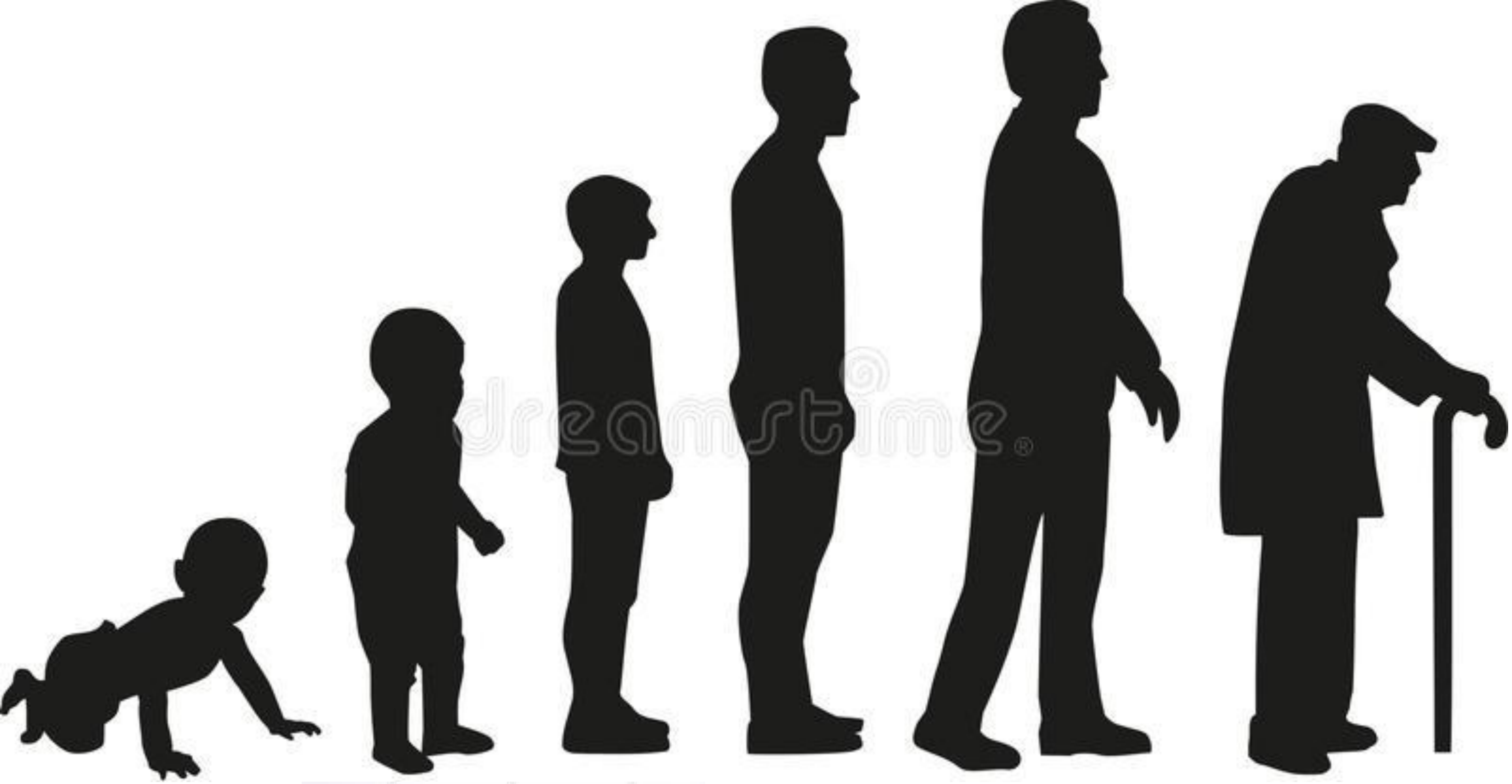
Life’s Scaling Laws

AK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- What are the common factors in all biological systems or living forms?

- What are the differences in biological systems?

Scale Terminology

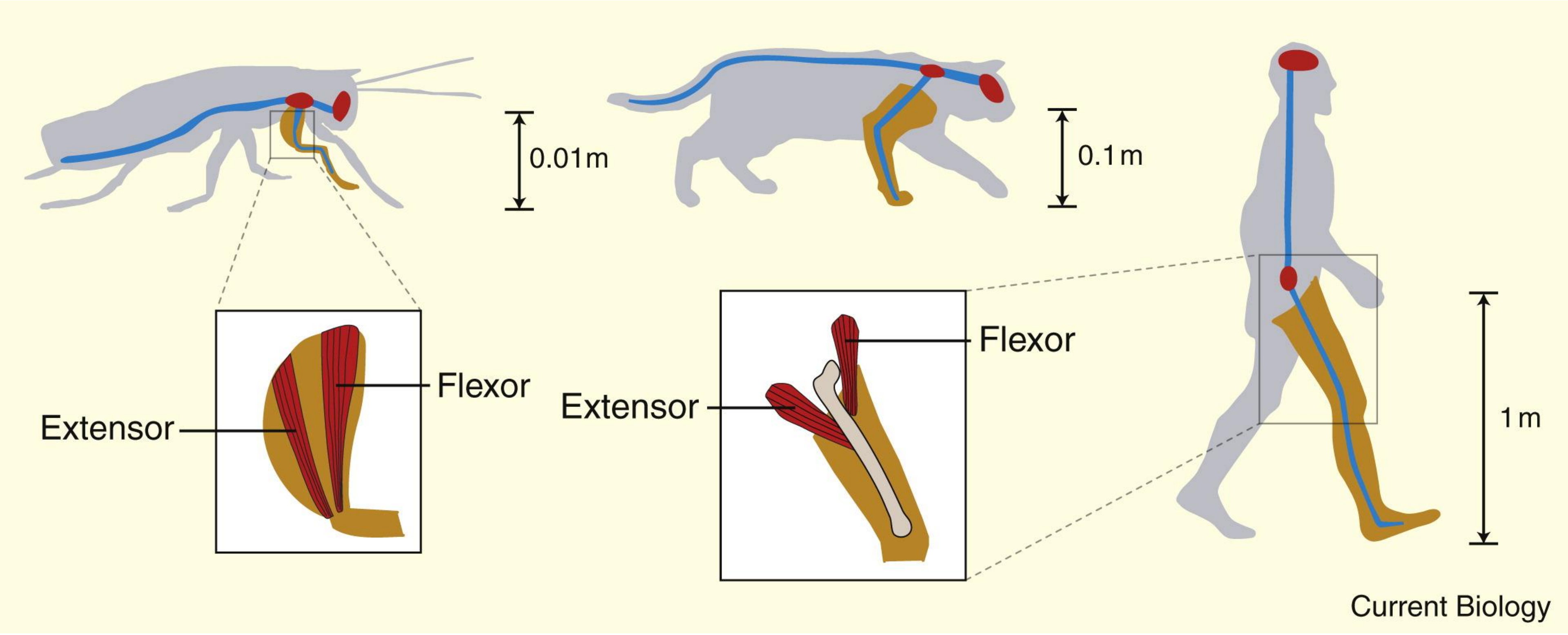
- Scale terminology – is not used consistently; leads to confusion

- ***Scale*** – refers to spatial or temporal dimension of an object or area

- vs –

- ***Level of organization*** – place within a biotic (or other organizational) hierarchy (e.g., organism, population, community, etc.)

Flying squirrel and mushroom

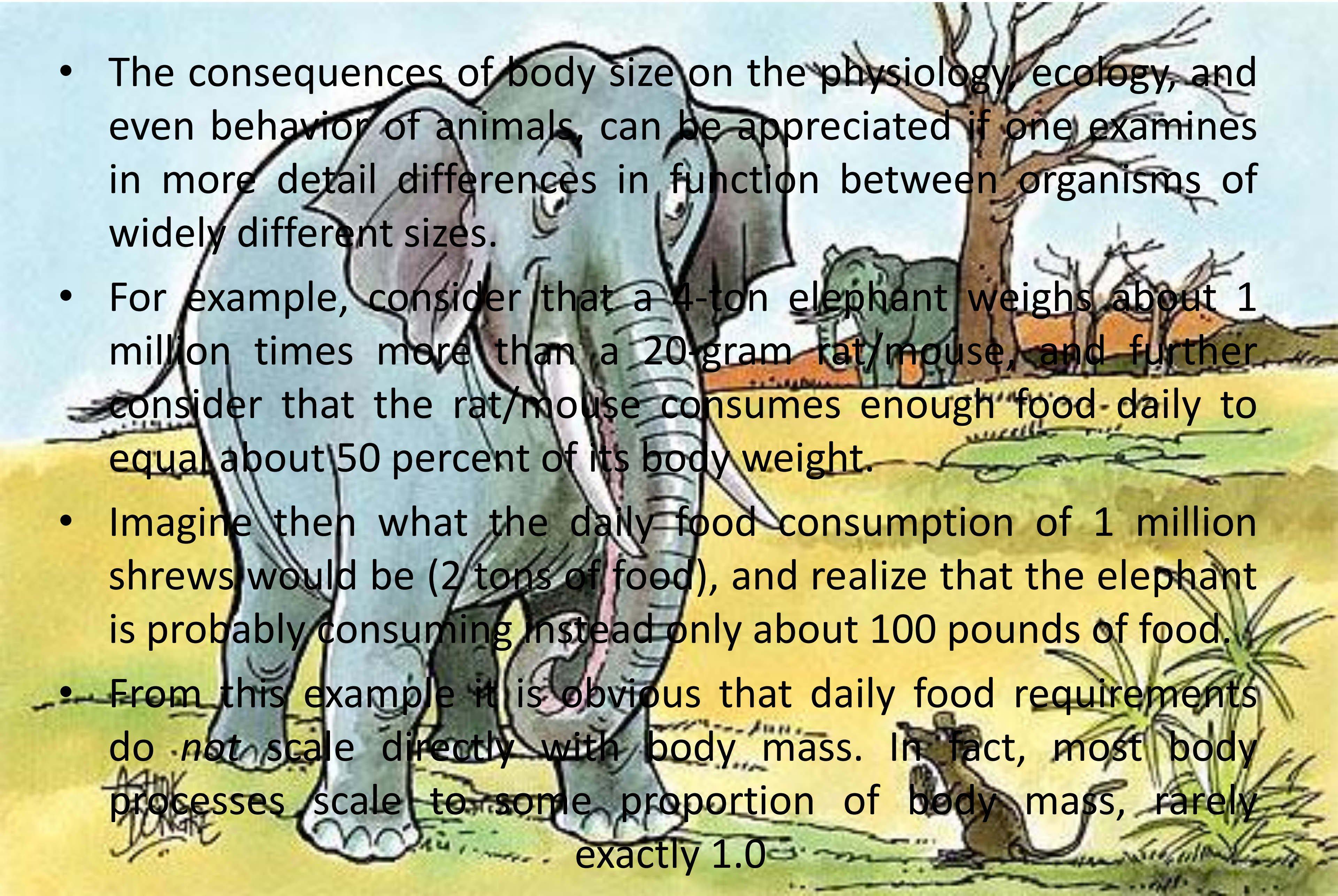


Current Biology 2009 19, R57-R61DOI: (10.1016/j.cub.2008.10.042)

Scaled up Cockroach

- Scaling can be defined as the structural and functional consequences of a change in size and scale among similarly organized animals.
- To examine what "consequences of a change in size" means, consider what would happen if one scaled up a cockroach simply by expanding it by a factor of 100 in each of its three dimensions.
- Its mass, which depends on volume, would increase by a factor of 1 million (100 x 100 x 100). The ability of its legs to support that mass, however, depends on the cross-sectional area of the leg, which has only increased by a factor of ten thousand (100 x 100).
- Similarly, its ability to take in oxygen through its outer surface will also grow only by ten thousand, since this too is a function of surface area.
- This disparity between the rapid growth in volume and the slower growth in surface area means the super-sized cockroach would be completely unable to support its weight or acquire enough oxygen for its greater body mass.

Does Food requirements scale up?



- The consequences of body size on the physiology, ecology, and even behavior of animals, can be appreciated if one examines in more detail differences in function between organisms of widely different sizes.
- For example, consider that a 4-ton elephant weighs about 1 million times more than a 20-gram rat/mouse, and further consider that the rat/mouse consumes enough food daily to equal about 50 percent of its body weight.
- Imagine then what the daily food consumption of 1 million shrews would be (2 tons of food), and realize that the elephant is probably consuming instead only about 100 pounds of food.
- From this example it is obvious that daily food requirements do *not* scale directly with body mass. In fact, most body processes scale to some proportion of body mass, rarely exactly 1.0

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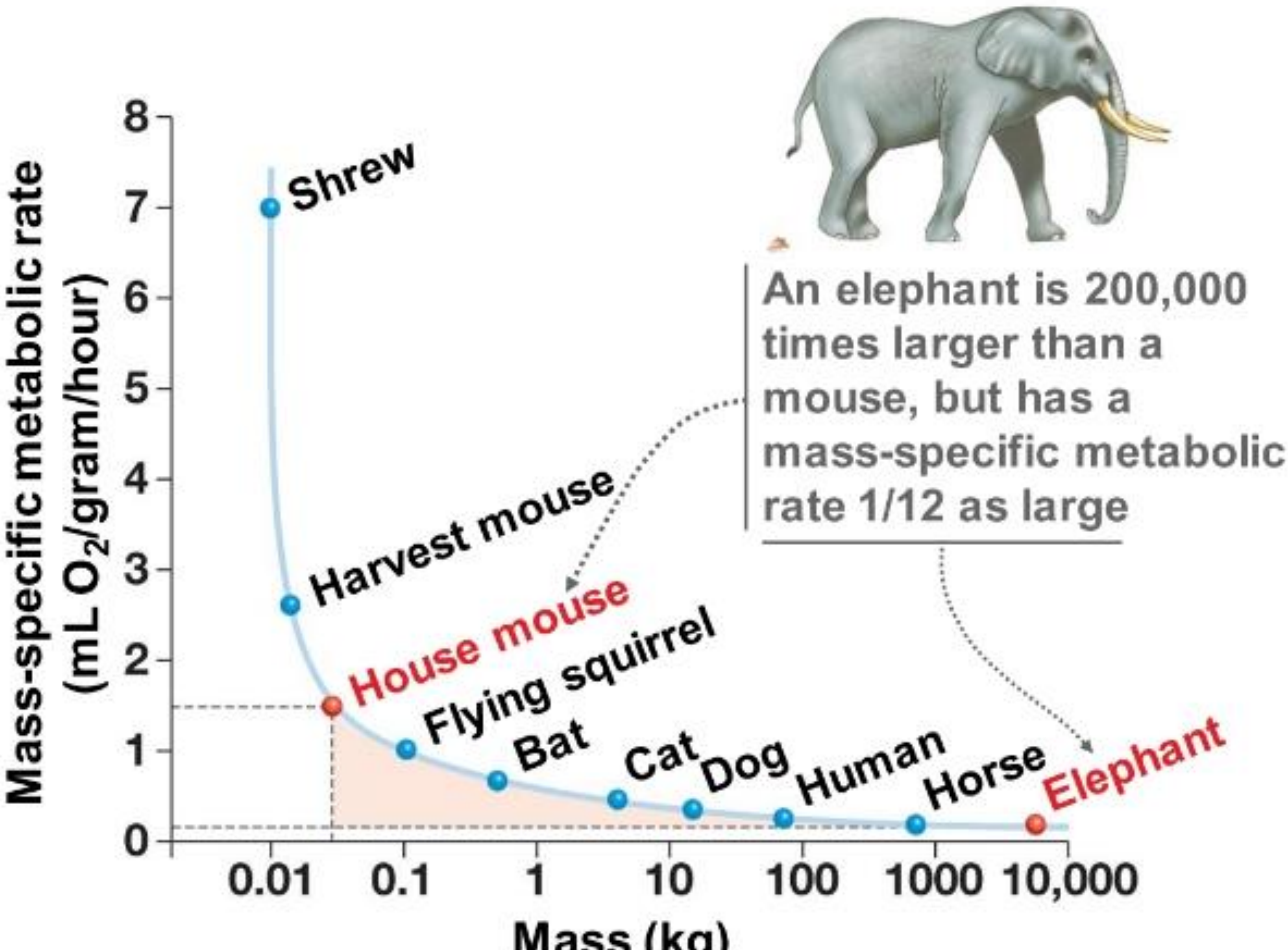
Of Mice and Elephants: A Matter of Scale

Species		
Mass	35 g	4,500,000 g
Metabolic rate	890 mm^3 0_2/g body mass/hr	75 mm^3 0_2/g body mass/hr

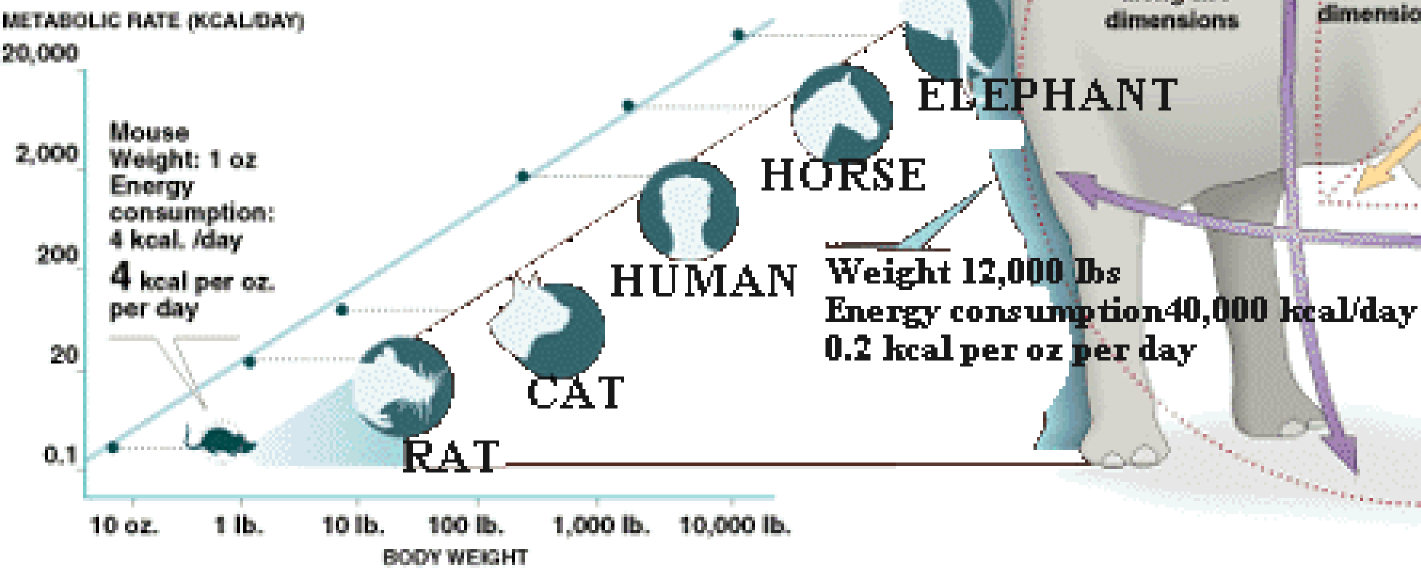

Mass-specific metabolic rate ($mL\ O_2$/gram/hour)
8
7
6
5
4
3
2
1
0
Shrew
Harvest mouse
House mouse
Flying squirrel
Bat
Cat
Dog
Human
Horse
Elephant
An elephant is 200,000 times larger than a mouse, but has a mass-specific metabolic rate 1/12 as large
0.01
0.1
1
10
100
1000
10,000
Mass (kg)

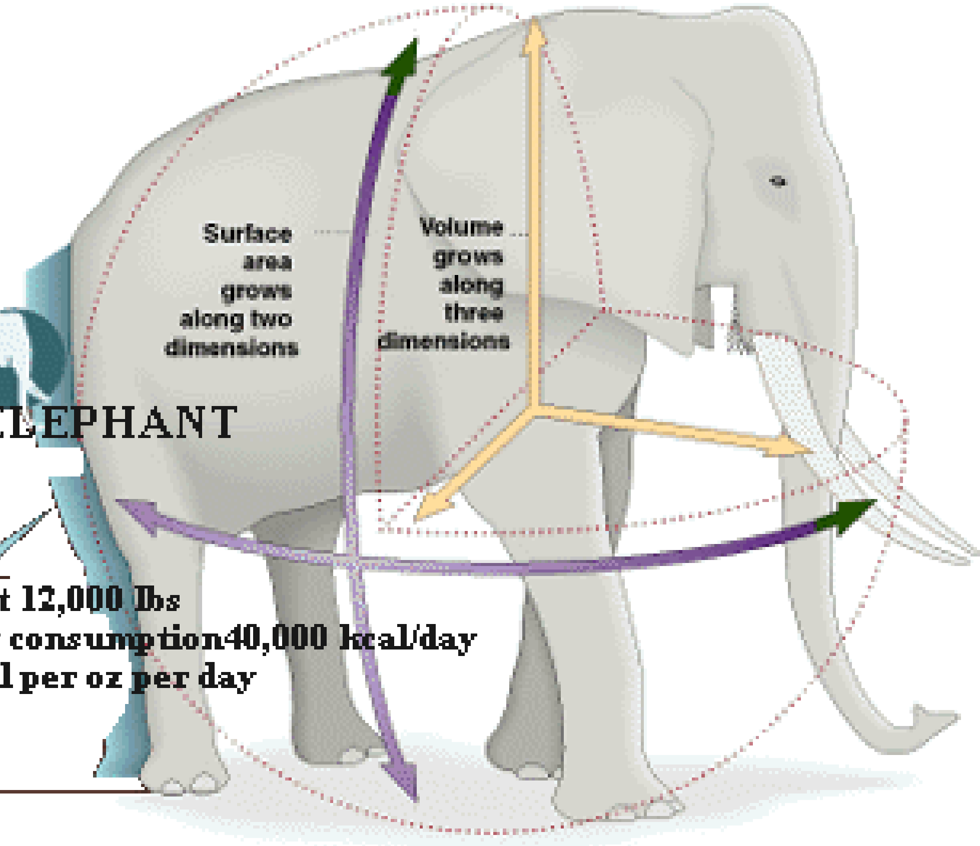
- Kleiber's law implies that the power required to sustain unit mass of an organism, *decreases* with size.
- Thus, to support one gram of a mouse requires three times the power needed for a dog and nine times that for an elephant!
- In this sense it is clearly more efficient to be large.
- It is instructive to compare this with mechanical engines, which do indeed scale isometrically.
- For example, over nearly six orders of magnitude the power output of internal combustion engines scales linearly with mass (b = l) while their revolution rate scales as $M^{1/3}$.

From the Small to the Huge

Three scientists have proposed a novel theory to explain how characteristics like body size and energy consumption differ from species to species along fixed scales. Their theory derives from analysis of the circulatory system.

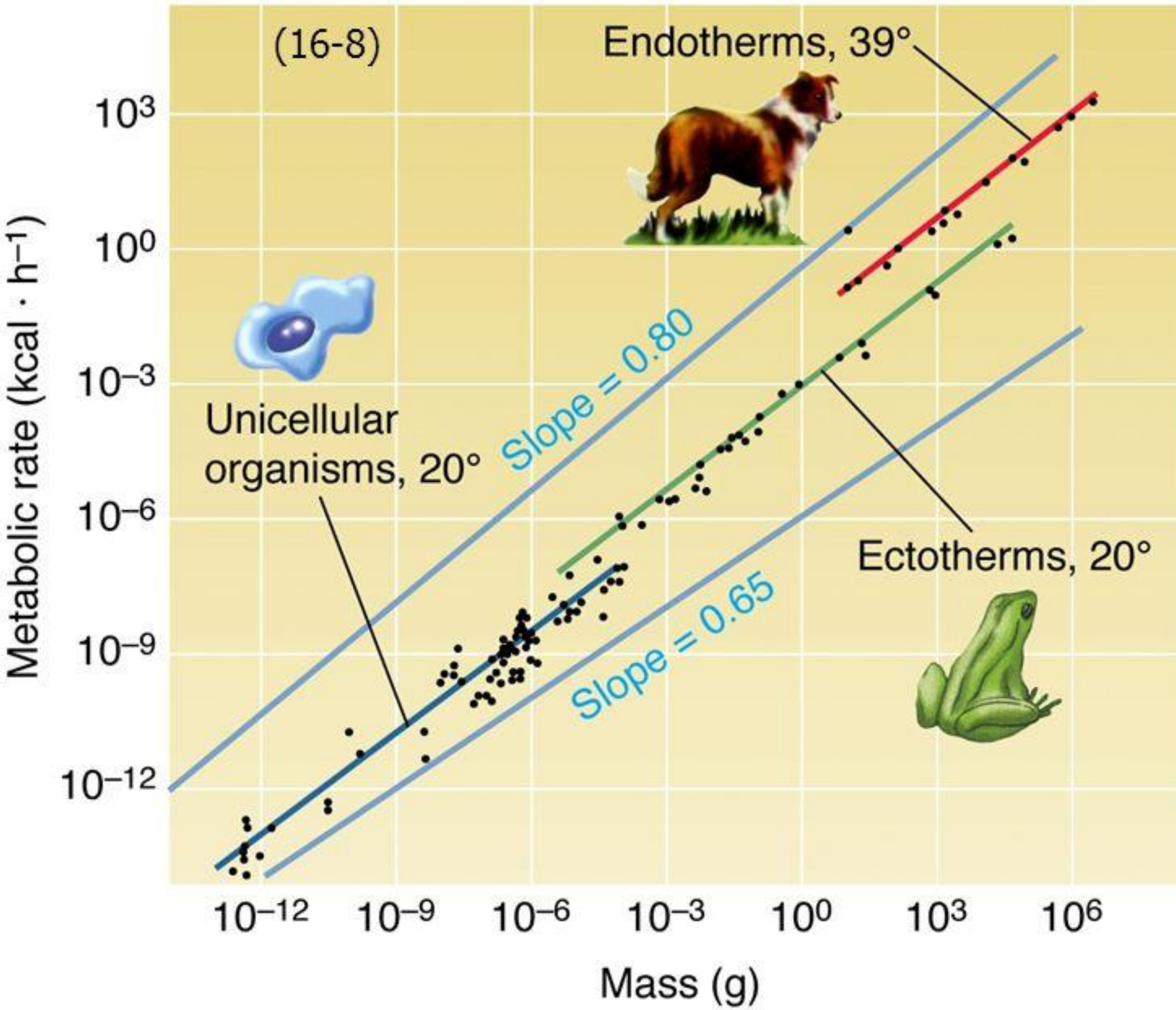
An Example of Scaling: Metabolic Rate





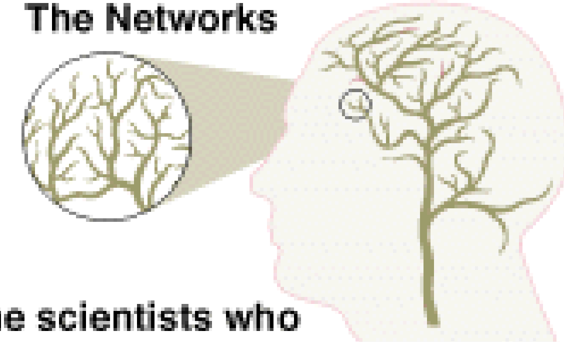
Size and Efficiency

The average elephant weighs 220,000 times as much as the average mouse, but requires only about 10,000 times as much energy in the form of food calories to sustain itself. The reason lies in the mathematical and geometric nature of networks that distribute nutrients and carry away wastes and heat. The bigger the animal, the more efficiently it uses energy.

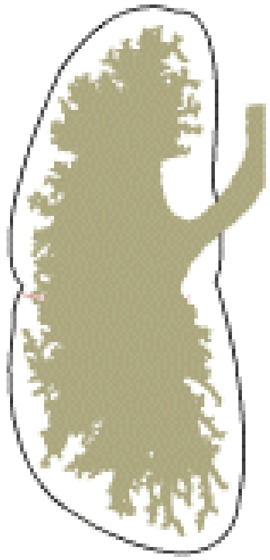

(16-8)
Endotherms, 39°
Unicellular organisms, 20°
Slope = 0.80
Slope = 0.65
Ectotherms, 20°
Metabolic rate (kcal · h⁻¹)
10^3
10^0
10^{-3}
10^{-6}
10^{-9}
10^{-12}
Mass (g)
10^{-12} 10^{-9} 10^{-6} 10^{-3} 10^0 10^3 10^6

The Networks

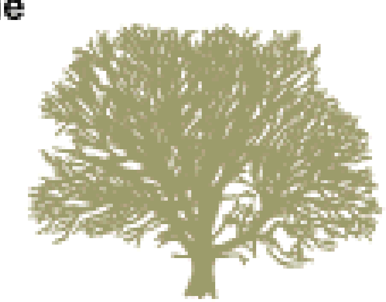
The scientists who developed the scaling theory took clues from naturally occurring networks that carry life-sustaining fluids in organisms in which each small part is a replica of the whole. No matter how big the organism, the ends of these fractal networks are always the same size, since individual cells are of similar size in all organisms.



CIRCULATORY SYSTEM



LUNGS



TREE BRANCHES

- Biological systems obey remarkably simple and systematic empirical scaling laws
  - Relate to how organism's features will change with size over many magnitudes
  - Fundamental quantities: metabolic rate, time scale, size
- All can be expressed with power law relationships with exponents that are simpe multiples of ¼ (e.g. ¼ , ¾ , 3/8)

- Allometric scaling
- Isometric scaling
- Fractal scaling / geometry

Allometric Analysis

- How can one determine the relationship of body processes to body mass?
- The best technique for uncovering the relationship is to plot one variable (for example, food requirements or metabolic rate) against body mass for groups of similar animals (for example, all mammals, or even more specifically, carnivorous mammals).
- Such a plot is called an X-Y regression. Using a statistical technique called least-squares regression gives an equation that best fits the data.

Allometric Analysis

- The equation for scaling of any variable to body mass is $Y = aW^b$,

$$Y = aW^b$$

  - where Y is the variable to be determined,
  - W is the animal body mass (or weight),
  - a and b are empirically derived constants from the regression.

- The exponent b is of particular interest, since it gives the scaling relationship one is looking for in nonlinear relations, such as that of **metabolism** and body mass.
- This mathematical technique is called **allometric analysis**.
- Allometric analysis can be used to predict the capacity or requirements of an unstudied animal, one that might be too rare to collect or too difficult to maintain in captivity for study.

Metabolism

- Using this technique, several interesting relationships between animal structure and function have been uncovered.
- Among the most well studied is the relationship between animal metabolism and body mass, introduced above, in which *M* (metabolism) scales to the 0.75 power of body weight ($M = aW^{0.75}$).
- This means that while the total energy needs per day of a large animal are greater than that of a small animal, the energy requirement *per gram* of animal (mass-specific metabolism) is much greater for a small animal than for a large animal.
- Why should this be the case? For birds and mammals that maintain a constant body temperature by producing heat, the increased mass-specific metabolism of smaller animals was once thought to be a product of their greater heat loss from their proportionately larger surface area-to-volume ratio.
- However, the same mathematical relationship between metabolism and body mass has been found to hold for all animals studied, and even unicellular organisms as well. Therefore, the relationship of metabolism to body size seems to represent a general biological rule, whose basis eludes scientific explanation at this time.

Metabolism

- Allometric analysis has shown that different body processes, involving different organs, scale with different exponents of body mass. For example, blood volume, heart weight, and lung volume all scale almost directly with body mass (exponent = 0.99–1.02).
- Thus, the oxygen delivery system (heart and lungs) is directly proportional to body mass, even though the metabolism, and thus oxygen requirements, of the body scale with body mass to the 0.75 power.
- If the hearts are proportionately the same size for large and small animals, but mass-specific oxygen requirements are higher for small animals, then this implies that hearts in small animals must pump faster to deliver the greater quantity of oxygenated blood.
- Similarly, lung ventilation rates of smaller animals must be higher than those of larger animals. Both predictions have been borne out by measurements that support this conclusion from the allometric analysis.

Body Size and Scaling

Size Matters in Physiology

Living Organisms Come in a Huge Range of Sizes!

- Pleuropneumonia-like organisms (*Mycoplasma*)
  - 0.1 pg (10^{-13} g)
- Rotifers
  - 0.01 μg (10^{-8} g)
- Blue Whale (*Balaenoptera musculus*)
  - 10,000 kg (10^{8} g)
- Giant Redwood Trees (*Sequoia* spp.) = even bigger!
- Living organisms range 10^{21+} in size
- Animals range 10^{16} in size

Size Profoundly Influences Physiology

- Gravity
  - Circulation
  - Movement and Locomotion
- Surface Area/Volume Ratio
  - Respiration
  - Digestion
  - Water Balance
  - Thermoregulation

Scaling

- Changes in body proportion often accompany changes in body size
  - both ontogenic and phylogenic
  - e.g. changes in proportions from human fetus to adult

Allometry

1. The study of differential growth

2. The study of biological scaling

Allometric Equation

- $Y = aX^b$ (a power function)
  - Y = body part being measured in relationship to the size of the organism
  - X = measure of size used for basis of comparison
    - usually a measure of whole body size
  - a = initial growth index
    - size of Y when X = 1
  - b = scaling exponent
    - proportional change in Y per unit X

Allometry is defined as the change of proportions with an increase in the size of a single species or between adults of related groups (Li, 2000). Allometric relations only exist when there is similarity of structure and function between biological units of different size. If completely different mechanisms are involved (e.g., the locomotion of bacteria compared to horses), then no allometric relationship would be expected.

There appear to be universal biological principles at work in scaling relationships, although the natures of these principles have not yet been fully explored. Allometric relationships among very divergent species seem to be scaled with body mass to some simple multiples of one-quarter power ($m^{1/4}$). Thus (Brown et al., 2000),

The leaf area of trees $\propto m^{3/4}$

The radii of mammalian aortas and radii of tree trunks $\propto m^{3/8}$

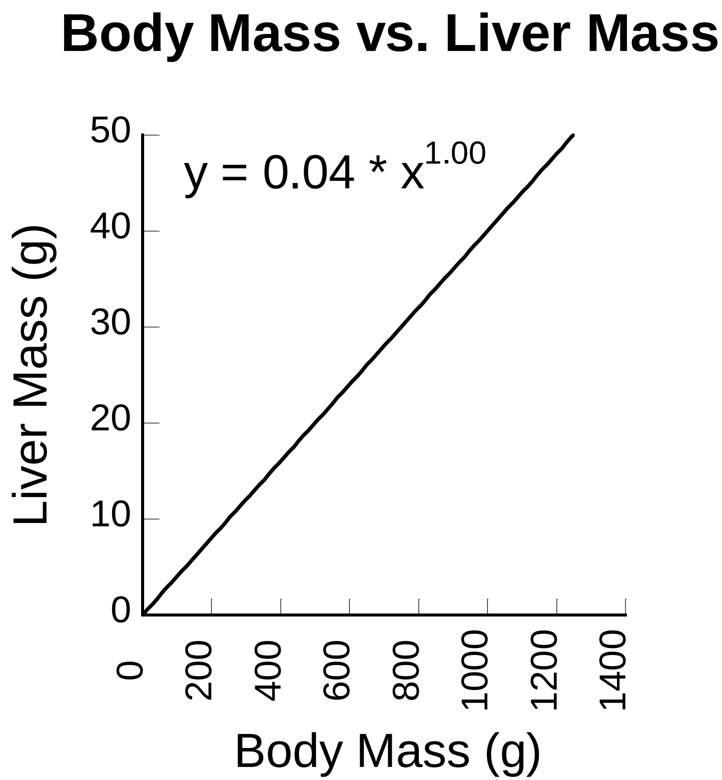
The circulation time of mammal blood, and of tree sap, and the cycle time of respiratory, cardiac, gestation, postembryonic development, life span $\propto m^{1/4}$

The biological rates, including mammalian heart rate and respiration rate $\propto m^{-1/4}$

Natural selection seems to have led to an economy of the design of structures and functions so that they just meet maximum demands. Any greater capacity would be biologically uneconomical (Brown et al., 2000). If evolution results in allometric relationships among BU, then it is only because the benefit-to-cost ratio of the function in question has been optimized.

The Scaling Exponent (b) Defines the Type of Scaling Relationship

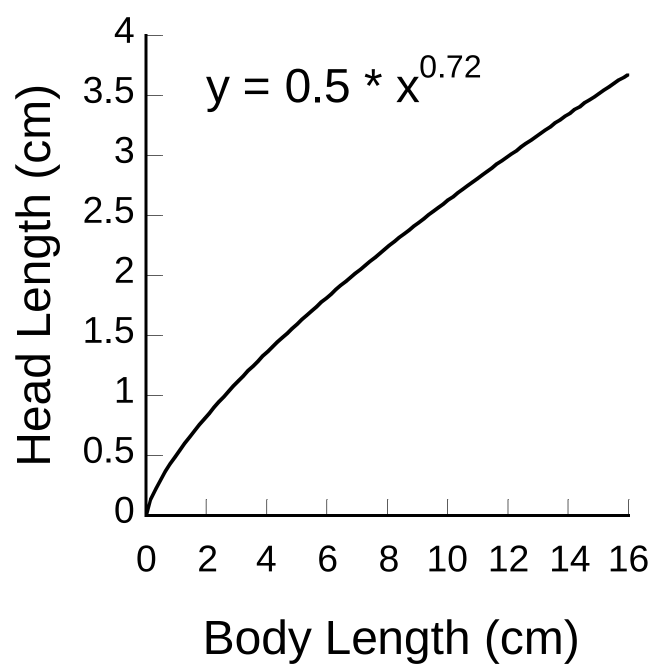
- If b = 1, there is no differential growth
  - the relative size of Y to X is the same at all values of X
  - *isometry* (geometric similarity)



The Scaling Exponent (b) Defines the Type of Scaling Relationship

- If b < 1, Y increases at a slower rate than X
  - as X increases, Y becomes relatively smaller
  - *negative allometry*

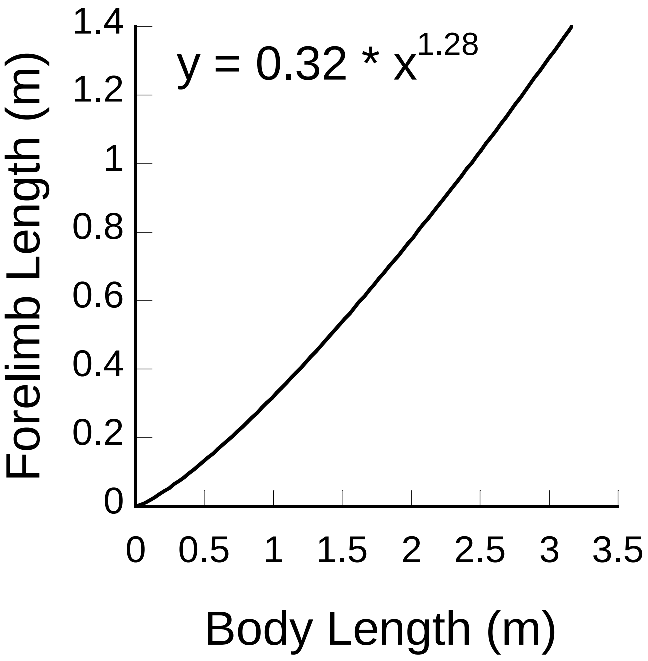
Head Length vs. Body Length



The Scaling Exponent (b) Defines the Type of Scaling Relationship

- If b > 1, Y increases at a faster rate than X
  - as X increases, Y becomes relatively larger
  - *positive allometry*

Forelimb Length vs. Body Length



Allometry

- Allometric Data Can Also Be Expressed as Linear Functions of Log-Transformed Data

$$Y = aX^b$$

$$\log Y = \log a + b \log X$$

  - the slope of the line (b) indicates the type of scaling relationship

Types of Scaling Relationships

- If $b = 1$, *isometry* (geometric similarity)
- If $b < 1$, *negative allometry*
- If $b > 1$, *positive allometry*

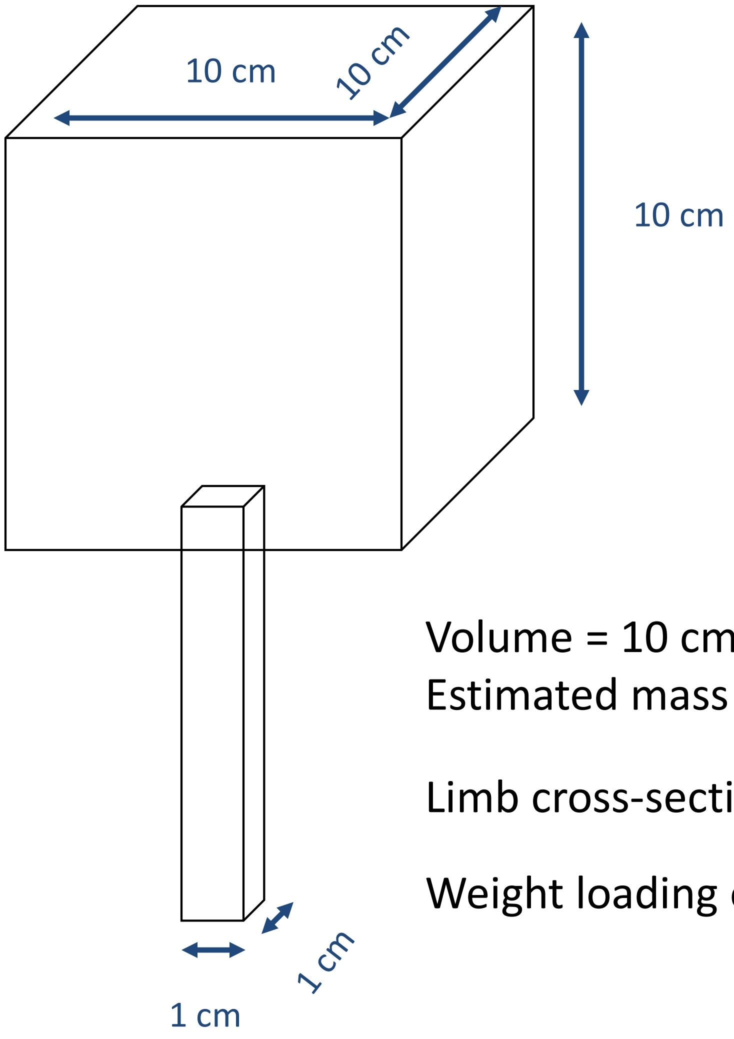
- The Catch:
  - Above is true only when we compare *like dimensions* (e.g. length to length, mass to mass).

Isometry for Different Dimensions

- Example: Head Length vs. Body Length
  - Linear dimension (m^1) vs. linear dimension (m^1)
  - Isometry: m^1/m^1, $b = 1/1 = 1.0$
- Example: Head Length vs. Body Mass
  - Linear Dimension (m^1) vs. Cubic Dimension (m^3)
  - Isometry: m^1/m^3, $b = 1/3 = 0.33$
- Example: Surface Area vs. Body Mass
  - Square Dimension (m^2) vs. Cubic Dimension (m^3)
  - Isometry: m^2/m^3, $b = 2/3 = 0.67$

Differential Scaling is Common

Example: Support of Weight by the Limbs



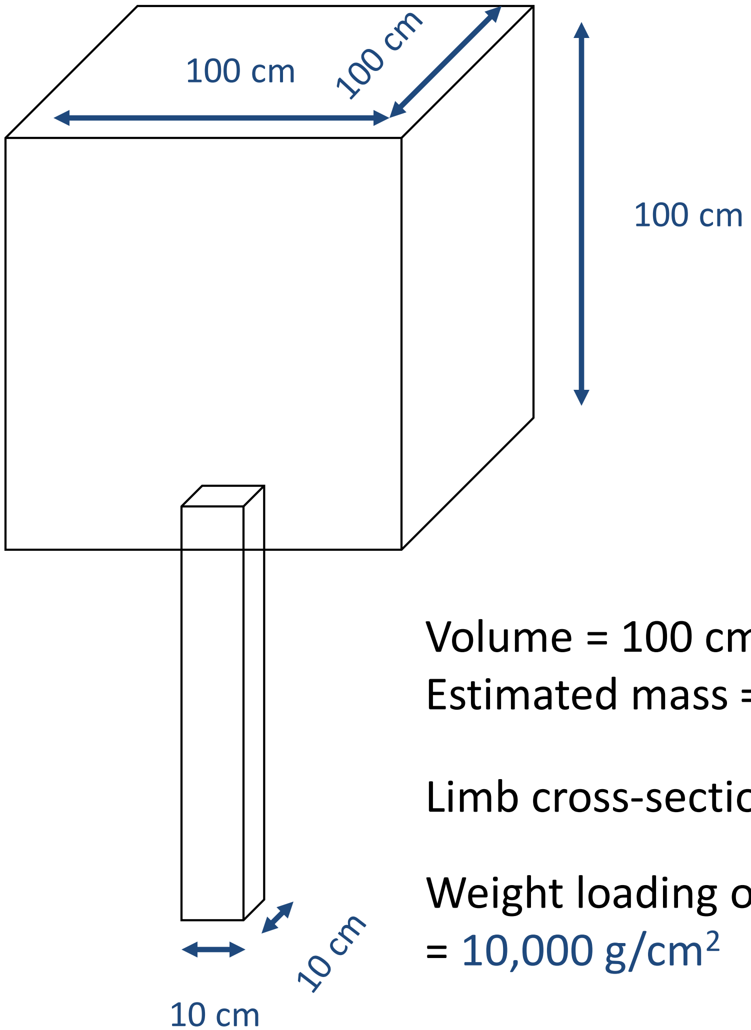
Hypothetical one-legged cuboid animal…

Volume = 10 cm X 10 cm X 10 cm = 1000 cm^3
Estimated mass = 1000 g

Limb cross-sectional area = 1 cm X 1 cm = 1 cm^2

Weight loading on limb = 1000g / 1 cm^2

Example: Support of Weight by the Limbs



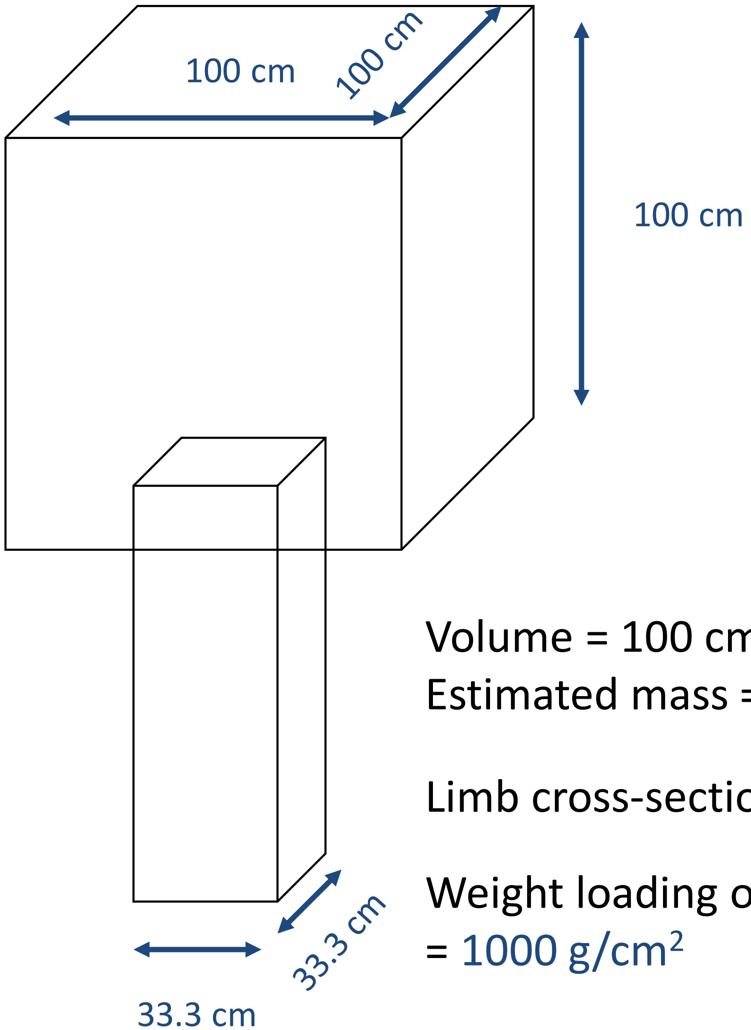
Increase all linear dimensions tenfold…

Volume = 100 cm X 100 cm X 100 cm = 1,000,000 cm^3
Estimated mass = 1,000,000 g

Limb cross-sectional area = 10 cm X 10 cm = 100 cm^2

Weight loading on limb = 1,000,000g / 100 cm^2
= 10,000 g/cm^2

Example: Support of Weight by the Limbs



Need a proportionately thicker limb bone to support the increased mass

Volume = 100 cm X 100 cm X 100 cm = 1,000,000 cm^3
Estimated mass = 1,000,000 g

Limb cross-sectional area = 33.3 cm X 33.3 cm = 1000 cm^2

Weight loading on limb = 1,000,000g / 1000 cm^2
= 1000 g/cm^2

Scaling of Skeleton Mass

- Expect b = 1 for isometry
- However, because of increased weight loading, may expect b > 1
- Typical scaling: b = 1.12
  - skeleton becomes relatively more massive with increased body size
  - compensates for increased weight loading

Scaling of Skeleton Mass

- Scaling of 1.12 does not fully compensate for weight loading with increased mass:
  - Length α Mass$^{1/3}$
  - Skeletal Mass α Cross-Sectional Area * Length
  - Cross-Sectional Area α Body Mass
  - Skeletal Mass α Body Mass * Length
  - Skeletal Mass α Body Mass * Body Mass$^{1/3}$
  - Skeletal Mass$^{4/3}$
  - Skeletal Mass$^{1.33}$ expected for isometry of weight loading

Scaling of Skeleton Mass

- Why not scale at 1.33?
  - Mass of skeleton contributes to mass of animal
  - increased skeletal mass limits movement and ability of skeleton to absorb physical shocks
    - the thicker the skeleton, the greater the chance of fracture

Scaling of Skeleton Mass

- How can animals increase in size without becoming “all skeleton”?
  - Animals accept lower safety factor
    - generally, skeleton is about 10x as strong as needed to support the animal’s weight
  - Decreased locomotor performance
  - Alter morphology to reduce stress on the skeleton
  - Alter chemical composition of skeleton
    - e.g. human limb bones - relatively more slender in adults

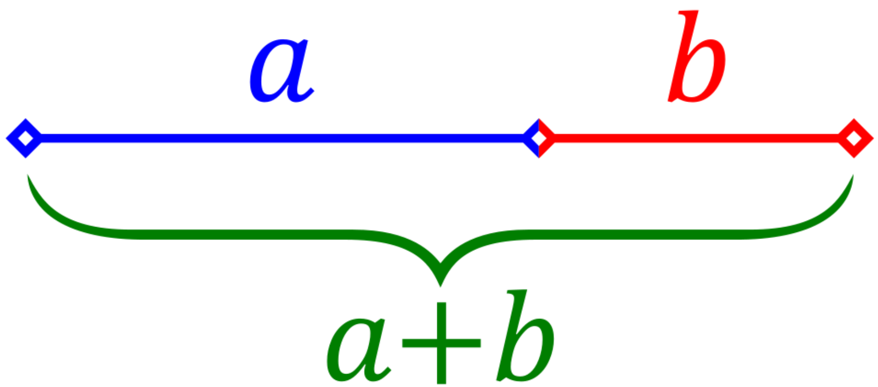
How Does Differential Scaling Arise?

- Differences in size among animals are due primarily to differences in cell number
- During embryonic development, cells differentiate and give rise to *germinal centers*
  - each part of an organism arises from one or more germinal centers

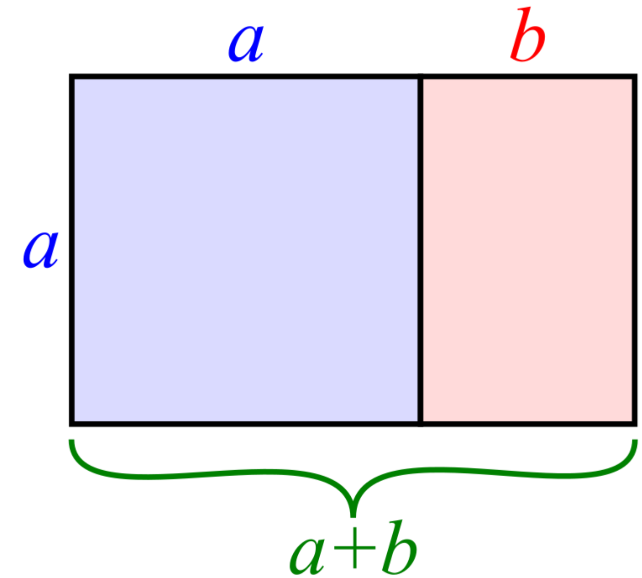
How Does Differential Scaling Arise?

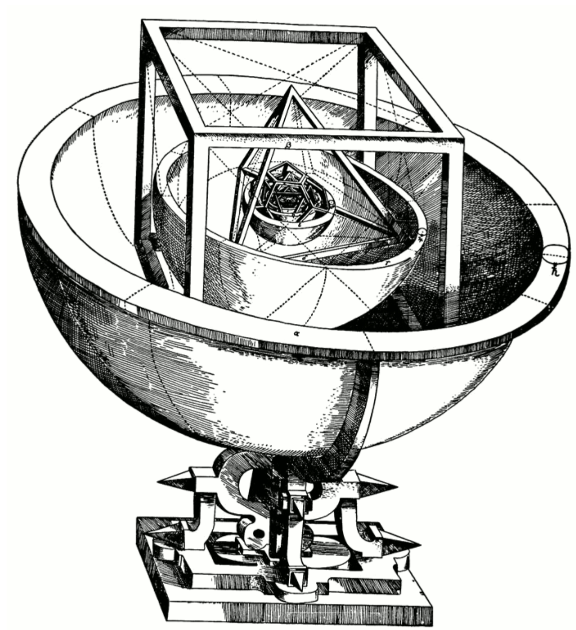
- Rate at which a part grows depends on number of germinal centers and rate of cell division
- For $Y = aX^b$
  - $a \propto$ number of germinal centers contributing to a particular body region
  - $b \propto$ ratio of the frequencies of cell division between Y and X

Golden Ratio

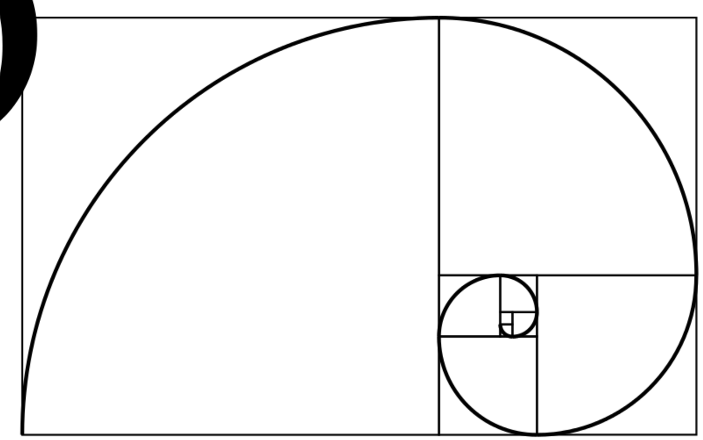


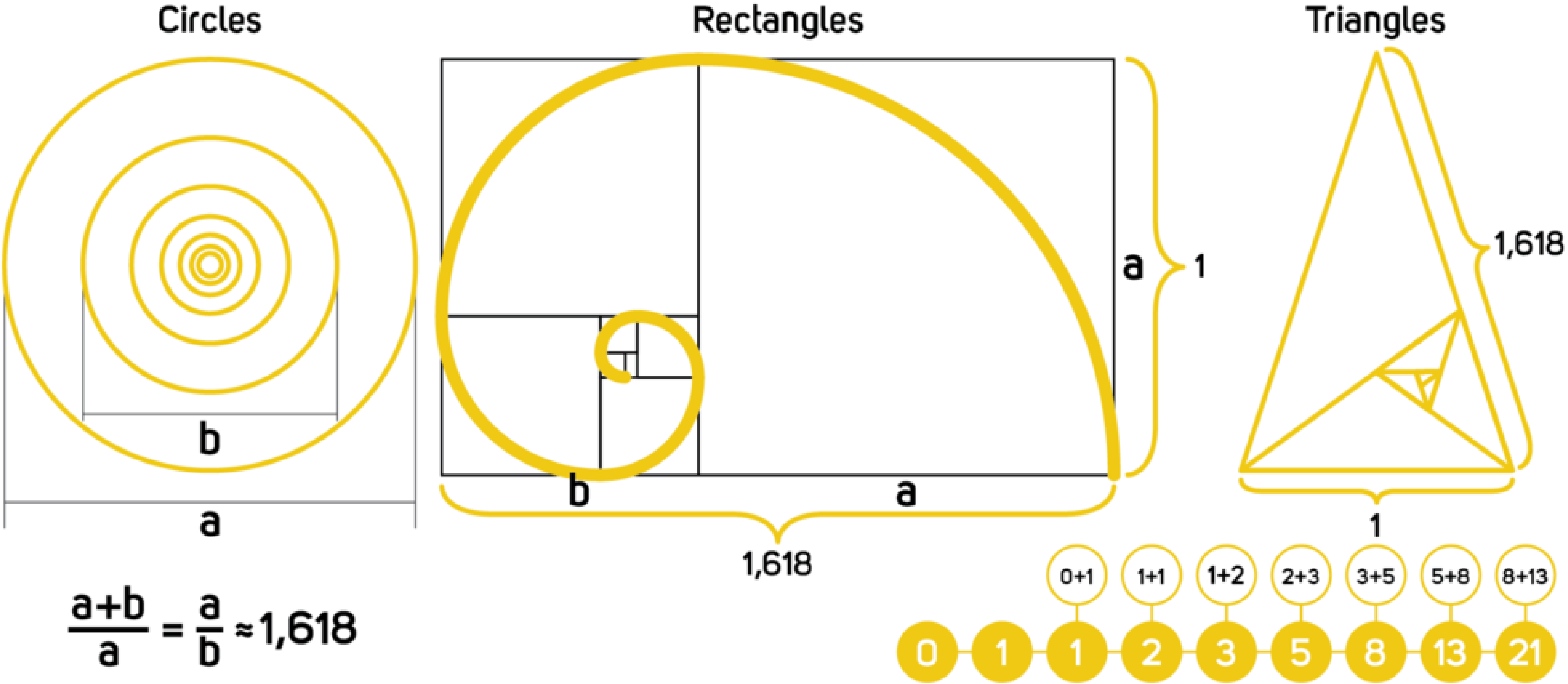
$a+b$ is to a as a is to b





Φφ




Circles
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Triangles
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$\frac{a+b}{a} = \frac{a}{b} \approx 1{,}618$
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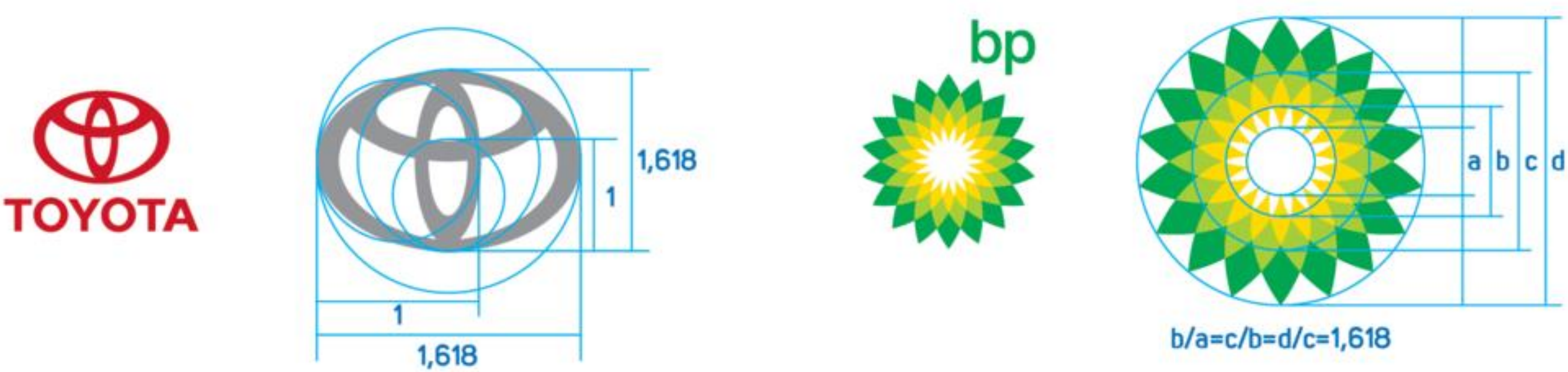
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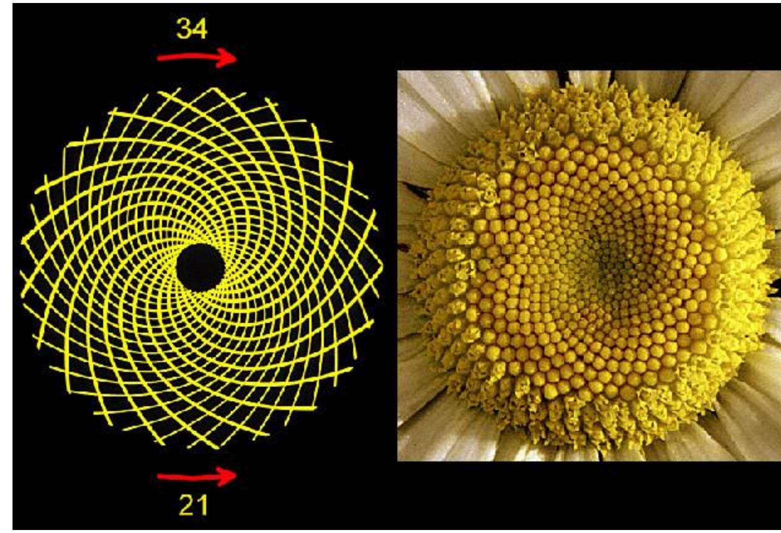
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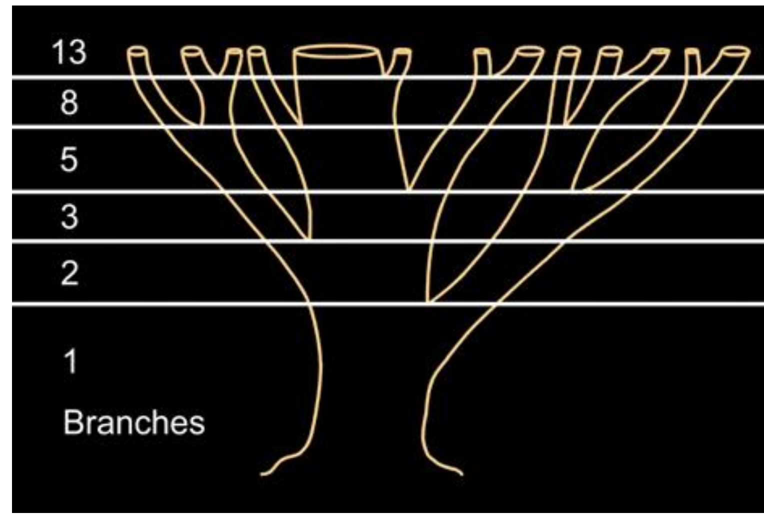
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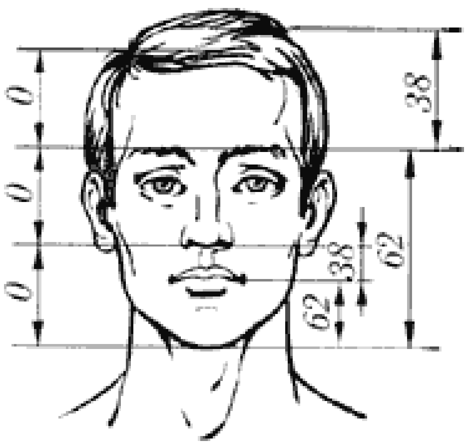
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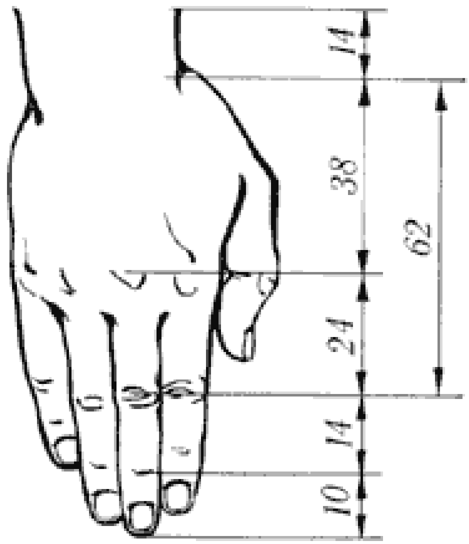
14
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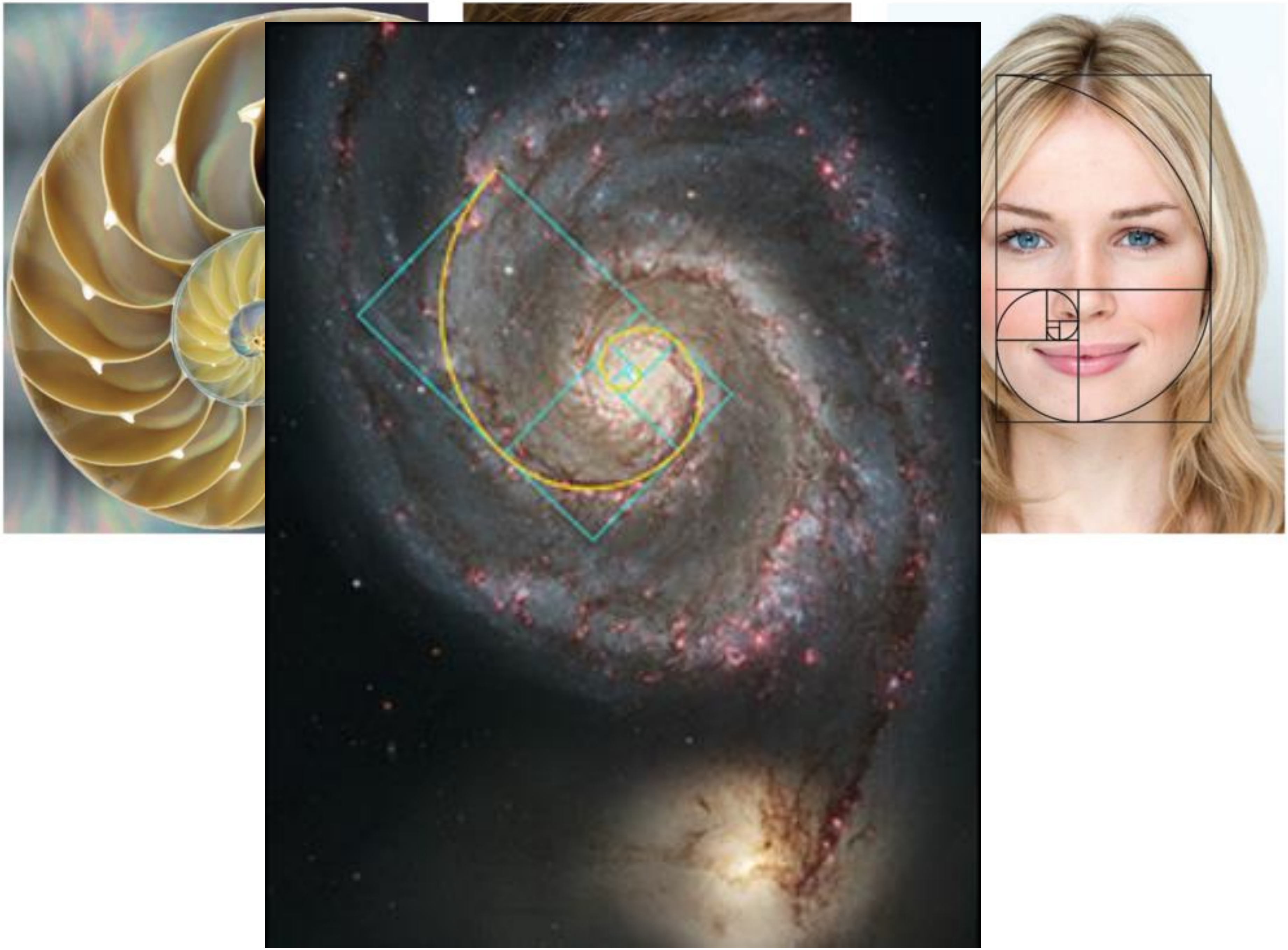
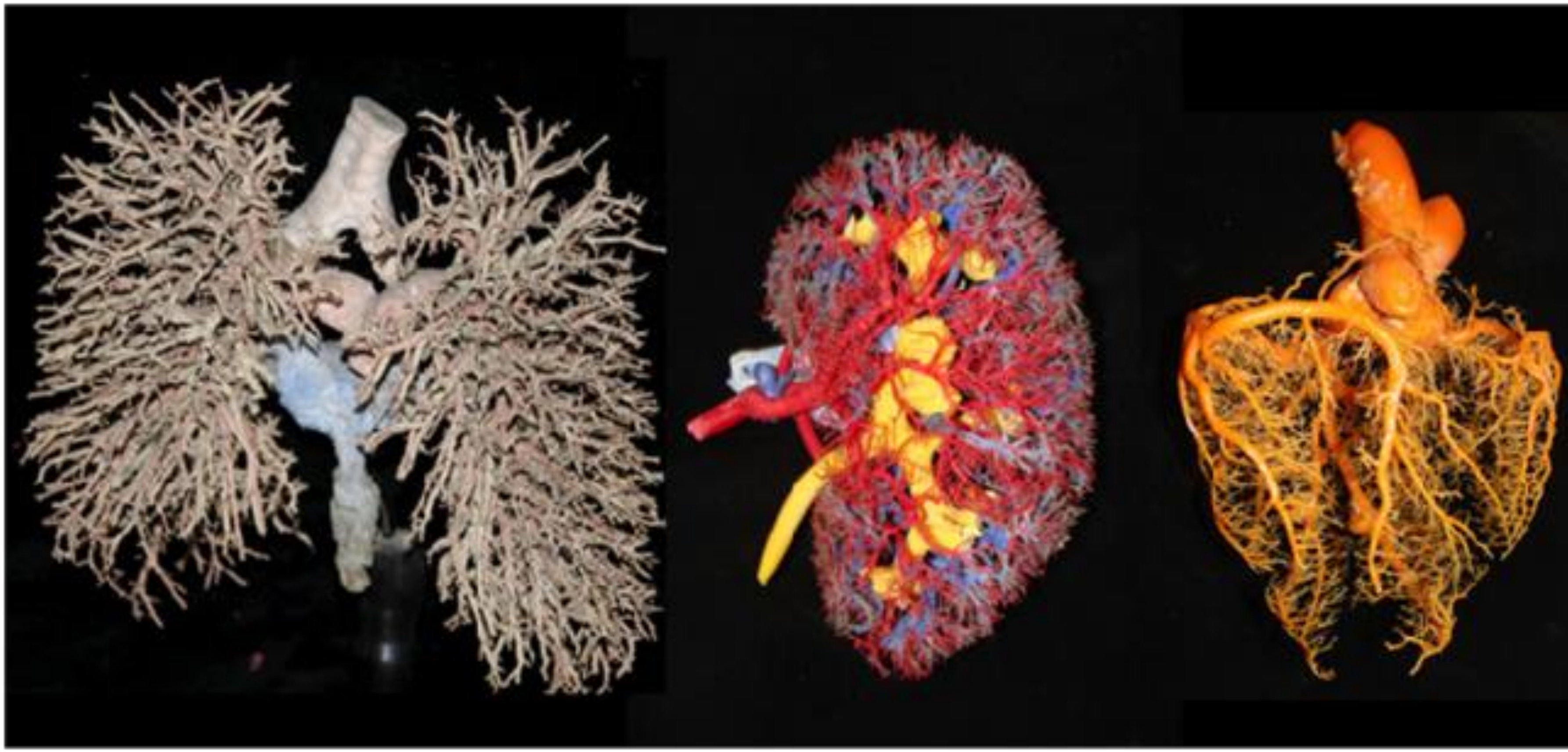
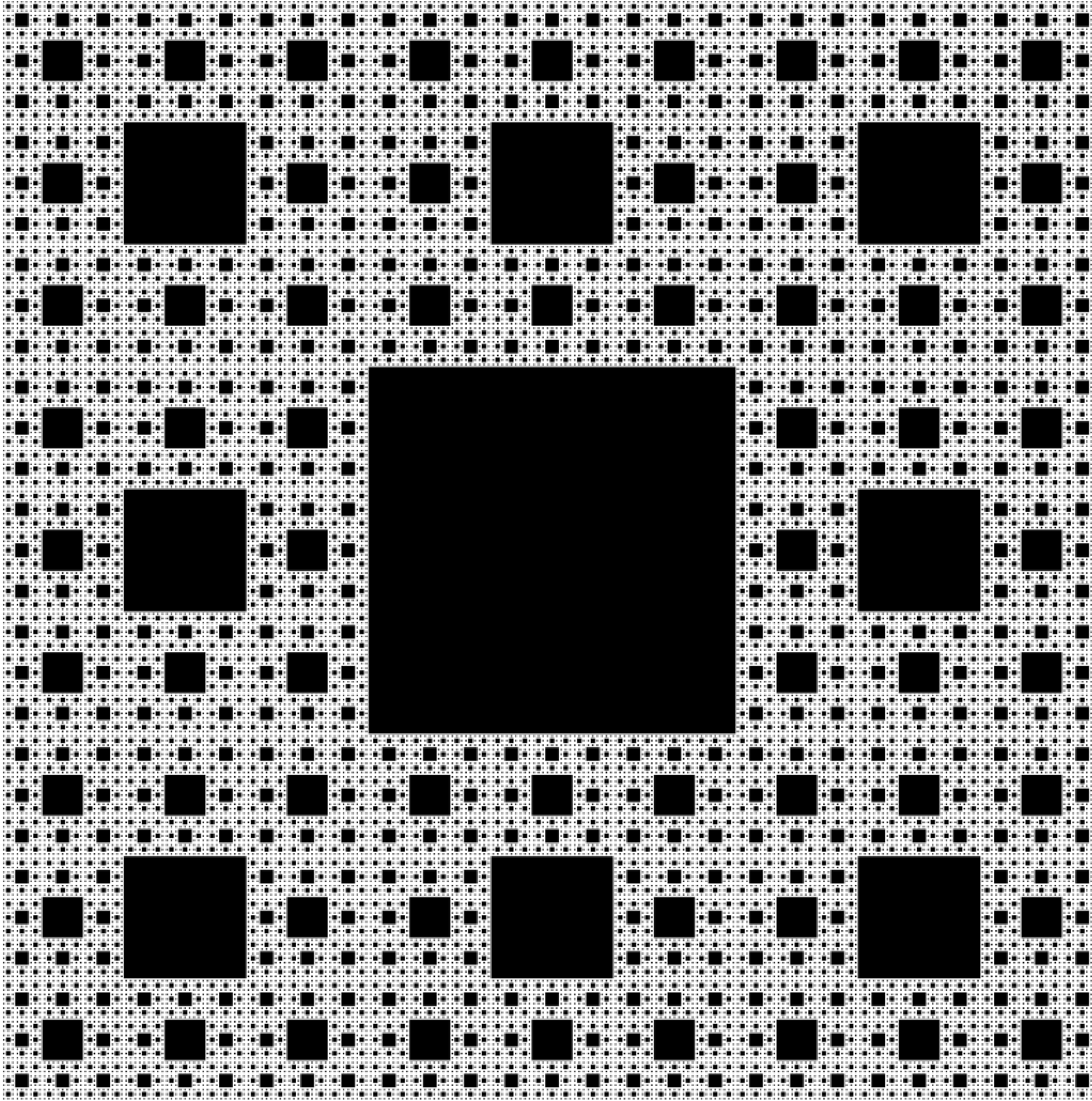


- Fractals exhibit similar patterns at increasingly small scales, also known as **expanding symmetry** or **unfolding symmetry**; If this replication is exactly the same at every scale





Key Scaling Questions

- Finding the characteristic scale of spatial heterogeneity or pattern (so-called "scaling techniques");
- Defining what a "patch" is, and devising aggregate descriptions of collections of patches (their sizes, diversity, and such), to more complex summaries - Connectedness, fractal geometry, and percolating networks;
- How these aspects of pattern are interrelated in landscapes, and how they vary according to physiography and landscape history.

What factors drive pattern?

- The physical template of environmental constraints -- soils, topography, climate;
- Biotic processes -- establishment and growth, dispersal, and mortality;
- Disturbance regimes -- fires, floods, storms, and human land use.

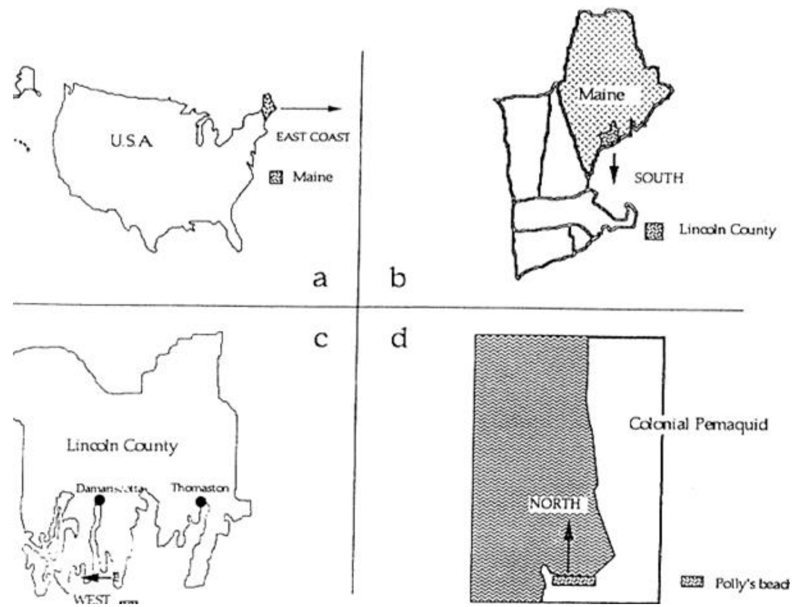
Scale - Environmental Imperative

- 1980s & 1990s – importance of scale in ecology widely published and discussed

- Pressing environmental issues over large areas brought role of scale to forefront:
  - Acid rain
  - Global climate change
  - Habitat fragmentation
  - Conservation biology
  - Disturbance regimes
  - Fire and bugs!

Scale – Lessons Learned

- "Lessons learned" from scale studies (esp. last 20 years):
  - No single scale is appropriate for study of all ecological problems
  - A challenge to understand how data collected at finer scales (e.g., small plots) relates to larger areas.
  - Can these results be extrapolated? CAUTION the scaling up/down problem



Scale – Lessons Learned

- "Lessons learned"…con't:
  - Changing the quadrat size (grain) or the extent of the area often yields a different numerical result or pattern
  - Disparate results from different studies of the same variable/organism might be due to differences in scale

Scale – Lessons Learned

- "Lessons learned" …con't:
  - Spatial and temporal scales important to humans are not necessarily the scales relevant to other organisms or processes
  - **Biological interactions most likely occur at multiple scales (biocomplexity idea)**