The Geometry

of Growth and Form

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Comments on a much loved book:

"On Growth and Form," first published in 1917.
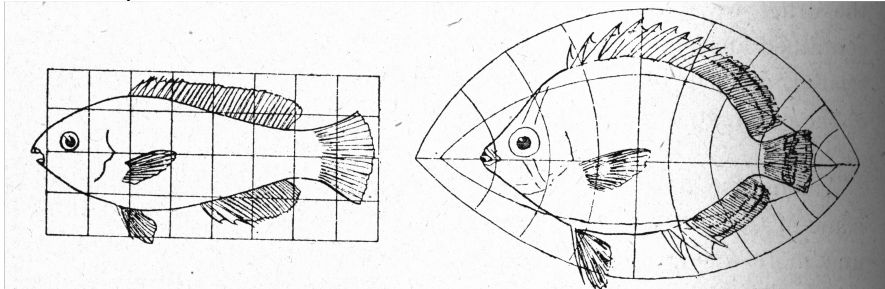

D'ARCY THOMPSON (1860-1948)

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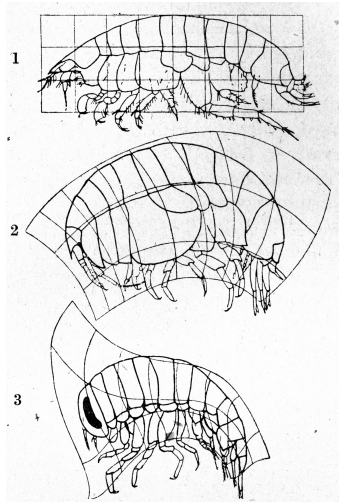
Porcupine-fish and Sunfish
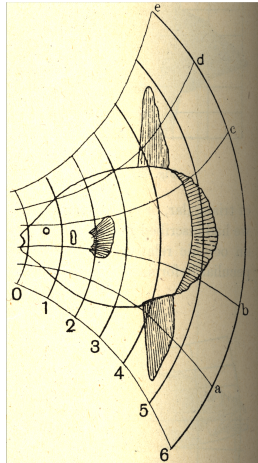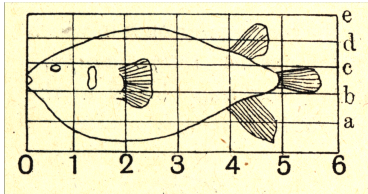
"··· on the right I have deformed its vertical coordinates into a system of concentric circles, and its horizontal coordinates into a system of curves which, approximately and provisionally, are made to resemble a system of hyperbolas [to obtain] a representation of the closely allied **sunfish**."
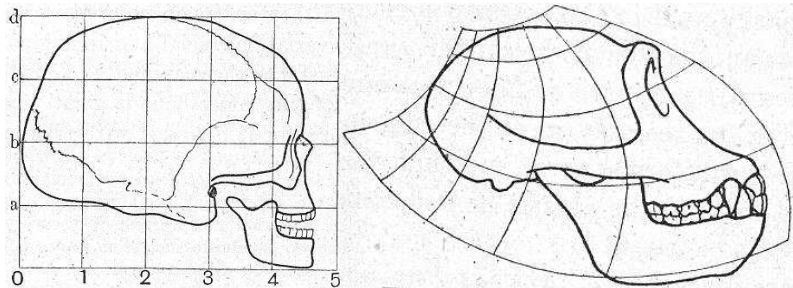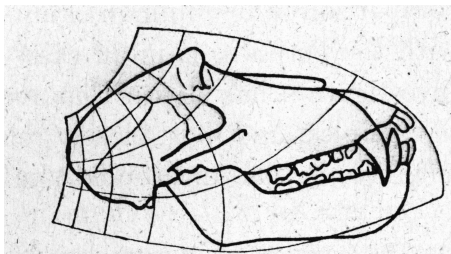
Three Marine Crustacea:

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.

"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."

MY 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?

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

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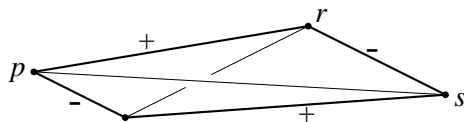
They form a finite dimensional Lie group:

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.
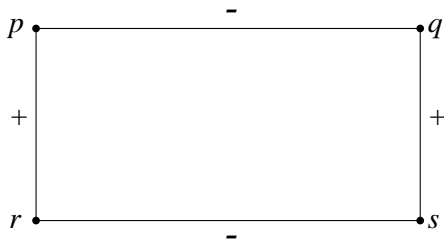
Two Dimensional Examples

If we identify $\mathbb{R}^2$ with the complex numbers, then

$$[p, q, r, s] = \left| \frac{(p-r)(q-s)}{(p-q)(r-s)} \right|$$

= absolute value of the classical cross-ratio.

For a rectangle

the distance cross-ratio is given by

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

Inversion

Lemma 2. The **inversion**

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

maps $\mathbb{R}^n \cup \infty$ to itself,
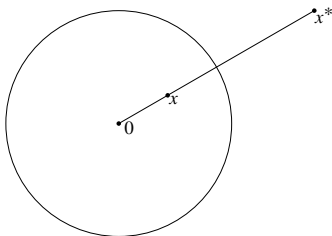

preserving distance cross-ratios:

$$[p^*, q^*, r^*, s^*] = [p, q, r, s]. \qquad (1)$$

Equation (1) follows easily from the identity

$$\|x^* - y^*\| = \frac{\|x - y\|}{\|x\| \cdot \|y\|}. \qquad (2)$$

Proof of (2) for $n = 2$**.** Identifying $\mathbb{R}^2$ with $\mathbb{C}$, note that

$$z^* = z/(z\bar{z}) = 1/\bar{z}, \qquad \text{with} \quad |1/\bar{z} - 1/\overline{w}| = |(z - w)/(zw)|.$$

Since any two vectors in $\mathbb{R}^n$ are contained in a copy of $\mathbb{R}^2$, this proves (2) for any n, and (1) follows. $\square$

The Möbius Group in dimensions $n \geq 1$.

Define the **Möbius group** $M\ddot{o}b(n)$ to be the group of all transformations of $\mathbb{R}^n \cup \infty$ which preserve the distance cross-ratio $[p, q, r, s]$. This makes sense for any $n \geq 1$.

Other descriptions which hold for all $n \geq 1$:

• $M\ddot{o}b(n)$ is generated by inversion, together with all similarity transformations of $\mathbb{R}^n$. (This follows from Lemmas 1 and 2.)

• 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 $\mathbb{R}^n \cup \infty$.

• $M\ddot{o}b(n)$ 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.

• $M\ddot{o}b(n)$ is isomorphic:
    to the group of all isometries of hyperbolic $(n+1)$-space,
   or to the projective orthogonal group $PO(n+1, 1)$.

For $n \geq 2$, a smooth 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.
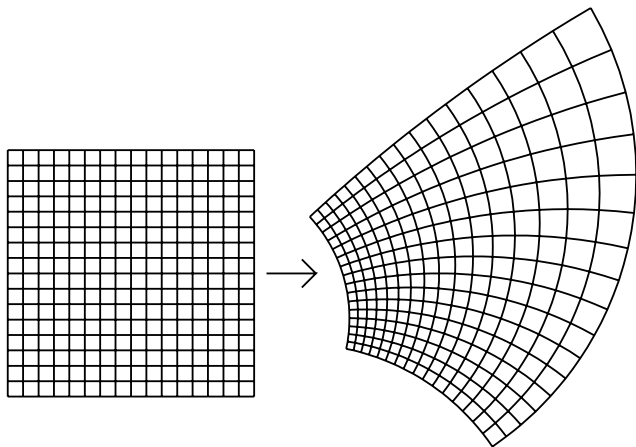
*RECALL THE QUESTION: To what extent is it true that individuals of closely related species can be transformed, one into the other, by a **conformal transformation** which carries every significant feature of one into the corresponding feature of the other?*

One difficulty was well known to Thompson:
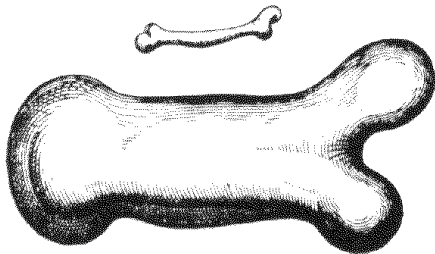
Comparison between bones of a small animal and a large animal   (from Galileo's "Two New Sciences").
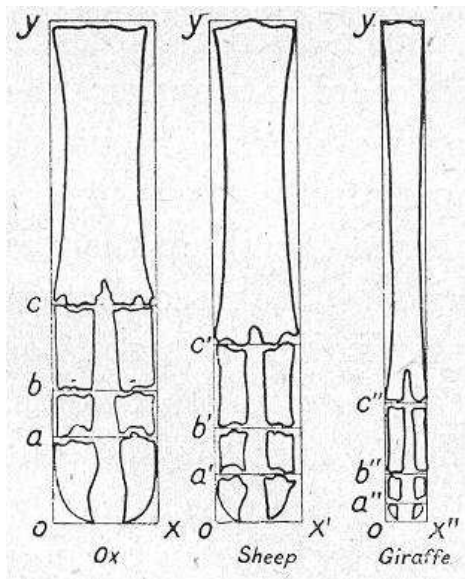
Elephant and Deer

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 supporting strength only by a factor of c^2.

If nature tried to create an elephant sized deer by a linear change of scale, the result would be unable to support its own weight!
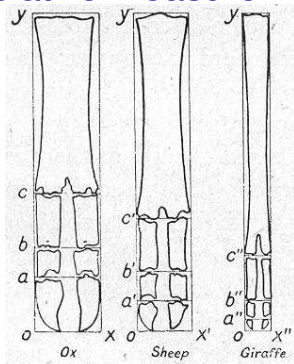
Ox   Sheep   Giraffe

Relative measurements

	o	a	b	c	y	$\frac{cy}{oa}$
Ox :	0	18	27	42	100	3.2
Sheep :	0	10	19	36	100	6.4
Giraffe :	0	5	10	24	100	15.2

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

Cross-ratios in the vertical direction are much closer:

	$[o, a, b, c]$		$[a, b, c, y]$	
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 :	$[0, 5, 10, 24] = 2.71$,		$[5, 10, 24, 100] = 4.50$	

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 distance 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	11.6
$\left(\frac{\Delta y}{\Delta x}\right)^2$	$\approx$	23.	34.	135.

Thus we have a paradox: Vertical cross-ratios don't change very much between these three species;
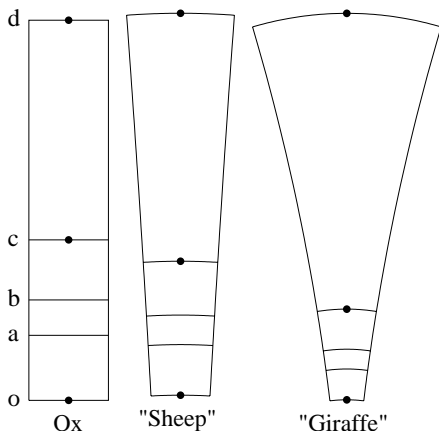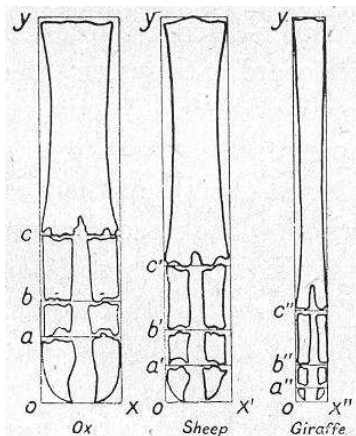
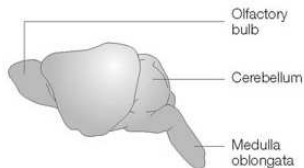but 2-dimensional distance cross-ratios change a lot !
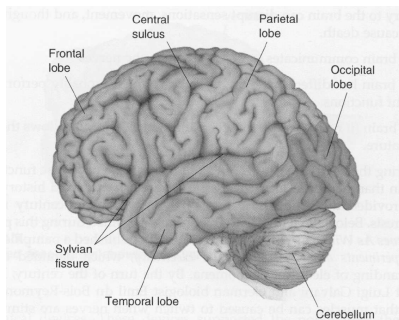
Graphical test for conformality

The action of the Möbius group $Möb(2)^+$ on $\mathbb{R}^2 \cup \infty$ is simply 3-transitive.

We can take three marked points on Thompson's **Ox** figure, and choose the unique element of $Möb(2)^+$ which carries them to the three corresponding points on the **Sheep** (or **Giraffe**) figure.

A Very Different Example: The Brain.

Mouse   Human

Starting with the relatively smooth brain of a simpler mammal, natural selection leads to a huge expansion of the surface area, with much smaller expansion of overall size.
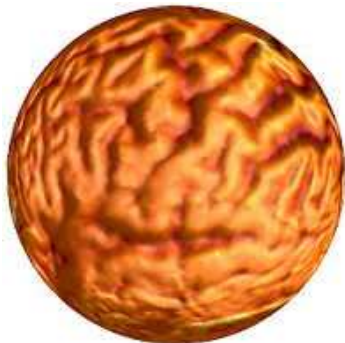
Clearly this is NOT a Möbius transformation.

The evolutionary solution— drastic wrinkling and furrowing of the outer layers of the brain— seems to be far from conformal.

But think only of the Surface of the Brain.

Image of the human brain surface, conformally mapped onto S^2

from Gu, Wang, Chan, Thompson, and Yau.

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

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.

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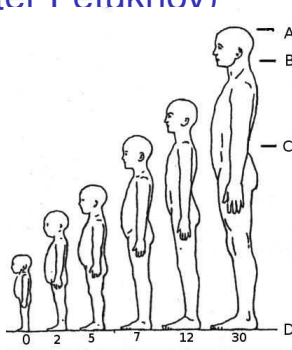
| Age	AB (head)	BC (torso)	CD (legs)	$\frac{CD}{AB}$	[A, B, C, D]
0	10.6	18.3	28.6	2.70	4.47
4	18.9	31.4	58.4	3.09	4.09
7	21.0	35.3	71.7	3.41	4.00
10	22.5	38.0	80.6	3.58	3.96
20	25.3	51.8	109.9	4.34	4.48

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

Finger growth

If we consider only a very small region of the body, then conformal growth would approximately be growth by a similarity transformation.

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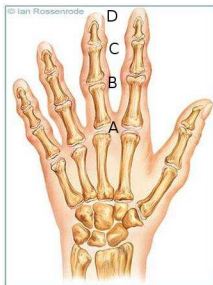
Age	AB	BC	CD	Ratios	[A, B, C, D]
4	2.42	1.43	0.96	(.51 : .30 : .18)	4.24
8	3.00	1.88	1.19	(.49 : .31 : .20)	4.19
14	3.56	2.27	1.46	(.49 : .31 : .20)	4.18
21	4.41	2.78	1.76	(.49 : .31 : .20)	4.21

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

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

namely the **projective group**

$$Proj(n) \cong PGL(n+1, \mathbb{R})$$

consisting of all projective transformations from the real projective space $\mathbb{RP}^n \supset \mathbb{R}^n$ *to itself.*

Could this be the right group for modeling changes in shape?

Would it fit the data better?

Caution. It may be easier to match data with the projective group, just because it has more free parameters.

$$\dim\big(M\ddot{o}b(3)\big) = 10, \qquad \dim\big(Proj(3)\big) = 15.$$

(To study only changes in **shape**, we should quotient by the 7 dimensional group of similarity transformations, leaving 3 free parameters for *Möb*(3), and 8 for *Proj*(3).)
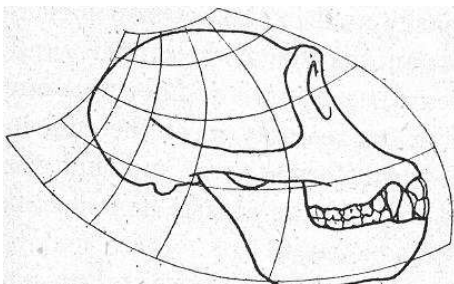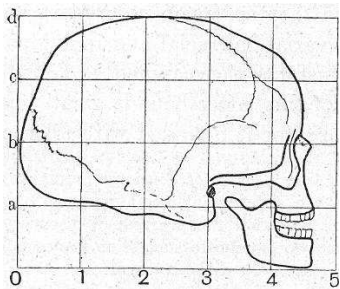
The group *Proj*(2) is simply 4-transitive, for 4-tuples in $\mathbb{RP}^2$ which are not collinear.
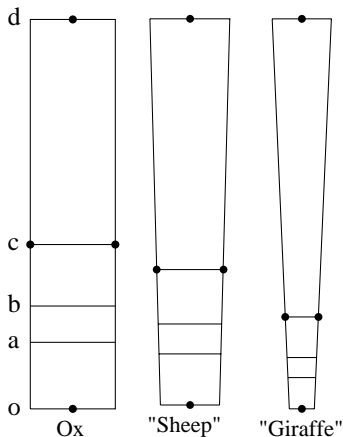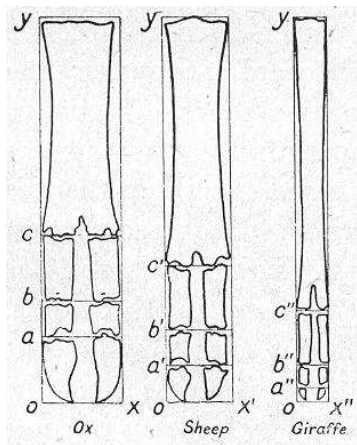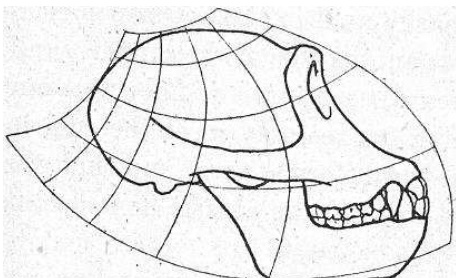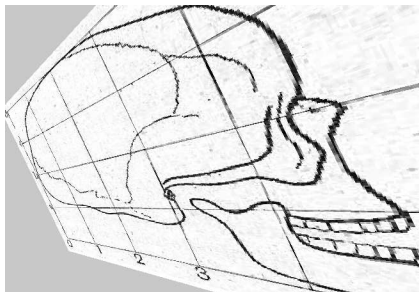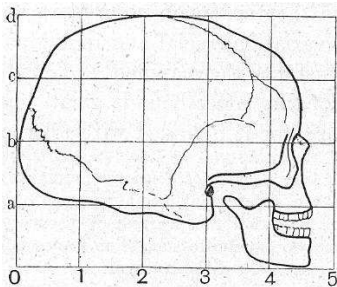
A Conformal Chimp?

Here is an attempt to convert a human skull to a chimp skull by a conformal transformation.

A Projective Chimp?

Now an attempt to convert a human skull to a chimp skull by a projective transformation.

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 species
are evolving towards the same optimal configuration,
or does it occur simply because there are such strong
constraints on what forms are evolutionarily possible?

One approach to this problem, by Thomas and Reif, sounds quite interesting.

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.

(However, their description is quite vague by mathematical standards, and seems difficult to test.)

The geometrically simplest way to change the relative size of different body parts would be 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.

But natural selection will surely deviate from conformality whenever the deviation confers a clear selective advantage. **There clearly is a great deal of deviation from conformality, and the projective group doesn't seem to work any better.**

However, there seems to be a real tendency to preserve cross-ratios, at least along many straight lines, even when the transformation is far from conformal or projective.

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

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.

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