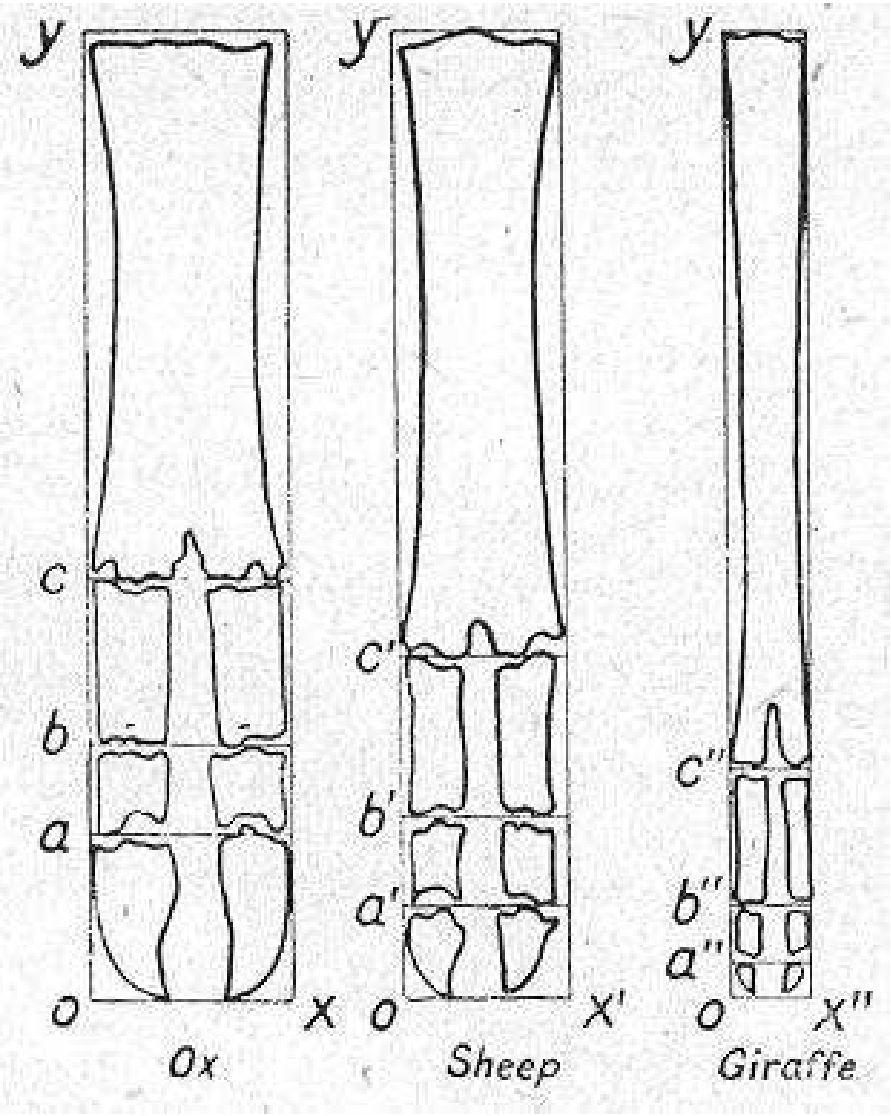


Galileo's comparison between bones of a small animal and a large animal.

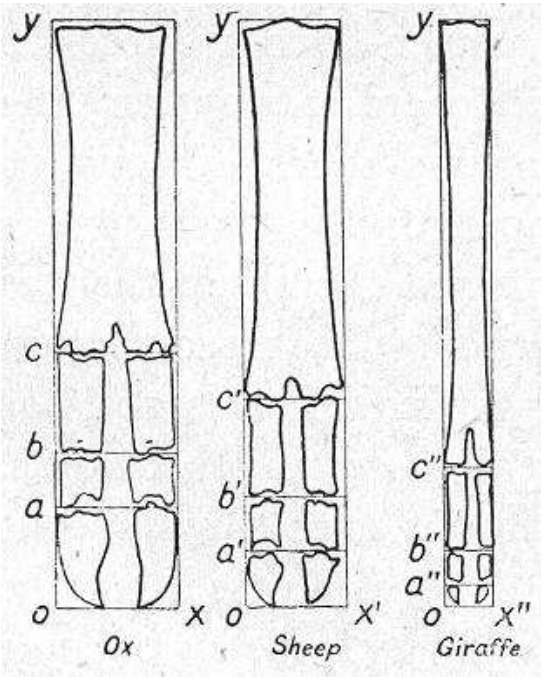
Elephant and Deer

If we try to increase the dimensions of an organism by a constant factor of c, then the weight will increase by a factor of c^3, but the suporting strength only by a factor of c^2. If nature tried to created an elephant sized deer by a linear change of scale, the result would be unable to support its own weight.

A comparison of foot bones for three species.



Relative measurements (with 0y=100).



	$0a$:	ab :	bc :	cy	$\frac{cy}{0a}$
Ox :	.18	.9	.15	.58	3.2
Sheep :	.10	.9	.17	.64	6.4
Giraffe :	.5	.5	.14	.76	15.2

Thus the distance ratio $\frac{cy}{0a}$ for a giraffe is almost five times the corresponding distance ratio for an ox.

Corresponding **cross-ratios** in the vertical direction are much closer to each other:

	$[0,\ a\ ,\ b,\ c]$	$[\ a,\ b\ ,\ c,\ y]$
Ox :	$[0, 18\ ,\ 27, 42] = 2.40$,	$[18,\ 27\ ,\ 42, 100] = 3.36$
Sheep :	$[0, 10\ ,\ 19, 36] = 2.91$,	$[10, 19\ ,\ 36, 100] = 3.66$
Giraffe :	$[0,\ 5\ ,\ 10, 24] = 2.71$,	$[\ 5, 10\ ,\ 24, 100] = 4.50$

2-dimensional cross-ratios

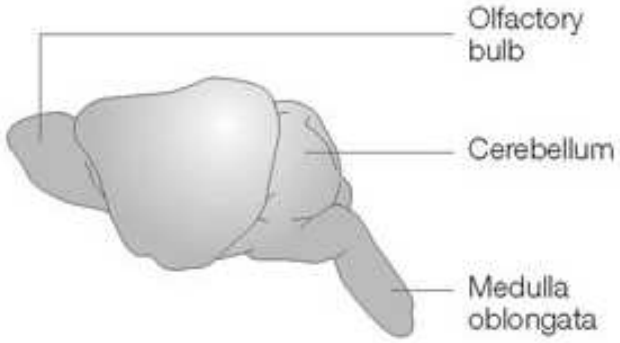
However, if we consider changes in both the x and y coordinates, then the cross-ratios change much more.
For a rectangle with edge lengths Δx and Δy, recall that the cross ratio of the four vertices of the rectangle, appropriately ordered, is $(\Delta y/\Delta x)^2$.
For the rectangles drawn by Thompson, we get the following:

		Ox	Sheep	Giraffe
$\frac{\Delta y}{\Delta x}$	$\approx$	4.8	5.8	11.5
$\left(\frac{\Delta y}{\Delta x}\right)^2$	$\approx$	23	34	132.

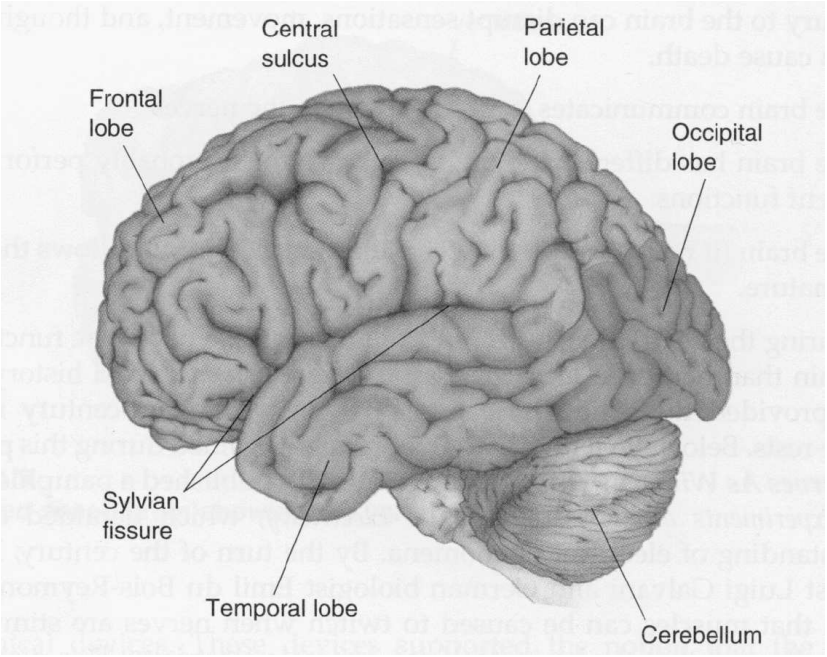
Thus we have a paradox: Vertical cross-ratios don't change much between these species;

but 2-dimensional cross-ratios change a lot !

Another Example: Evolution of the Brain.



Mouse



Human

Starting with the relatively smooth brain of a simpler mammal, if natural selection leads to an expansion of the surface area without expanding the overall size, then Möbius transformations simply cannot work. The evolutionary solution—drastic wrinkling and furrowing of the outer layers of the brain—seems to be far from conformal.

Conformal Maps of the Brain.

However, the surface of the brain is a surface of genus zero, conformally isomorphic to S^2.

Conformal mapping of from the surface of the brain to a sphere seems to be relatively stable, so that it can actually be used as an effective tool in medical imaging.

(Work of Gu, Wang, Chan, Thompson, and Yau.)

Perhaps the expansion of the cerebral cortex is roughly conformal **if we consider only the two-dimensional surface** ?

Growth.

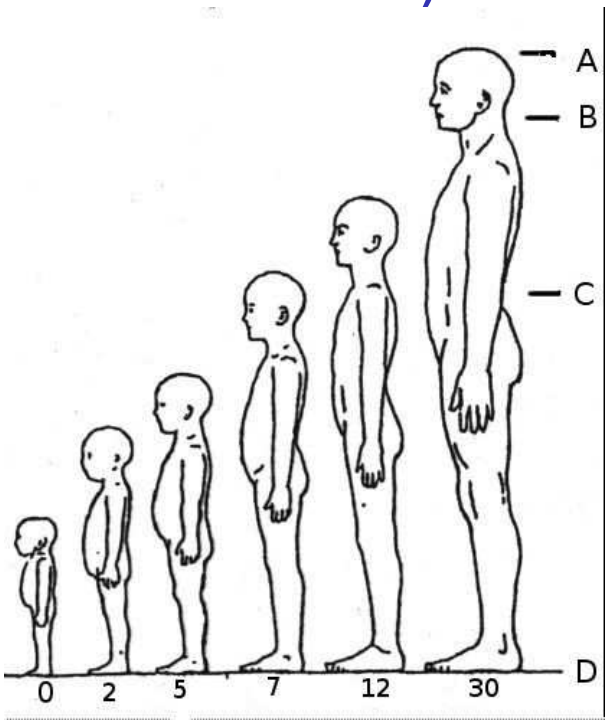
Organisms seem to grow by transformations which are roughly conformal.

As an example, a human child has a relatively large head and small torso in comparison to an adult. The ratio of head size to torso size is not at all invariant under growth.

However, if we look at the transformation which carries each point of a child's body to the corresponding point of an adult's body, then it does seem to be very roughly conformal.

In particular, cross-ratios change far less than simple ratios of distances.

Human growth (after Petukhov)



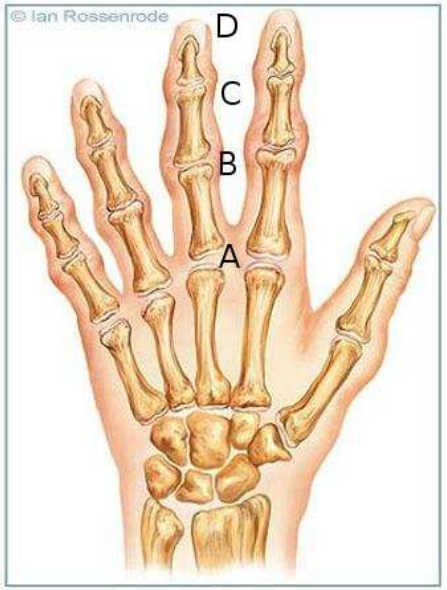
The legs grow almost twice as much as the head; but the cross-ratios remain relatively stable.

Age	AB (head)	BC (torso)	CD (legs)	$\frac{CD}{AB}$	$[A, B, C, D]$
0	10.6	18.3	28.6	2.70	4.47
4	18.9	31.4	58.4	3.09	4.09
7	21.0	35.3	71.7	3.41	4.00
10	22.5	38.0	80.6	3.58	3.96
20	25.3	51.8	109.9	4.34	4.48

Finger growth

If we consider only a very small region of the body, then conformal growth is approximately growth by similarity transformations.

Consider growth of the middle finger.



Age	AB	BC	CD	Ratios	$[A, B, C, D]$
4	2.42	1.43	0.96	(.51 : .30 : .18)	4.24
8	3.00	1.88	1.19	(.49 : .31 : .20)	4.19
14	3.56	2.27	1.46	(.49 : .31 : .20)	4.18
21	4.41	2.78	1.76	(.49 : .31 : .20)	4.21

In this case ratios, and hence cross-ratios, are quite stable.

Conclusions

The geometrically simplest way to change the relative size of different body parts is by a conformal transformation.

It seems plausible that this simplest solution will often be the most efficient, so that natural selection tend to choose it.

However, natural selection will surely deviate from conformality whenever the deviation confers a clear selective advantage.

The Problem: There does seem to be a real tendency to preserve cross-ratios, for example in the vertical direction, even when the transformation is far from conformal.

Is this a real effect? If so, why does it occur?

Possible Explanations

1. Engineering Explanation. Transformations which preserve appropriate cross-ratios confer some selective advantage. They are more efficient, and hence tend to be chosen by natural selection.

2. Control Mechanism Explanation. The bio-chemical systems which regulate growth tend to yield transformations which preserve cross-ratios, even when other patterns of growth would work just as well or better.

3. Skeptical Explanation. Perhaps these approximately preserved cross-ratios are just numerical accidents, with no biological meaning at all.

Another Possibility: The Projective Group

There is a quite different group which preserves the cross-ratios for any four points lying in a straight line,

namely the group of all **projective transformations** from the 3-dimensional real projective space $\mathbb{RP}^3 \supset \mathbb{R}^3$ to itself.

This would seem to fit the data better!

This group,

$$PGL(4, \mathbb{R}) \;=\; GL(4, \mathbb{R})/(\text{diagonal matrices})\,,$$

is much bigger than the conformal group (15 dimensional instead of 10 dimensional).

On the other hand, it is hard to imagine any reason for natural selection to choose projective transformations.

A Related Problem: Convergent Evolution.

There are many examples of animals which have similar features, although they are not closely related.

Some form of eye has evolved independently at least 40 different times.

Venomous stings have evolved independently in jellyfish, spiders, scorpions, centipedes, insects, molluscs, snakes, stingrays, stonefish, platypus, and in some plants (nettles).

Genetic analysis often shows that animals which were thought to be close relatives are actually very distantly related.

The progression from dissimilar ancestors to similar descendants is called **Convergent Evolution**.

Problem. Does this convergence occur because both animals are evolving towards the same optimal configuration,

or does it occur simply because there are such strong constraints on what forms are evolutionarily possible?

Skeleton Space.

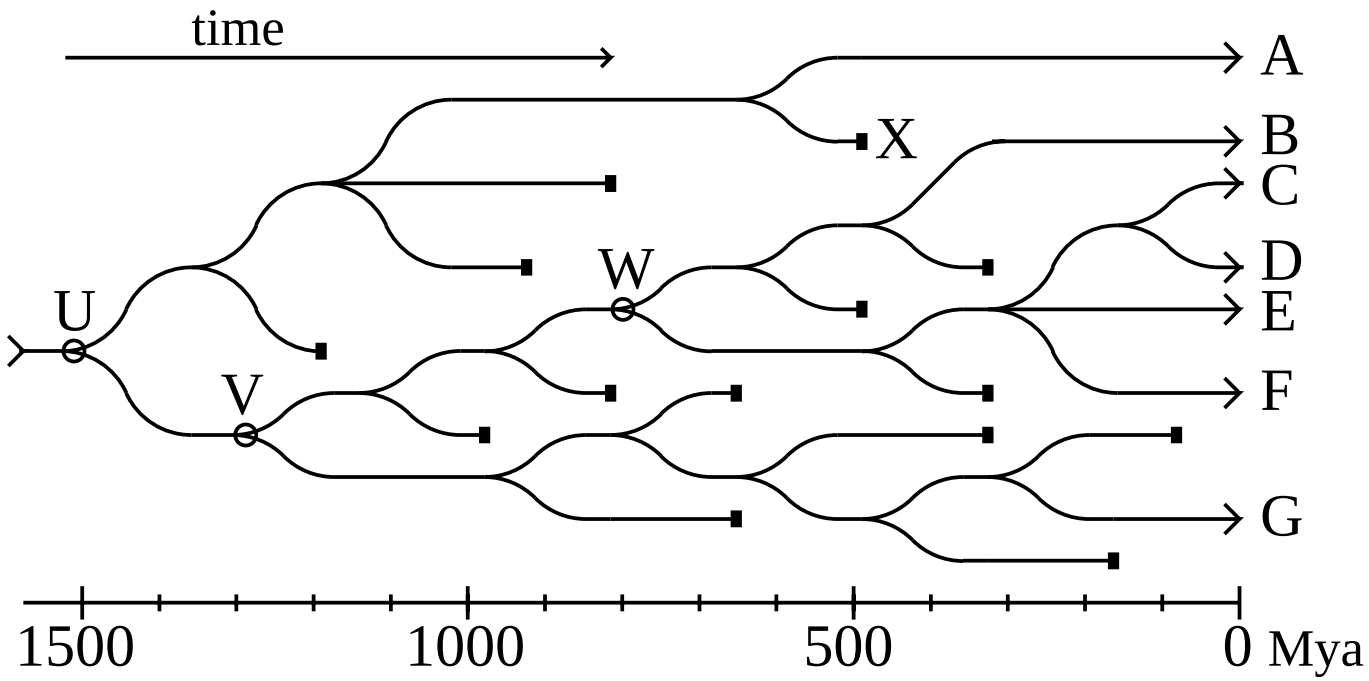
One approach to this problem, by Thomas and Reif, sounds very interesting, although it is quite vague by mathematical standards.

They describe an enormous abstract “space” of theoretically possible skeletal configurations.

Their claim: There is a much smaller subset of efficient configurations which form a “*topological attractor*”.

Evolution of any organism must inevitably converge towards this subset of efficient configurations.

Part 2. The Tree Model for Evolution.



Hypothesis. The histories of the various species over time can be described by a tree:

- Any two species have a common ancestor species.
- A species may become extinct,
  or may bifurcate into two or more related species;
  but once separated, two species can never come back together.

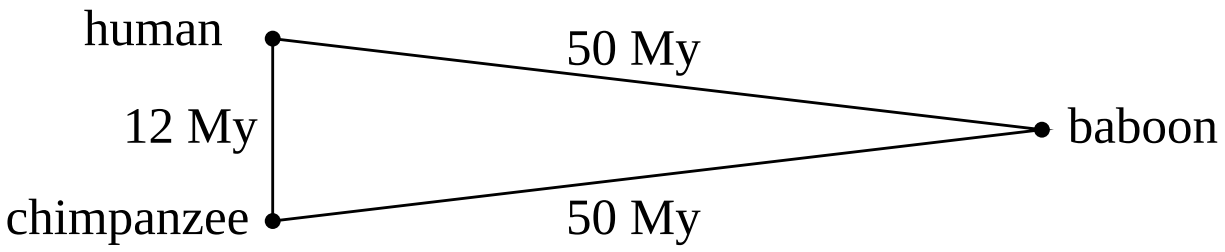
Evolutionary distance.

This tree has a natural metric $\int |dt|$, measured in years.

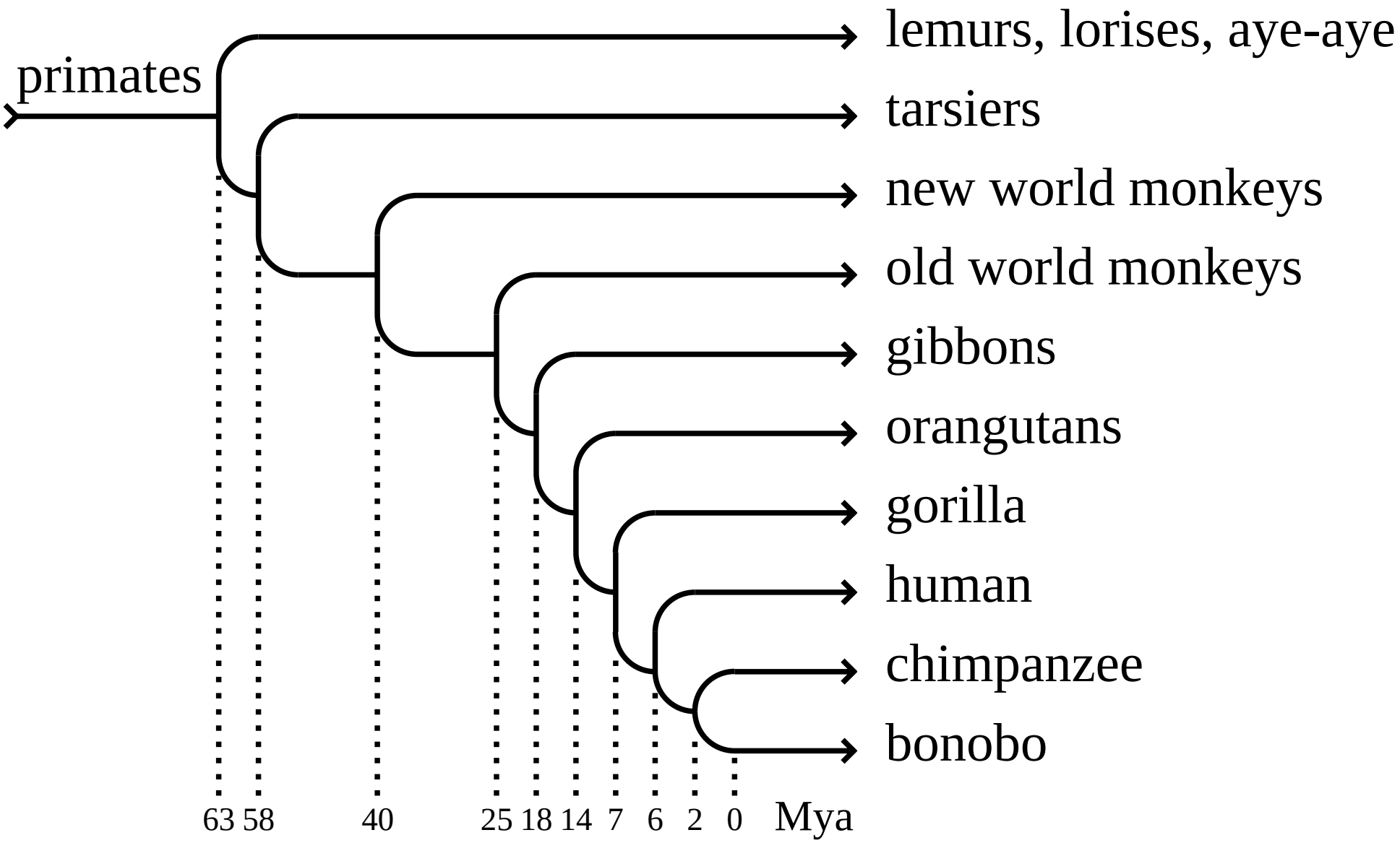
In particular, the **evolutionary distance** between two present day species is defined to be **2y**, where **y** is the number of years since a common ancestor was alive.

Ultrametric property: In terms of this distance, any three present day species form the vertices of an isosceles or equilateral triangle, the two longest sides being equal.

Example:



Tree for Primate Evolution



One Difficulty: the Concept of “Species.”

An example:

Lesser Black-Backed Gull

Herring Gull

These are two distinct species in Europe. But as we move west across America, Alaska, and through Siberia, the Herring Gull gradually changes. By the time we get back to Western Europe, it has become a Lesser Black-Backed Gull!

Non-transitivity

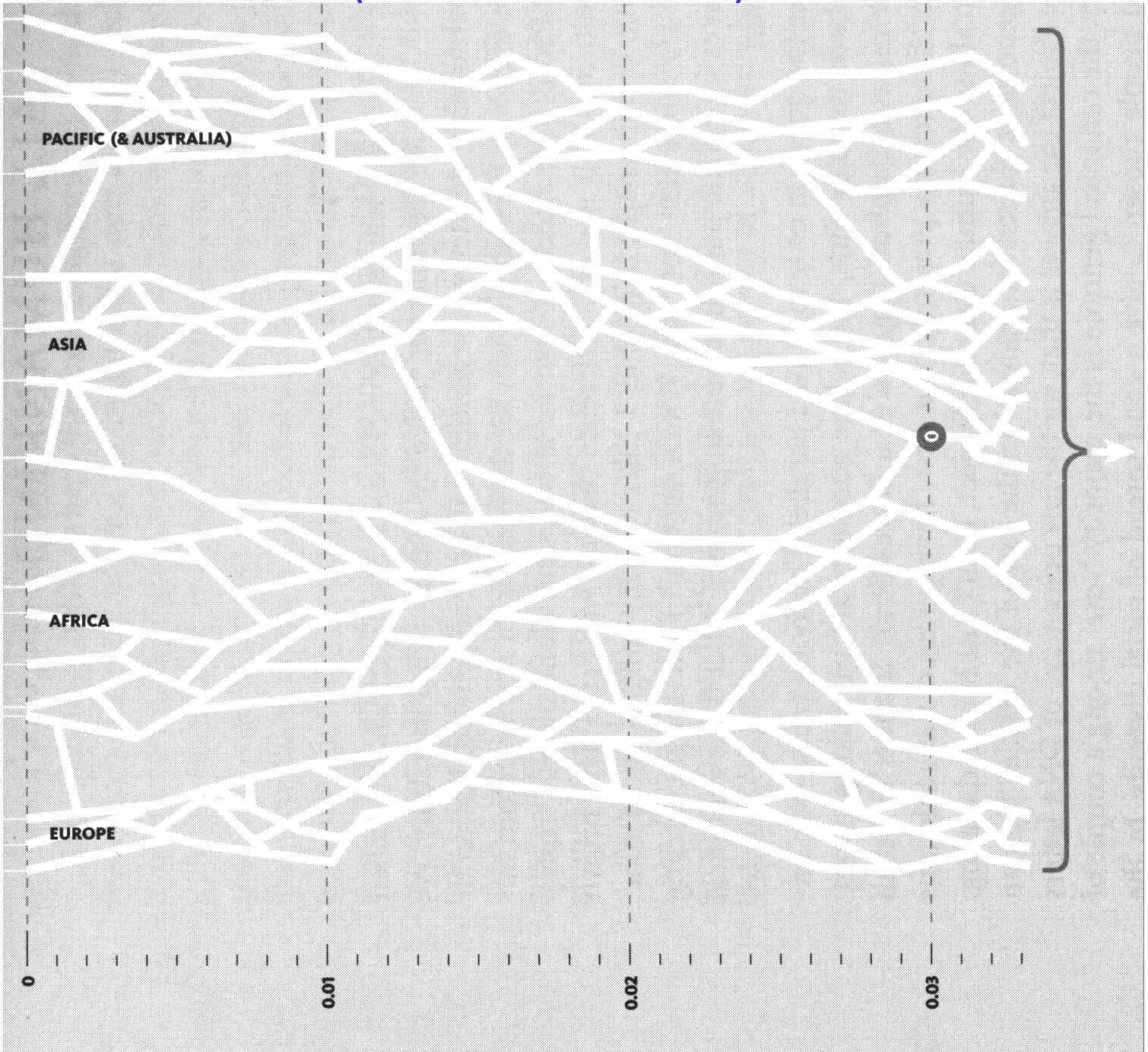
Two groups of animals are often said to belong to the **same species** if they mate with each other and produce fertile offspring.

But this is not a transitive relation!

Hence this definition of species can't be taken literally.

In fact, each solid line in the Evolutionary Tree Model (representing a species), is actually an abstraction, representing an enormously complicated tangle of matings and births.

Human evolution (after Dawkins)



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