Unit 9: Biological Scaling

9.1 Intro: What ‘scaling’ means

9.2 Examples of Scaling, optional log-log explanation

9.3 Zipf’s Law

9.4 Metabolic Scaling

9.5 Kleiber’s Law, WBE Model, Summary

Scaling: How do properties of systems (organisms, economies, cities) change or remain the same as their size is varied?

Scaling:

FIG. 1 Archeologist's hammer used for scale (www.sciencedirect.com)

Scaling:

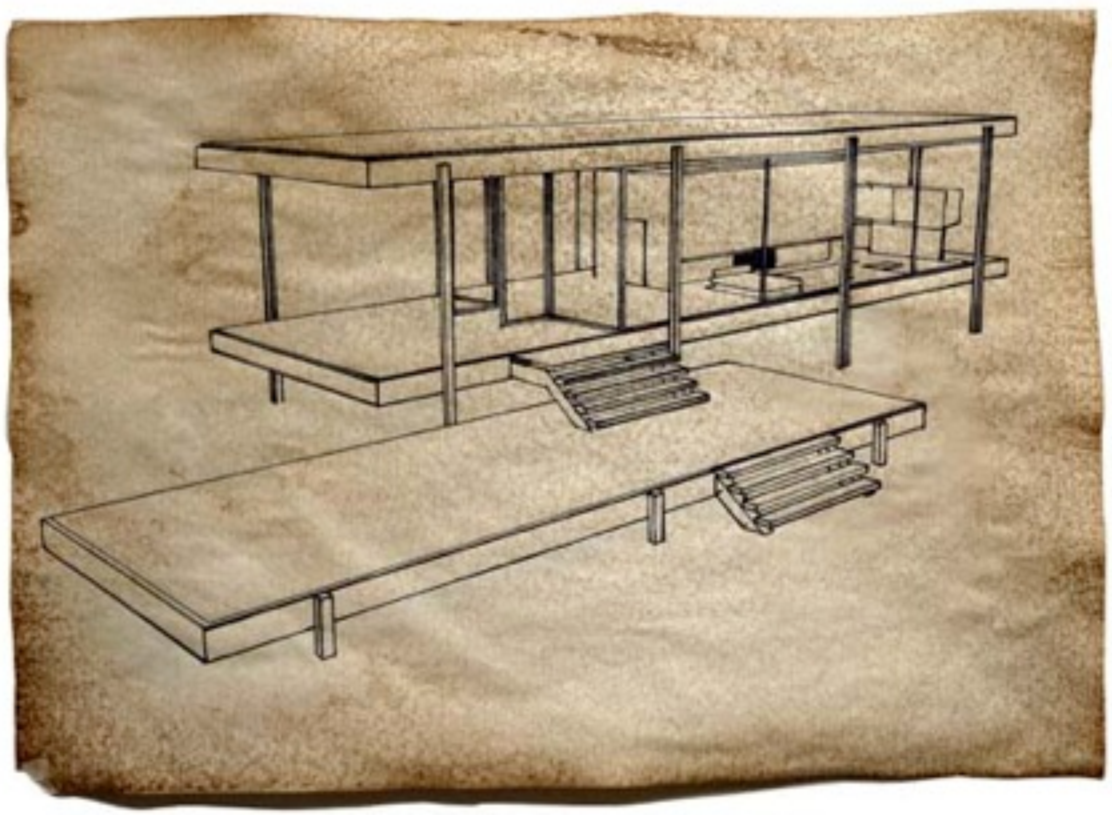

FIG. 2 Scale Drawing
(www.eamonokane.com)

FIG. 3 Scale model 1 : 200
(www.willstrange.net)

Some definitions:

Order of magnitude: a fixed ratio, usually 10, used in scaling where each class is ten times the amount that proceeded it, i.e. 10, 100, 1000 etc.

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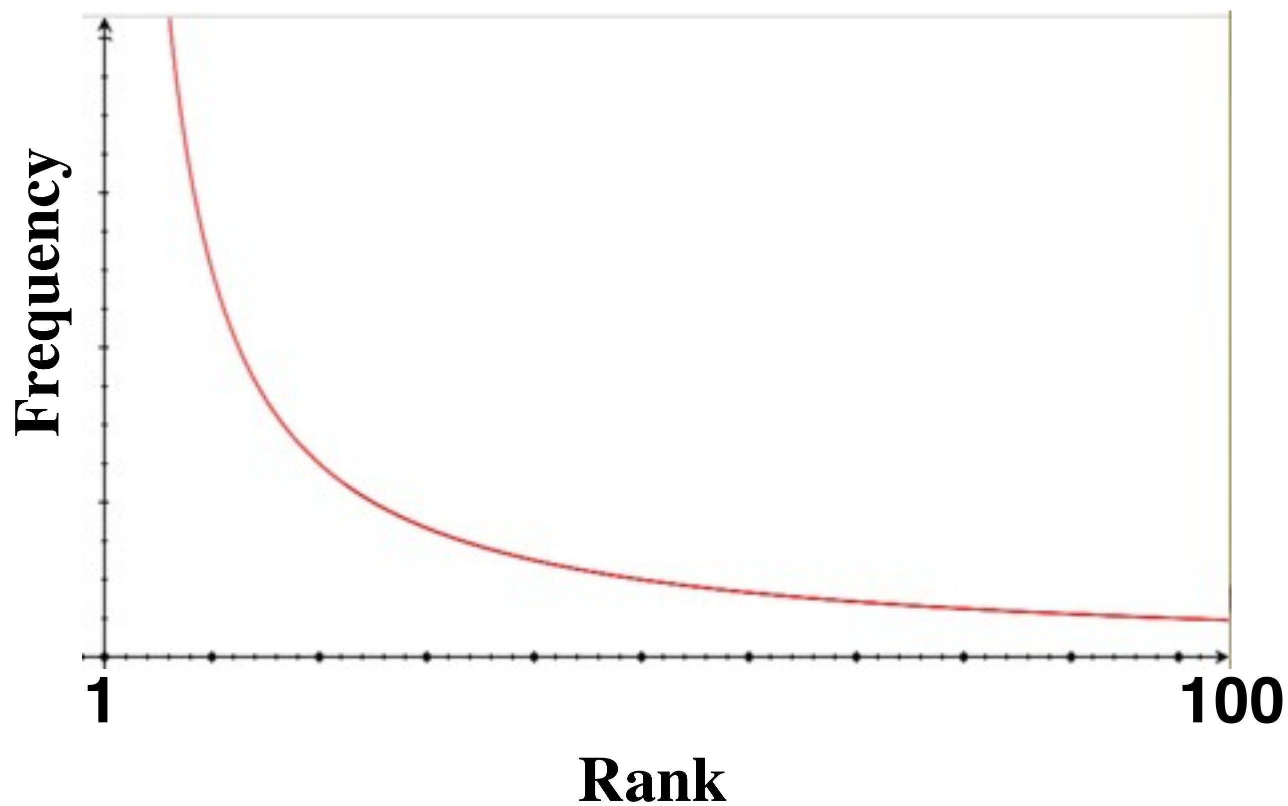
$\propto$ **:** a mathematical symbol meaning proportional to or ‘scales with’ such that one side of an equation is equal to a fixed ratio of the other,

i.e. y = 2x could be written as $y \propto x$

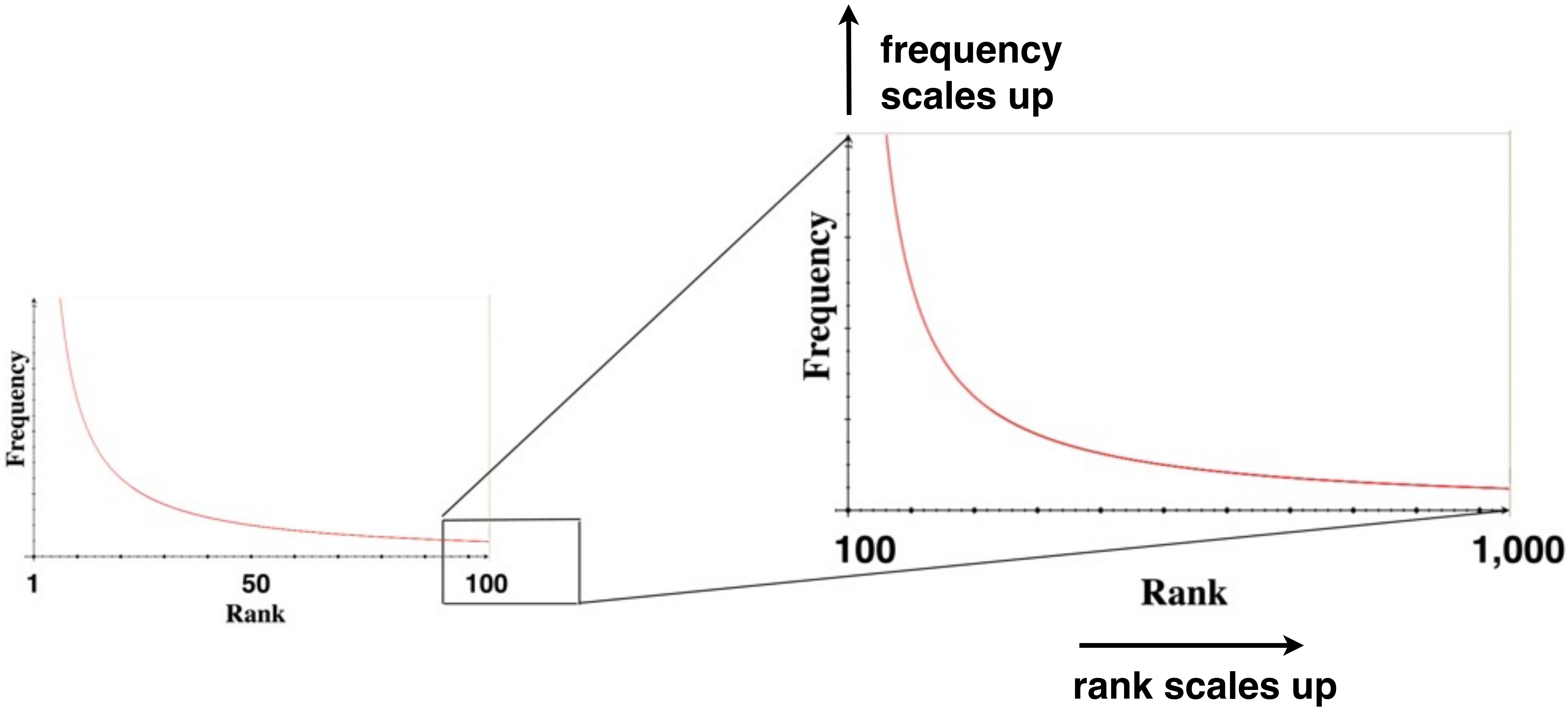
Power laws:

y = c x^z where z is an integer or fraction and c is a constant.

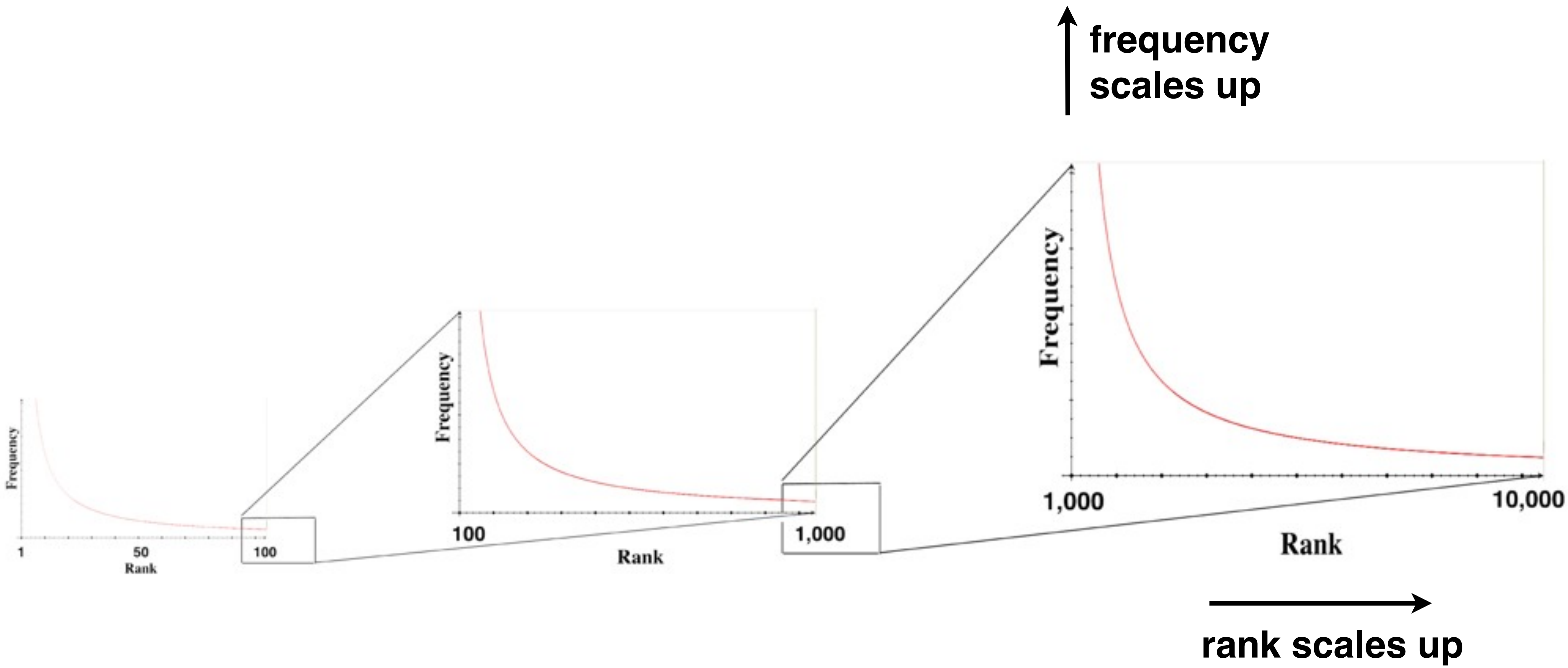


$$y \propto \frac{1}{x}$$

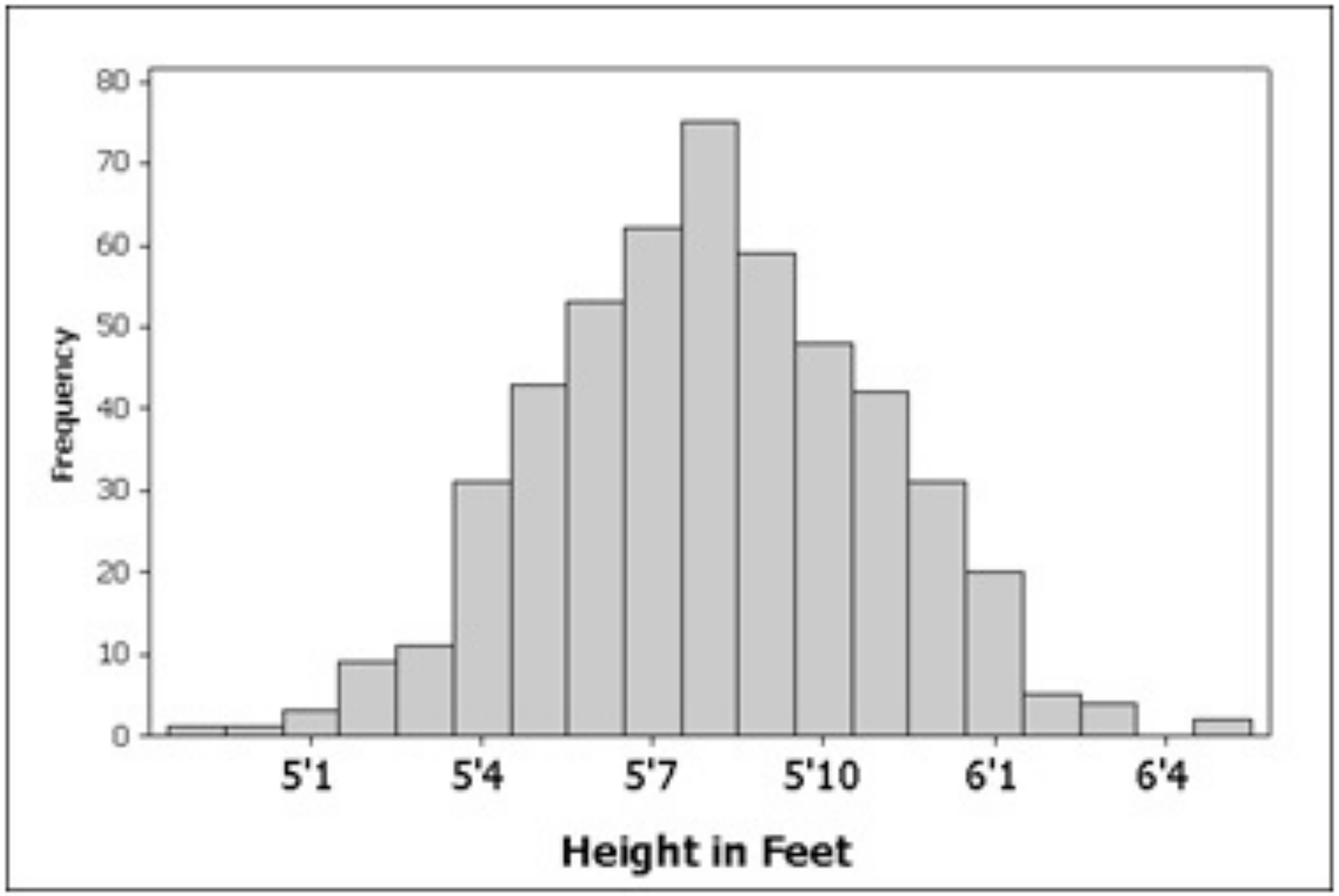
Scale free distribution:



Scale free distribution:

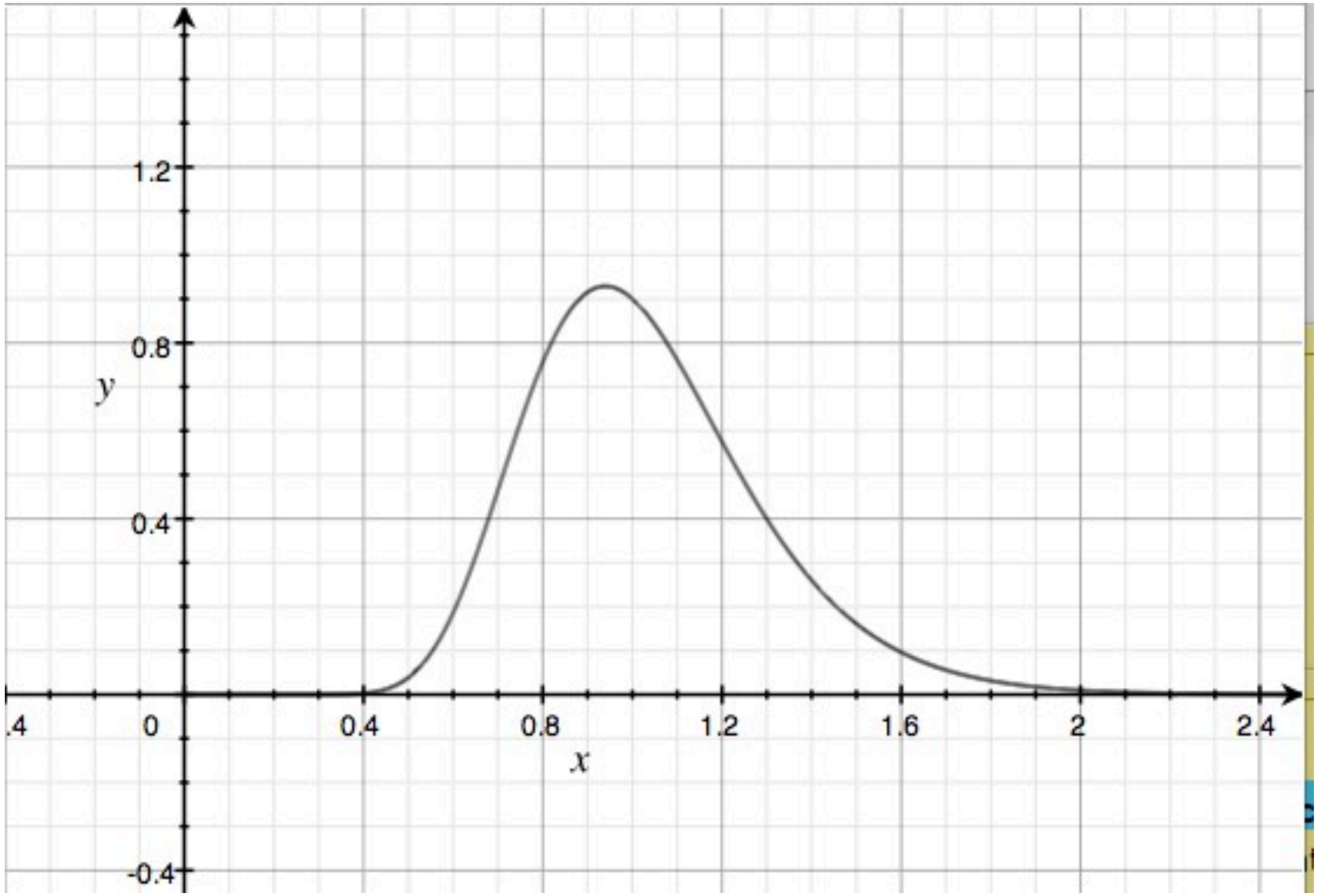


Scale Free distributions versus Bell Curves:



http://www.measuringusability.com
/images/height-normal.png

Normal Distributions:



For this unit, we will be using normal distributions very generally and it is not necessary to know the formula for this distribution.

1. relative small number of high frequency events.

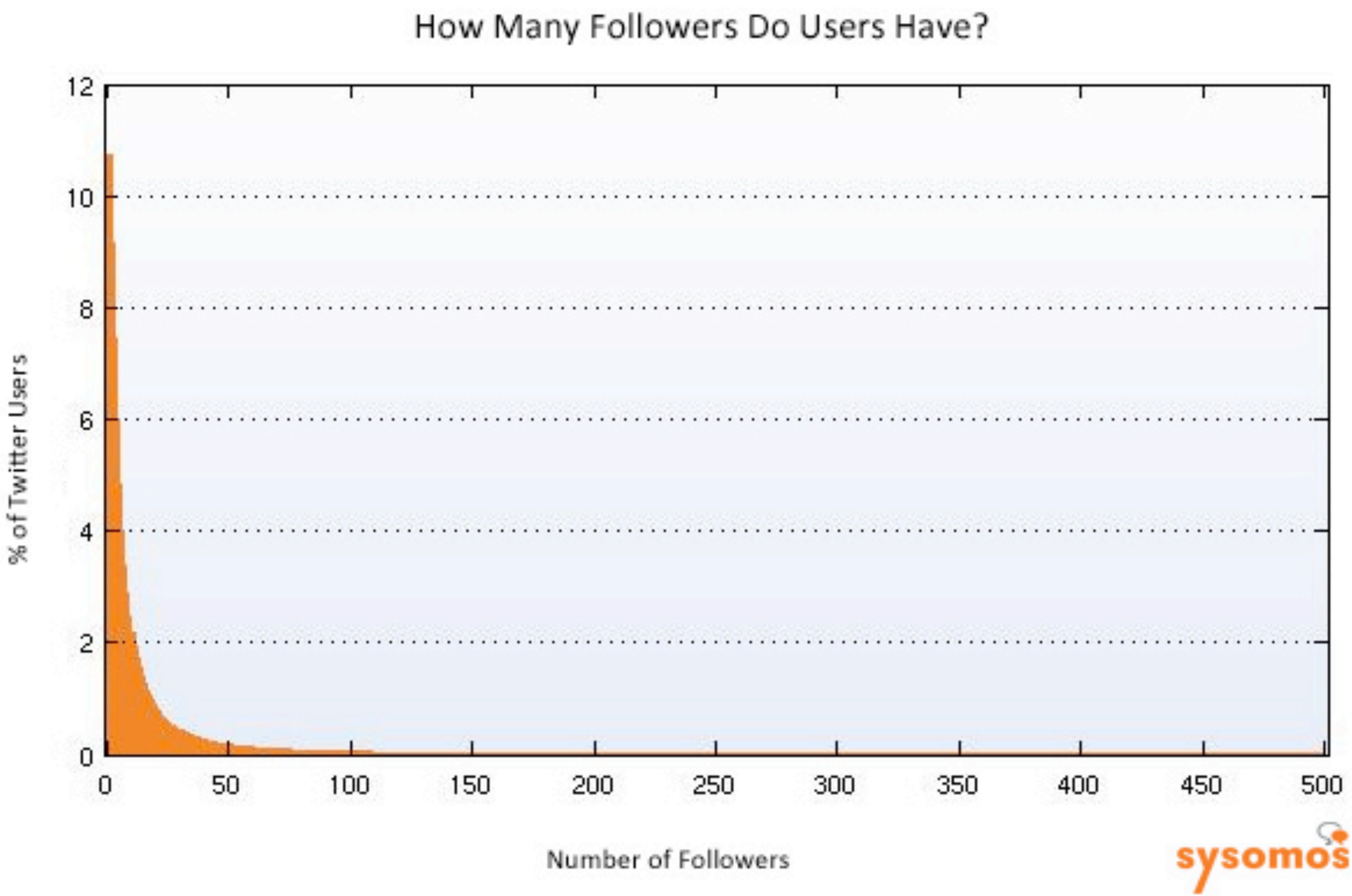
2. Events with frequencies over a very large range of different values.

3. self-similarity.

4. scale-free distributions are characterized mathematically as power laws.

Examples of Power Laws:

Twitter users and followers



Examples of Power Laws:

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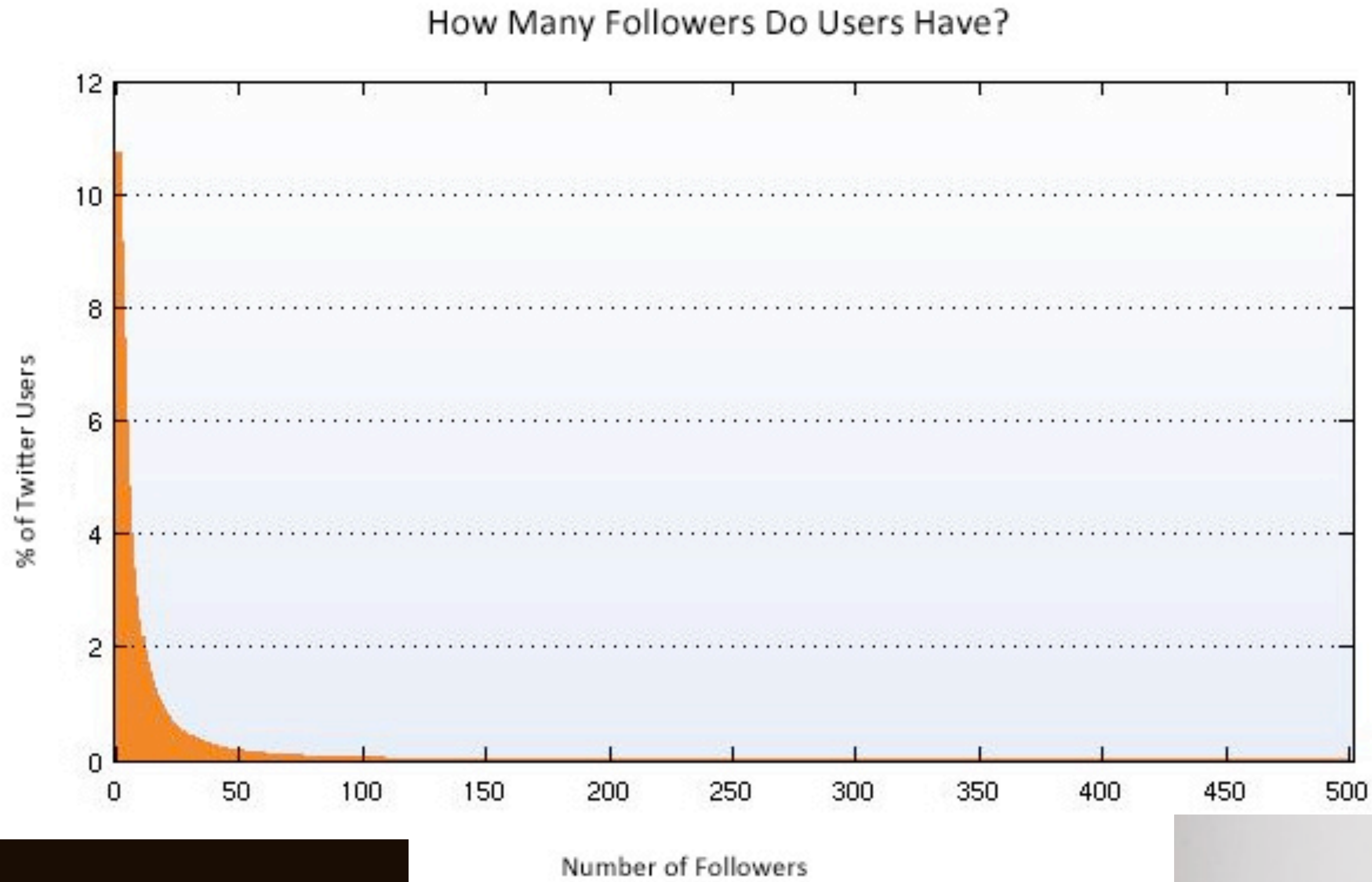


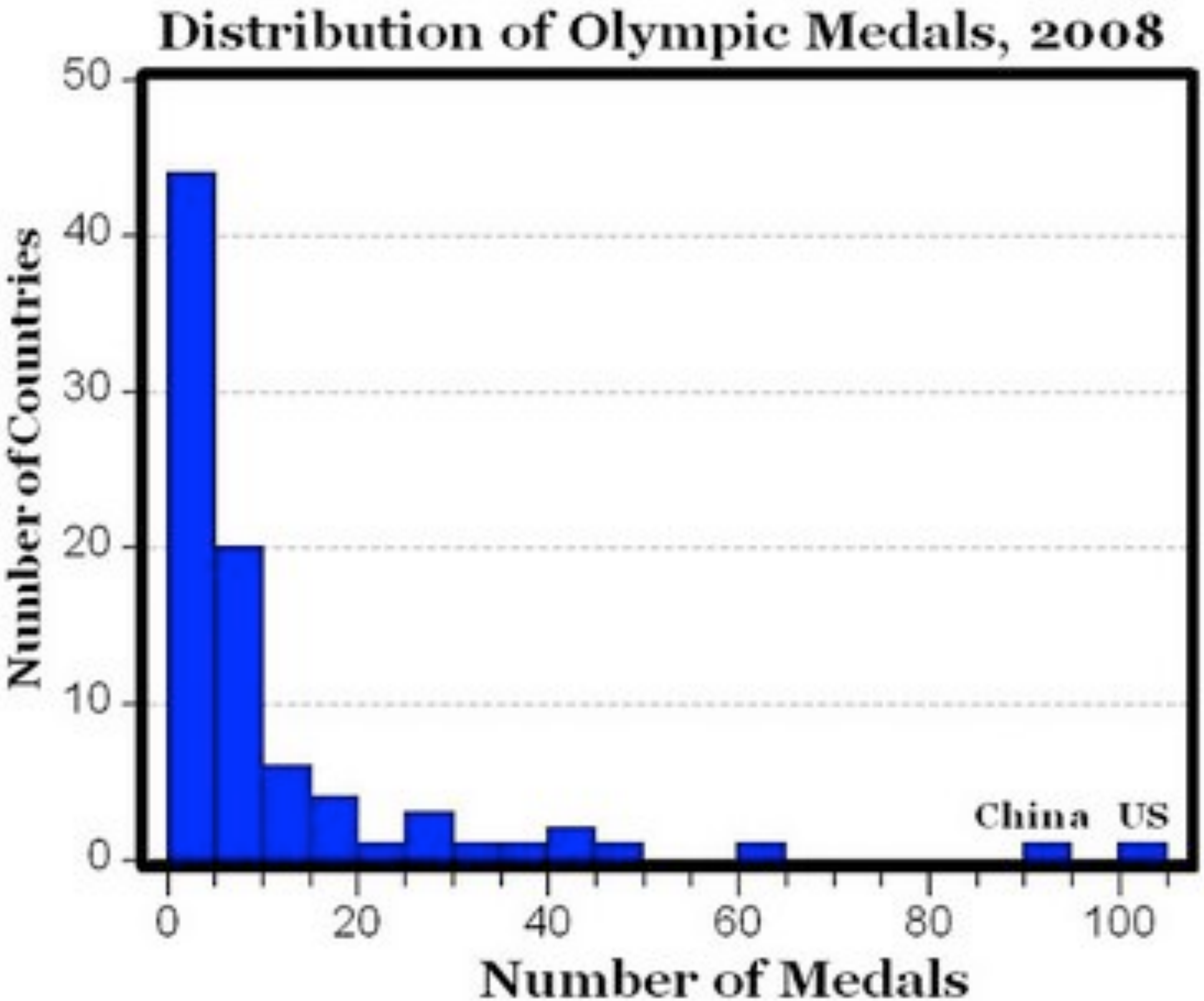
COMPLEXITY EXPLORER

Complexity Explorer has 818 followers

http://media.nbcdfw.com/images/640*360/051512+britney+spears.jpg

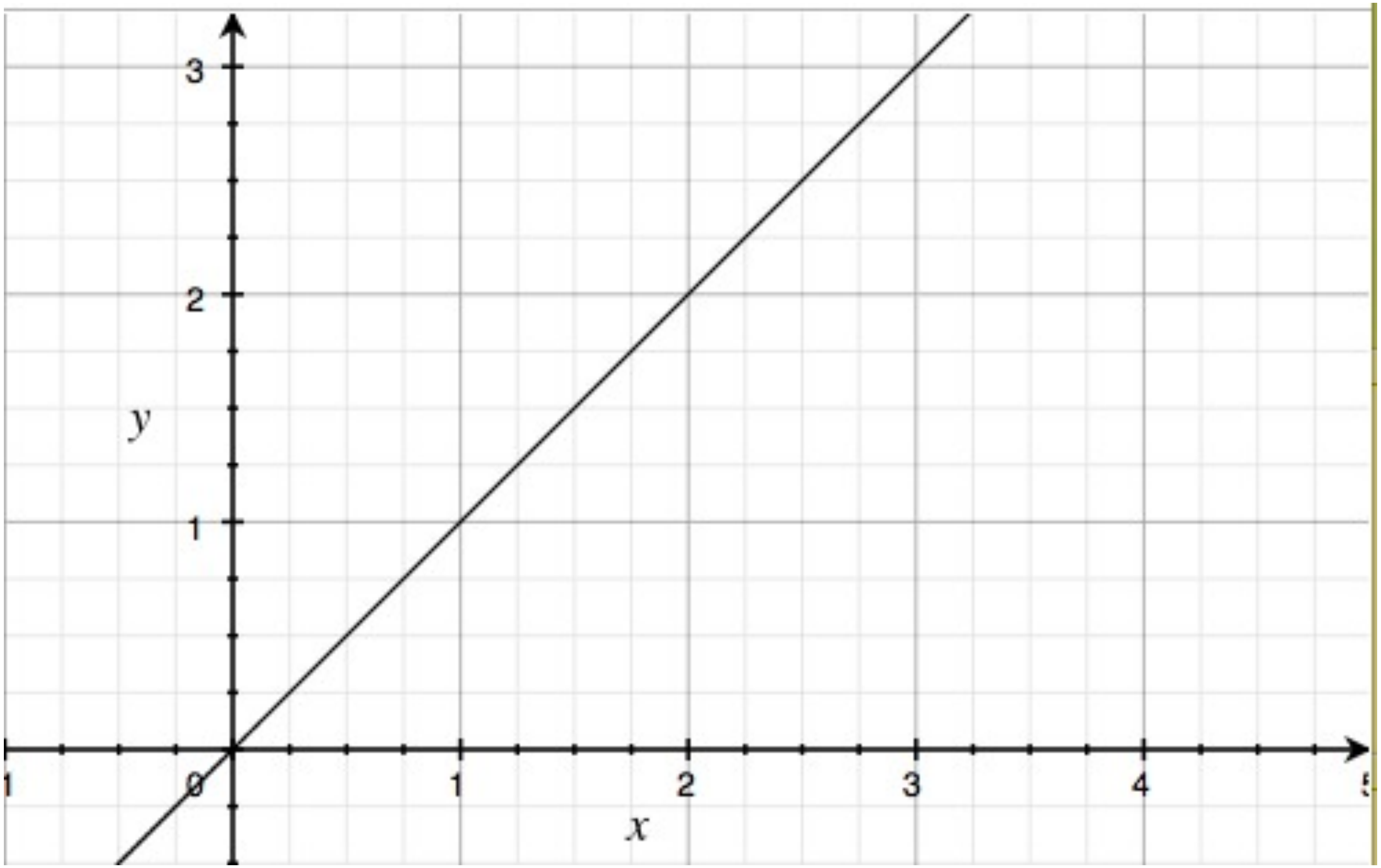
Britney Spears has 26 million Twitter followers

Examples of Power Laws:



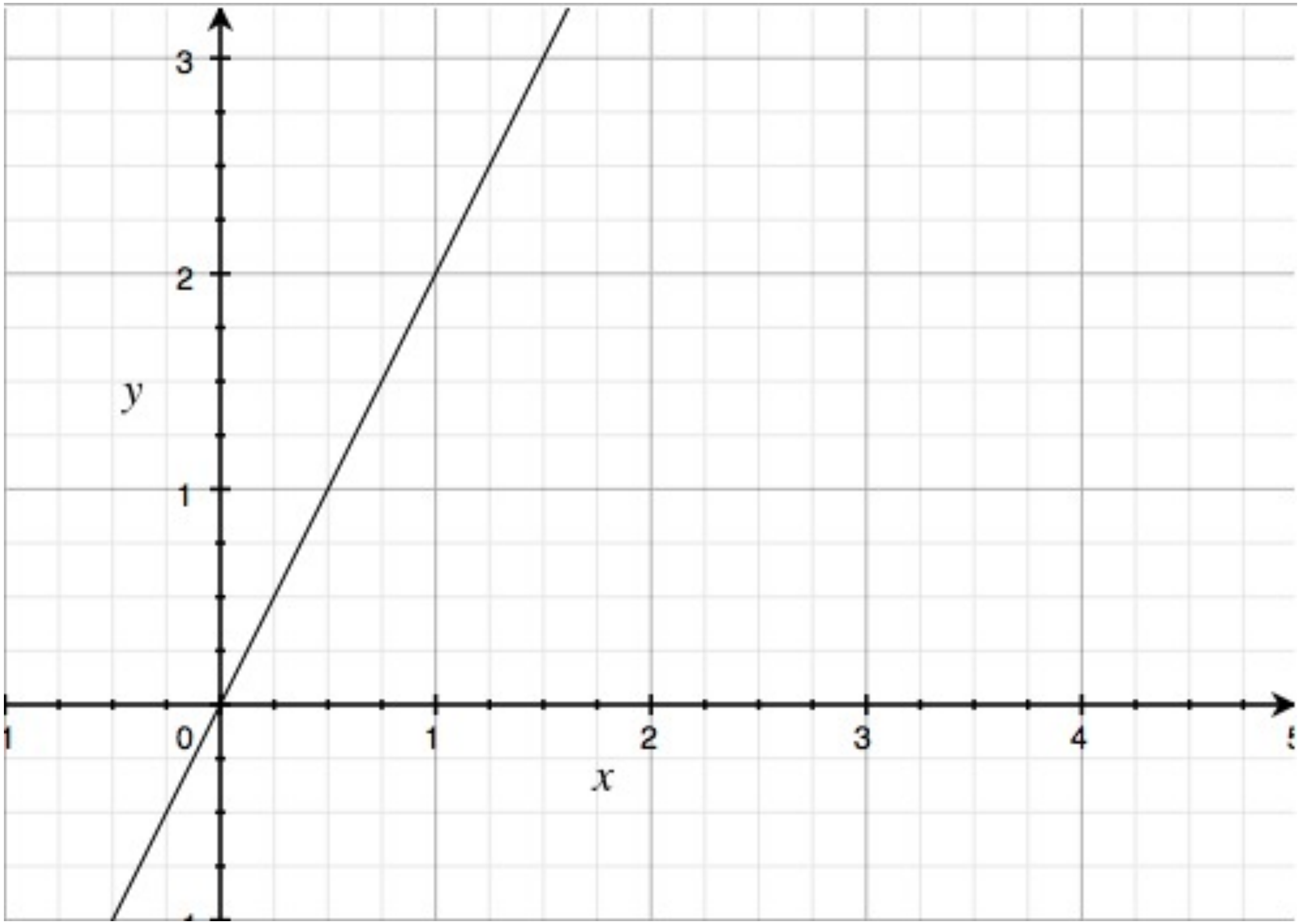
http://mjperry.blogspot.com/2008/08/more-on-medal-inequality-at-2008.html

Some basics:



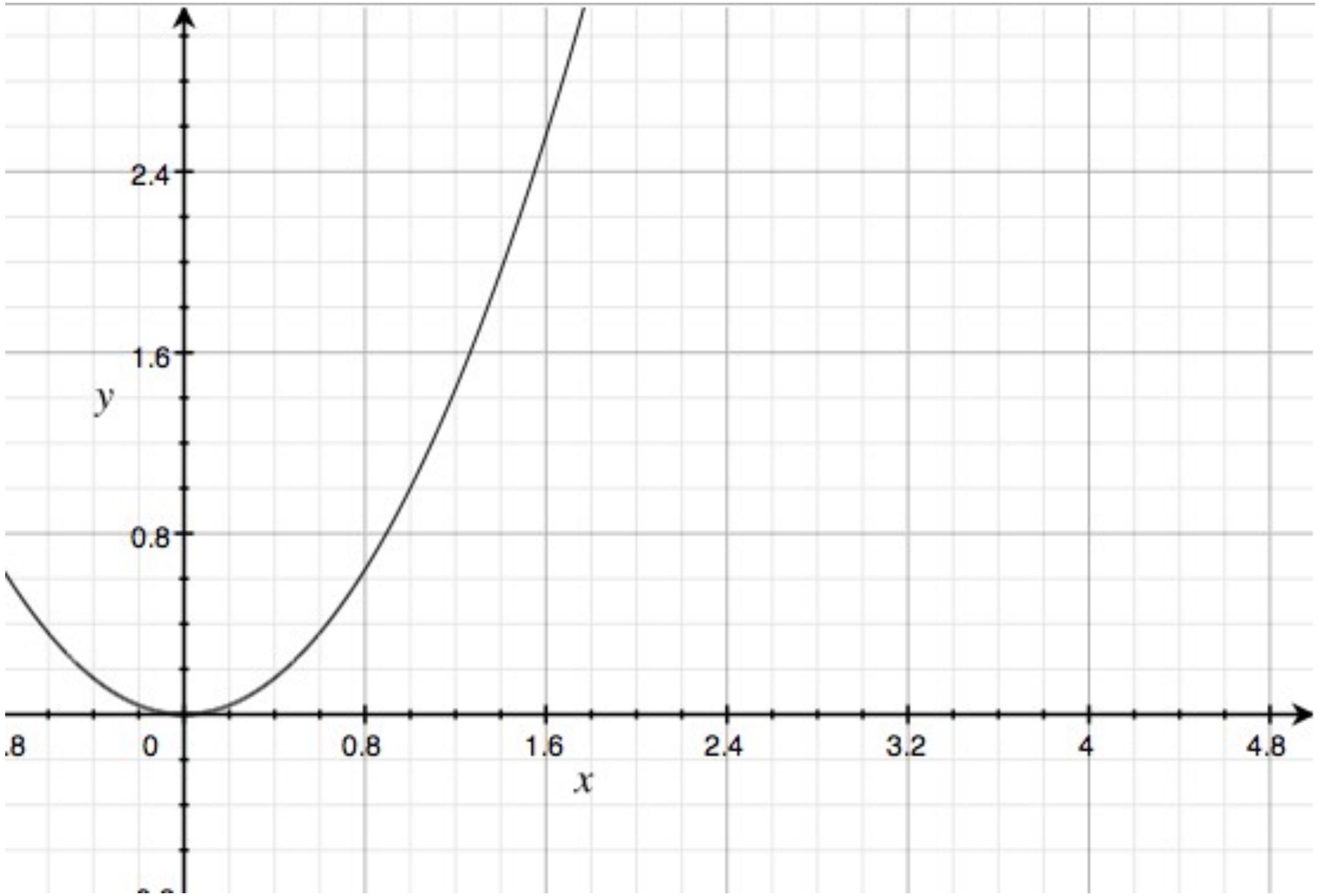
$$y = x$$

Some basics:



$$y = 2x$$

Some basics:



$$y = x^2$$

Power law:

$\boldsymbol{y = c\,x^{z}}$ where z is an integer or fraction and c is a constant.

Logarithm basics:

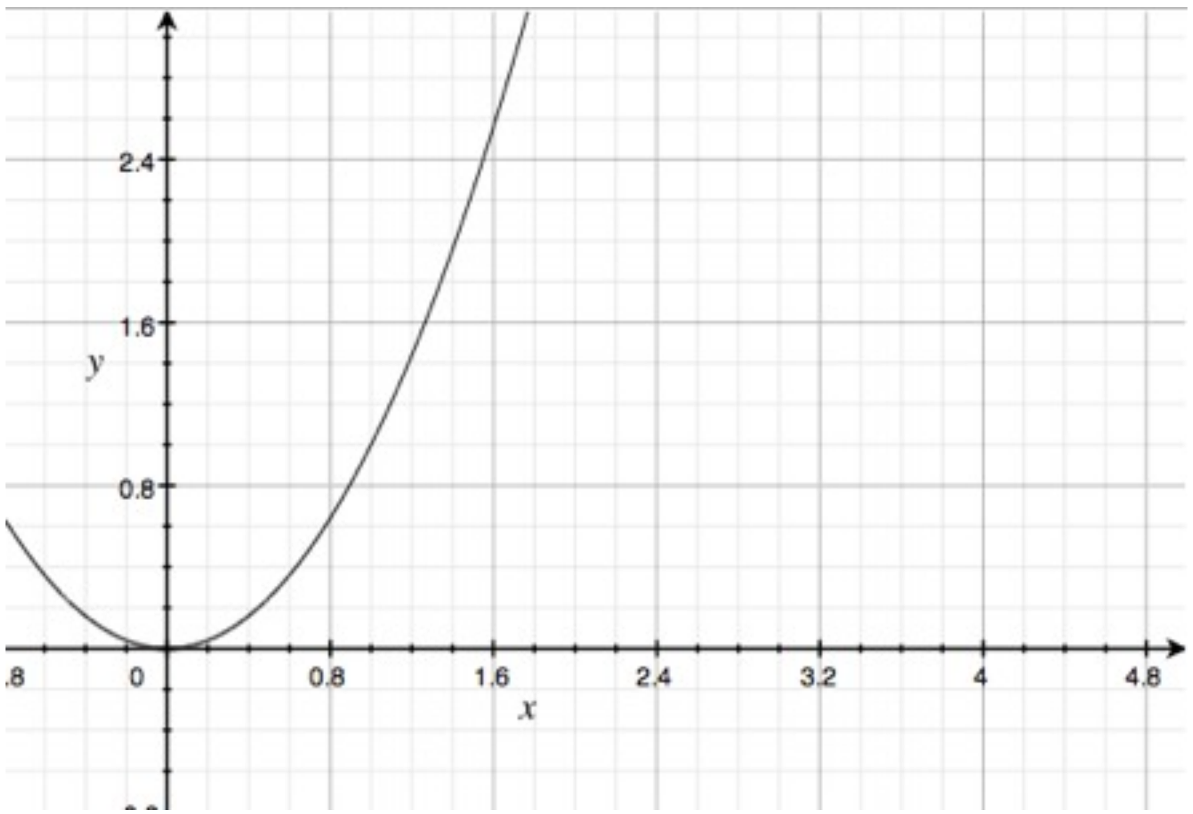
$\log_{10} u = v$ means that $10^{v} = u$

i.e., $\log_{10} 100 = 2$, or $10^{2} = 100$

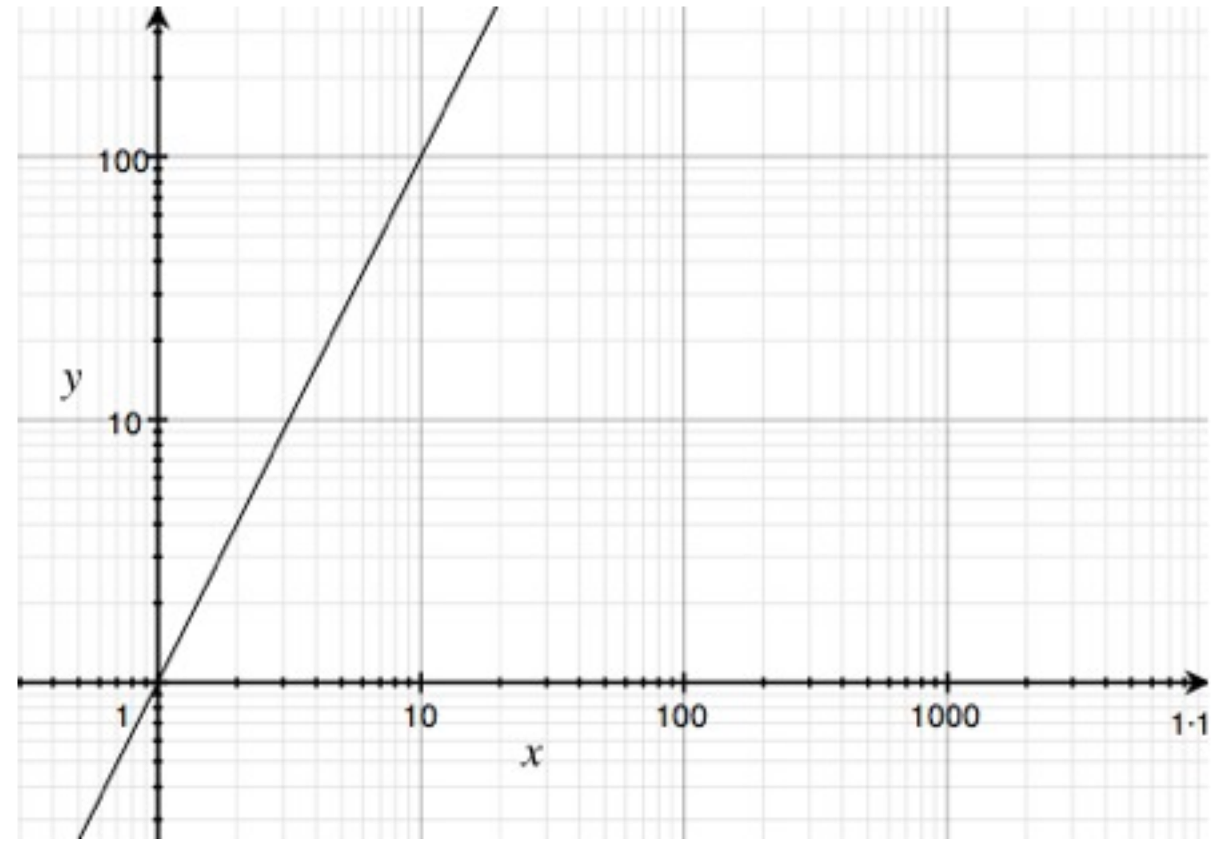
Power property: $\log_{10} u^{n} = n \log_{10} u$,

i.e. $\log_{10} 100^{2} = 2 \log_{10} 100 = 4$ or $\log_{10}$ 10,000.

Some basics:



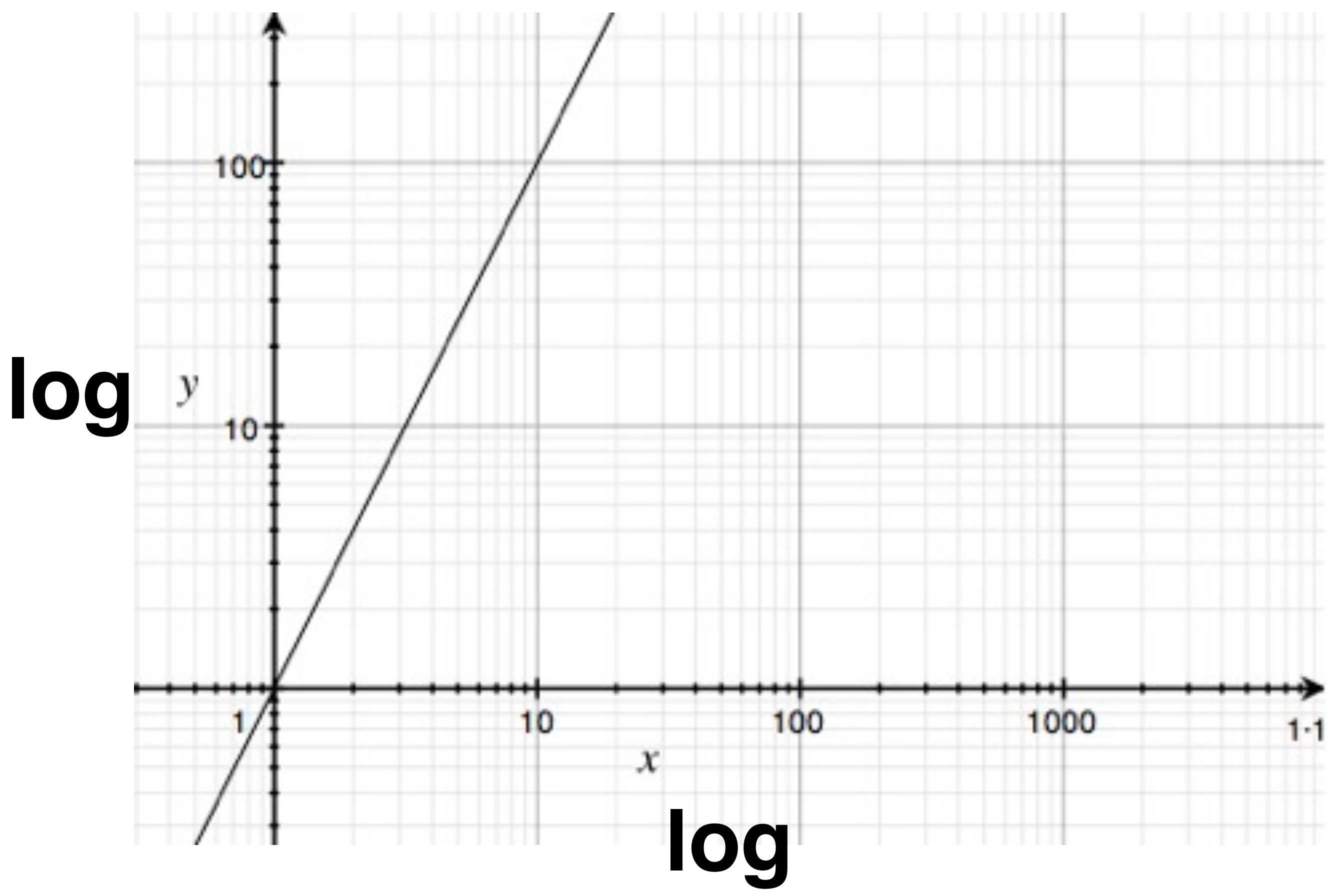
$$y = x^2$$



$$\log y = \log x^2$$

$$\log y = 2 \log x$$

All that is necessary to know about logarithms for this unit is that a power law looks like a straight line on a log-log plot.



Fractional exponents:

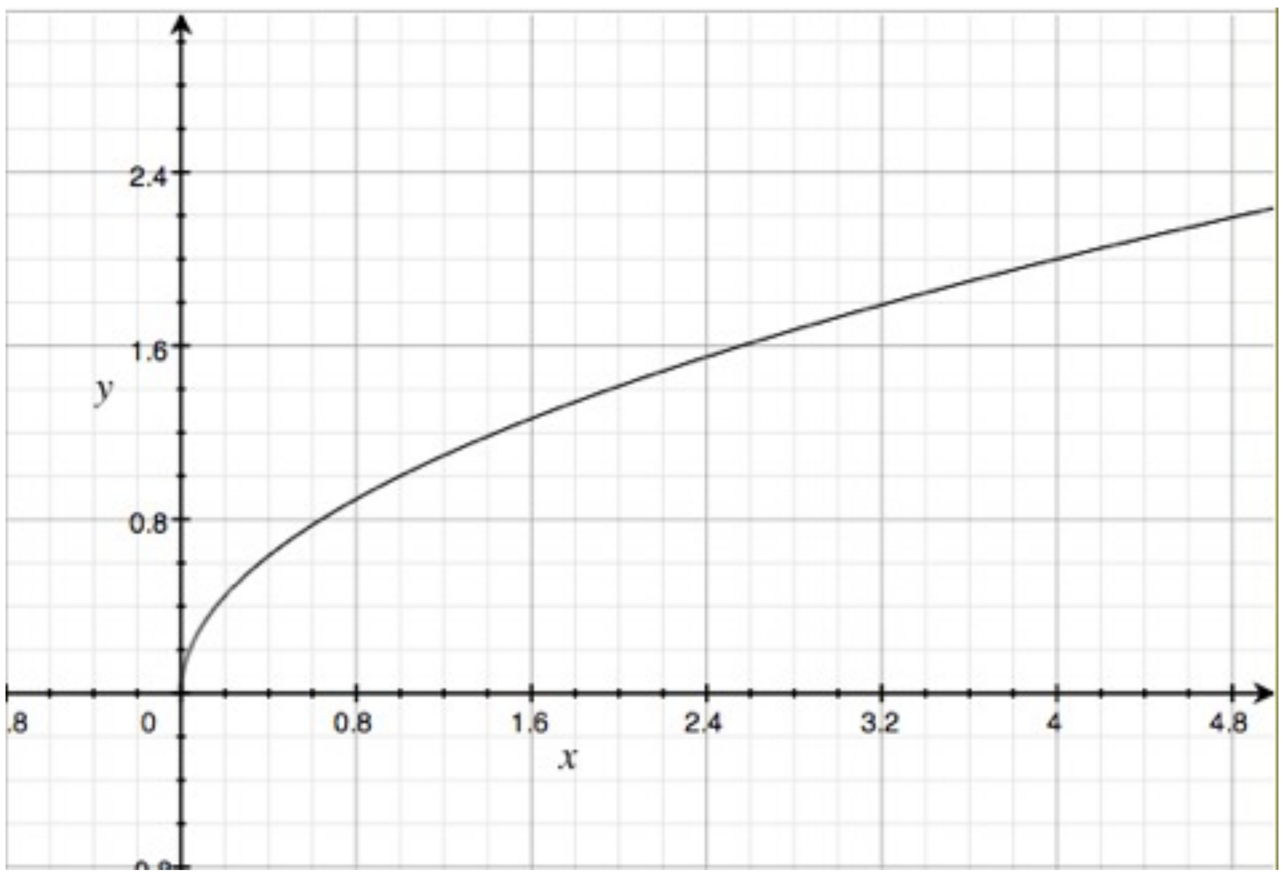
$$x^{\frac{u}{v}} = \sqrt[v]{x^{u}}$$

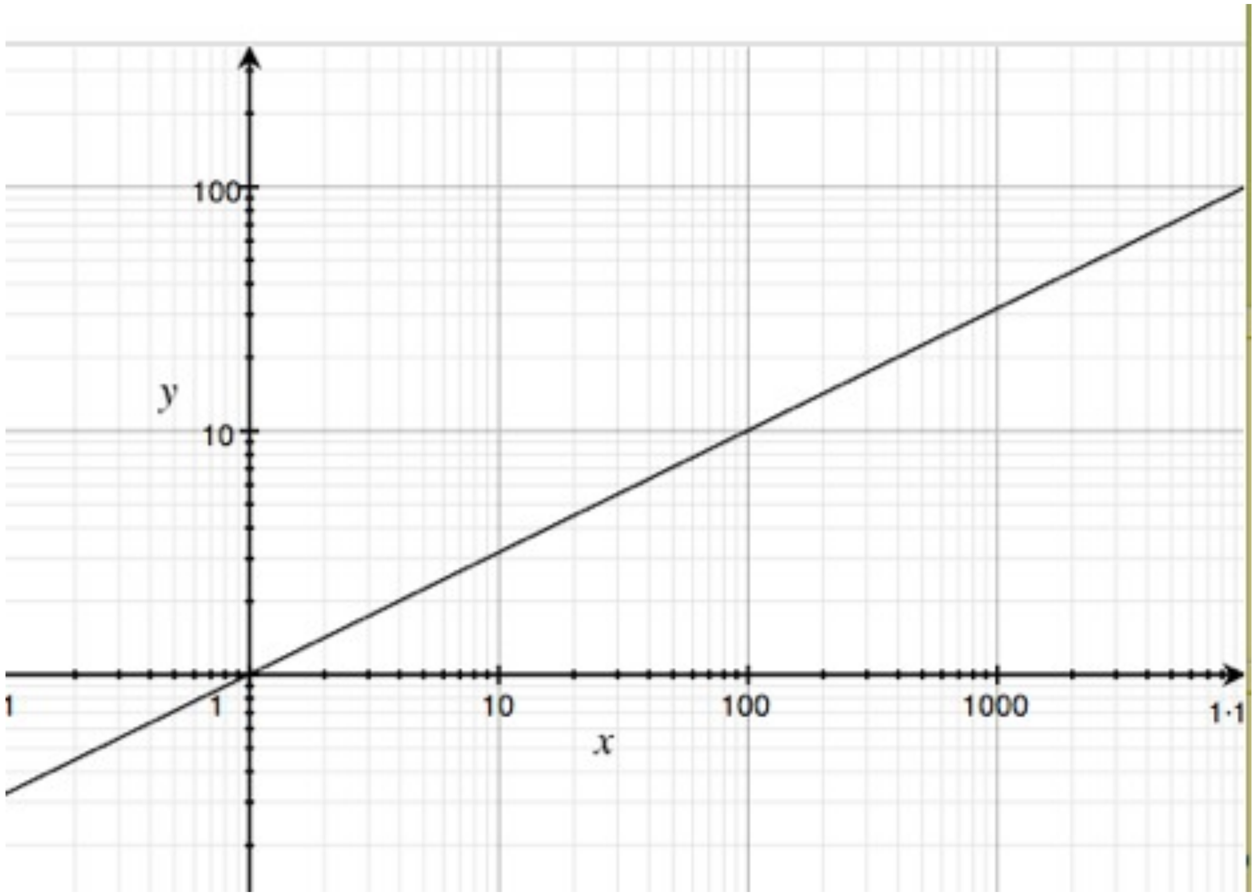
$$x^{-u} = \frac{1}{x^{u}}$$

$$x^{-\frac{u}{v}} = \frac{1}{\sqrt[v]{x^{u}}}$$

therefore: $2^{-\frac{1}{2}} = \frac{1}{\sqrt{2}}$

Some basics:





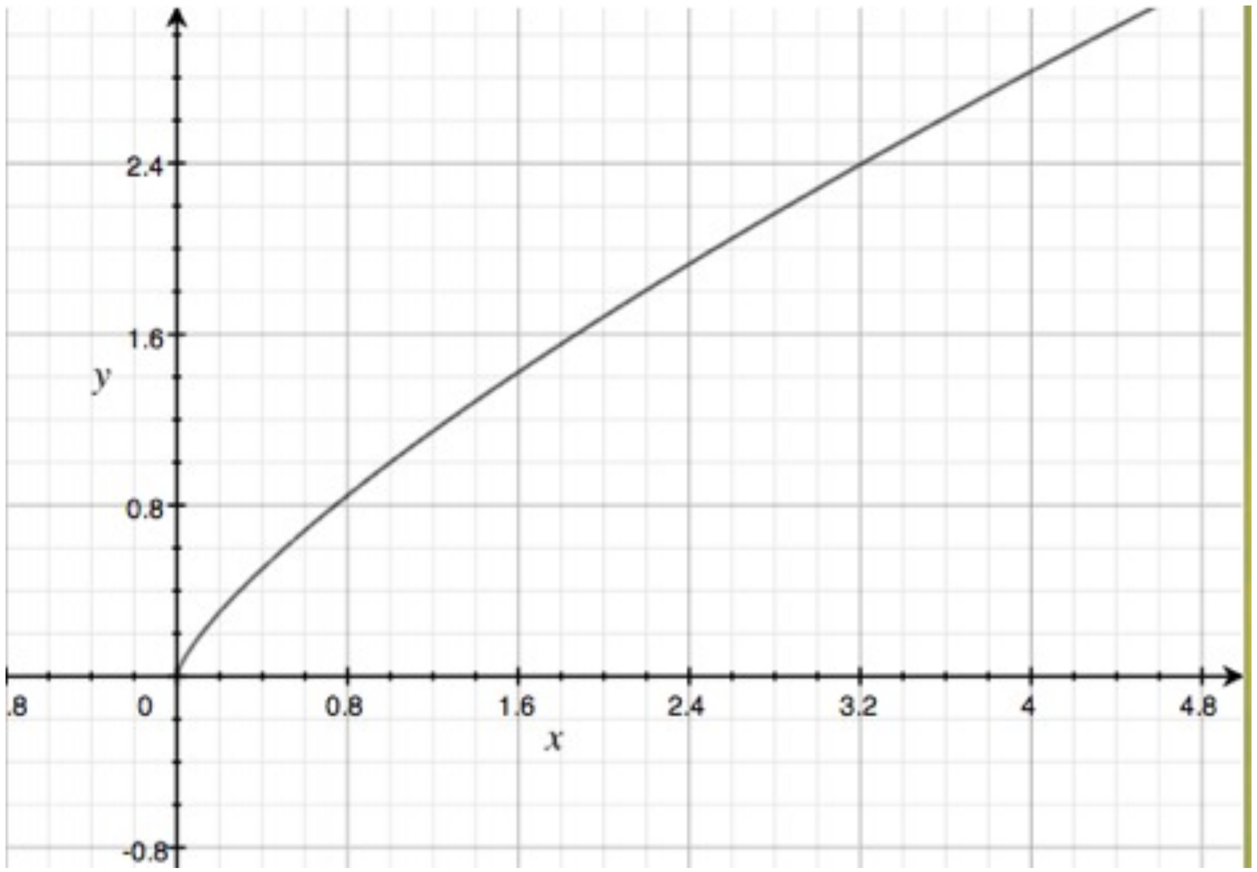
$$y = x^{\frac{1}{2}}$$

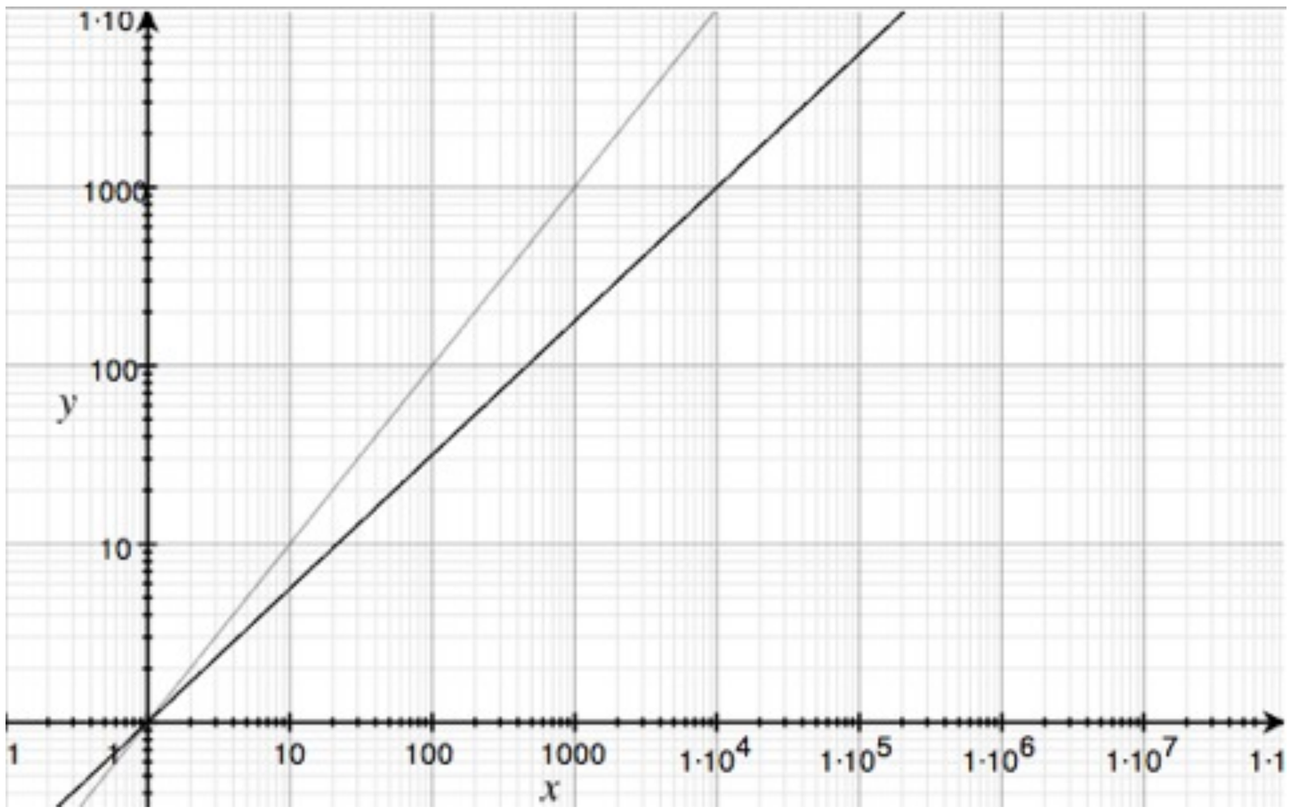
$$y = \sqrt{x}$$

$$\log y = \tfrac{1}{2}\log x$$

$$slope = \tfrac{1}{2}(sublinear)$$

Some basics:





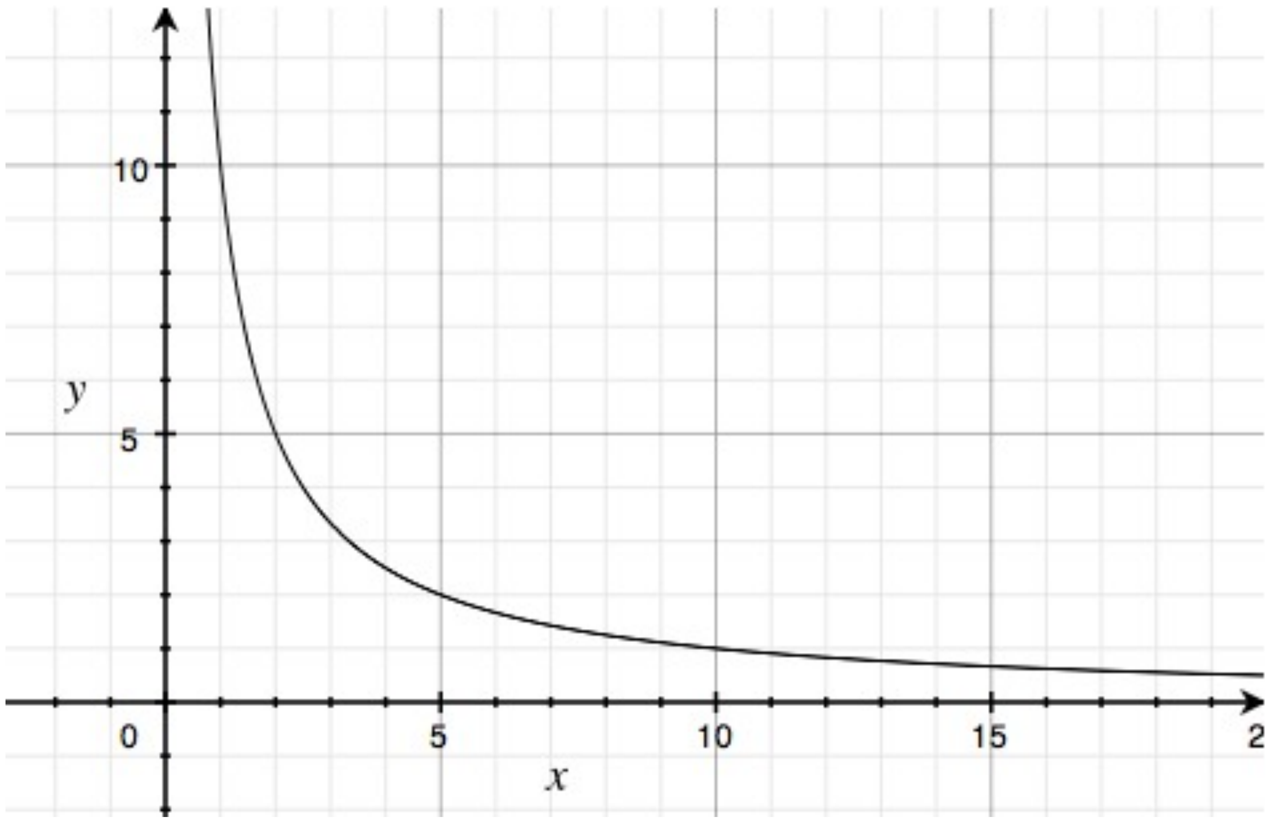
$$y = x^{\frac{3}{4}}$$

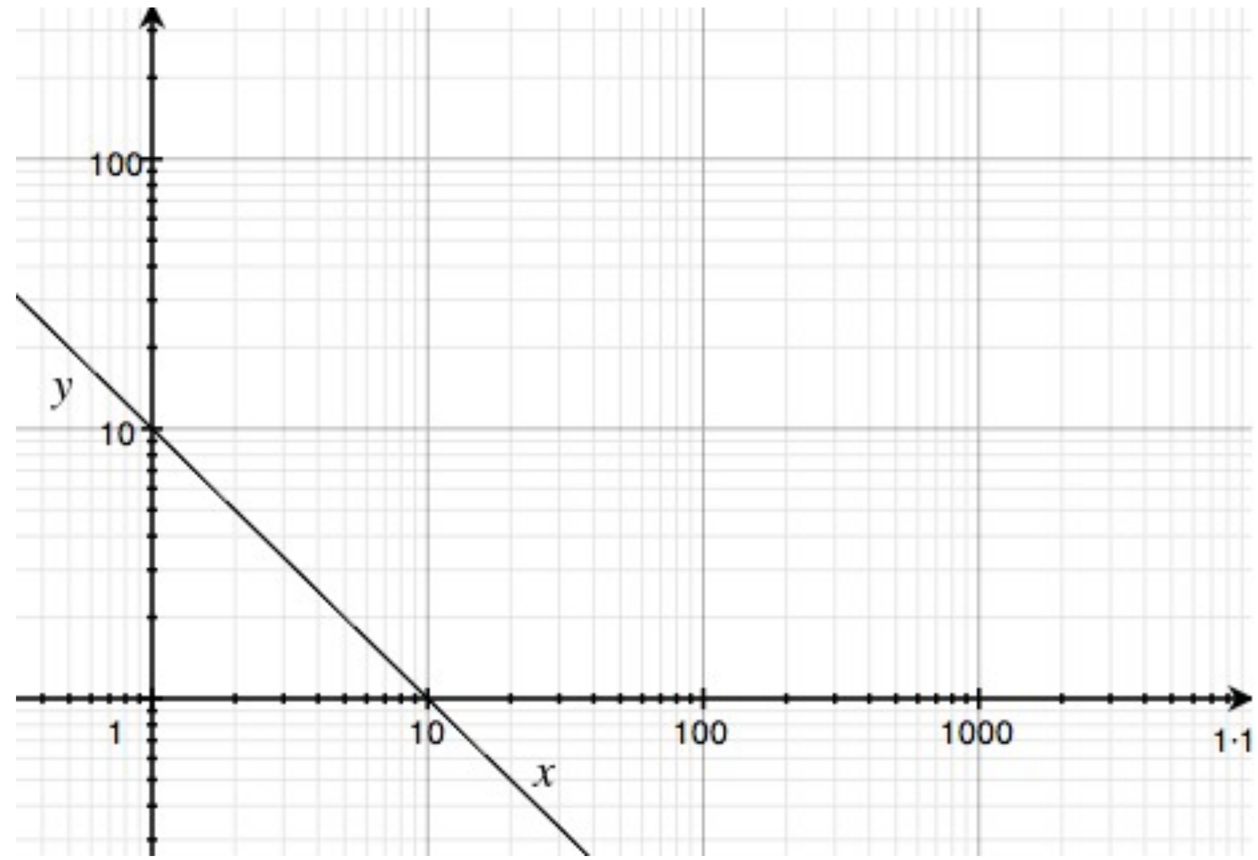
$$y = \sqrt[4]{x^3}$$

$$\log y = \frac{3}{4} \log x$$

$$slope = \frac{3}{4} \; (sublinear)$$

Some basics:





$$y \propto x^{-1}$$

$$y \propto \frac{1}{x}$$

$$\log y \propto -1 \log x$$

$$slope = -1$$

Hausdorff dimension:

$$D = \frac{\log M}{\log N}$$

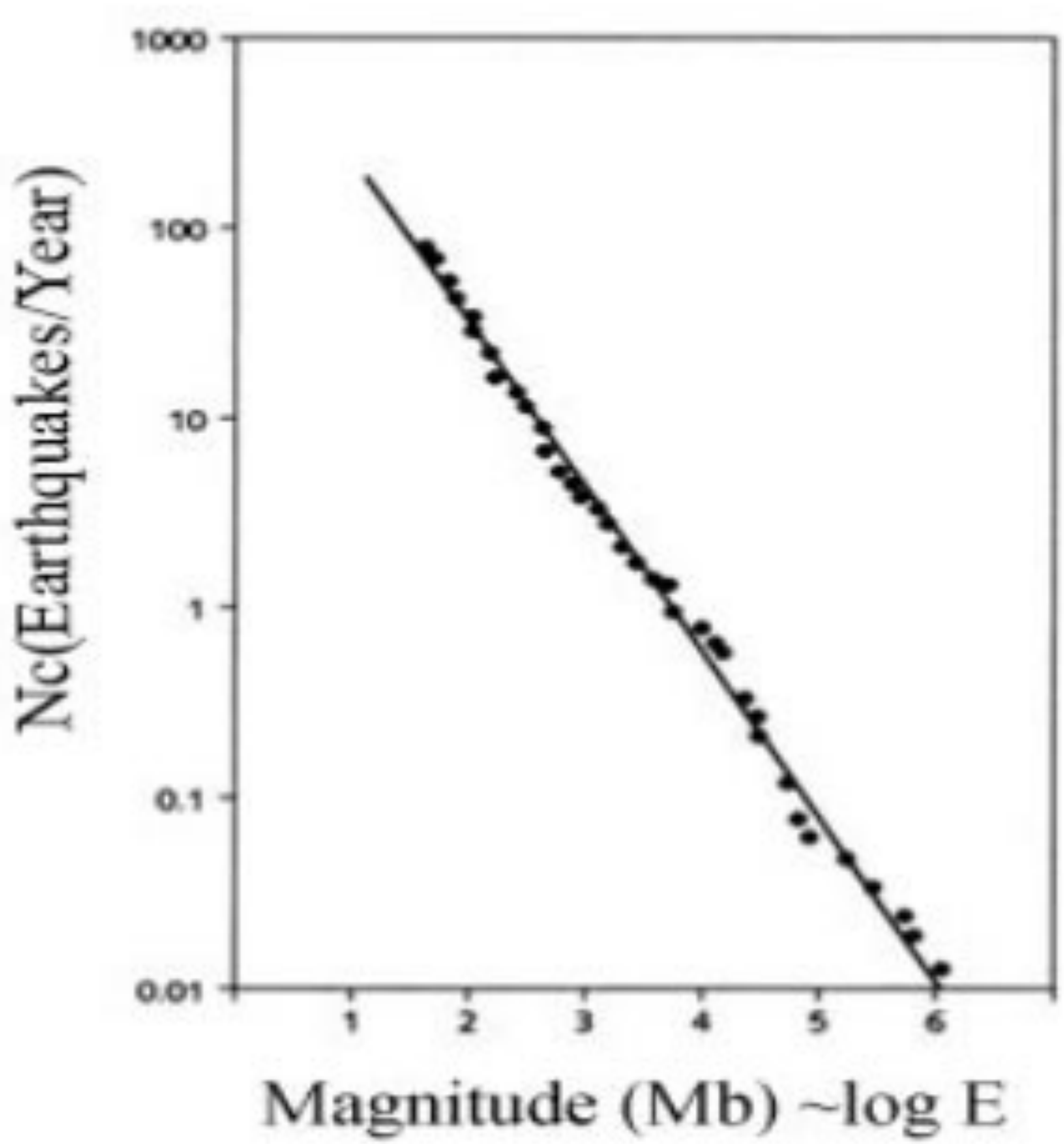
$$\log M = D \log N$$

$$\log M = \log N^{D}$$

$$M = N^{D}$$

Some examples of power law scaling in nature

Gutenberg-Richter law of earthquake magnitudes



By: Bak [1]

Kleiber's Law:

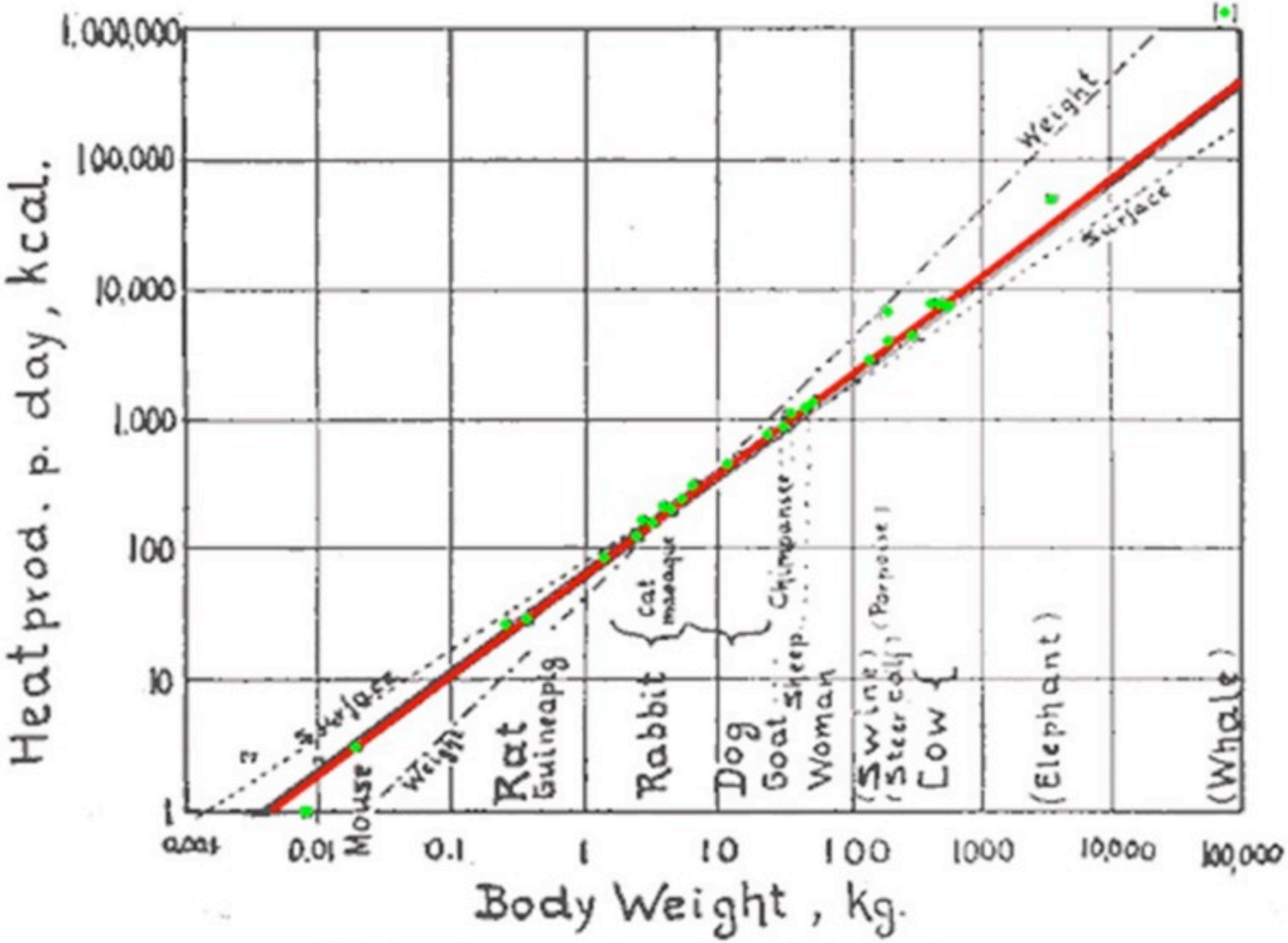
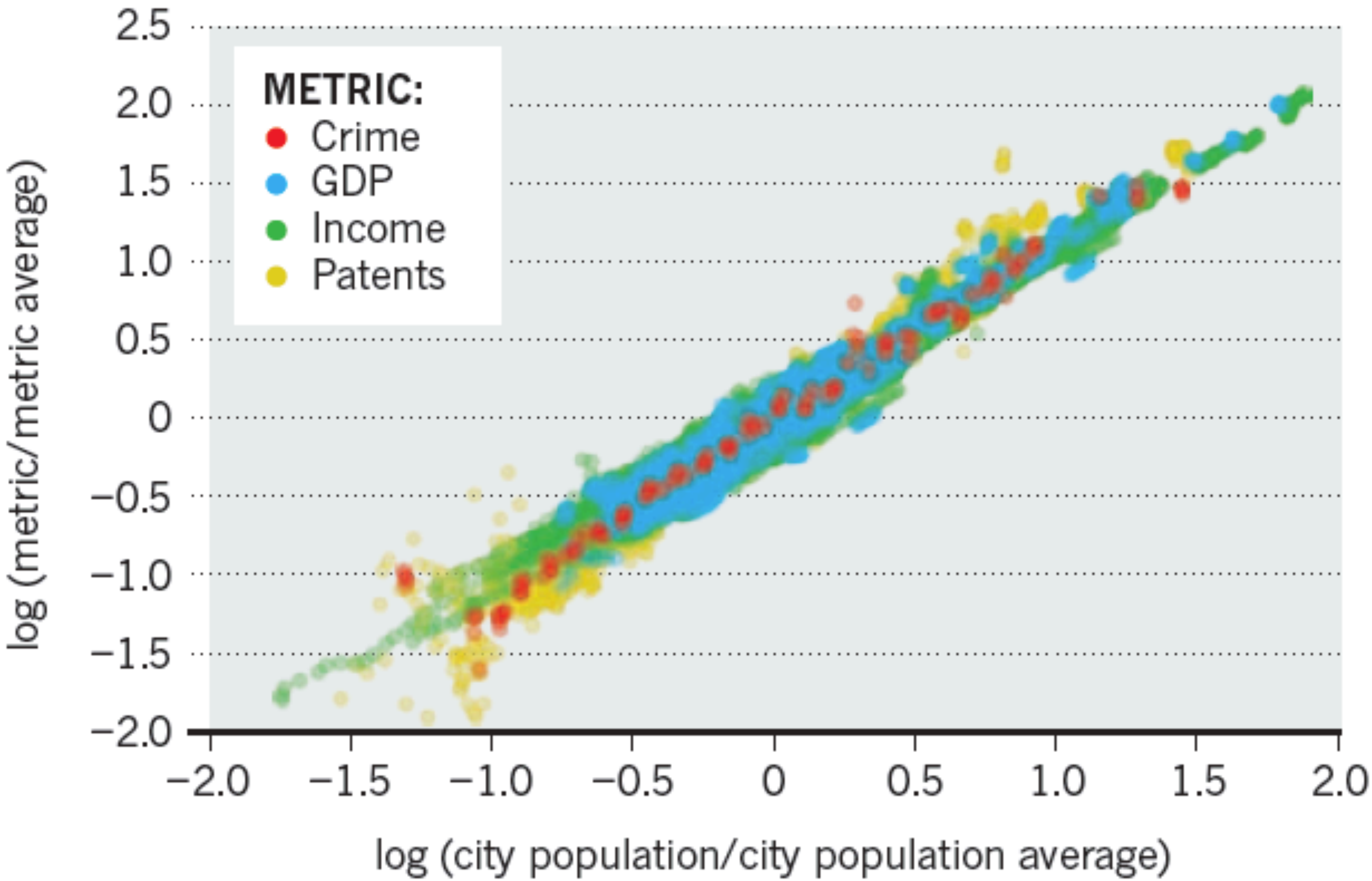


Fig. 1. Log. metabol. rate/log body weight

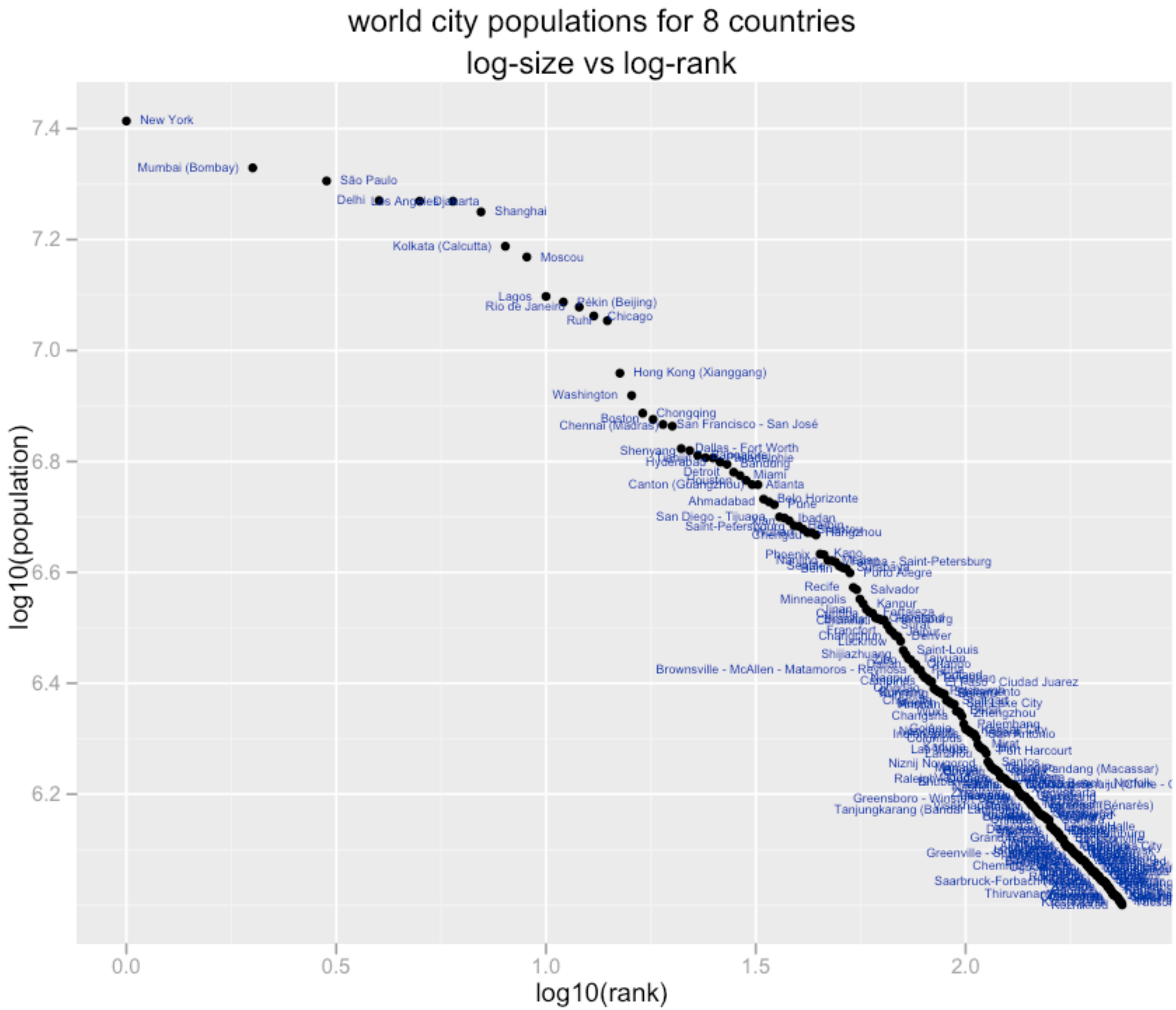
FIG. Body size versus metabolic rate for a variety of species. Kleiber (1947). Kleiber's original units were weight and calories. Today units of mass and watts are typical.

From **A Unified Theory of Urban Living,** L. Bettencourt and G. West, Nature, 467, 912–913, 2010

Scaling crime, income, etc. with city population



City populations



http://brenocon.com/blog/2009/05/zipfs-law-and-world-city-populations/

Zipf's law:

$$frequency \propto \frac{1}{rank}$$

$$y \propto \frac{1}{x}$$

$$y \propto x^{-1}$$

$$y \propto -1 \log x$$

FIG. George Kinglsey Zipf 1902 - 1950. George Kingsley Zipf, was an American linguist and philologist who studied statistical occurrences in different languages. Zipf was Chairman of the German Department and University Lecturer at Harvard

Zipf's law:

Jack and Jill

BY MOTHER GOOSE

Jack and Jill went up the hill
To fetch a pail of water;
Jack fell down and broke his crown,
and Jill came tumbling after.

Zipf's law:

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Jack and Jill went up the hill
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Jack fell down and broke his crown,
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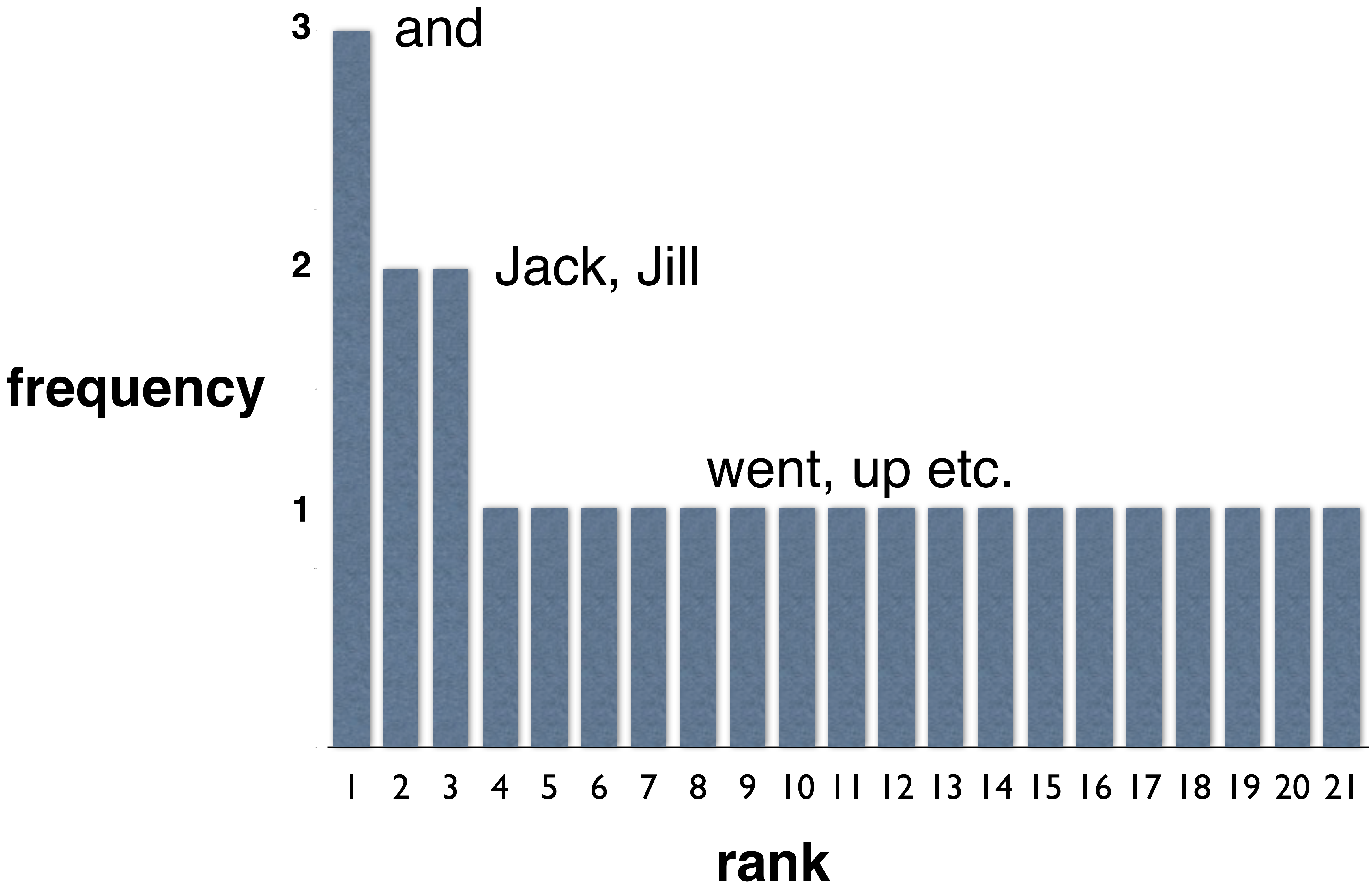
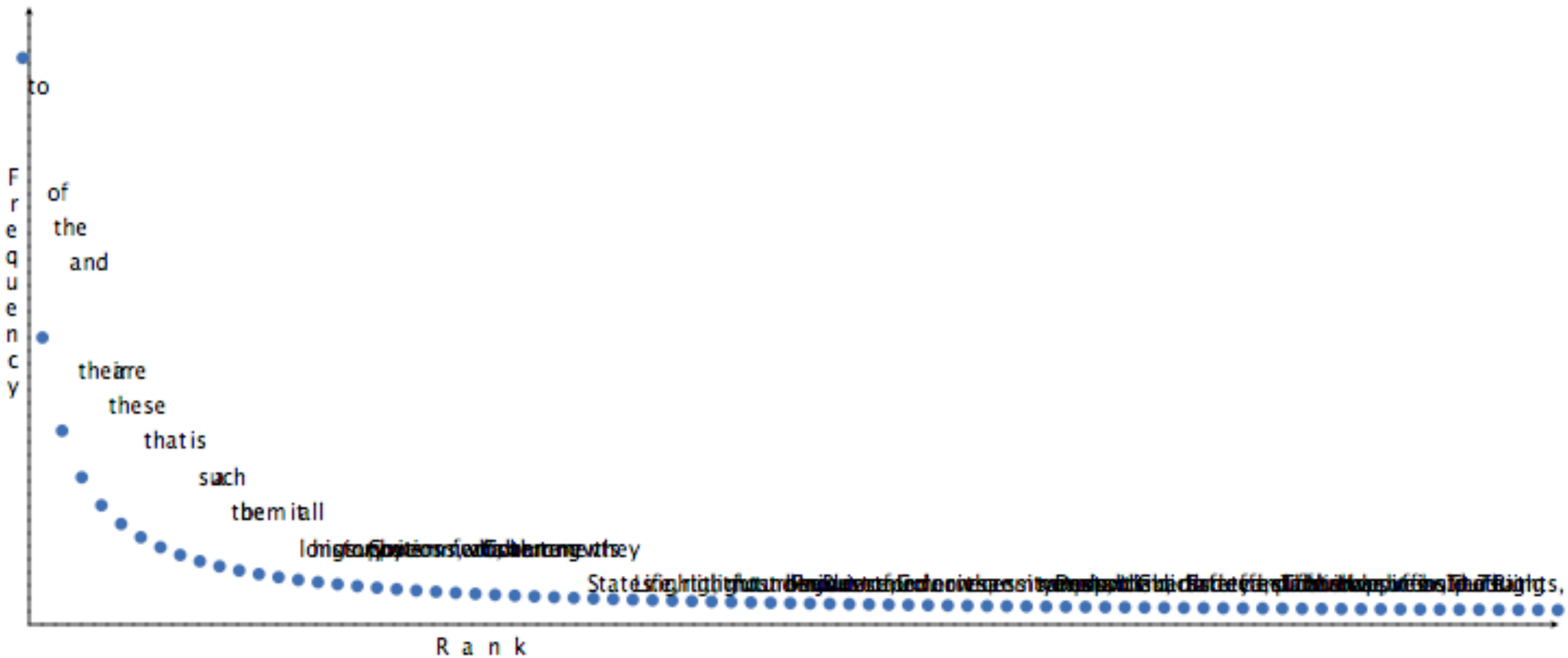
word	rank	frequency
and	1	3
Jill	2	2
Jack	3	2
went	4	1
up	5	1
the	6	1
hill	7	1
to	8	1
fetch	9	1
a	10	1
pail	11	1
of	12	1
water	13	1
fell	14	1
down	15	1
broke	16	1
his	17	1
crown	18	1
came	19	1
tumbling	20	1
after	21	1

Zipf's law:



3
and
2
Jack, Jill
frequency
went, up etc.
1
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21
rank

Zipf's law:



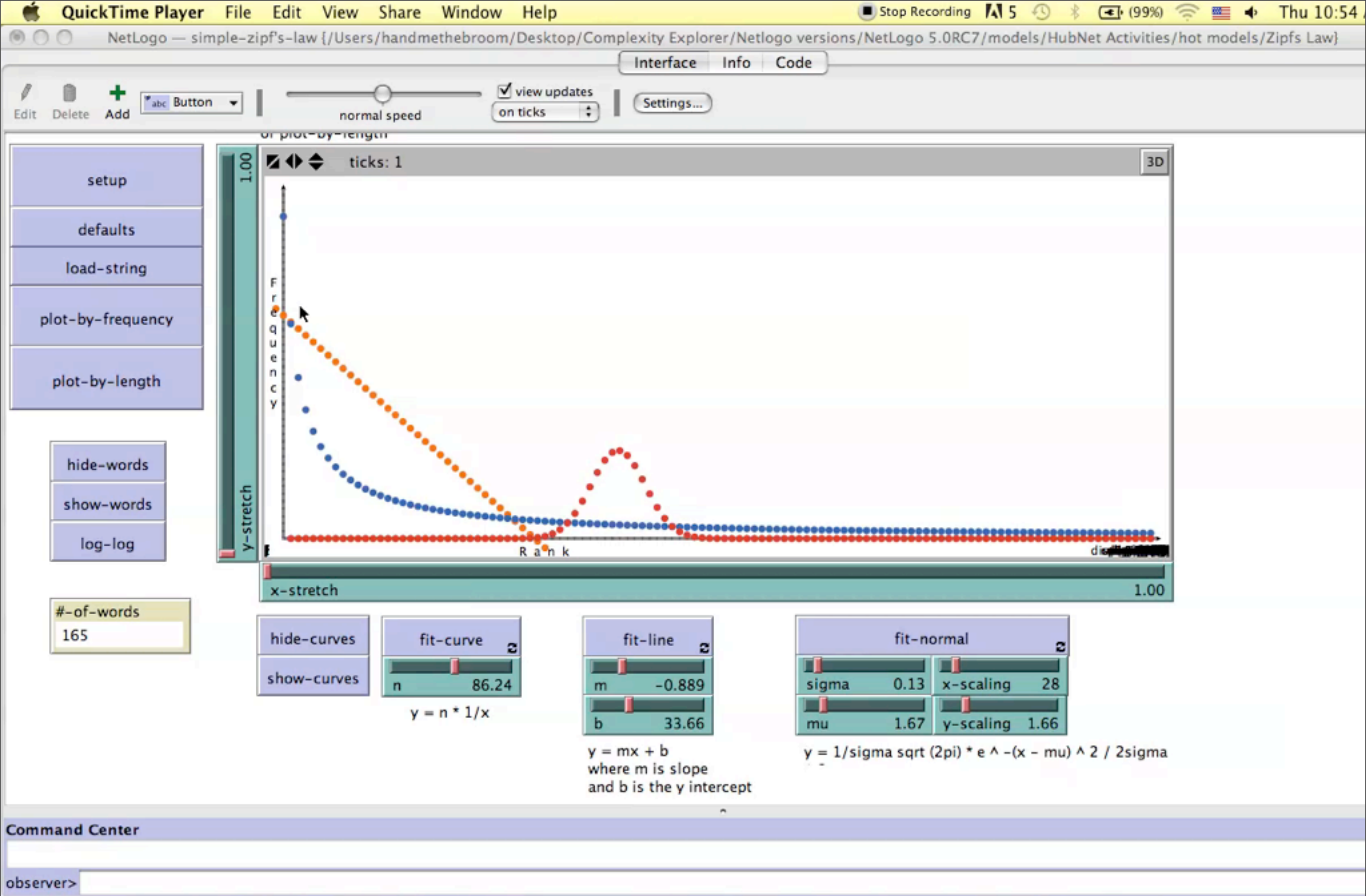


FIG. Zipf's Law Netlogo model: simple-zipf's-law.nlogo.

What causes these distributions?

Preferential attachment is the well-known idea that "the rich get richer". That is, the probability that individuals (e.g., people, cities, web pages) will attain some quantity (e.g., friends, money, population, links) is proportional to the amount of the quantity they already have.

Metabolic Scaling:

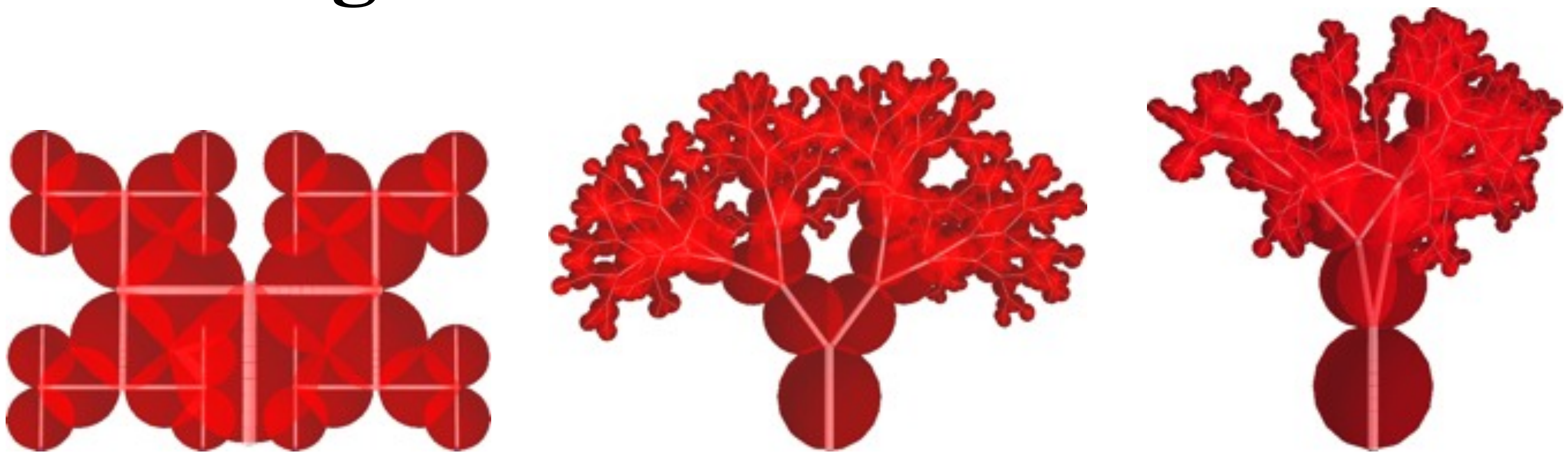


FIG. Three networks produced with *simple-fractal-scaling.nlogo*.

Of Mice and Elephants: a Matter of Scale

By GEORGE JOHNSON
Published: January 12, 1999

Scientists, intent on categorizing everything around them, sometimes divide themselves into the lumpers and the splitters. The lumpers, many of whom flock to the unifying field of theoretical physics, search for hidden laws uniting the most seemingly diverse phenomena: Blur your vision a little and lightning bolts and static cling are really the same thing. The splitters, often drawn to the biological sciences, are more taken with diversity, reveling in the 34,000 variations on the theme spider, or the 550 species of coniferous trees.

But there are exceptions to the rule. When two biologists and a physicist, all three of the lumper persuasion, recently joined forces at the Santa Fe Institute, an interdisciplinary research center in northern New Mexico, the result was an advance in a problem that has bothered scientists for decades: the origin of biological scaling. How is one to explain the subtle ways in which various characteristics of living creatures -- their life spans, their pulse rates, how fast they burn energy -- change according to their body size?

FIG. 8 New York Times Article, Jan 12, 1999.

Some definitions:

Allometry: The study of the relationship of body size to shape in biology, physiology etc.

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Metabolism: The chemical reactions in the cells of an organism which convert nutrients to energy and sustain life.

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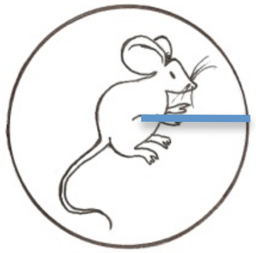
Body Mass: Amount of matter in an organism measured in grams.

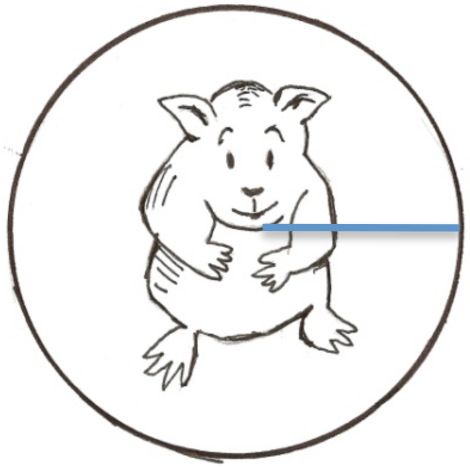
Mouse

Hamster

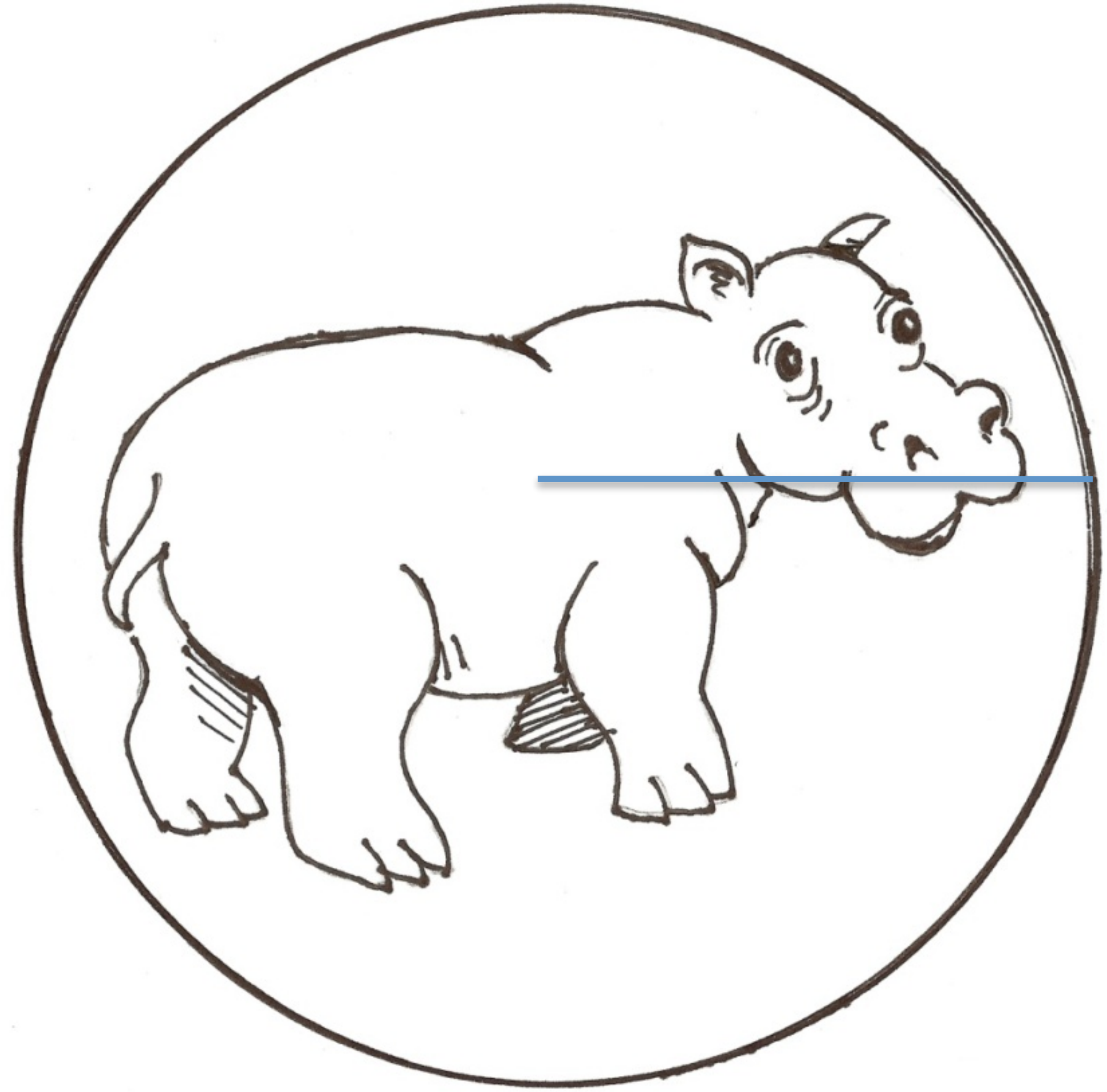
Hippo



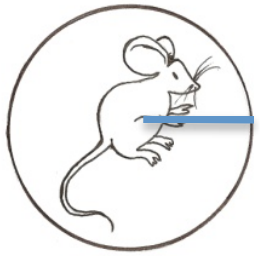
Mouse



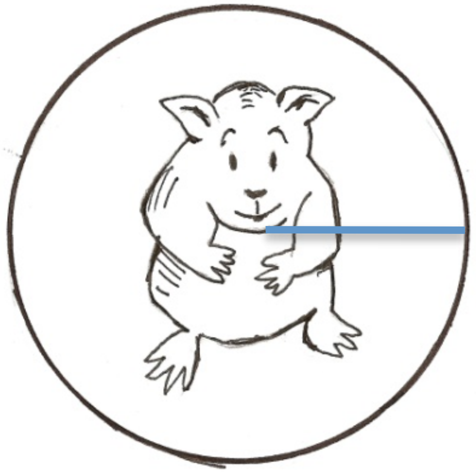
Hamster
Radius = 2 × Mouse radius



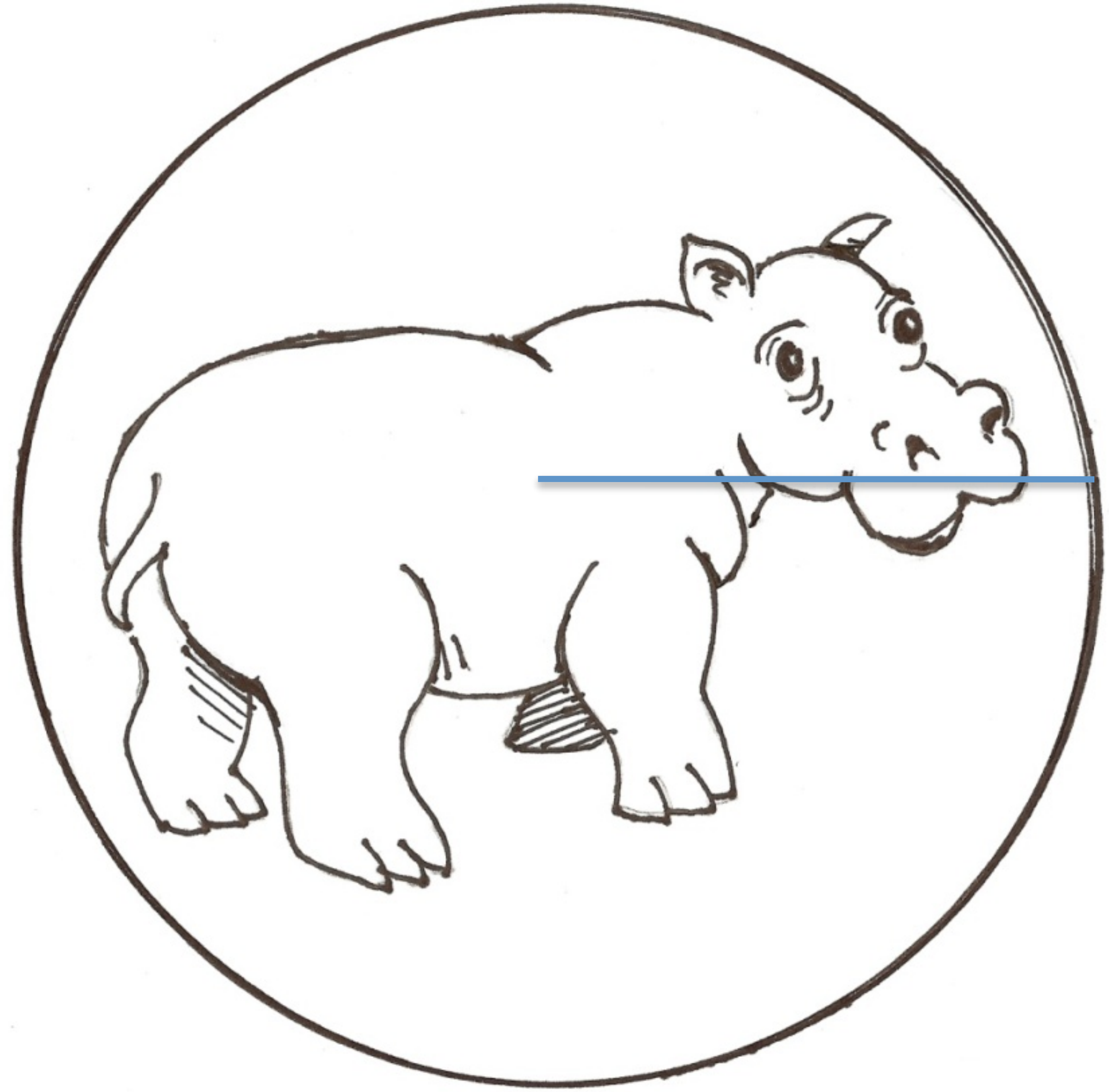
Hippo
Radius = 50 × Mouse radius



Mouse



Hamster
Radius = 2 × Mouse radius



Hippo
Radius = 50 × Mouse radius

Hypothesis 1: metabolic rate ∝ body mass

Mouse

Hamster
Radius = 2 × Mouse radius

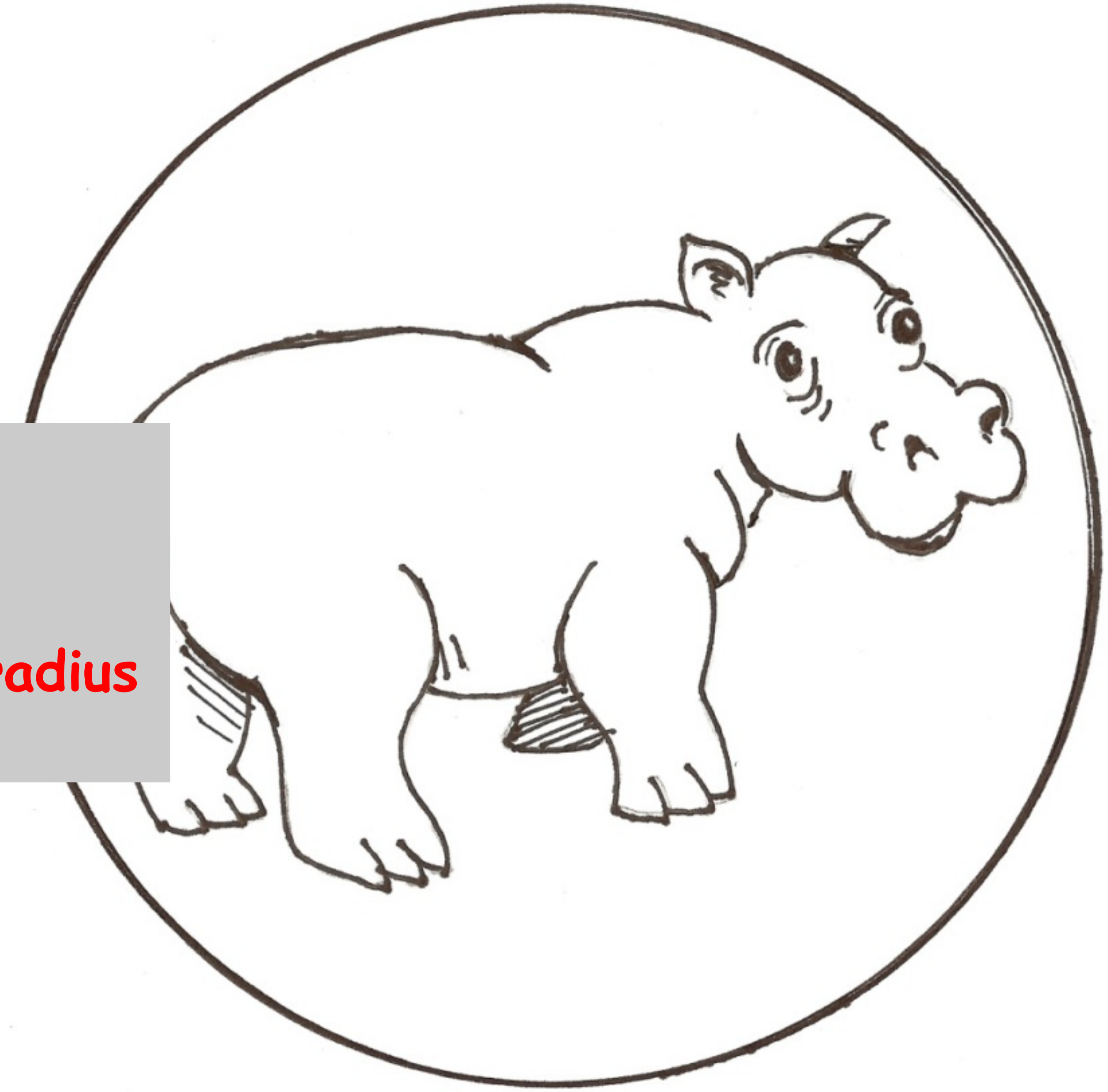
Volume of a sphere: $\frac{4}{3}\pi r^3$

Surface area of a sphere: $4\pi r^2$

Hippo
Radius = 50 × Mouse radius

Hypothesis 1: metabolic rate ∝ body mass

Mouse



Hamster
Radius = 2 × Mouse radius
Mass ∝ **8 × Mouse radius**
Surface area ∝ **4 × Mouse radius**

Volume of a sphere: $\frac{4}{3}\pi r^3$

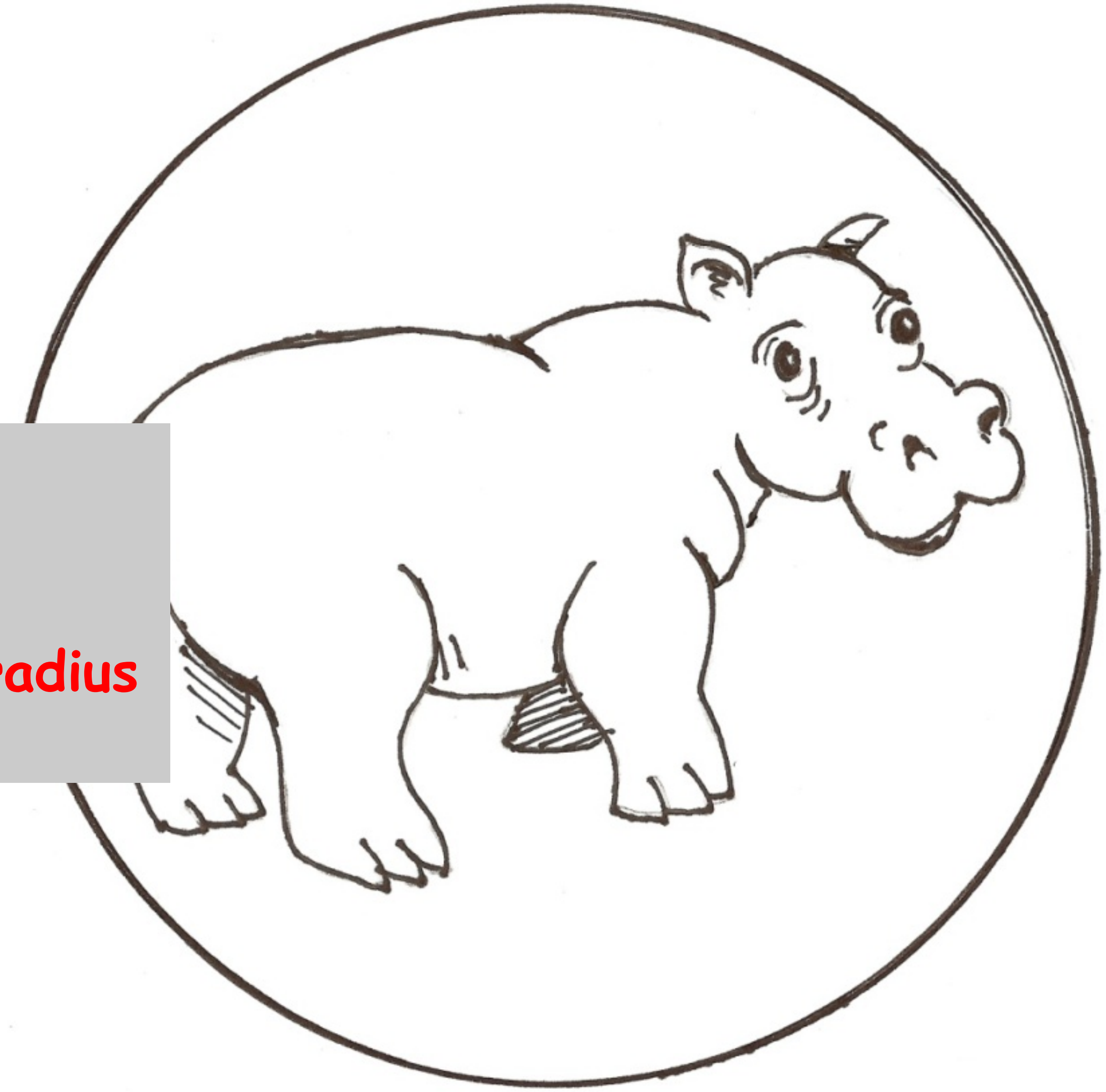
Surface area of a sphere: $4\pi r^2$

Hippo
Radius = 50 × Mouse radius

Hypothesis 1: metabolic rate ∝ body mass

Problem:
mass is proportional to **volume** of animal
but heat can radiate only from **surface** of animal

Mouse



Hamster
Radius = 2 × Mouse radius
Mass ∝ **8 × Mouse radius**
Surface area ∝ **4 × Mouse radius**

Volume of a sphere: $\frac{4}{3}\pi r^3$

Surface area of a sphere: $4\pi r^2$

Hypothesis 1: metabolic rate ∝ body mass

Problem:
mass is proportional to **volume** of animal
but heat can radiate only from **surface** of animal

Hippo
Radius = 50 × Mouse radius
Mass ∝ **125,000 × Mouse radius**
Surface area ∝ **2,500 × Mouse radius**

Biological scaling: Area preserving and surface hypothesis

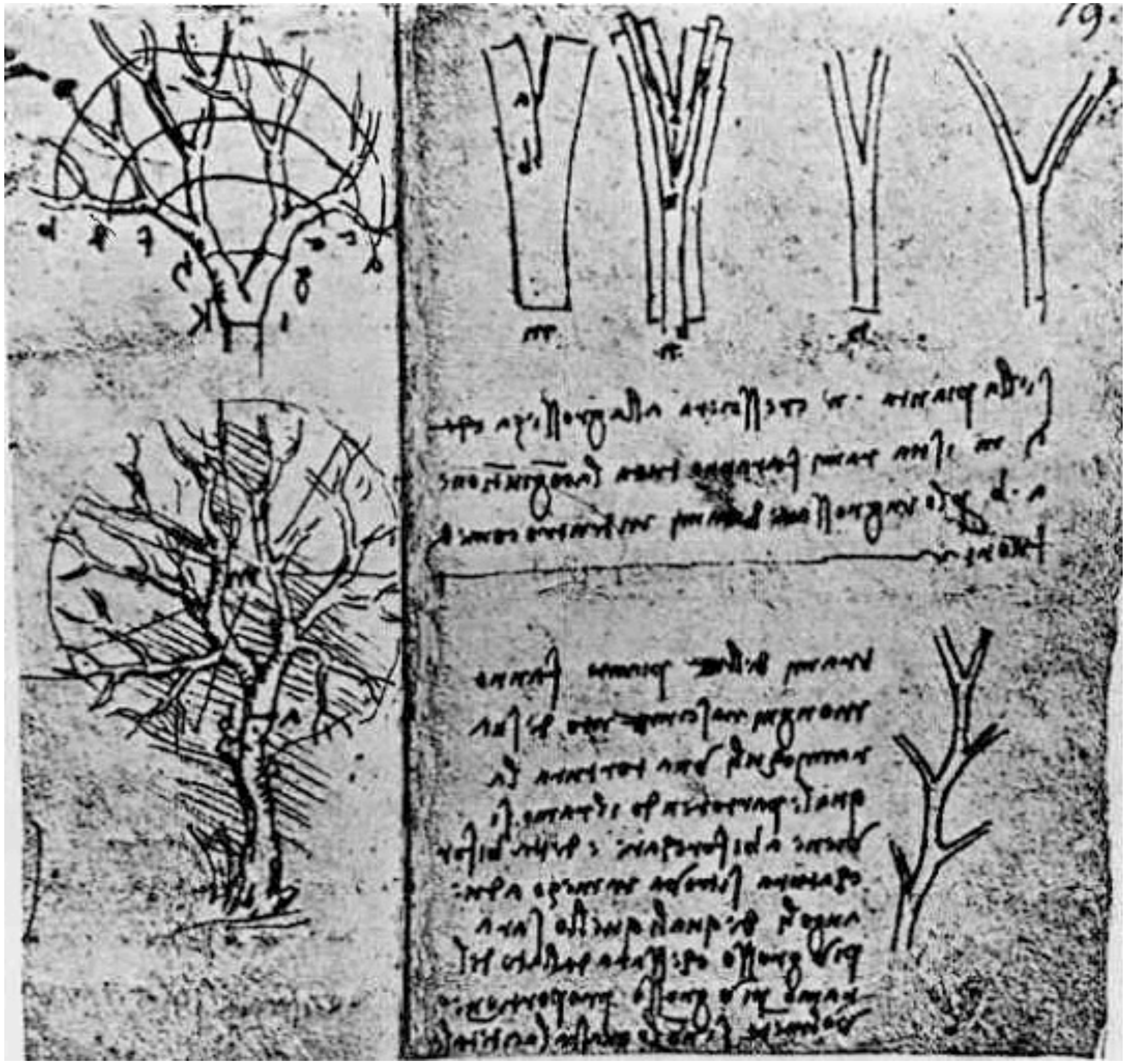


FIG. Da Vinci sketch showing area preserving branches in a bifurcating fractal structure.

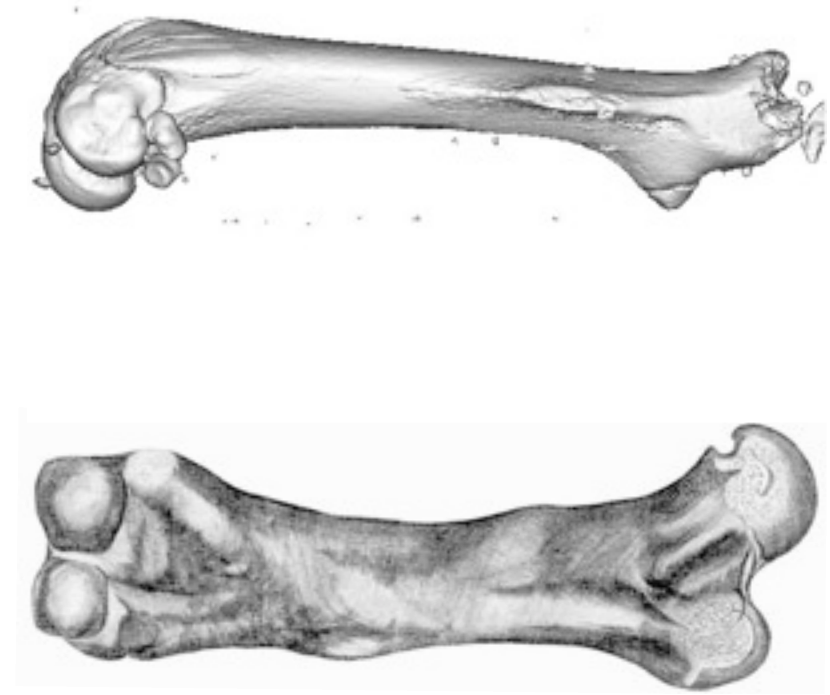


FIG. Femur bone of a mastodon (bottom) compared to that of a mouse (top) shown at the same scale.

FIG. Skeleton of a cat.

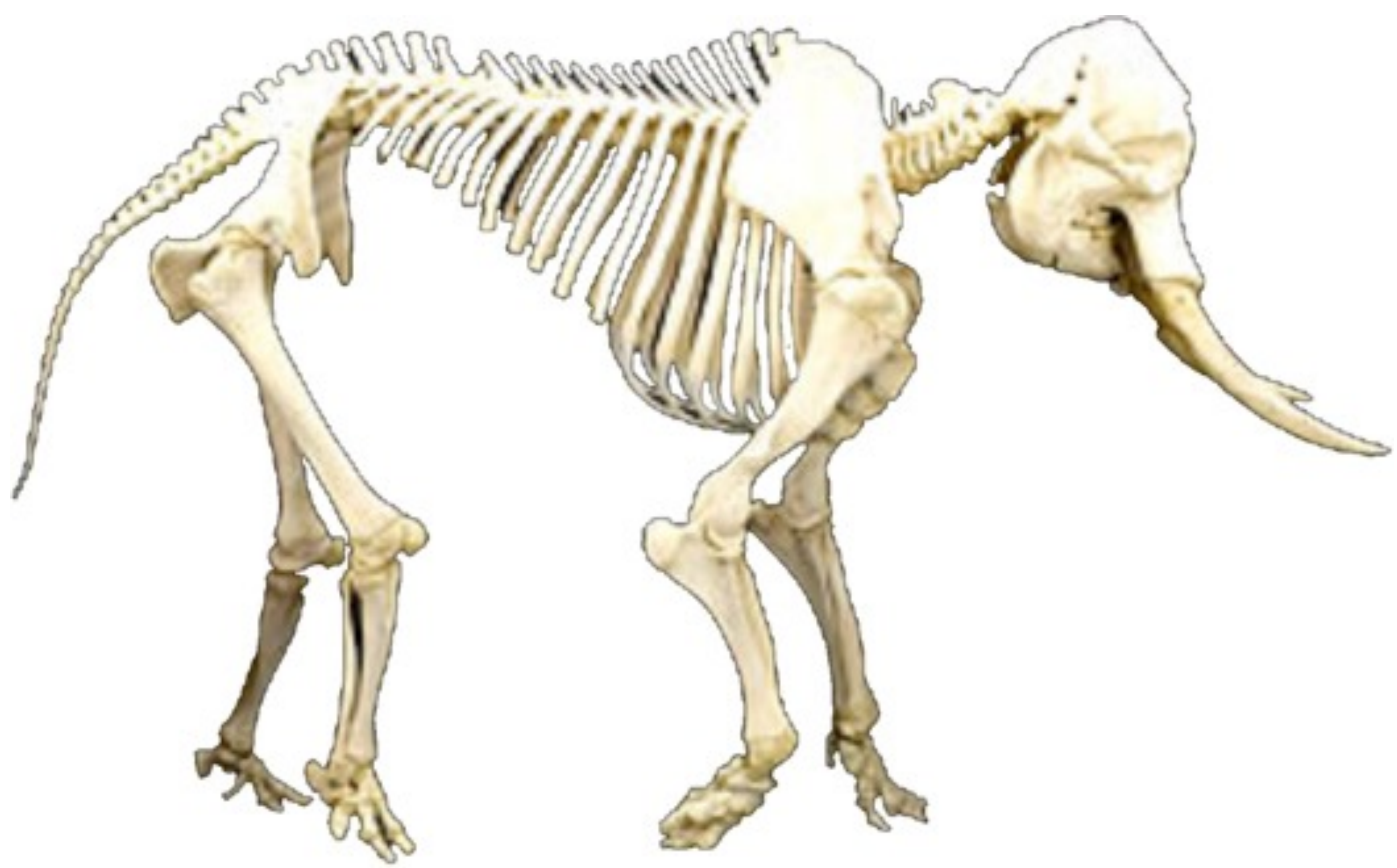


FIG. Skeleton of an elephant.

Surface hypothesis:

Volume of a sphere: $\frac{4}{3}\pi r^3$ "Volume of a sphere scales as the radius cubed"

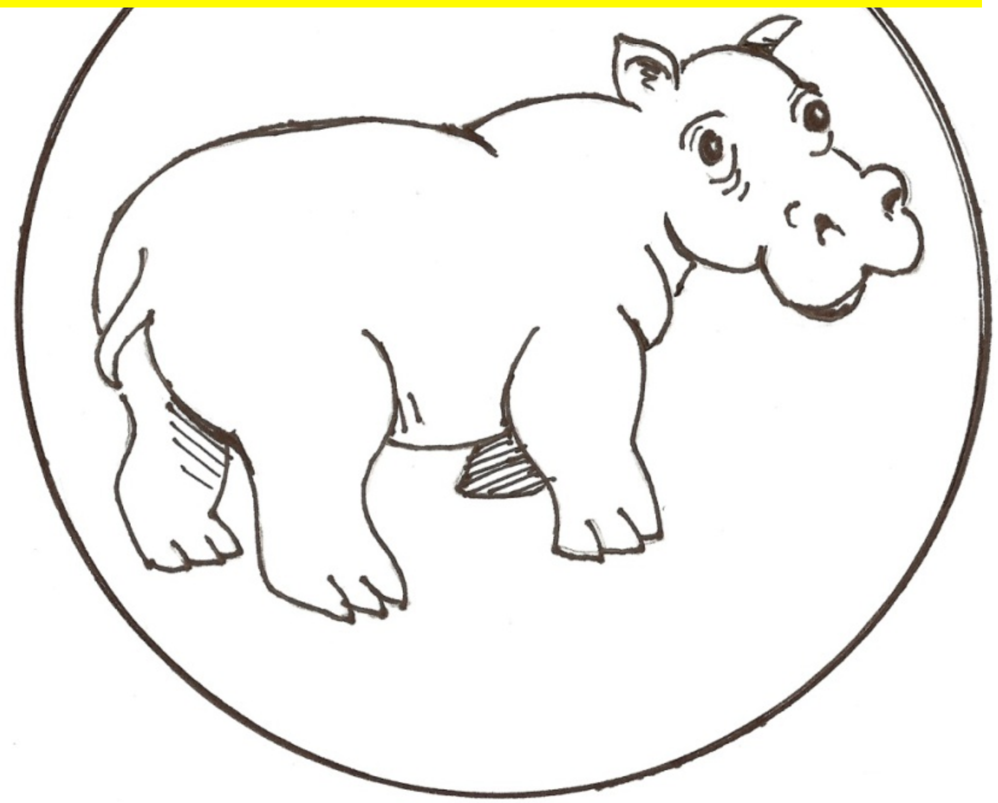
Surface area of a sphere: $4\pi r^2$ "Surface area of a sphere scales as the radius squared"

Surface area scales with volume to the 2/3 power.

Hypothesis 2 ("Surface Hypothesis): metabolic rate $\propto$ mass$^{2/3}$

mouse

hamster
(8 × mouse mass)

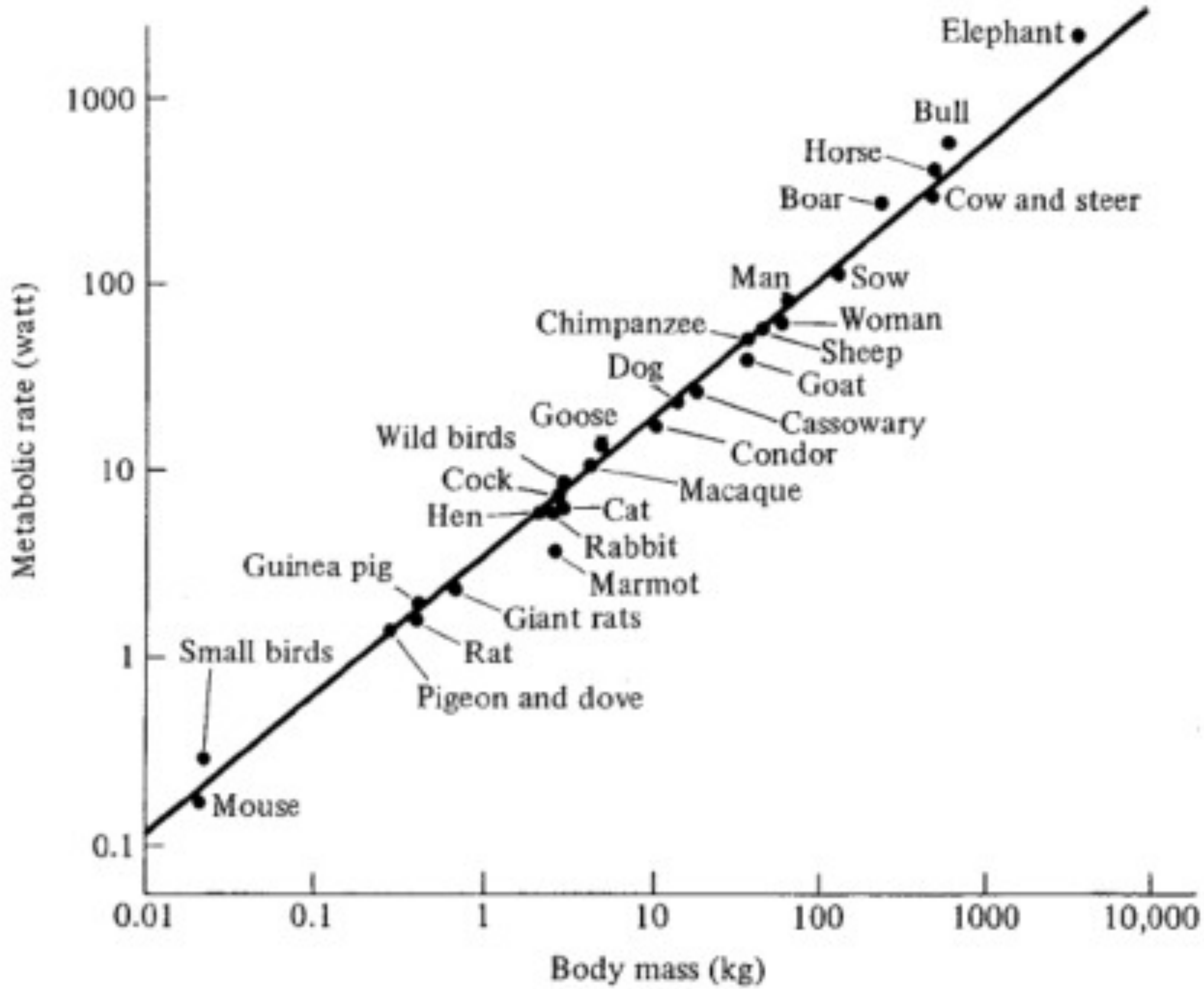


hippo
(125,000 × mouse mass)

$$y = cx^{\frac{2}{3}}$$

Actual data:

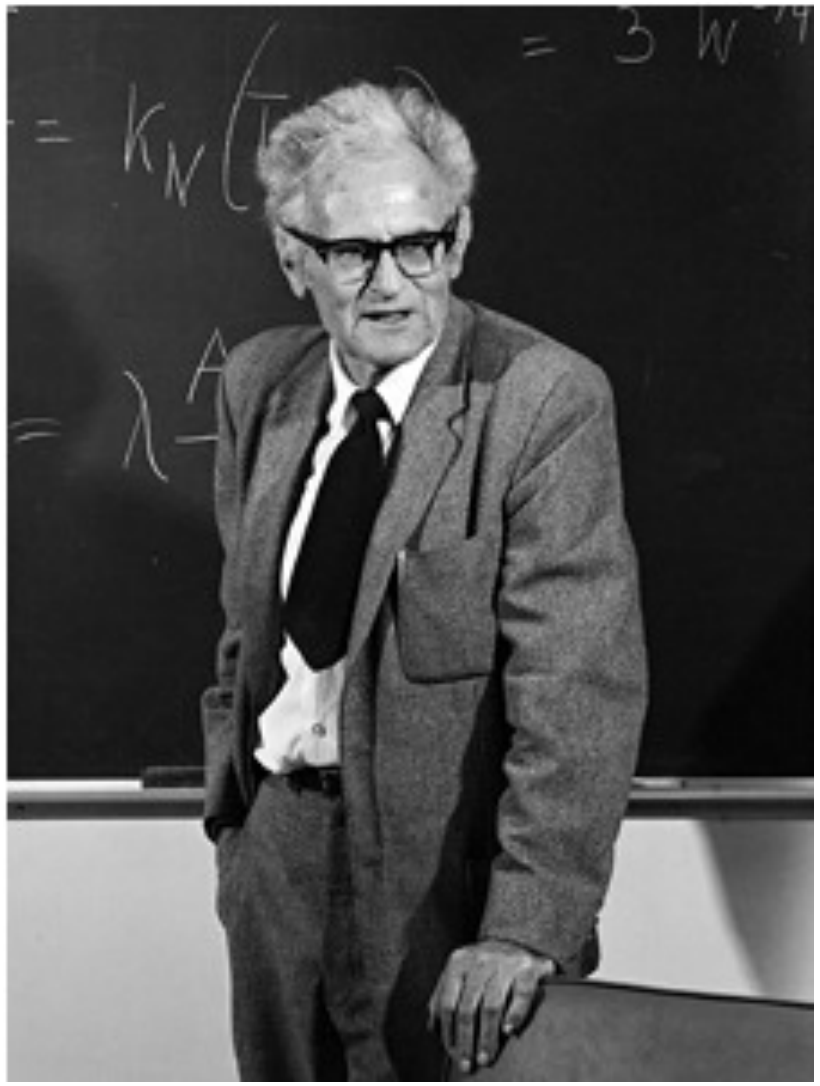
$y = x^{3/4}$



Hypothesis 3 ("Kleiber's law): metabolic rate $\propto$ mass$^{3/4}$

$$y = cx^{\frac{3}{4}}$$

Kleiber's Law:



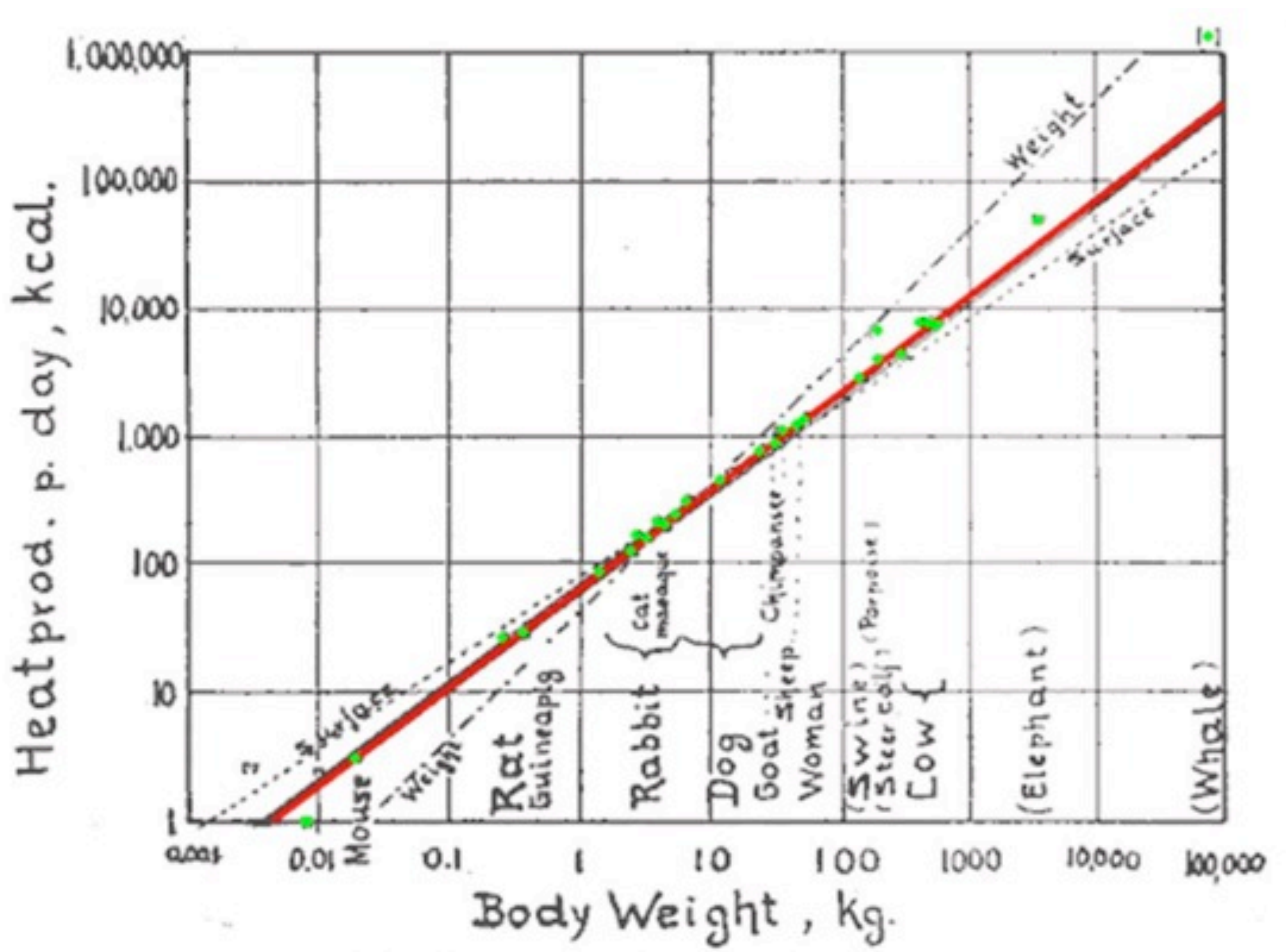
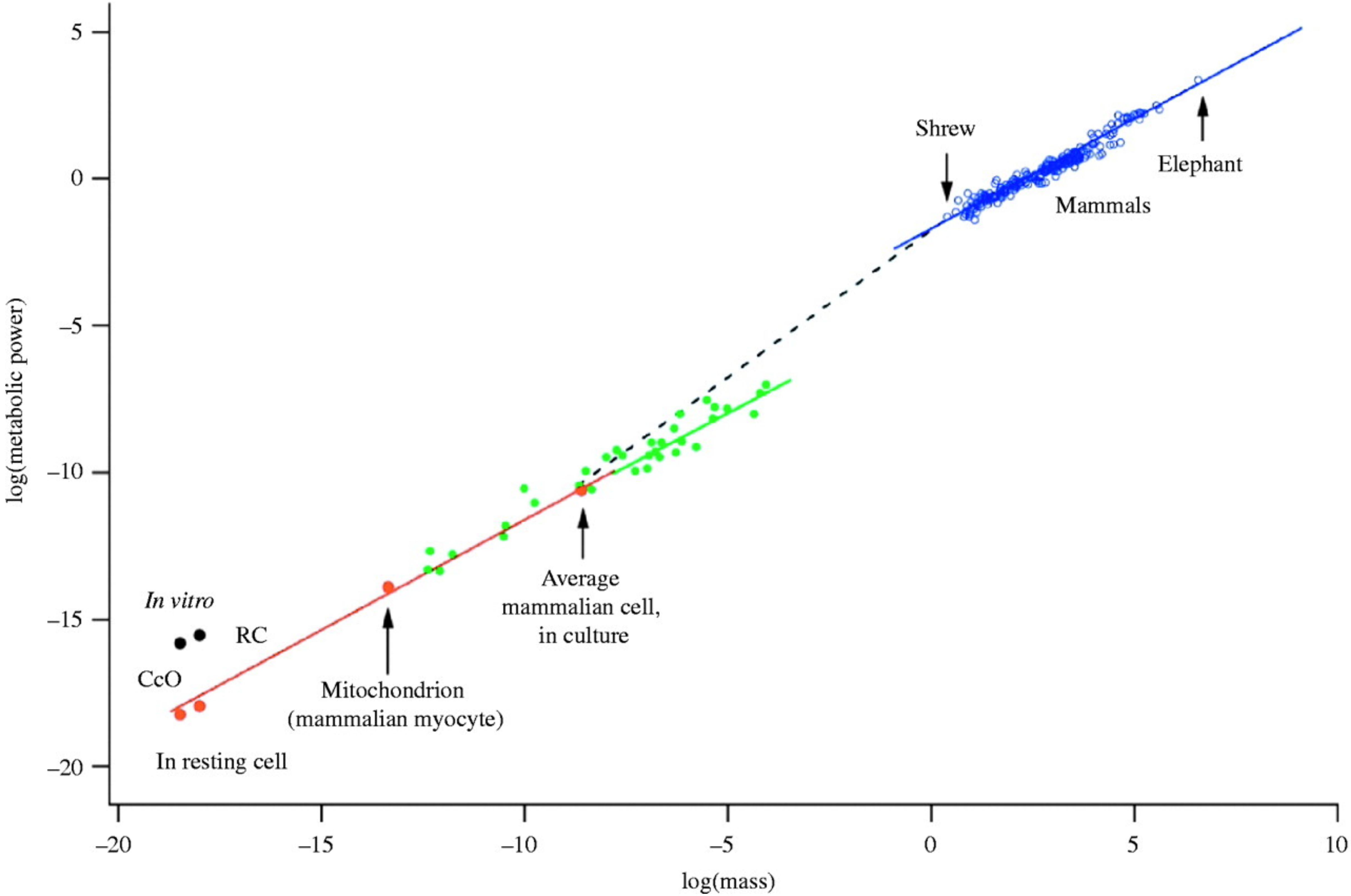


Fig. 1. Log. metabol. rate/log body weight

http://upload.wikimedia.org/wikipedia/commons/b/b7/Kleiber1947.jpg

FIG. Max Kleiber 1893 - 1976, was a Swiss agricultural biologist and professor of Animal Physiology at University of California, Davis from 1929 - 1960

Kleiber's Law:



Kleiber's law extends over 21 orders of magnitude

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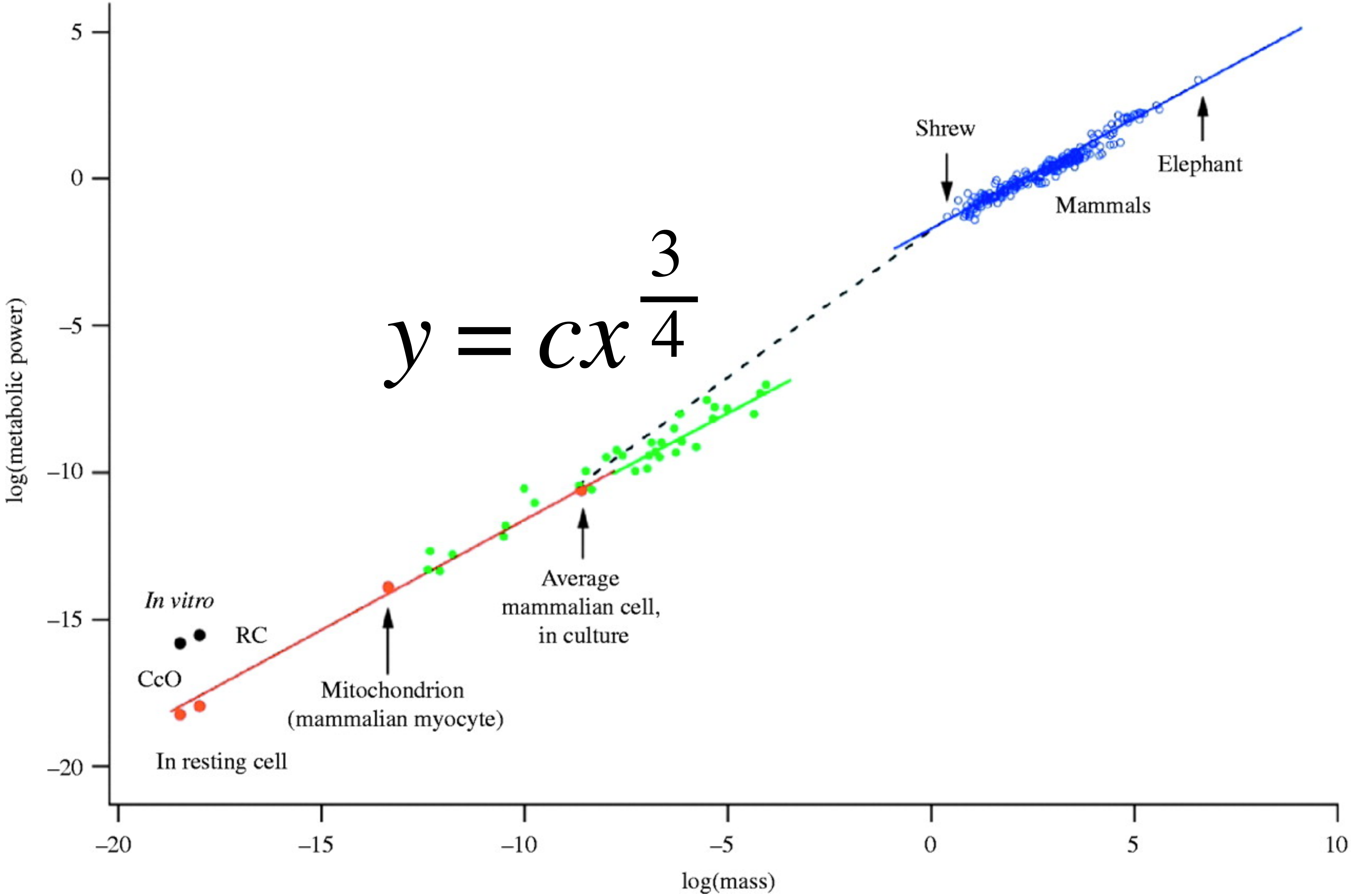
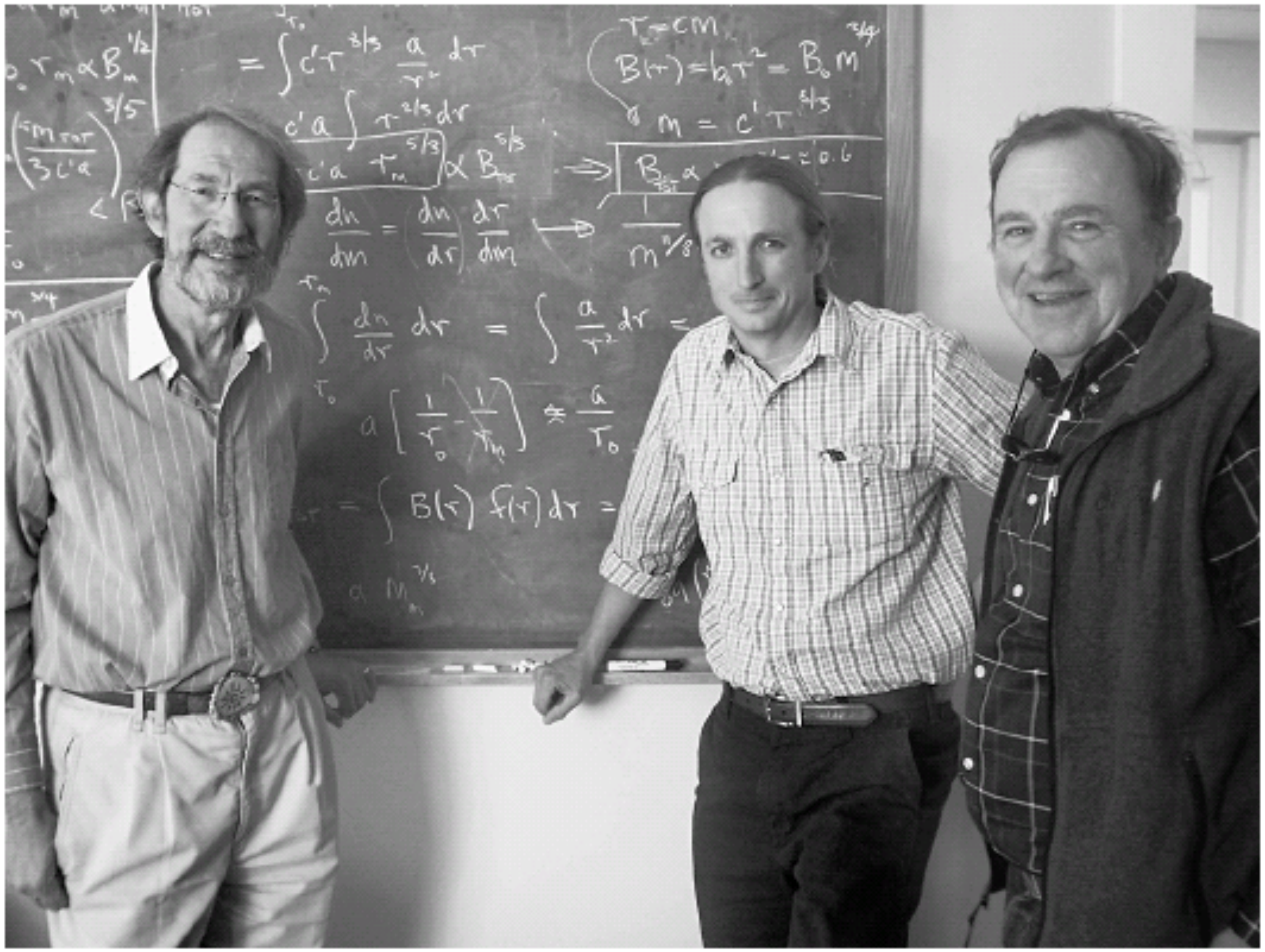


$$y = cx^{\frac{3}{4}}$$

Kleiber's law extends over 21 orders of magnitude

West, Brown, and Enquist's Theory (1990s)

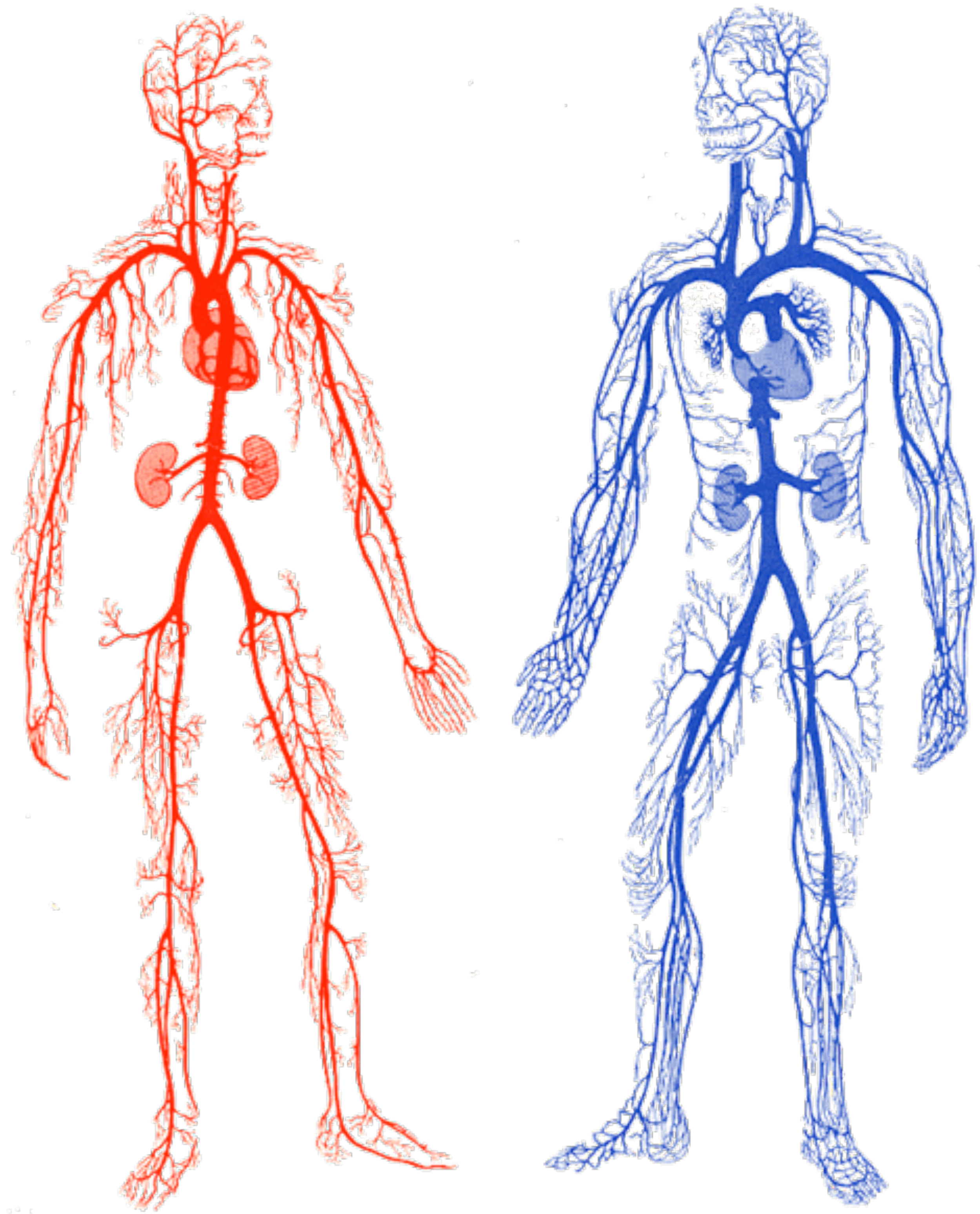


Left to right: Geoffrey West, Brian Enquist, and James Brown.

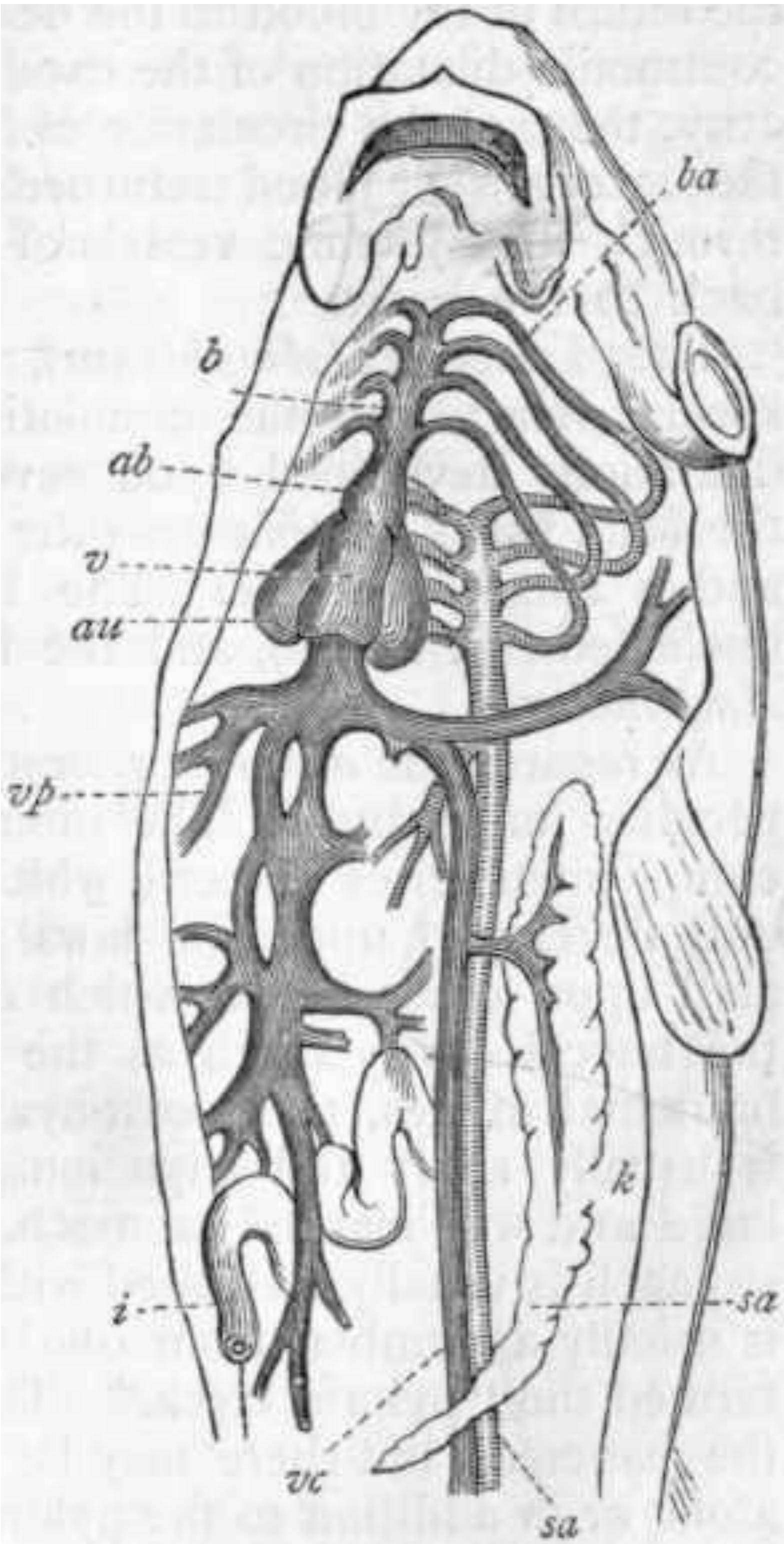
West, Brown Enquist Model: area *and* volume Preserving:

http://www.cwu.edu/~ratlifja/Fractals.html

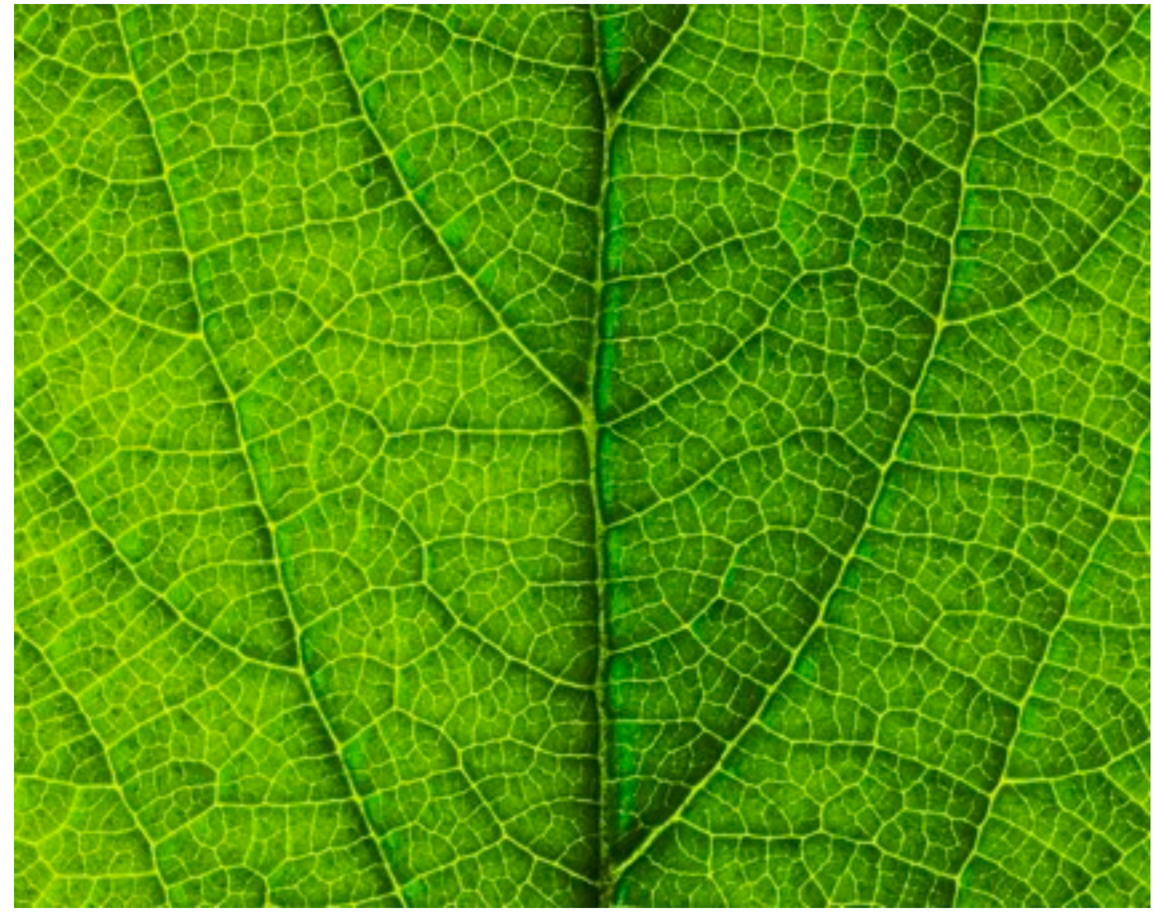
http://twistedsifter.com/2012/05/picture-of-the-day-fractal-patterns-in-dried-out-desert-rivers/



http://scienceinspiration.blogspot.com/2012/04/human-circulatory-system.html



http://chestofbooks.com/animals/Manual-Of-Zoology/Division-I-Ichthyopsida-Class-I-Pisces-Part-5.html#.UXWGO2C7OeY



http://fineartamerica.com/featured/fractal-leaf-abstract-0063-thom-gourley.html

http://www.beyondthextramile.com/fractal_art.html

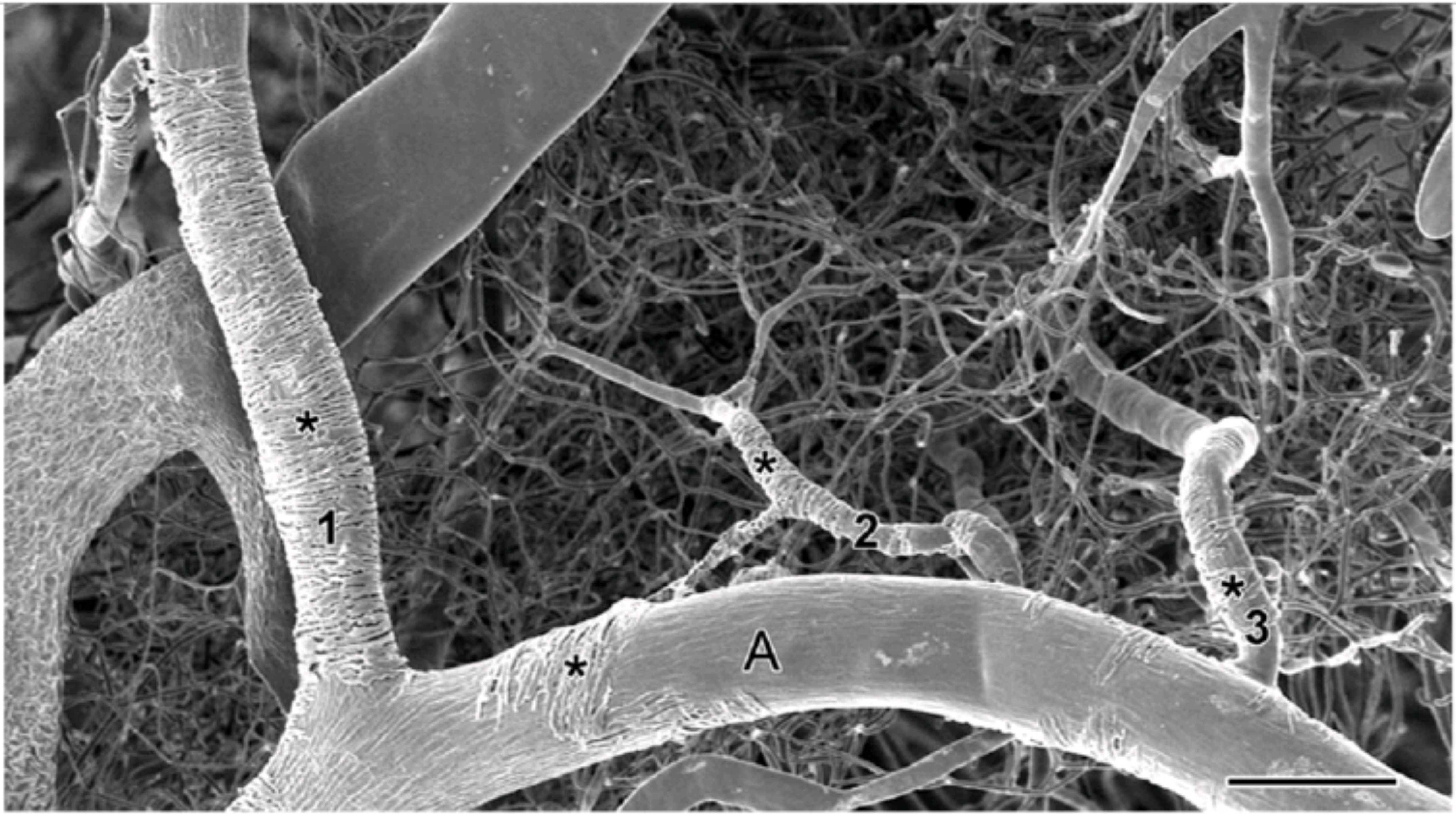
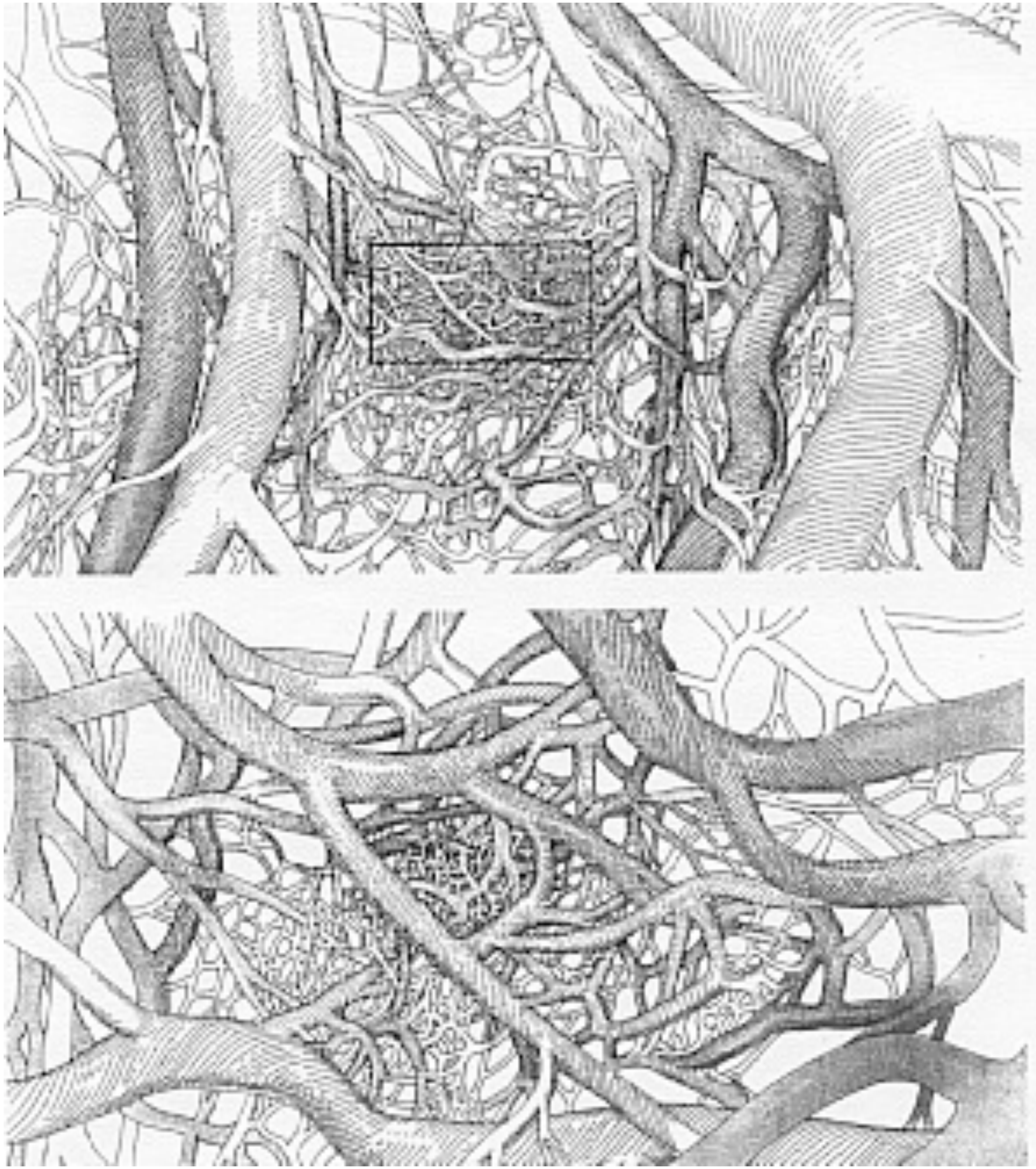


Figure 6. Scanning electron micrograph revealing vasculature within the area corresponding to the maximum acoustically evoked intrinsic signal. The arteries (A) and vein (V) can be clearly distinguished. 1, 2, 3: three types of arterial collateral vessels (see text). Note evidence of smooth muscle banding (asterisk symbols) on arteriole walls. Bar = 100 μm.

http://pubpages.unh.edu/~jel/brain_imaging/control_capillary.html



http://glimmerveen.nl/le/chaos.html

Other Observed Biological Scaling Laws

Heart rate $\propto$ body mass$^{-1/4}$

Blood circulation time $\propto$ body mass$^{1/4}$

Life span $\propto$ body mass$^{1/4}$

Growth rate $\propto$ body mass$^{-1/4}$

Heights of trees $\propto$ tree mass$^{1/4}$

Sap circulation time in trees $\propto$ tree mass$^{1/4}$

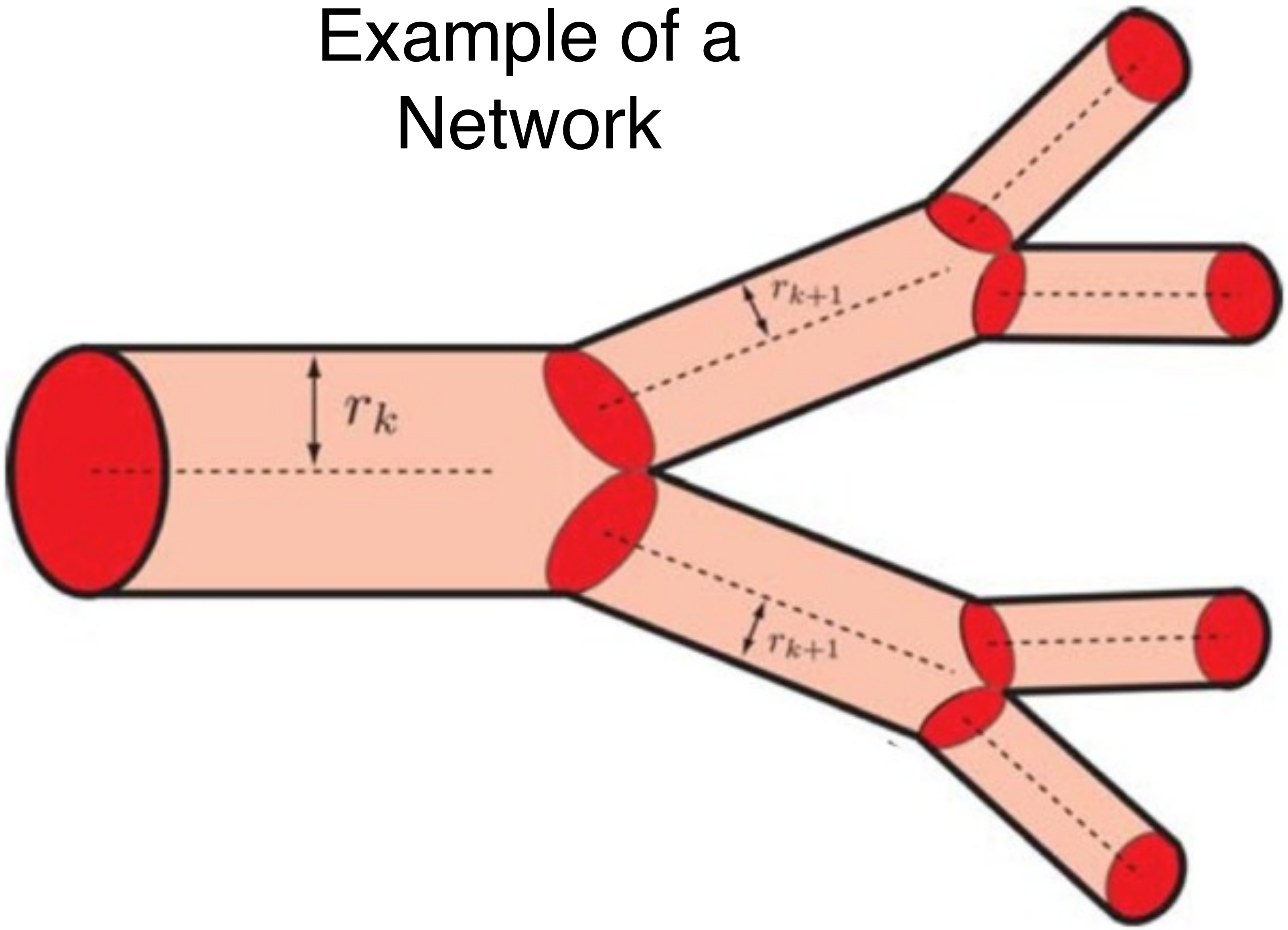
“An intriguing consequence of these ‘quarter-power’ scaling laws is the emergence of invariant properties, which physicists recognize as usually reflecting fundamental underlying constraints. For example, the mammalian life span increases as approximately mass $^{1/4}$, whereas heart rate decreases as mass $^{-1/4}$, so the number of heartbeats per lifetime is approximately invariant (about 1.5 billion independent of size)” (West, Brown 2004).

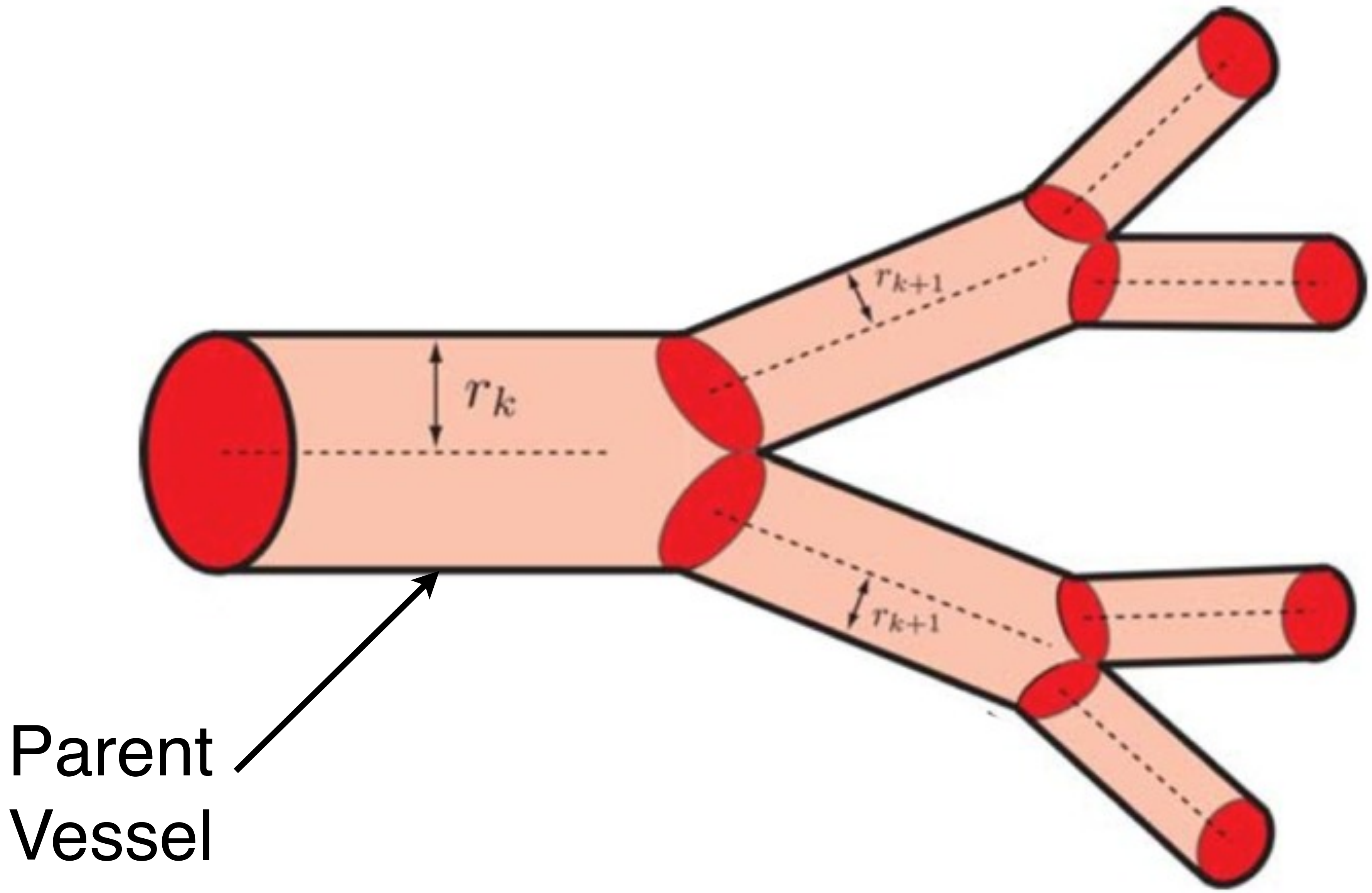
WBE model:

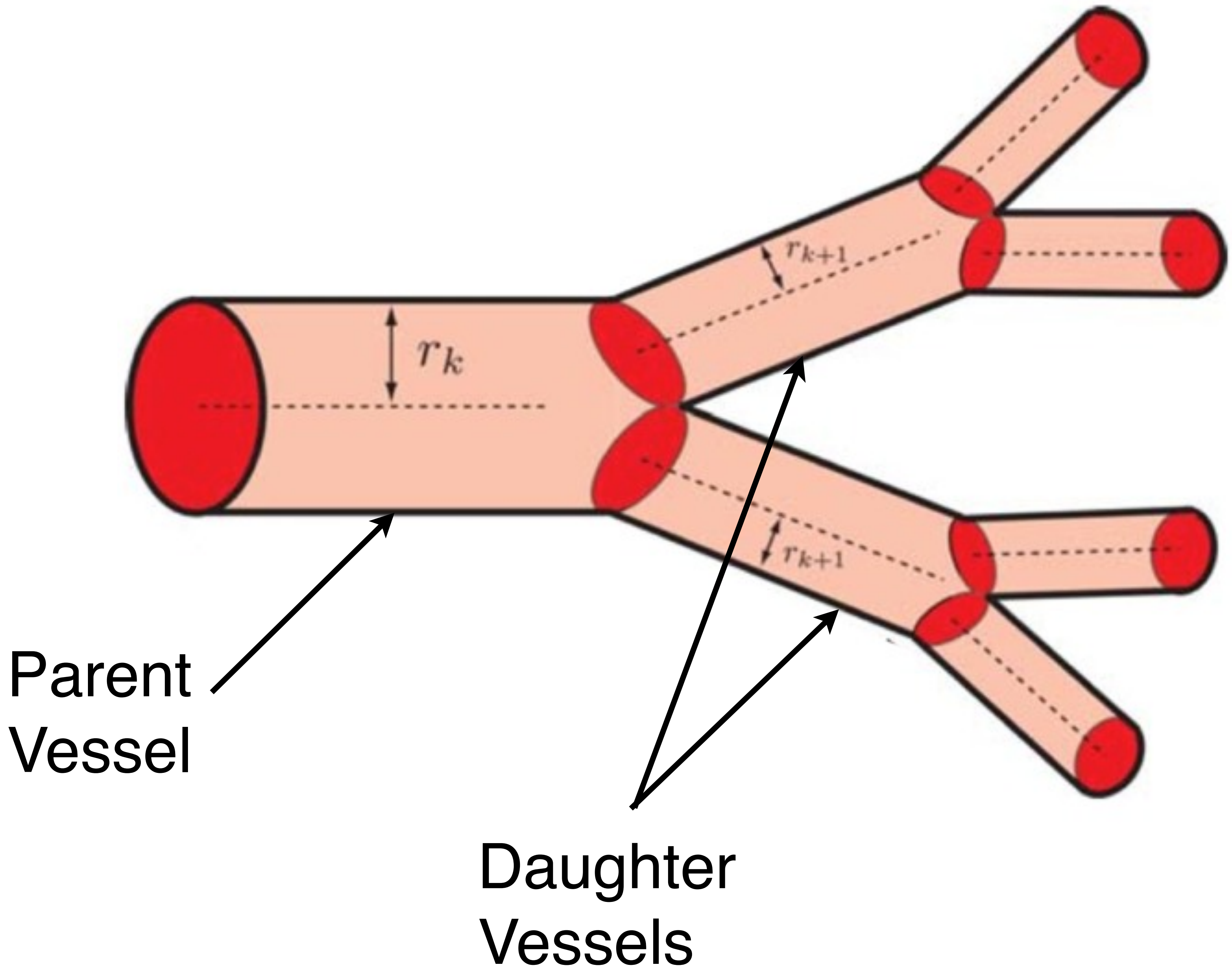
The West Brown Enquist model is derived from the relationship between the metabolism of an organism as measured by the *number of capillaries, i.e. terminal nodes in the network* compared to the mass of an an organism *as measured by the network volume which is the volume of blood in the vessels*.

number of capillaries / network volume

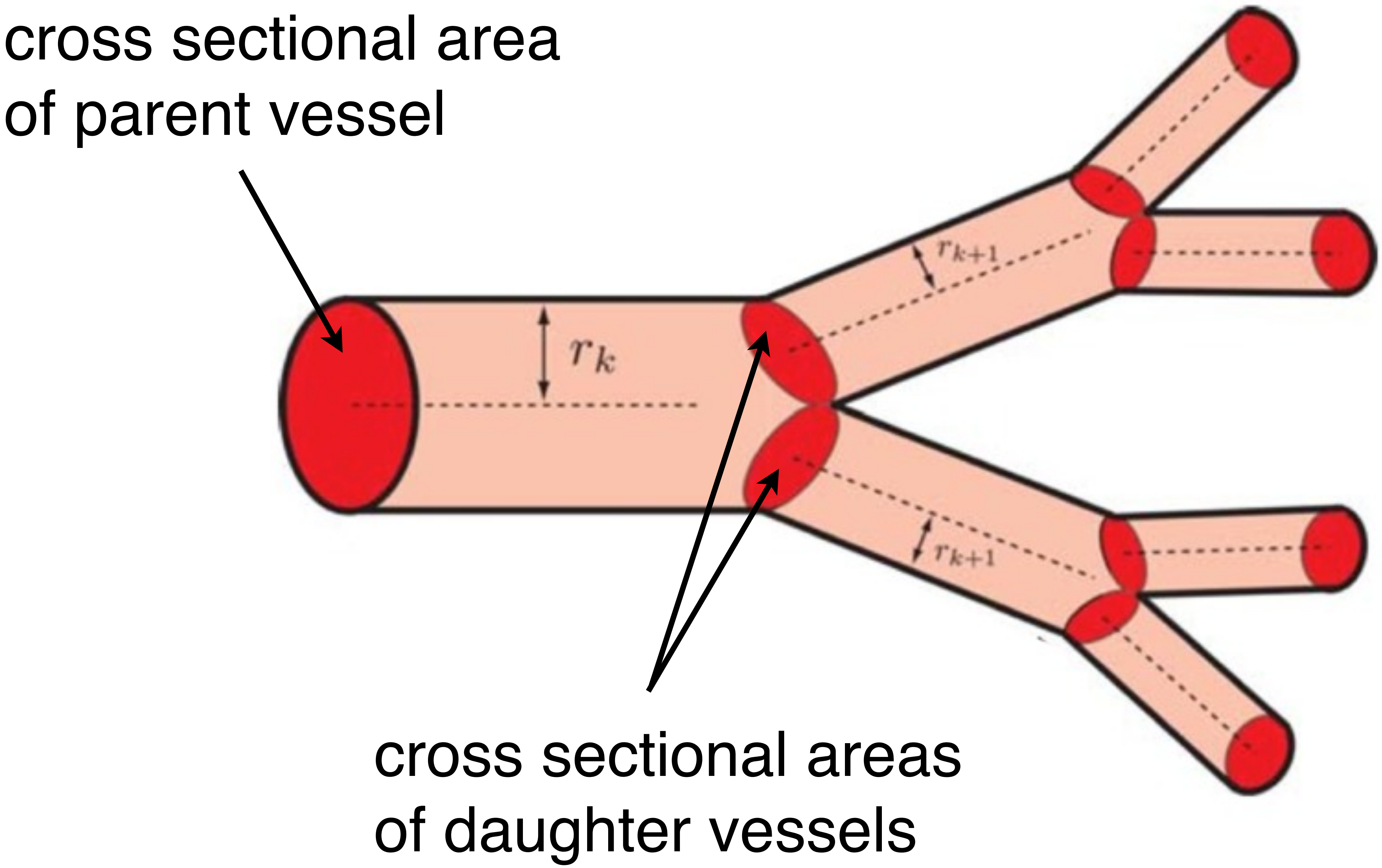
Example of a
Network



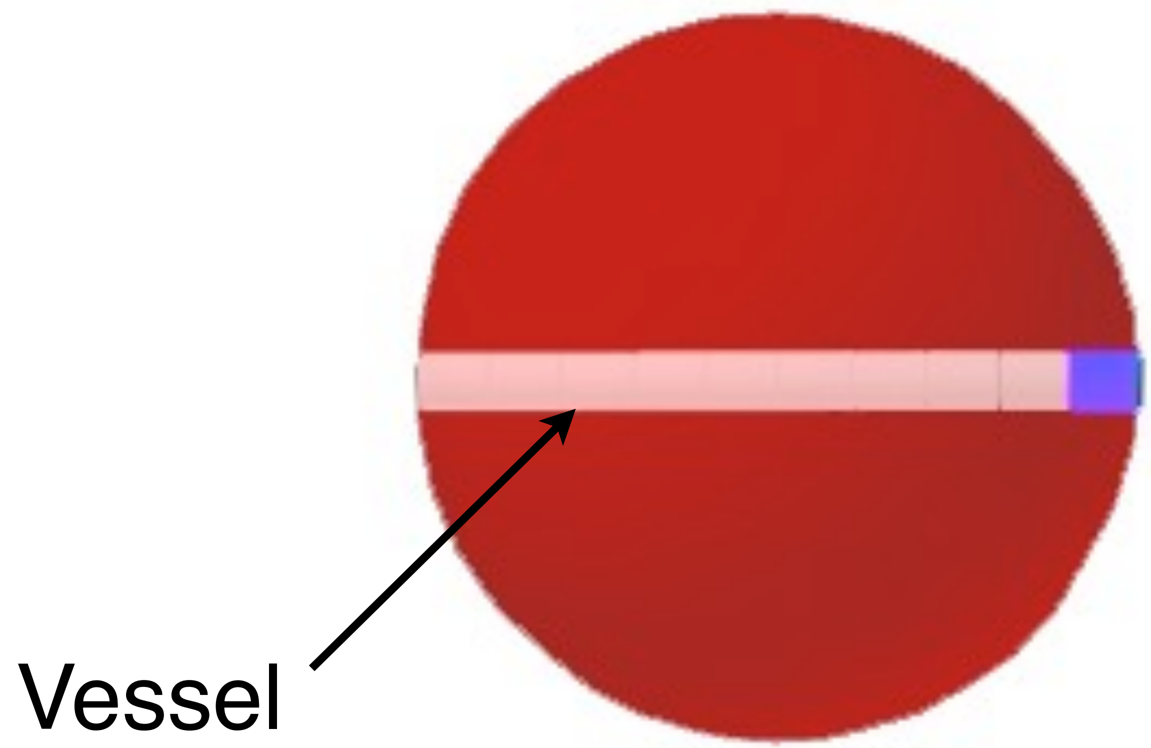

r_k
r_{k+1}
r_{k+1}
Parent
Vessel


r_k
r_{k+1}
r_{k+1}
Parent Vessel
Daughter Vessels

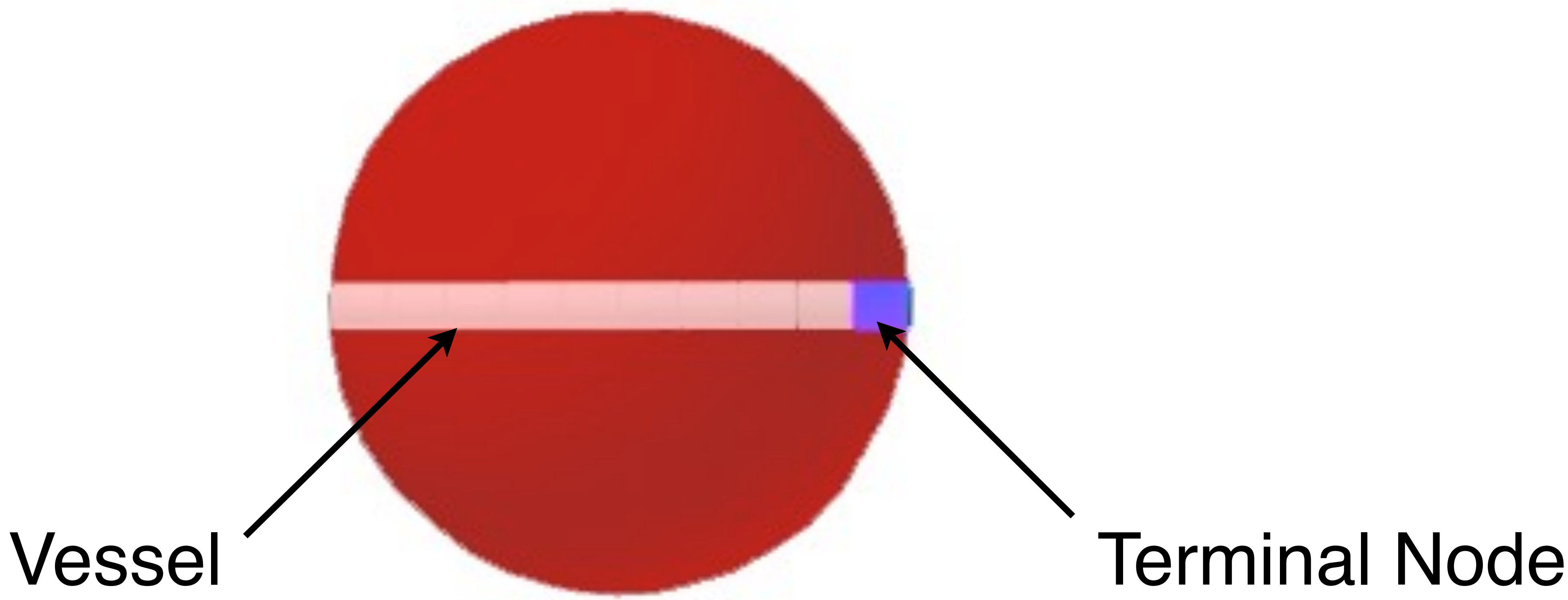
Area Preserving:



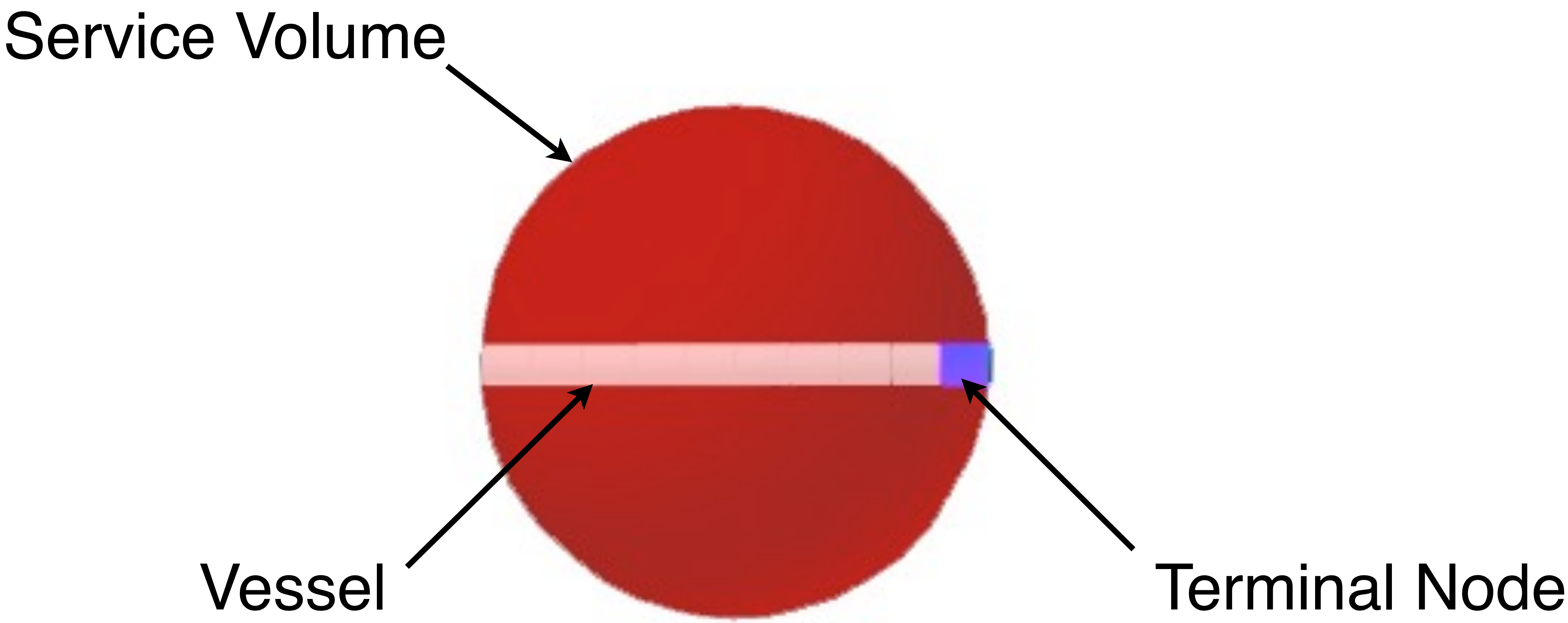
Volume Preserving:



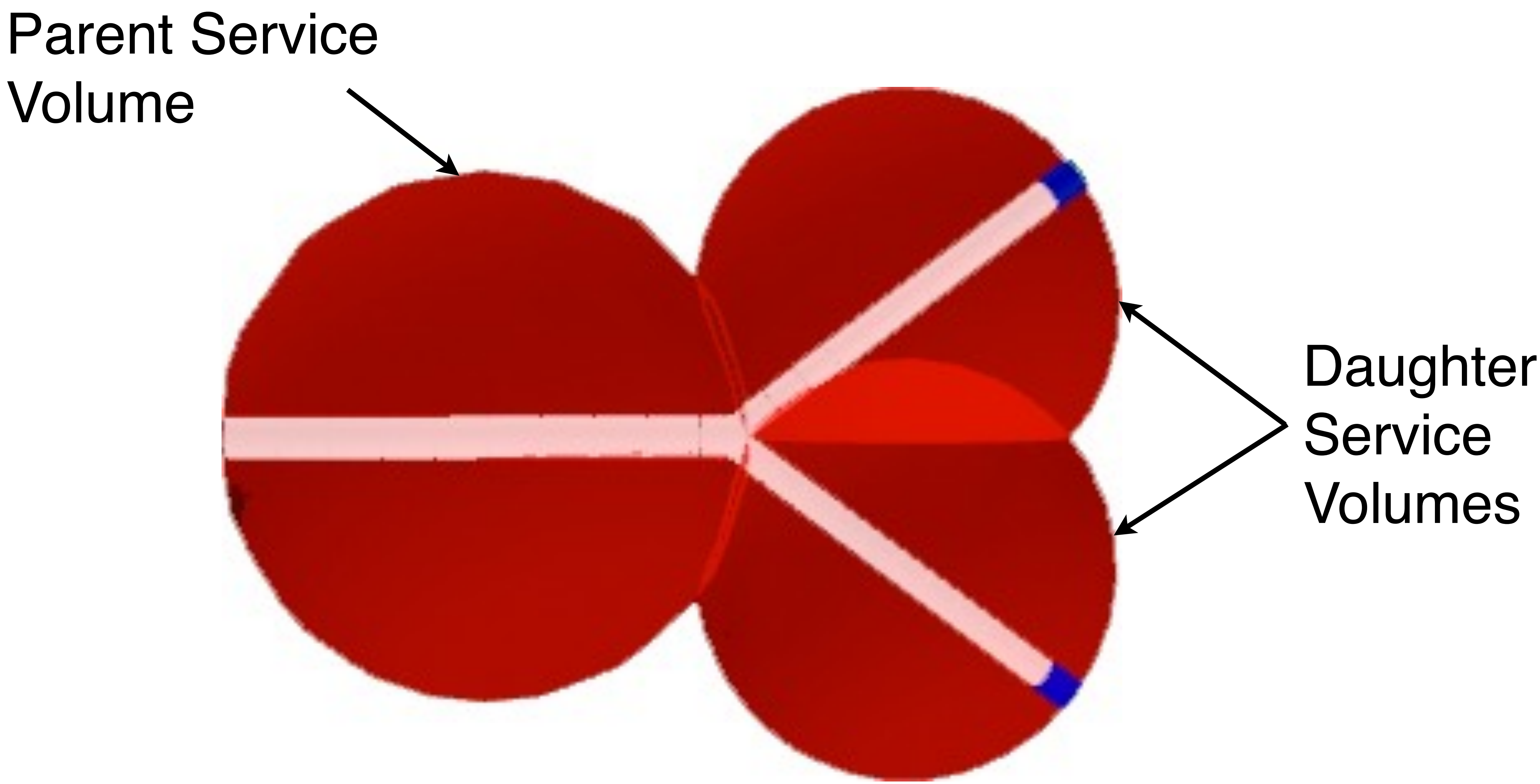
Volume Preserving:



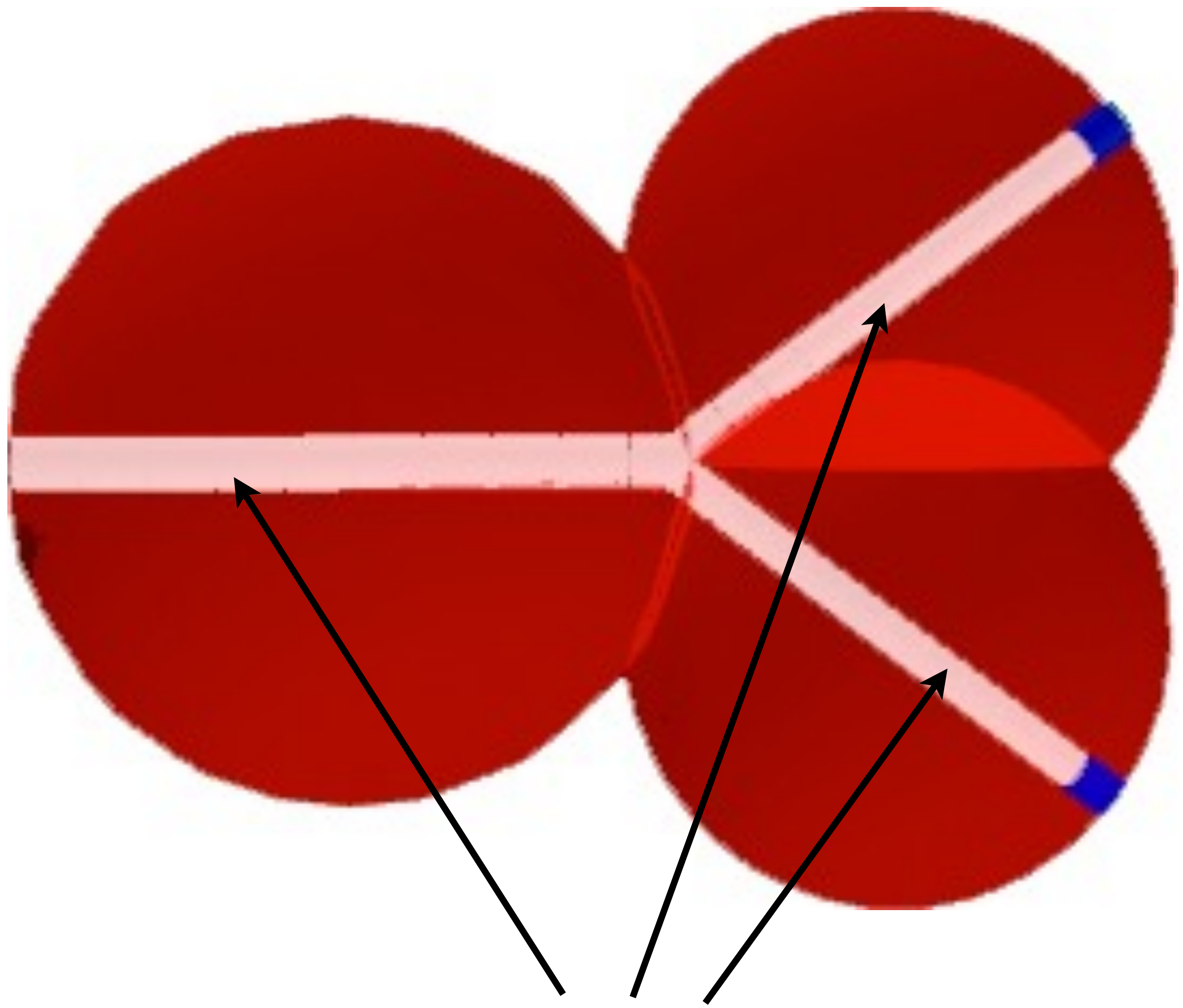
Volume Preserving:



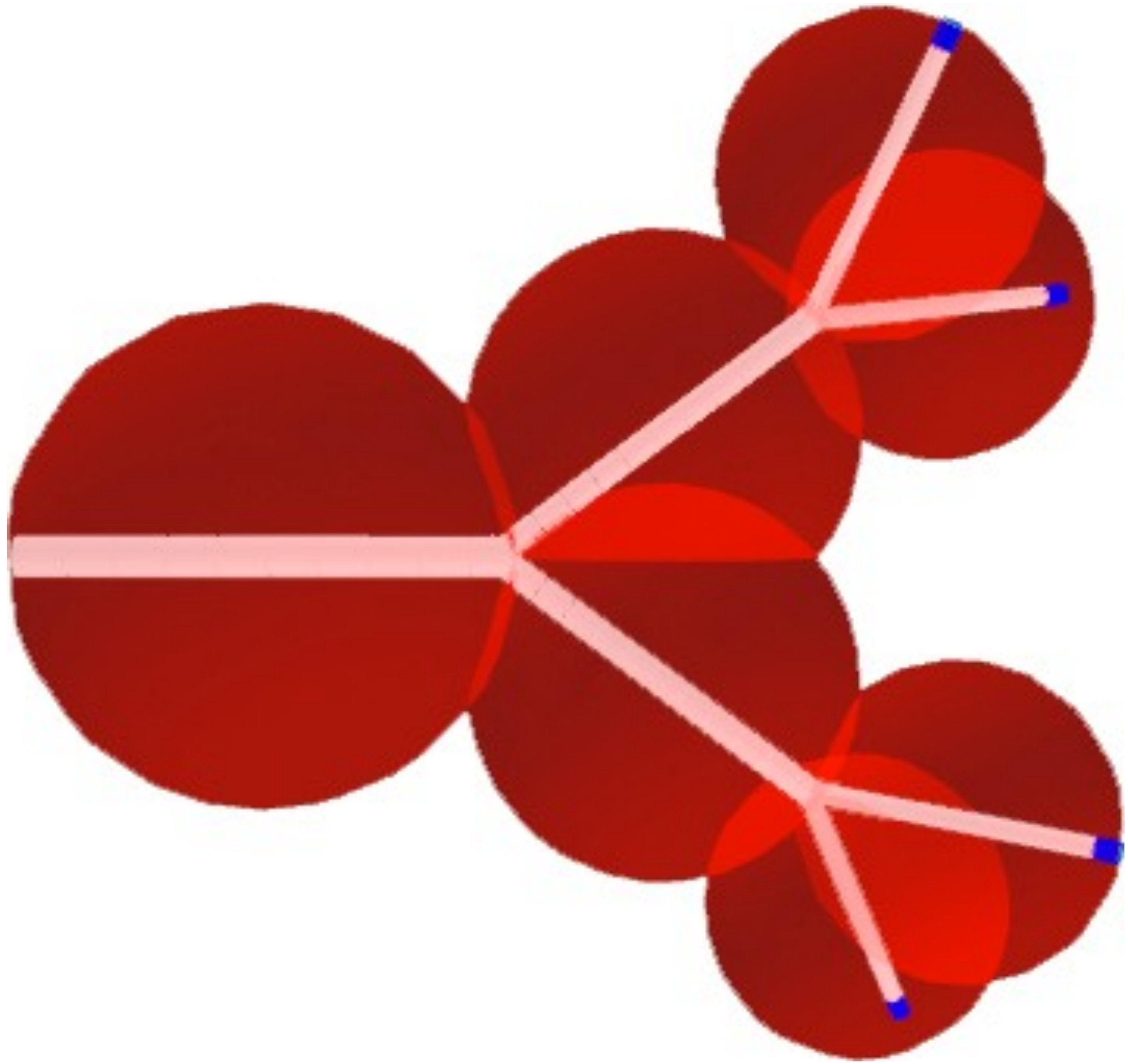
Area Preserving and Volume Preserving:

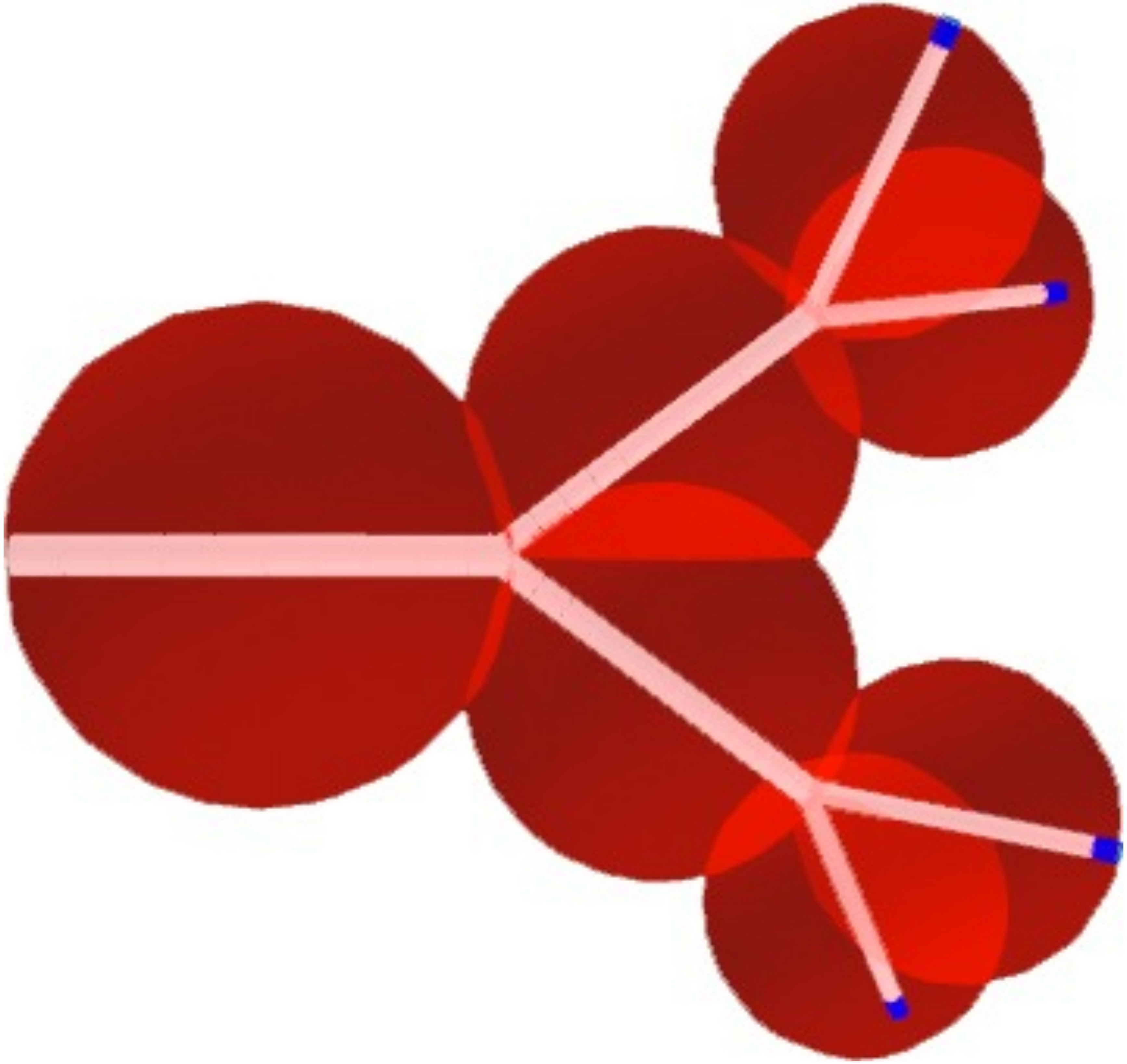


Area Preserving and Volume Preserving:



Network Volume = sum of
the volume of the vessels

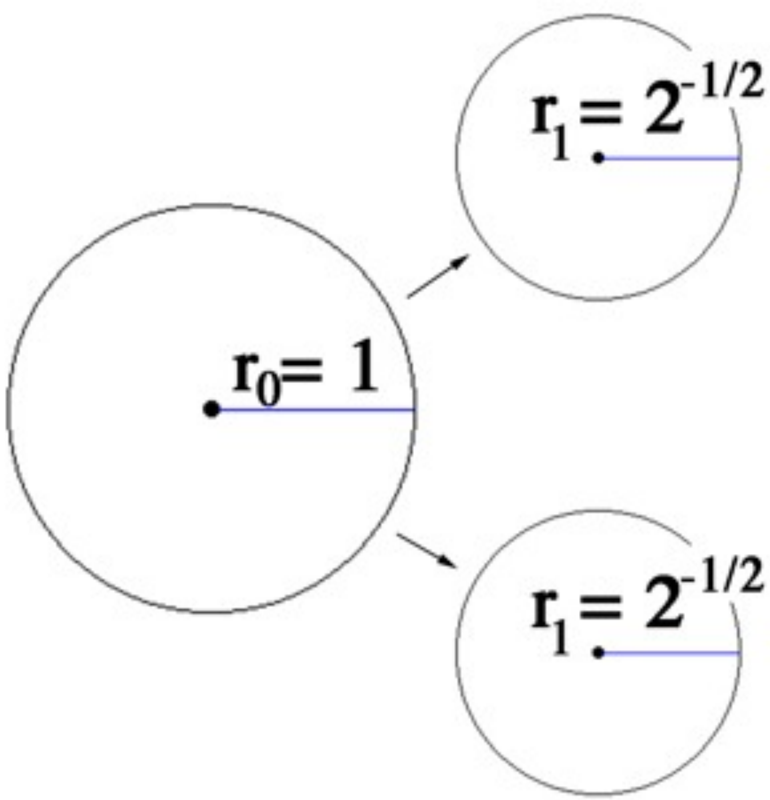


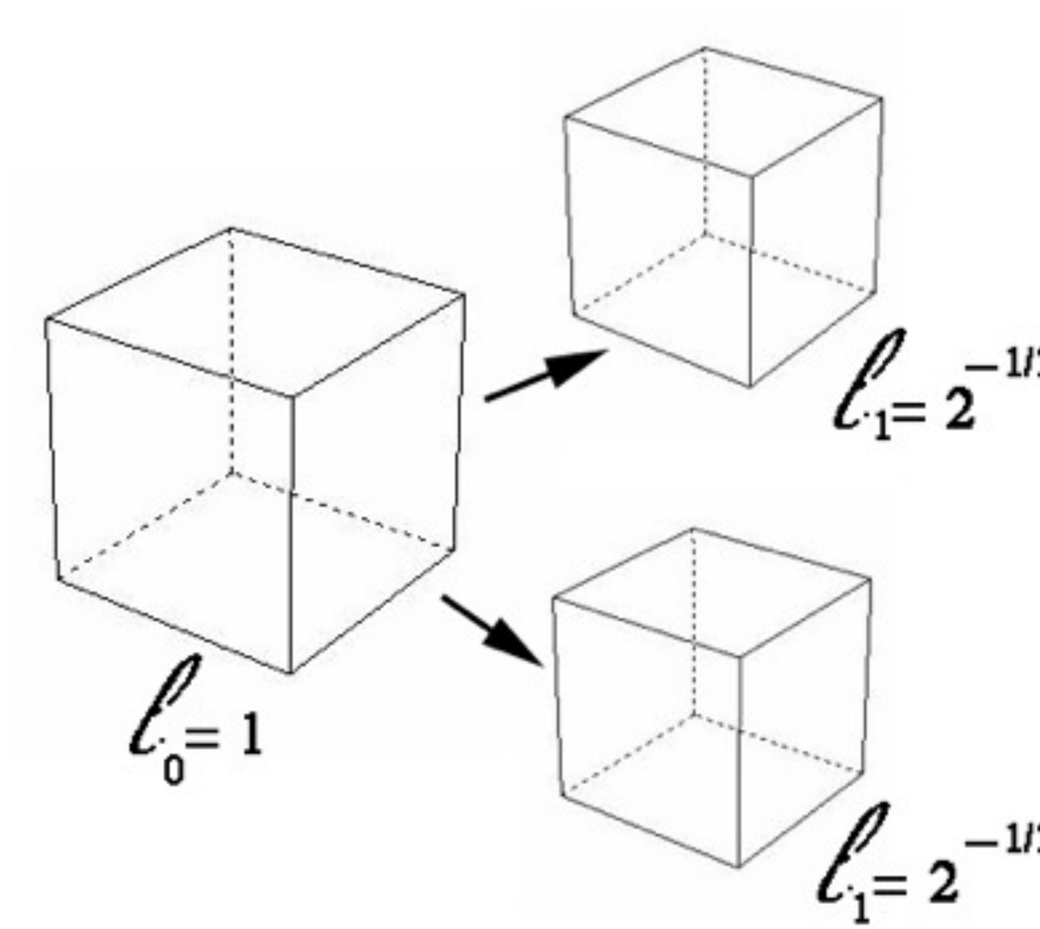


number of capillaries / network volume

Area Preserving

Volume Preserving





$$\beta = \mathbf{r_{k+1} / r_k = n^{-1/2}}$$

$$\lambda = \ell_{\mathbf{k+1}} / \ell_{\mathbf{k}} = \mathbf{n^{-1/3}}$$

WBE meets the Surface Hypothesis:

Now that we have studied both the West Brown Enquist hypothesis and the Surface hypothesis, it is intriguing to note the similarities between them. Recall in the surface hypothesis the power law exponent was 2/3. This is basically a relationship between a two dimensional surface and a three dimensional volume. In the WBE model the exponent is 3/4 which suggests a relationship between a three dimensional volume and a fourth dimension or *hyper-volume*. This has led Geoffrey West to suggest that biological organisms have adapted fractal networks which in essence utilize an added dimension. It is this property of life that allows for increased efficiency over that predicted by conventional models.

“Unlike the genetic code, which has evolved only once in the history of life, fractal-like distribution networks that confer an additional effective fourth dimension have originated many times. Examples include extensive surface areas of leaves, gills, lungs, guts, kidneys, chloroplasts, and mitochondria, the whole-organism branching architectures of trees, sponges, hydrozoans, and crinoids, and the treelike networks of diverse respiratory and circulatory systems. It is not surprising, therefore, that even unicellular organisms exhibit quarter-power scaling, including the 3/4-power scaling law for metabolic rate. Although living things occupy a three-dimensional space, their internal physiology and anatomy operate as if they were four-dimensional.” (West et al. 1999).

Controversy:

In the West Brown Enquist model, abstractions of real networks, such as vascular networks in human beings, are necessarily generalized to apply to many examples where definitions may become more ambiguous or serve as analogies rather than strict associations between the mathematical model and real world networks. For instance, in microbial organisms it is not clear what constitutes a service volume (or network for that matter). Further ambiguity is introduced in referring to spatial networks as *fourth* dimensional. Analogy and description gets a little blurry in WBE and has fed criticism. For a good outline of the major critical camps concerning WBE, see ‘Complexity a Guided Tour’ (Mitchell 2009) and ‘Metabolic scaling: Consensus or Controversy?’ (Agutter, Wheatley 2004).

Summary:

http://www.ajo.com/article/S0002-9394(99)00411-0/abstract

http://www.ajo.com/article/S0002-9394(99)00411-0/abstract

Appendix:

Assumptions of the WBE model:

- ***The network is space filling.*** WBE uses averaged networks which are cross sectional area preserving and space-filling, meaning they distribute to all service areas in an organism.
- ***The energy loss of fluid flow through the network is minimized.*** Network efficiency in terms of resources distribution and energy use has been selected for through the evolutionary processes of any particular organism.
- ***Capillary characteristics are the same across species.*** The terminal units of all members of a given taxonomy are the same size, i.e. capillaries are invariant within a taxon. A related concept is that individual cells are the same size in different organisms.

Appendix:

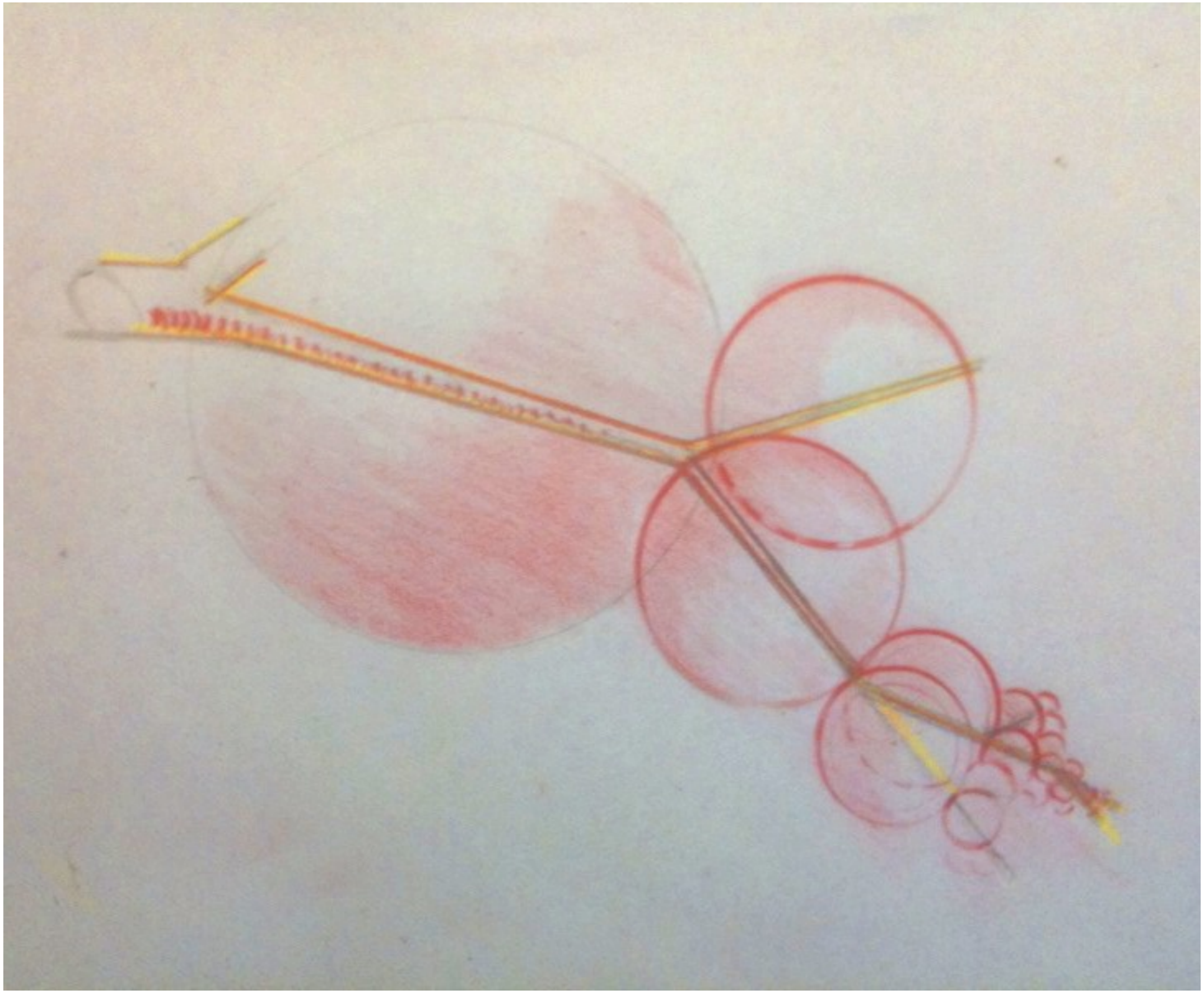


FIG. Space filling fractal network showing both area preserving and volume preserving characteristics..

Appendix:
Formal WBE derivation but not necessary to know for this course:

M - mass (linearly proportional to volume of blood) $M \propto V_{blood}$

B - metabolism (linearly proportional to number of invariant terminal units) $B \propto V_{cap} N_{cap} \propto N_{cap}$

n - branching ratio. For this model is bifurcating so is = 2

N - number of nodes at a given level k

$\mathbf{r_k}$ - radius at a given level

$\boldsymbol{\ell_k}$ - length at a given level

T - the terminal level in the network, this is the level with capillaries.

$$M \propto V_{blood} = \sum_{k=0}^{T} N_k \pi r_k^2 \ell_k$$ *sum of the number of vessels' volumes*

$\pi \ell_k r_k^2$ = *volume of a single tube at level k*

$$= \sum_{k=0}^{T} n^k \pi (\lambda^{-(T-k)} \ell_N)(\beta^{-2(T-k)} r_N^2)$$ ❄ *number of vessels*

n = 2 for bifurcating network

$$= \pi r_T^2 \ell_T \sum n^k \lambda^{-(T-k)} \beta^{-2(T-k)}$$

volume of a single capillary

$$= n^T V_T \sum n^{-(T-k)} \lambda^{-(T-k)} \beta^{-2(T-k)}$$

$N_T = N_{cap}$ $V_T = V_{cap}$

$$= n^T V_{cap} \sum 1 / (n \lambda \beta^2)^{(T-k)}$$ *sum of geometric series**

$$= V_{cap}\ n^{(4T/3+1/3)} - n^T / n^{1/3} - 1$$

lim as $T \to \infty$ = $n^{4/3}$ *all but leading term drop out*

$$M \propto V_{blood} \propto V_{cap}\, n^{(4T/3)} \propto V_{cap}\, \underbrace{(n^T)}_{N_{cap}}{}^{4/3} \text{ for } T \to \infty$$

$$M \propto V_{blood} \propto V_{cap}\ N_{cap}^{4/3}$$

$M \propto V_{blood} \propto B^{4/3}$ because [$B = N_T B_T$ (invariant) $\propto N_T$ $\therefore$ $\mathbf{B \propto M^{3/4}}$

❄ $\dfrac{\ell_k}{\ell_T} = (\ell_k / \ell_{k+1})(\ell_{k+1} / \ell_{k+2}) \ldots (\ell_{T-1} / \ell_T)$

(λ^{-1}) $(\lambda^{-1}) \ldots$

$(T-k)$

$\ell_k = (\lambda^{-(T-k)}) \ell_T$

$\boldsymbol{\lambda} = (\ell_{k+1} / \ell_k) = n^{-1/3}$

$r_k = (\beta^{-(T-k)}) r_T$

$\boldsymbol{\beta} = (r_{k+1} / r_k) = n^{-1/2}$

$$\sum_{k=0}^{T} 1 / (n \lambda \beta^2)^{(T-k)}$$

let $k' = T - k$

let $x = (n \lambda \beta^2)^{-1}$

$$\sum_{K'=0}^{T} x^{k'} = (n(n^{1/3} n^{1})^{-1} = n^{1/3}$$

$x^{T+1} - 1 / x - 1$ *(geometric series)*

$n^{T+1/3} - 1 / n^{1/3} - 1$