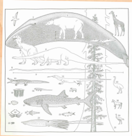
Scaling—a Plenitude of Power Laws

Principles of Complex Systems
CSYS/MATH 300, Fall, 2011

Prof. Peter Dodds

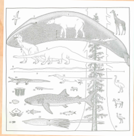
Department of Mathematics & Statistics | Center for Complex Systems | Vermont Advanced Computing Center | University of Vermont



Outline

Scaling-at-large
- Allometry
- Examples
- A focus: Metabolism
- Measuring exponents
- History: River networks
- Earlier theories
- Geometric argument
- Blood networks
- River networks
- Conclusion

References



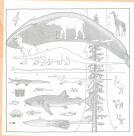
Scalingarama

General observation:

Systems (complex or not)
that cross many spatial and temporal scales
often exhibit some form of scaling.

Outline—All about scaling:

- Definitions.
- Examples.
- How to measure your power-law relationship.
- Metabolism and river networks.
- Mechanisms giving rise to your power-laws.



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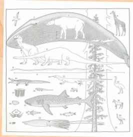

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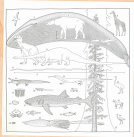

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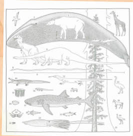
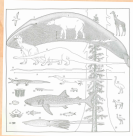


Definitions

A power law relates two variables x and y as follows:

$$y = cx^{\alpha}$$

- α is the scaling exponent (or just exponent)
- (α can be any number in principle but we will find various restrictions.)
- c is the prefactor (which can be important!)



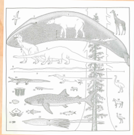
Definitions

- The prefactor c must balance dimensions.
- eg., length ℓ and volume v of common nails are related as:

$$\ell = cv^{1/4}$$

- Using $[\cdot]$ to indicate dimension, then

$$[c] = [l]/[V^{1/4}] = L/L^{3/4} = L^{1/4}.$$



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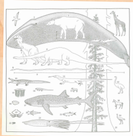

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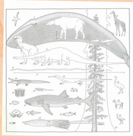


Looking at data

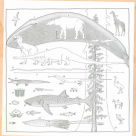
- Power-law relationships are linear in log-log space:

$$y = cx^{\alpha}$$

$$\Rightarrow \log_b y = \alpha \log_b x + \log_b c$$

with slope equal to α, the scaling exponent.

- Much searching for straight lines on log-log or double-logarithmic plots.
- Good practice: Always, always, always use base 10.
- Talk only about orders of magnitude (powers of 10).



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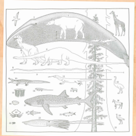

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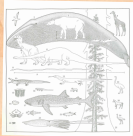

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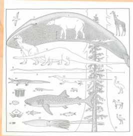
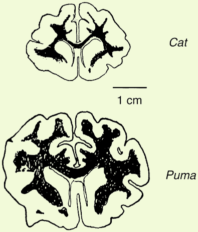
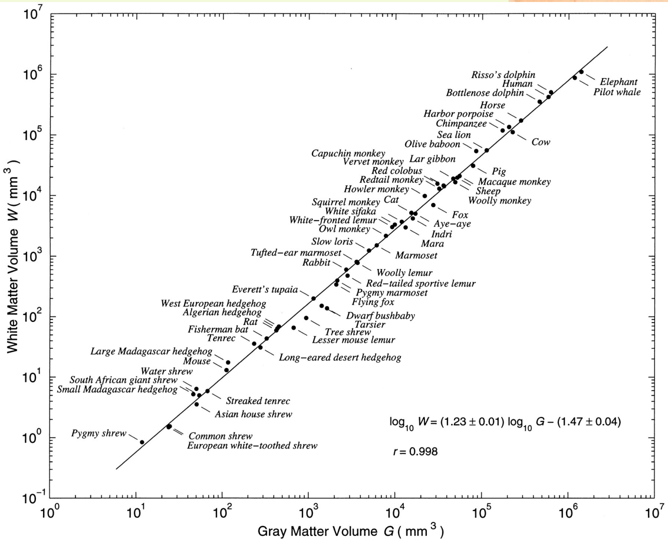


A beautiful, heart-warming example:





- G = volume of gray matter: ‘computing elements’
- W = volume of white matter: ‘wiring’
- $W \sim cG^{1.23}$
- from Zhang & Sejnowski, PNAS (2000) [44]

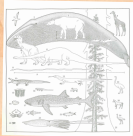
Why is $\alpha \simeq 1.23$?

Quantities (following Zhang and Sejnowski):

- G = Volume of gray matter (cortex/processors)
- W = Volume of white matter (wiring)
- T = Cortical thickness (wiring)
- S = Cortical surface area
- L = Average length of white matter fibers
- p = density of axons on white matter/cortex interface

A rough understanding:

- $G \sim ST$ (convolutions are okay)
- $W \sim \frac{1}{2}pSL$
- $G \sim L^3$
- Eliminate S and L to find $W \propto G^{4/3}/T$



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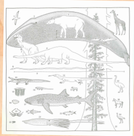

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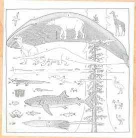

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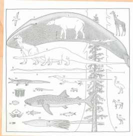

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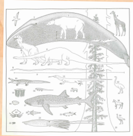

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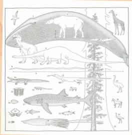

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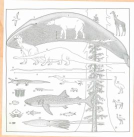

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- $G \sim L^3 \leftarrow$ this is a little sketchy...
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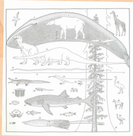
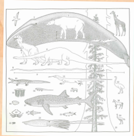


Why is $\alpha \simeq 1.23$?

A rough understanding:

- We are here: $W \propto G^{4/3}/T$
- Observe weak scaling $T \propto G^{0.10\pm0.02}$.
- (Implies $S \propto G^{0.9} \rightarrow$ convolutions fill space.)
- $\Rightarrow W \propto G^{4/3}/T \propto G^{1.23\pm0.02}$



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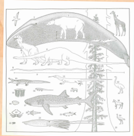

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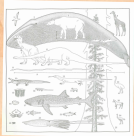

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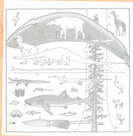
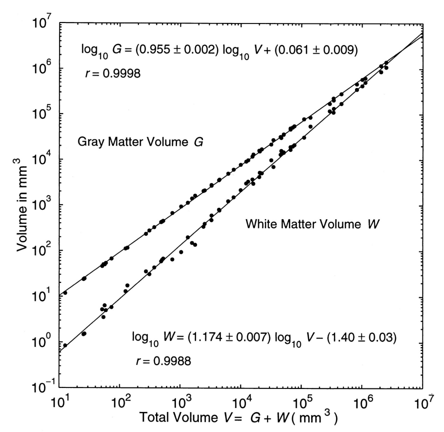
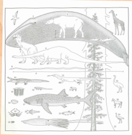


Trickiness:



- With $V = G + W$, some power laws must be approximations.
- Measuring exponents is a hairy business...



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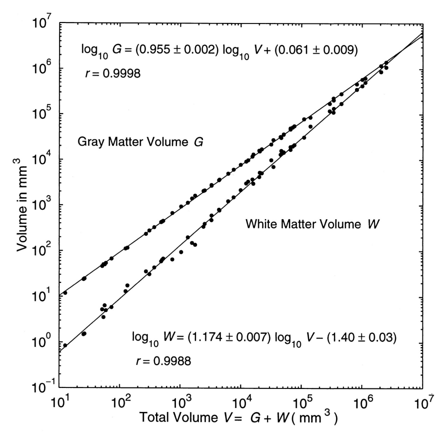

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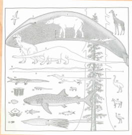
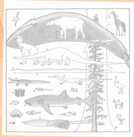


Good scaling:

General rules of thumb:

- *High quality:* scaling persists over three or more orders of magnitude for each variable.
- *Medium quality:* scaling persists over three or more orders of magnitude for only one variable and at least one for the other.
- *Very dubious:* scaling 'persists' over less than an order of magnitude for both variables.



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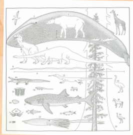

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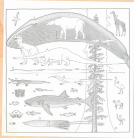

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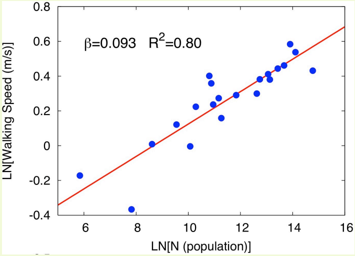
Unconvincing scaling:

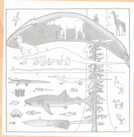
Average walking speed as a function of city population:



Two problems:

1. use of natural log, and
2. minute varation in dependent variable.

- from Bettencourt et al. (2007) [4]; otherwise very interesting—see later.

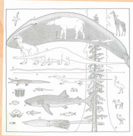


Definitions

Power laws are the signature of scale invariance:

Scale invariant 'objects'
look the 'same'
when they are appropriately
rescaled.

- Objects = geometric shapes, time series, functions, relationships, distributions,...
- 'Same' might be 'statistically the same'
- To rescale means to change the units of measurement for the relevant variables



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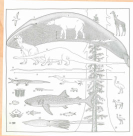

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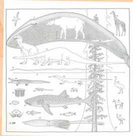

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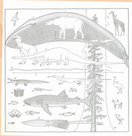
- 'Same' might be 'statistically the same'
- To rescale means to change the units of measurement for the relevant variables



Scale invariance

Our friend $y = cx^{\alpha}$:

- If we rescale x as $x = rx'$ and y as $y = r^{\alpha} y'$,
- then

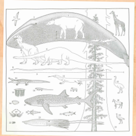
$$r^{\alpha} y' = c(rx')^{\alpha}$$

-

$$\Rightarrow y' = c r^{\alpha} x'^{\alpha} r^{-\alpha}$$

-

$$\Rightarrow y' = c x'^{\alpha}$$



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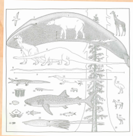

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$$\Rightarrow y' = cr^{\alpha}x'^{\alpha}r^{-\alpha}$$

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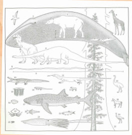
$$\Rightarrow y' = cx'^{\alpha}$$



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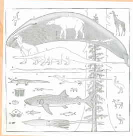

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- Original form cannot be recovered.
- Scale matters for the exponential.

More on $y = ce^{-\lambda x}$:

- Say $x_0 = 1/\lambda$ is the characteristic scale.
- For $x \gg x_0$, y is small,
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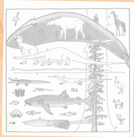
- More on this later with size distributions.



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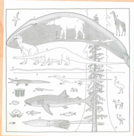

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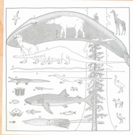

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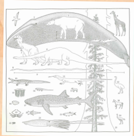

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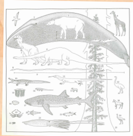

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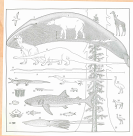

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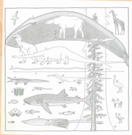
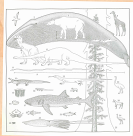


Outline

Scaling-at-large

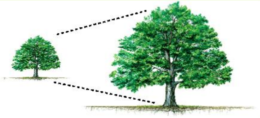
- Allometry
- Examples
- A focus: Metabolism
- Measuring exponents
- History: River networks
- Earlier theories
- Geometric argument
- Blood networks
- River networks
- Conclusion

References



Definitions:

Isometry:



- Dimensions scale linearly with each other.

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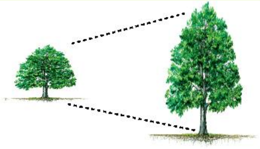

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Allometry: (⊞)

- Refers to differential growth rates of the parts of a living organism's body part or process.
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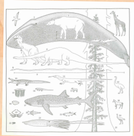

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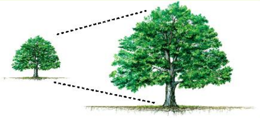

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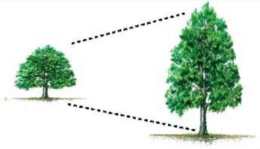

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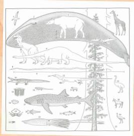

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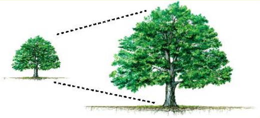

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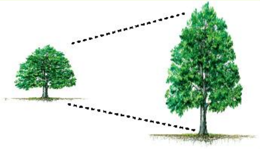

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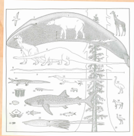


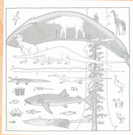
Definitions

Isometry versus Allometry:

- Iso-metry = ‘same measure’
- Allo-metry = ‘other measure’

Confusingly, we use allometric scaling to refer to both:

1. Nonlinear scaling of a dependent variable on an independent one (e.g., $y \propto x^{1/3}$)
2. The relative scaling of correlated measures (e.g., white and gray matter).



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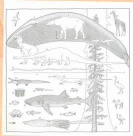

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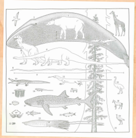

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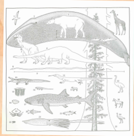
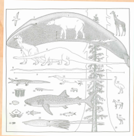
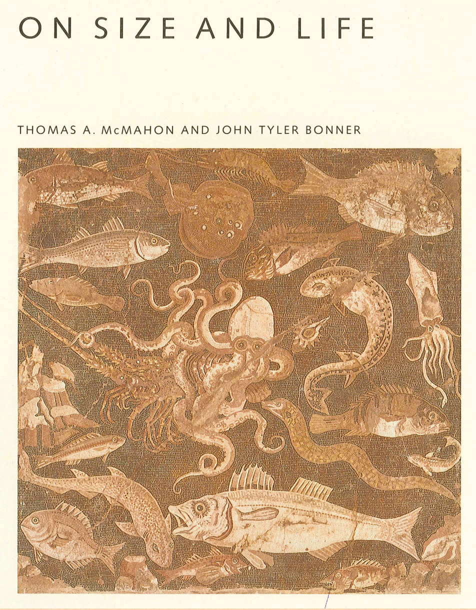


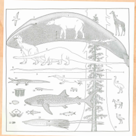
Outline



A wonderful treatise on scaling:



McMahon and Bonner, 1983 [28]

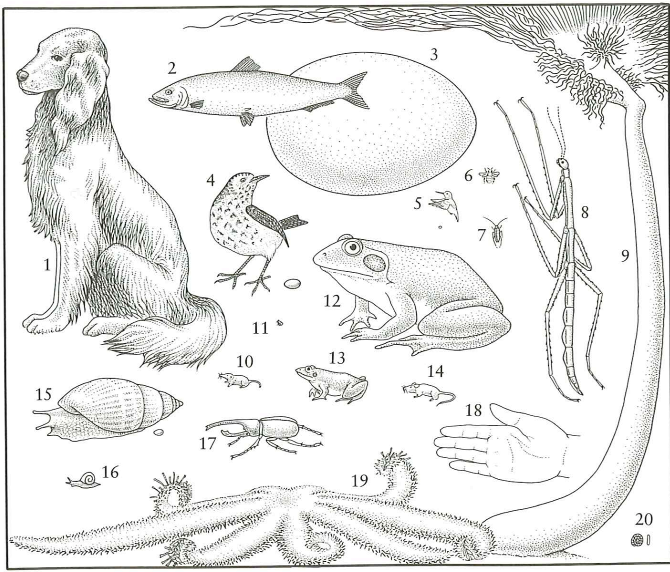


The many scales of life:

The biggest living things (*left*). All the organisms are drawn to the same scale. *1*, The largest flying bird (albatross); *2*, the largest known animal (the blue whale), *3*, the largest extinct land mammal (*Baluchitherium*) with a human figure shown for scale; *4*, the tallest living land animal (giraffe); *5*, *Tyrannosaurus*; *6*, *Diplodocus*; *7*, one of the largest flying reptiles (*Pteranodon*); *8*, the largest extinct snake; *9*, the length of the largest tapeworm found in man; *10*, the largest living reptile (West African crocodile); *11*, the largest extinct lizard; *12*, the largest extinct bird (*Aepyornis*); *13*, the largest jellyfish (*Cyanea*); *14*, the largest living lizard (Komodo dragon); *15*, sheep; *16*, the largest bivalve mollusc (*Tridacna*); *17*, the largest fish (whale shark); *18*, horse; *19*, the largest crustacean (Japanese spider crab); *20*, the largest sea scorpion (Eurypterid); *21*, large tarpon; *22*, the largest lobster; *23*, the largest mollusc (deep-water squid, *Architeuthis*); *24*, ostrich; *25*, the lower 105 feet of the largest organism (giant sequoia), with a 100-foot larch superposed.

p. 2, McMahon and Bonner[28]

The many scales of life:



Medium-sized creatures (*above*). *1*, Dog; *2*, common herring; *3*, the largest egg (*Aepyornis*); *4*, song thrush with egg; *5*, the smallest bird (hummingbird) with egg; *6*, queen bee; *7*, common cockroach; *8*, the largest stick insect; *9*, the largest polyp (*Branchiocerianthus*); *10*, the smallest mammal (flying shrew); *11*, the smallest vertebrate (a tropical frog); *12*, the largest frog (goliath frog); *13*, common grass frog; *14*, house mouse; *15*, the largest land snail (*Achatina*) with egg; *16*, common snail; *17*, the largest beetle (goliath beetle); *18*, human hand; *19*, the largest starfish (*Luidia*); *20*, the largest free-moving protozoan (an extinct nummulite).

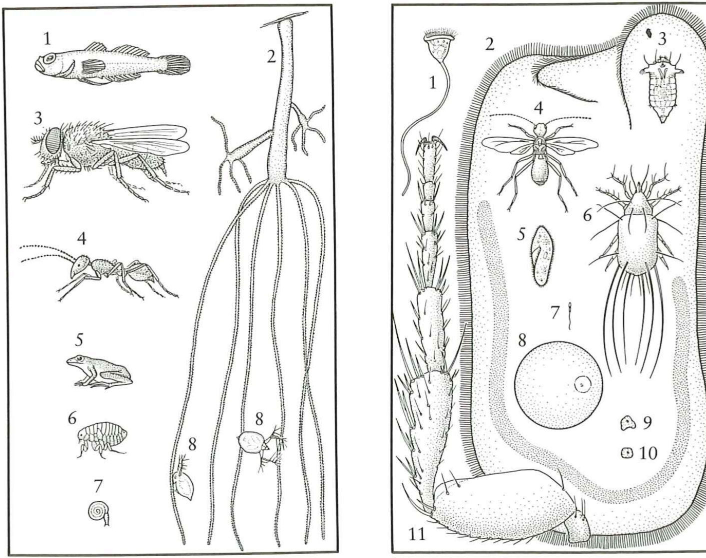
p. 3, McMahon and Bonner [28]

The many scales of life:

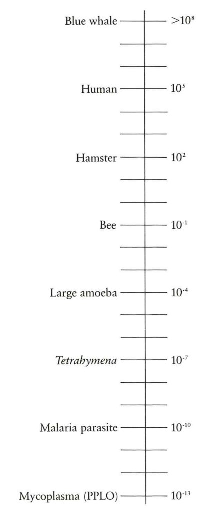
Small, "naked-eye" creatures (*lower left*). *1*, One of the smallest fishes (*Trimmatom nanus*); *2*, common brown hydra, expanded; *3*, housefly; *4*, medium-sized ant; *5*, the smallest vertebrate (a tropical frog, the same as the one numbered *11* in the figure *above*); *6*, flea (*Xenopsylla cheopis*); *7*, the smallest land snail; *8*, common water flea (*Daphnia*).

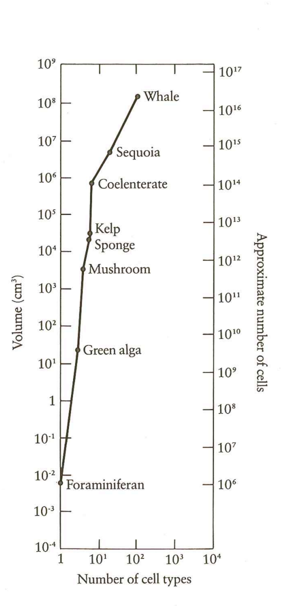
The smallest "naked-eye" creatures and some large microscopic animals and cells (*below right*). *1*, *Vorticella*, a ciliate; *2*, the largest ciliate protozoan (*Bursaria*); *3*, the smallest many-celled animal (a rotifer); *4*, smallest flying insect (*Elaphis*); *5*, another ciliate (*Paramecium*); *6*, cheese mite; *7*, human sperm; *8*, human ovum; *9*, dysentery amoeba; *10*, human liver cell; *11*, the foreleg of the flea (numbered *6* in the figure to the *left*).

3, McMahon and Bonner [28]

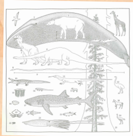


Size range (in grams) and cell differentiation:



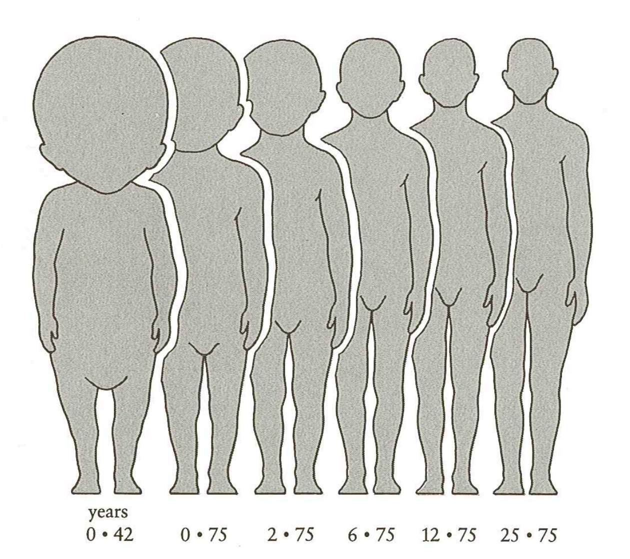


p. 3, McMahon and Bonner [28]

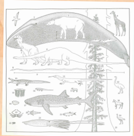


The UNIVERSITY of VERMONT

Non-uniform growth:

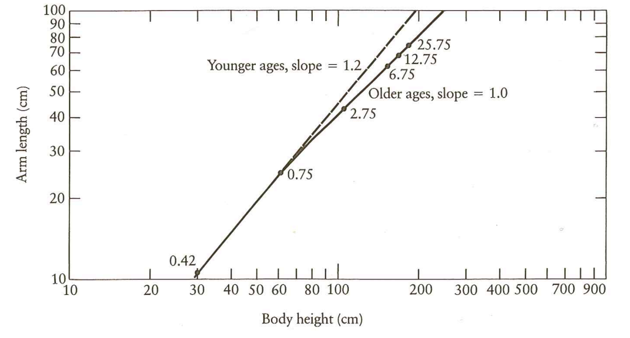


p. 32, McMahon and Bonner [28]



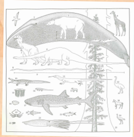
Non-uniform growth—arm length versus height:

Good example of a break in scaling:

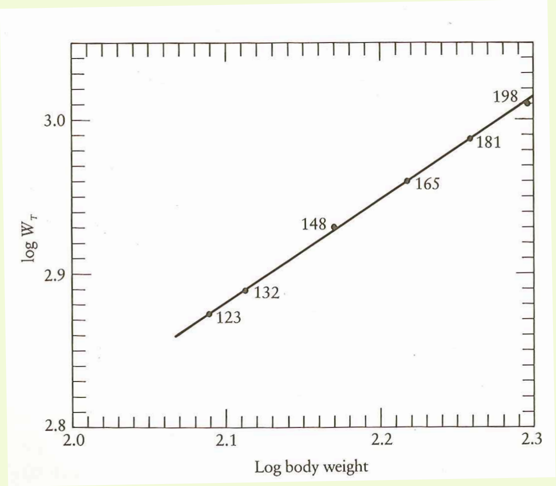


A crossover in scaling occurs around a height of 1 metre.

p. 32, McMahon and Bonner [28]

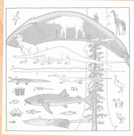


Weightlifting: $M_{\mathrm{worldrecord}} \propto M_{\mathrm{lifter}}^{2/3}$

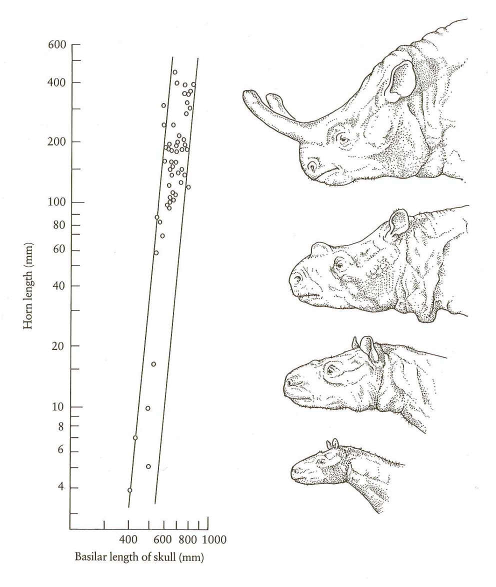


Idea: Power $\sim$ cross-sectional area of isometric lifters.

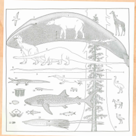
p. 53, McMahon and Bonner [28]



Titanothere horns: $L_{\mathrm{horn}} \sim L_{\mathrm{skull}}^4$

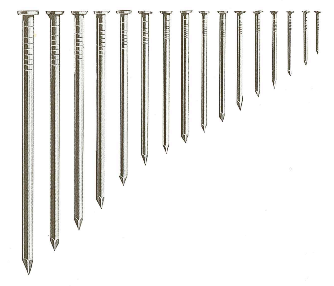


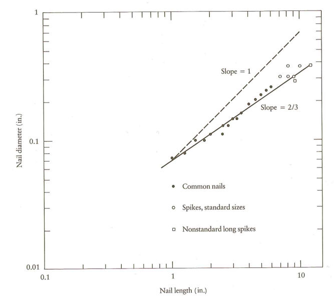
p. 36, McMahon and Bonner [28]; a bit dubious.



The allometry of nails:

Observed: Diameter $\propto$ Length$^{2/3}$ or $d \propto \ell^{2/3}$.

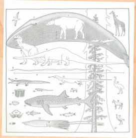




Since $\ell d^2 \propto$ Volume v:

- Diameter $\propto$ Mass$^{3/8}$ or $d \propto v^{3/8}$.
- Length $\propto$ Mass$^{1/4}$ or $\ell \propto v^{1/4}$.
- Nails lengthen faster than they broaden (c.f. trees).

p. 58–59, McMahon and Bonner [28]



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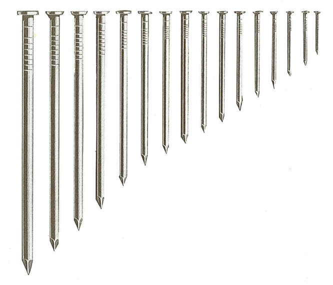

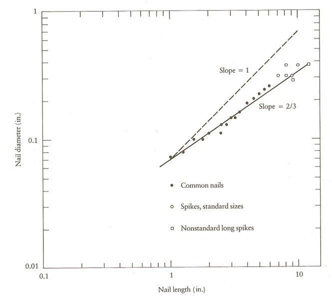

Since $\ell d^2 \propto$ Volume v:

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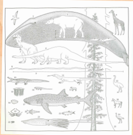
- Nails lengthen faster than they broaden (c.f. trees).

p. 58–59, McMahon and Bonner [28]



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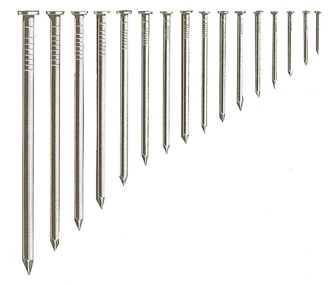

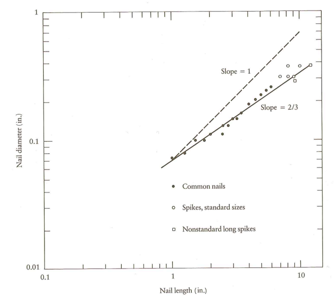

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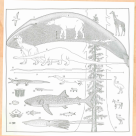

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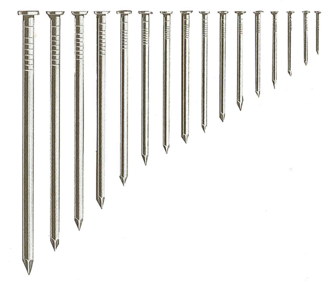

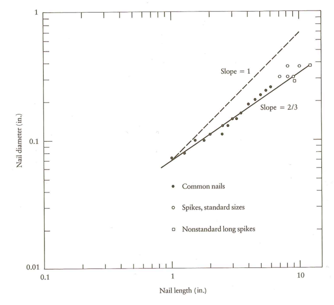

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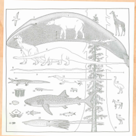

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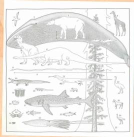

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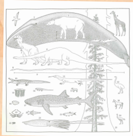

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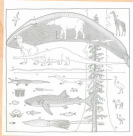

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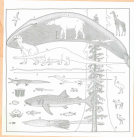

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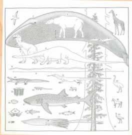

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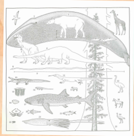

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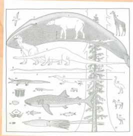

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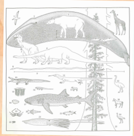
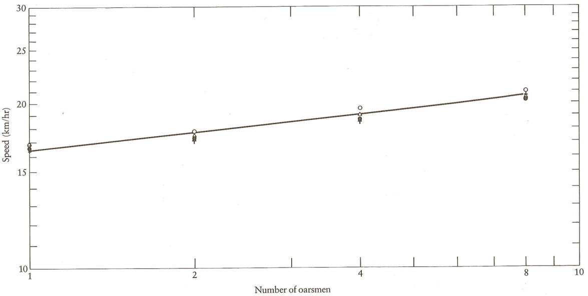


Rowing: Speed $\propto$ (number of rowers)$^{1/9}$

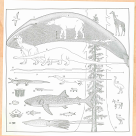
Shell dimensions and performances.

No. of oarsmen	Modifying description	Length, l (m)	Beam, b (m)	l/b	Boat mass per oarsman (kg)	Time for 2000 m (min) I	II	III	IV
8	Heavyweight	18.28	0.610	30.0	14.7	5.87	5.92	5.82	5.73
8	Lightweight	18.28	0.598	30.6	14.7				
4	With coxswain	12.80	0.574	22.3	18.1				
4	Without coxswain	11.75	0.574	21.0	18.1	6.33	6.42	6.48	6.13
2	Double scull	9.76	0.381	25.6	13.6				
2	Pair-oared shell	9.76	0.356	27.4	13.6	6.87	6.92	6.95	6.77
1	Single scull	7.93	0.293	27.0	16.3	7.16	7.25	7.28	7.17



From further back:

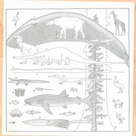
- Zipf (more later)
- Survey by Naroll and von Bertalanffy [31]
  "The principle of allometry in biology and the social sciences"
  General Systems, Vol 1., 1956.



Scaling in Cities:

- “Growth, innovation, scaling, and the pace of life in cities”
  Bettencourt et al., PNAS, 2007. [4]
- Quantified levels of
  - Infrastructure
  - Wealth
  - Crime levels
  - Disease
  - Energy consumption

  as a function of city size N (population).



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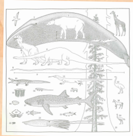
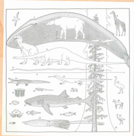


Scaling in Cities:

Table 1. Scaling exponents for urban indicators vs. city size

Y	*β*	95% CI	Adj-R^2	Observations	Country–year
New patents	1.27	[1.25,1.29]	0.72	331	U.S. 2001
Inventors	1.25	[1.22,1.27]	0.76	331	U.S. 2001
Private R&D employment	1.34	[1.29,1.39]	0.92	266	U.S. 2002
"Supercreative" employment	1.15	[1.11,1.18]	0.89	287	U.S. 2003
R&D establishments	1.19	[1.14,1.22]	0.77	287	U.S. 1997
R&D employment	1.26	[1.18,1.43]	0.93	295	China 2002
Total wages	1.12	[1.09,1.13]	0.96	361	U.S. 2002
Total bank deposits	1.08	[1.03,1.11]	0.91	267	U.S. 1996
GDP	1.15	[1.06,1.23]	0.96	295	China 2002
GDP	1.26	[1.09,1.46]	0.64	196	EU 1999–2003
GDP	1.13	[1.03,1.23]	0.94	37	Germany 2003
Total electrical consumption	1.07	[1.03,1.11]	0.88	392	Germany 2002
New AIDS cases	1.23	[1.18,1.29]	0.76	93	U.S. 2002–2003
Serious crimes	1.16	[1.11, 1.18]	0.89	287	U.S. 2003
Total housing	1.00	[0.99,1.01]	0.99	316	U.S. 1990
Total employment	1.01	[0.99,1.02]	0.98	331	U.S. 2001
Household electrical consumption	1.00	[0.94,1.06]	0.88	377	Germany 2002
Household electrical consumption	1.05	[0.89,1.22]	0.91	295	China 2002
Household water consumption	1.01	[0.89,1.11]	0.96	295	China 2002
Gasoline stations	0.77	[0.74,0.81]	0.93	318	U.S. 2001
Gasoline sales	0.79	[0.73,0.80]	0.94	318	U.S. 2001
Length of electrical cables	0.87	[0.82,0.92]	0.75	380	Germany 2002
Road surface	0.83	[0.74,0.92]	0.87	29	Germany 2002

Data sources are shown in *SI Text*. CI, confidence interval; Adj-R^2, adjusted R^2; GDP, gross domestic product.



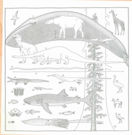
Scaling in Cities:

Intriguing findings:

- Global supply costs scale sublinearly with N ($\beta < 1$).
  - Returns to scale for infrastructure.
- Total individual costs scale linearly with N ($\beta = 1$)
  - Individuals consume similar amounts independent of city size.
- Social quantities scale superlinearly with N ($\beta > 1$)
  - Creativity (# patents), wealth, disease, crime, ...

Density doesn't seem to matter...

- Surprising given that across the world, we observe two orders of magnitude variation in area covered by agglomerations (⊞) of fixed populations.



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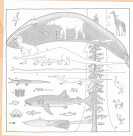

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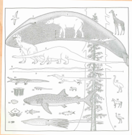

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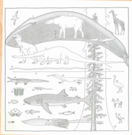


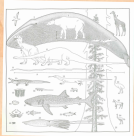
Ecology—Species-area law: (⊞)

Allegedly (data is messy):

- $$N_{\text{species}} \propto A^{\beta}$$
- On islands: $\beta \approx 1/4$.
- On continuous land: $\beta \approx 1/8$.

A focus:

- How much energy do organisms need to live?
- And how does this scale with organismal size?



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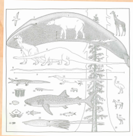
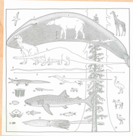


Outline

Scaling-at-large

Allometry
Examples
A focus: Metabolism
Measuring exponents
History: River networks
Earlier theories
Geometric argument
Blood networks
River networks
Conclusion

References



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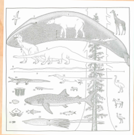
Animal power

Fundamental biological and ecological constraint:

$$P = c\,M^{\alpha}$$

$P =$ basal metabolic rate

$M =$ organismal body mass



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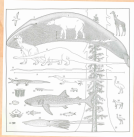
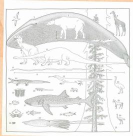


$P = c M^{\alpha}$

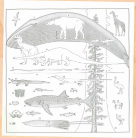
Prefactor c depends on body plan and body temperature:



$P = c M^{\alpha}$

Prefactor c depends on body plan and body temperature:

Birds	39–41 $^{\circ}C$
Eutherian Mammals	36–38 $^{\circ}C$
Marsupials	34–36 $^{\circ}C$
Monotremes	30–31 $^{\circ}C$



What one might expect:

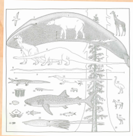
$\alpha = 2/3$

- Dimensional analysis suggests an energy balance surface law:

$$P \propto S \propto V^{2/3} \propto M^{2/3}$$

- Lognormal fluctuations:
  Gaussian fluctuations in $\log P$ around $\log cM^{\alpha}$.
- Stefan-Boltzmann law (⊞) for radiated energy:

$$\frac{\mathrm{d}E}{\mathrm{d}t} = \sigma \varepsilon S T^4 \propto S$$



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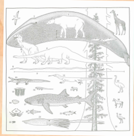

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$$P \propto S \propto V^{2/3} \propto M^{2/3}$$

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  Gaussian fluctuations in $\log P$ around $\log cM^{\alpha}$.
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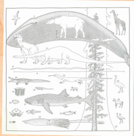
$$\frac{\mathrm{d}E}{\mathrm{d}t} = \sigma\varepsilon S T^4 \propto S$$



What one might expect:

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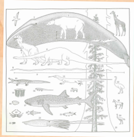
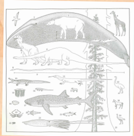


The prevailing belief of the church of quarterology

$$\boxed{\alpha = 3/4}$$

$$P \propto M^{3/4}$$



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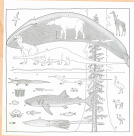

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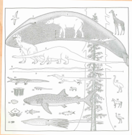
Most obvious concern:

$$3/4 - 2/3 = 1/12$$

- An exponent higher than 2/3 points suggests a fundamental inefficiency in biology.
- Organisms must somehow be running 'hotter' than they need to balance heat loss.



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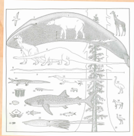
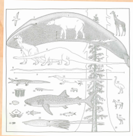


Related putative scalings:

Wait! There's more!:

- number of capillaries $\propto M^{3/4}$
- time to reproductive maturity $\propto M^{1/4}$
- heart rate $\propto M^{-1/4}$
- cross-sectional area of aorta $\propto M^{3/4}$
- population density $\propto M^{-3/4}$



The great 'law' of heartbeats:

Assuming:

- Average lifespan $\propto M^{\beta}$
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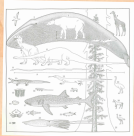
- Irrelevant but perhaps $\beta = 1/4$.

Then:

- Average number of heart beats in a lifespan



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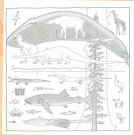

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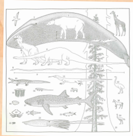

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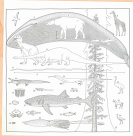

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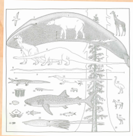

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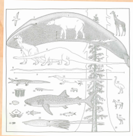

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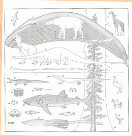

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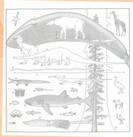
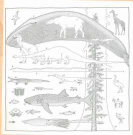
- $\approx$ 1.5 billion....



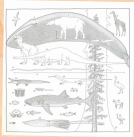
History

1840's: Sarrus and Rameaux [36] first suggested $\alpha = 2/3$.



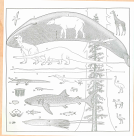
History

1883: Rubner [34] found $\alpha \simeq 2/3$.



History

1930's: Brody, Benedict study mammals. [7]
Found $\alpha \simeq 0.73$ (standard).



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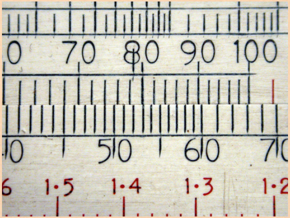
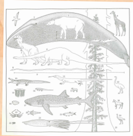


- 1932: Kleiber analyzed 13 mammals. [23]
- Found $\alpha = 0.76$ and suggested $\alpha = 3/4$.
- Scaling law of Metabolism became known as Kleiber's Law (⊞) (2011 Wikipedia entry is embarrassing).
- 1961 book: "The Fire of Life. An Introduction to Animal Energetics". [24]



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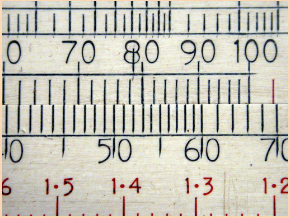

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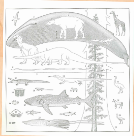
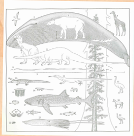


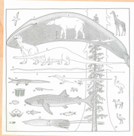
History

1950/1960: Hemmingsen [19, 20]
Extension to unicellular organisms.
$\alpha = 3/4$ assumed true.



History

1964: Troon, Scotland: [5]
3rd symposium on energy metabolism.
$\alpha = 3/4$ made official . . .



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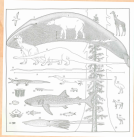
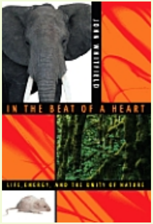


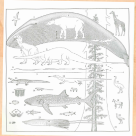
Today

- 3/4 is held by many to be the one true exponent.



In the Beat of a Heart: Life, Energy, and the Unity of Nature—by John Whitfield

and ensuing madness...



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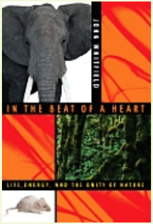

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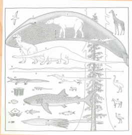

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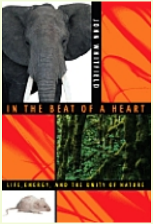

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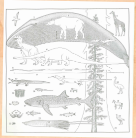
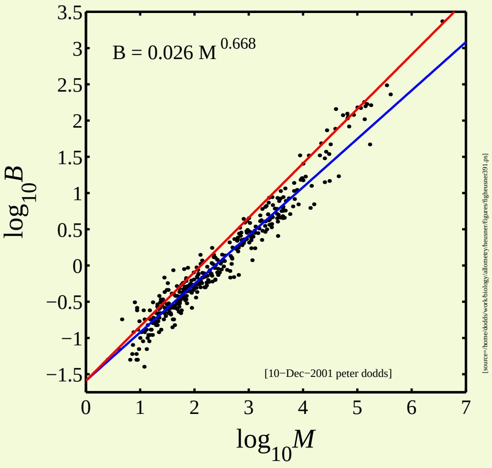
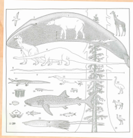
- But—much controversy...
- See ‘Re-examination of the “3/4-law” of metabolism’ Dodds, Rothman, and Weitz [12] and ensuing madness...



Some data on metabolic rates



- Heusner's data (1991) [21]
- 391 Mammals
- blue line: 2/3
- red line: 3/4.
- $(B = P)$



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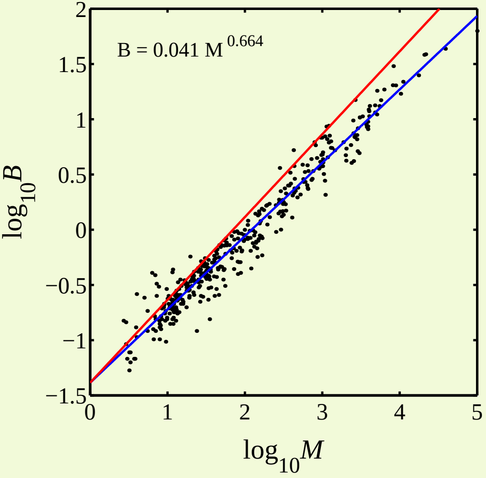

- Bennett and Harvey's data (1987) [3]
- 398 birds
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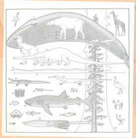
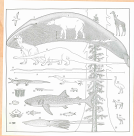
- red line: 3/4.
- ($B = P$)

- Passerine vs. non-passerine issue...



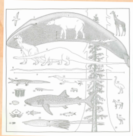
Outline



Linear regression

Important:

- Ordinary Least Squares (OLS) Linear regression is only appropriate for analyzing a dataset $\{(x_i, y_i)\}$ when we know the x_i are measured without error.
- Here we assume that measurements of mass M have less error than measurements of metabolic rate B.
- Linear regression assumes Gaussian errors.



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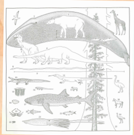

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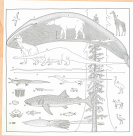
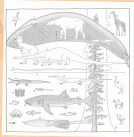


Measuring exponents

More on regression:

If (a) we don't know what the errors of either variable are,



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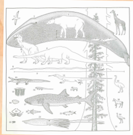

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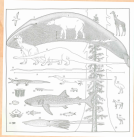
Standardized Major Axis Linear Regression. [35, 33]



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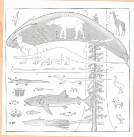
(aka Reduced Major Axis = RMA.)

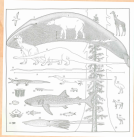


Measuring exponents

For Standardized Major Axis Linear Regression:

$$\text{slope}_{\text{SMA}} = \frac{\text{standard deviation of } y \text{ data}}{\text{standard deviation of } x \text{ data}}$$

- Very simple!
- Scale invariant.



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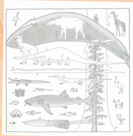

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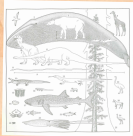


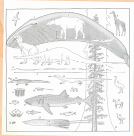
Measuring exponents

Relationship to ordinary least squares regression is simple:

$$\begin{aligned} \text{slope}_{\text{SMA}} &= r^{-1} \times \text{slope}_{\text{OLS } y \text{ on } x} \\ &= r \times \text{slope}_{\text{OLS } x \text{ on } y} \end{aligned}$$

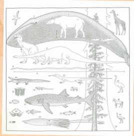
where r = standard correlation coefficient:

$$r = \frac{\sum_{i=1}^{n}(x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\sum_{i=1}^{n}(x_i - \bar{x})^2}\sqrt{\sum_{i=1}^{n}(y_i - \bar{y})^2}}$$



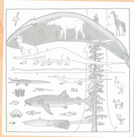
Heusner's data, 1991 (391 Mammals)

range of M	N	$\hat{\alpha}$
≤ 0.1 kg	167	0.678 ± 0.038
≤ 1 kg	276	0.662 ± 0.032
≤ 10 kg	357	0.668 ± 0.019
≤ 25 kg	366	0.669 ± 0.018
≤ 35 kg	371	0.675 ± 0.018
≤ 350 kg	389	0.706 ± 0.016
≤ 3670 kg	391	0.710 ± 0.021



Bennett and Harvey, 1987 (398 birds)

M_{max}	N	$\hat{\alpha}$
≤ 0.032	162	0.636 ± 0.103
≤ 0.1	236	0.602 ± 0.060
≤ 0.32	290	0.607 ± 0.039
≤ 1	334	0.652 ± 0.030
≤ 3.2	371	0.655 ± 0.023
≤ 10	391	0.664 ± 0.020
≤ 32	396	0.665 ± 0.019
≤ 100	398	0.664 ± 0.019



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$$H_0 : \alpha = \alpha' \text{ and } H_1 : \alpha \neq \alpha'.$$

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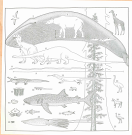

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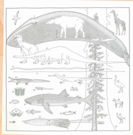

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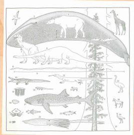

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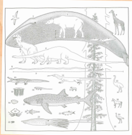

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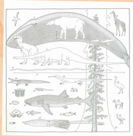
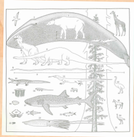


Revisiting the past—mammals

Full mass range:

	N	$\hat{\alpha}$	$p_{2/3}$	$p_{3/4}$
Kleiber	13	0.738	$< 10^{-6}$	0.11
Brody	35	0.718	$< 10^{-4}$	$< 10^{-2}$
Heusner	391	0.710	$< 10^{-6}$	$< 10^{-5}$
Bennett and Harvey	398	0.664	0.69	$< 10^{-15}$



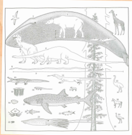
Revisiting the past—mammals

$M \leq 10$ kg:

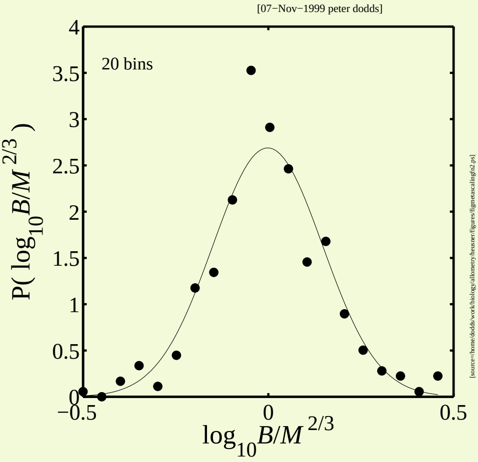
	N	$\hat{\alpha}$	$p_{2/3}$	$p_{3/4}$
Kleiber	5	0.667	0.99	0.088
Brody	26	0.709	$< 10^{-3}$	$< 10^{-3}$
Heusner	357	0.668	0.91	$< 10^{-15}$

$M \geq 10$ kg:

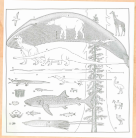
	N	$\hat{\alpha}$	$p_{2/3}$	$p_{3/4}$
Kleiber	8	0.754	$< 10^{-4}$	0.66
Brody	9	0.760	$< 10^{-3}$	0.56
Heusner	34	0.877	$< 10^{-12}$	$< 10^{-7}$



Fluctuations—Things look normal...



- $P(B|M) = 1/M^{2/3} f(B/M^{2/3})$
- Use a Kolmogorov-Smirnov test.

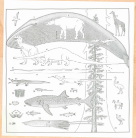


Analysis of residuals

1. Presume an exponent of your choice: 2/3 or 3/4.
2. Fit the prefactor ($\log_{10} c$) and then examine the residuals:

$$r_i = \log_{10} B_i - (\alpha' \log_{10} M_i - \log_{10} c).$$

3. H_0: residuals are uncorrelated
   H_1: residuals are correlated.
4. Measure the correlations in the residuals and compute a p-value.



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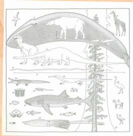

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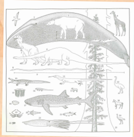

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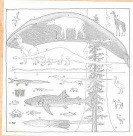

Analysis of residuals

We use the spiffing Spearman Rank-Order Correlation Coefficient (⊞)

Basic idea:

- Given $\{(x_i, y_i)\}$, rank the $\{x_i\}$ and $\{y_i\}$ separately from smallest to largest. Call these ranks R_i and S_i.
- Now calculate correlation coefficient for ranks, r_s:
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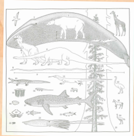
$$r_s = \frac{\sum_{i=1}^{n}(R_i - \bar{R})(S_i - \bar{S})}{\sqrt{\sum_{i=1}^{n}(R_i - \bar{R})^2}\sqrt{\sum_{i=1}^{n}(S_i - \bar{S})^2}}$$
- Perfect correlation: x_i's and y_i's both increase monotonically.



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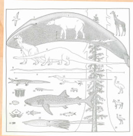

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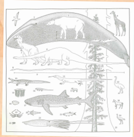

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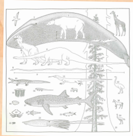

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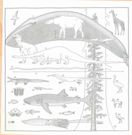
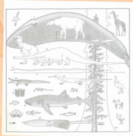


Analysis of residuals

We assume all rank orderings are equally likely:

- r_s is distributed according to a Student's t-distribution (⊞) with $N - 2$ degrees of freedom.
- Excellent feature: Non-parametric—real distribution of x's and y's doesn't matter.
- Bonus: works for non-linear monotonic relationships as well.
- See Numerical Recipes in C/Fortran (⊞) which contains many good things.[32]



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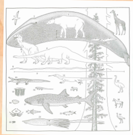

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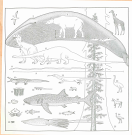

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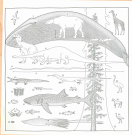

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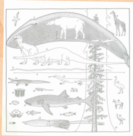
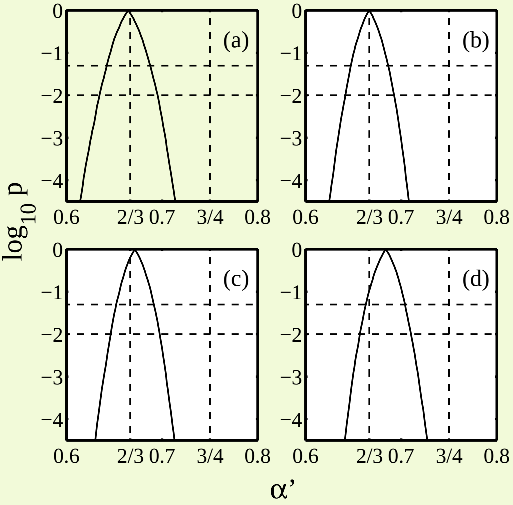


Analysis of residuals—mammals

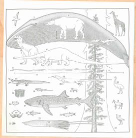


(a) $M < 3.2$ kg,

(b) $M < 10$ kg,

(c) $M < 32$ kg,

(d) all mammals.



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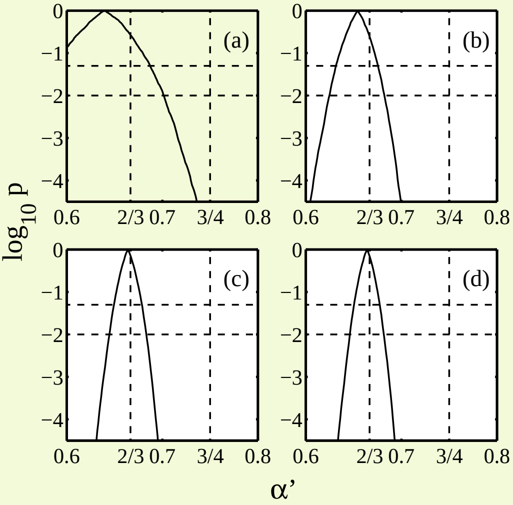
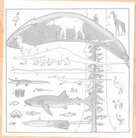
Analysis of residuals—birds

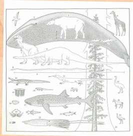


(a) $M < 0.1$ kg,
(b) $M < 1$ kg,
(c) $M < 10$ kg,
(d) all birds.



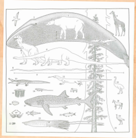
Other approaches to measuring exponents:

- Clauset, Shalizi, Newman: “Power-law distributions in empirical data” [8]
  SIAM Review, 2009.
- See Clauset’s page on measuring power law exponents (⊞) (code, other goodies).



Recap:

- So: The exponent $\alpha = 2/3$ works for all birds and mammals up to 10–30 kg
- For mammals $>$ 10–30 kg, maybe we have a new scaling regime
- Possible connection?: Economos (1983)—limb length break in scaling around 20 kg [13]
- But see later: non-isometric growth leads to lower metabolic scaling. Oops.



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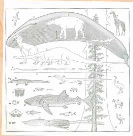

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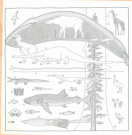

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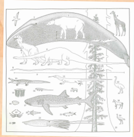

The widening gyre:

Now we're really confused (empirically):

- White and Seymour, 2005: unhappy with large herbivore measurements [43]. Pro $2/3$: Find $\alpha \simeq 0.686 \pm 0.014$.
- Glazier, BioScience (2006) [17]: "The 3/4-Power Law Is Not Universal: Evolution of Isometric, Ontogenetic Metabolic Scaling in Pelagic Animals."
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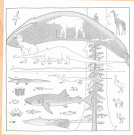

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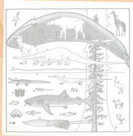

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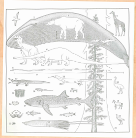

The widening gyre:

Now we're really confused (empirically):

- White and Seymour, 2005: unhappy with large herbivore measurements [43]. Pro $2/3$: Find $\alpha \simeq 0.686 \pm 0.014$.
- Glazier, BioScience (2006) [17]: "The 3/4-Power Law Is Not Universal: Evolution of Isometric, Ontogenetic Metabolic Scaling in Pelagic Animals."
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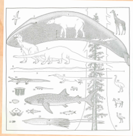
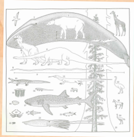
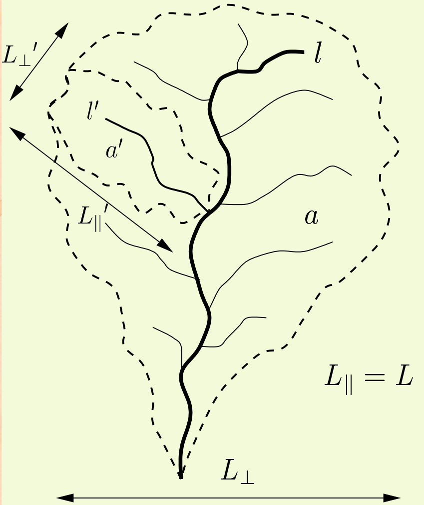


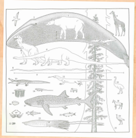
Outline



Basic basin quantities: a, l, $L_{\parallel}$, $L_{\perp}$:



- a = drainage basin area
- ℓ = length of longest (main) stream
- $L = L_{\parallel}$ = longitudinal length of basin



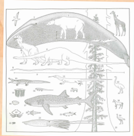
River networks

- 1957: J. T. Hack [18]
  "Studies of Longitudinal Stream Profiles in Virginia and Maryland"

$$\ell \sim a^h$$

$$h \sim 0.6$$

- Anomalous scaling: we would expect $h = 1/2$...
- Subsequent studies: $0.5 \lesssim h \lesssim 0.6$
- Another quest to find universality/god...
- A catch: studies done on small scales.



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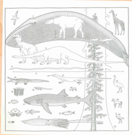

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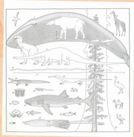

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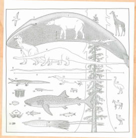

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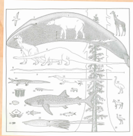
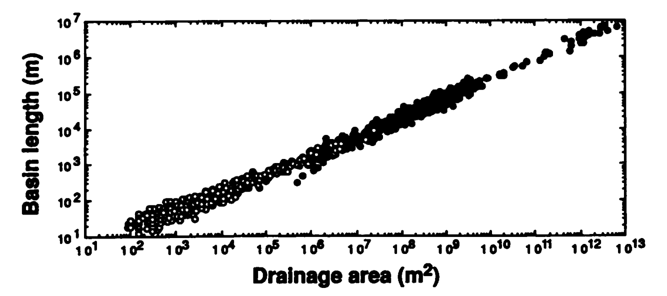


Large-scale networks:

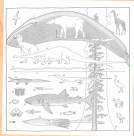
(1992) Montgomery and Dietrich [29]:



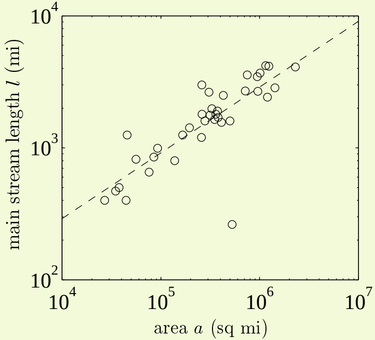
- Composite data set: includes everything from unchanneled valleys up to world's largest rivers.
- Estimated fit:

$$L \simeq 1.78 a^{0.49}$$

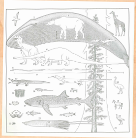
- Mixture of basin and main stream lengths.



World's largest rivers only:



- Data from Leopold (1994) [25, 11]
- Estimate of Hack exponent: $h = 0.50 \pm 0.06$

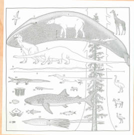


Outline

Scaling-at-large

- Allometry
- Examples
- A focus: Metabolism
- Measuring exponents
- History: River networks
- **Earlier theories**
- Geometric argument
- Blood networks
- River networks
- Conclusion

References



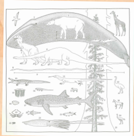
Earlier theories

Building on the surface area idea...

- Blum (1977) [6] speculates on four-dimensional biology:

$$P \propto M^{(d-1)/d}$$

- $d = 3$ gives $\alpha = 2/3$
- $d = 4$ gives $\alpha = 3/4$
- So we need another dimension...
- Obviously, a bit silly... [39]



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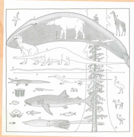

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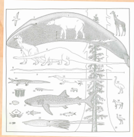

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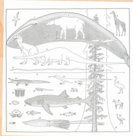

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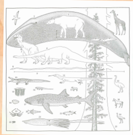

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- McMahon (70's, 80's): Elastic Similarity [26, 28]
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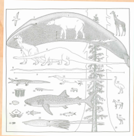

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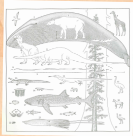

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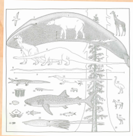

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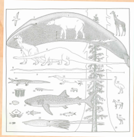

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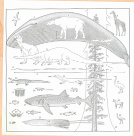
- 1960's: Rashevsky considers blood networks and finds a $2/3$ scaling.
- 1997: West *et al.* [42] use a network story to find $3/4$ scaling.



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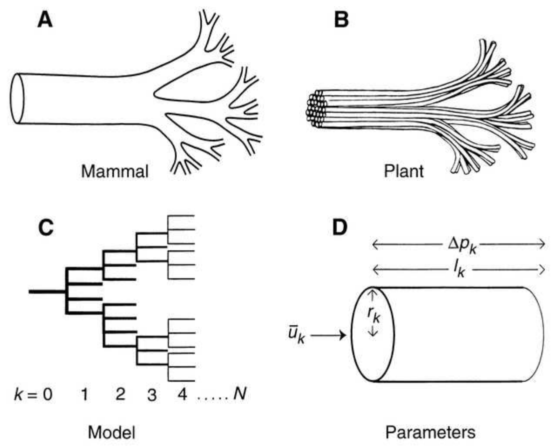
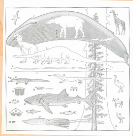




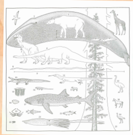
Nutrient delivering networks:

West et al.'s assumptions:

1. hierarchical network
2. capillaries (delivery units) invariant
3. network impedance is minimized via evolution

Claims:

- $P \propto M^{3/4}$
- networks are fractal
- quarter powers everywhere



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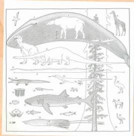

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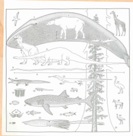

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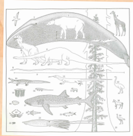

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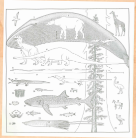

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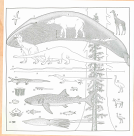


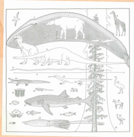
Impedance measures:

Poiseuille flow (outer branches):

$$Z = \frac{8\mu}{\pi} \sum_{k=0}^{N} \frac{\ell_k}{r_k^4 N_k}$$

Pulsatile flow (main branches):

$$Z \propto \sum_{k=0}^{N} \frac{h_k^{1/2}}{r_k^{5/2} N_k}$$



The UNIVERSITY of VERMONT

Not so fast . . .

Actually, model shows:

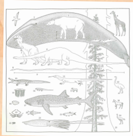
- $P \propto M^{3/4}$ does not follow for pulsatile flow
- networks are not necessarily fractal.

Do find:

- Murray's cube law (1927) for outer branches: [30]

$$r_0^3 = r_1^3 + r_2^3$$

- Impedance is distributed evenly.
- Can still assume networks are fractal.



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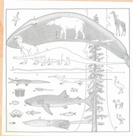

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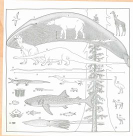

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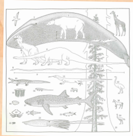

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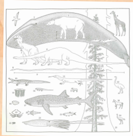


Connecting network structure to α

1. Ratios of network parameters:

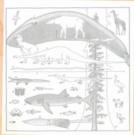
$$R_n = \frac{n_{k+1}}{n_k}, \; R_\ell = \frac{\ell_{k+1}}{\ell_k}, \; R_r = \frac{r_{k+1}}{r_k}$$

2. Number of capillaries $\propto P \propto M^\alpha$.

Soldiering on, assert:

- area-preservingness: $R_r = R_n^{-1/2}$
- space-fillingness: $R_\ell = R_n^{-1/3}$

$$\Rightarrow \alpha = 3/4$$



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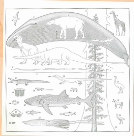

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$$\Rightarrow \quad \boxed{\alpha = -\frac{\ln R_n}{\ln R_r^2 R_\ell}}$$

(also problematic due to prefactor issues)

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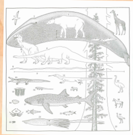

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2. Number of capillaries $\propto P \propto M^\alpha$.

$$\Rightarrow \boxed{\alpha = -\frac{\ln R_n}{\ln R_r^2 R_\ell}}$$

(also problematic due to prefactor issues)

Soldiering on, assert:

- area-preservingness: $R_r = R_n^{-1/2}$
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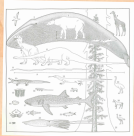
$$\Rightarrow \alpha = 3/4$$



Connecting network structure to α

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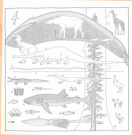
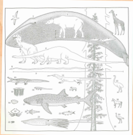


Data from real networks

Network	R_n	R_r^{-1}	R_ℓ^{-1}	$-\frac{\ln R_r}{\ln R_n}$	$-\frac{\ln R_\ell}{\ln R_n}$	α
West *et al.*	–	–	–	1/2	1/3	3/4
rat (PAT)	2.76	1.58	1.60	0.45	0.46	0.73
cat (PAT) (Turcotte *et al.*[41])	3.67	1.71	1.78	0.41	0.44	0.79
dog (PAT)	3.69	1.67	1.52	0.39	0.32	0.90
pig (LCX)	3.57	1.89	2.20	0.50	0.62	0.62
pig (RCA)	3.50	1.81	2.12	0.47	0.60	0.65
pig (LAD)	3.51	1.84	2.02	0.49	0.56	0.65
human (PAT)	3.03	1.60	1.49	0.42	0.36	0.83
human (PAT)	3.36	1.56	1.49	0.37	0.33	0.94



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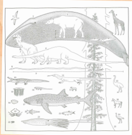

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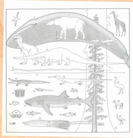

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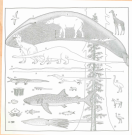
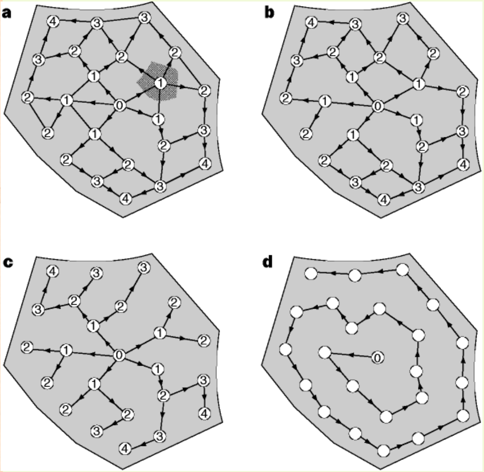
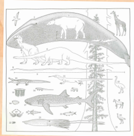


Simple supply networks



- Banavar et al., Nature, (1999) [1]
- Flow rate argument
- Ignore impedance
- Very general attempt to find most efficient transportation networks



Simple supply networks

- Banavar *et al.* find ‘most efficient’ networks with

$$P \propto M^{d/(d+1)}$$

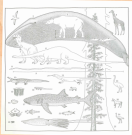
- ... but also find

$$V_{\mathrm{network}} \propto M^{(d+1)/d}$$

- $d = 3$:

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

- Consider a 3 g shrew with $V_{\mathrm{blood}} = 0.1\, V_{\mathrm{body}}$
- $\Rightarrow$ 3000 kg elephant with $V_{\mathrm{blood}} = 10\, V_{\mathrm{body}}$



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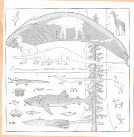

The UNIVERSITY of VERMONT

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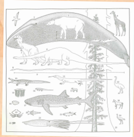

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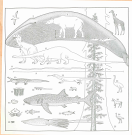

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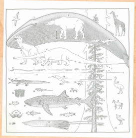
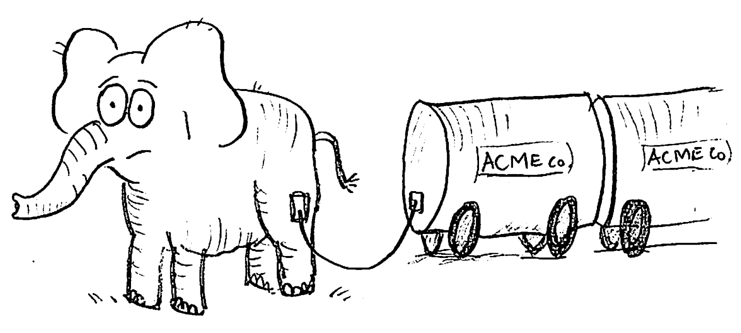
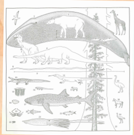


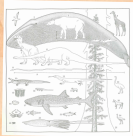
Simple supply networks

Such a pachyderm would be rather miserable:



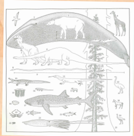


Outline



Geometric argument

- "Optimal Form of Branching Supply and Collection Networks." Dodds, Phys. Rev. Lett., 2010.[10]
- Consider one source supplying many sinks in a d-dim. volume in a D-dim. ambient space.
- Assume sinks are invariant.
- Assume sink density $\rho = \rho(V)$.
- Assume some cap on flow speed of material.
- See network as a bundle of virtual vessels:



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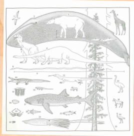

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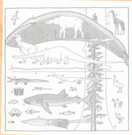

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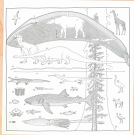

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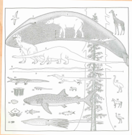

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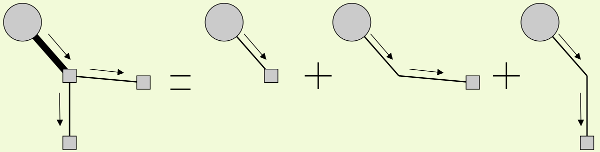
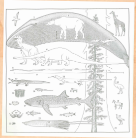
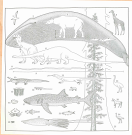




Geometric argument

- Q: how does the number of sustainable sinks N_{sinks} scale with volume V for the most efficient network design?
- Or: what is the highest α for $N_{\text{sinks}} \propto V^{\alpha}$?



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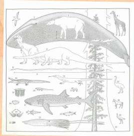
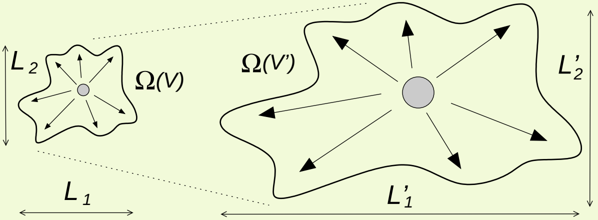


Geometric argument

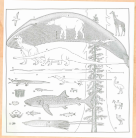
- Allometrically growing regions:



- Have d length scales which scale as

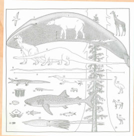
$$L_i \propto V^{\gamma_i} \text{ where } \gamma_1 + \gamma_2 + \ldots + \gamma_d = 1.$$

- For isometric growth, $\gamma_i = 1/d$.
- For allometric growth, we must have at least two of the $\{\gamma_i\}$ being different



Spherical cows and pancake cows:

- Question: How does the surface area S_{cow} of our two types of cows scale with cow volume V_{cow}? Insert question from assignment 3 (⊞)
- Question: For general families of regions, how does surface area S scale with volume V? Insert question from assignment 3 (⊞)



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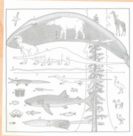
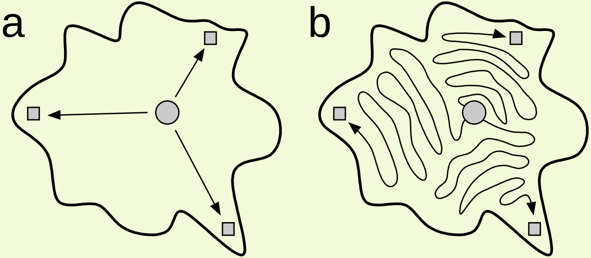
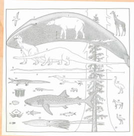


Geometric argument

- Best and worst configurations (Banavar et al.)



- Rather obviously:
  min $V_{\mathrm{net}} \propto \sum$ distances from source to sinks.



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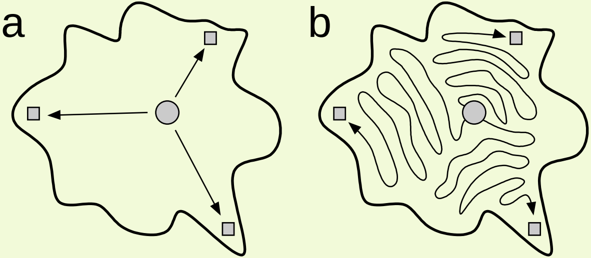

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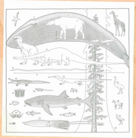


Minimal network volume:

Real supply networks are close to optimal:

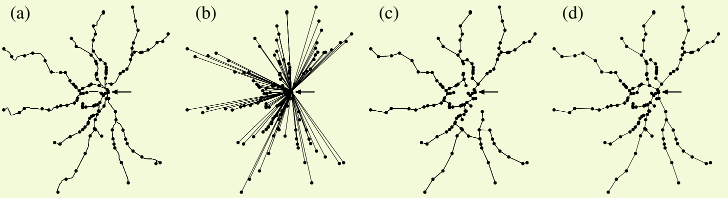
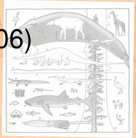


Figure 1. (a) Commuter rail network in the Boston area. The arrow marks the assumed root of the network. (b) Star graph. (c) Minimum spanning tree. (d) The model of equation (3) applied to the same set of stations.

(2006)

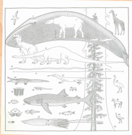


Gastner and Newman [15]: "Shape and efficiency in spatial distribution networks"

Minimal network volume:

Approximate network volume by integral over region:

$$\min V_{\text{net}} \propto \int_{\Omega_{d,D}(V)} \rho \, ||\vec{x}|| \, \mathrm{d}\vec{x}$$



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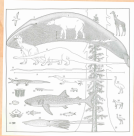
Insert question from assignment 3 (⊞)



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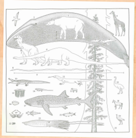


Geometric argument

- General result:

$$\boxed{\min V_{\mathrm{net}} \propto \rho V^{1+\gamma_{\max}}}$$

- If scaling is isometric, we have $\gamma_{\max} = 1/d$:

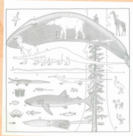
$$\min V_{\mathrm{net/iso}} \propto \rho V^{1+1/d} = \rho V^{(d+1)/d}$$

- If scaling is allometric, we have $\gamma_{\max} = \gamma_{\mathrm{allo}} > 1/d$: and

$$\min V_{\mathrm{net/allo}} \propto \rho V^{1+\gamma_{\mathrm{allo}}}$$

- Isometrically growing volumes require less network volume than allometrically growing volumes:

$$\frac{\min V_{\mathrm{net/iso}}}{\min V_{\mathrm{net/allo}}} \rightarrow 0 \text{ as } V \rightarrow \infty$$



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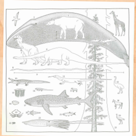

Geometric argument

- General result:

$$\boxed{\min V_{\text{net}} \propto \rho V^{1+\gamma_{\max}}}$$

- If scaling is isometric, we have $\gamma_{\max} = 1/d$:

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- If scaling is allometric, we have $\gamma_{\max} = \gamma_{\text{allo}} > 1/d$: and

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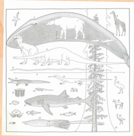

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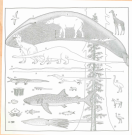
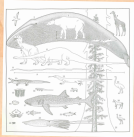


Outline

Scaling-at-large

- Allometry
- Examples
- A focus: Metabolism
- Measuring exponents
- History: River networks
- Earlier theories
- Geometric argument
- **Blood networks**
- River networks
- Conclusion

References

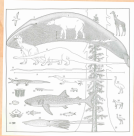


Blood networks

- Material costly $\Rightarrow$ expect lower optimal bound of $V_{\text{net}} \propto \rho V^{(d+1)/d}$ to be followed closely.
- For cardiovascular networks, $d = D = 3$.
- Blood volume scales linearly with body volume [40], $V_{\text{net}} \propto V$.
- Sink density must $\therefore$ decrease as volume increases:

$$\rho \propto V^{-1/d}.$$

- Density of suppliable sinks decreases with organism size.



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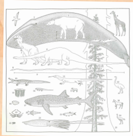

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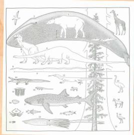

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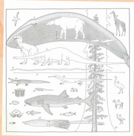

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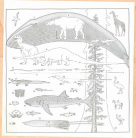


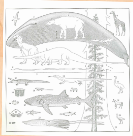
Blood networks

- Then P, the rate of overall energy use in Ω, can at most scale with volume as

$$P \propto \rho V$$

- For $d = 3$ dimensional organisms, we have

$$\boxed{P \propto M^{2/3}}$$



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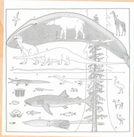

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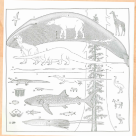

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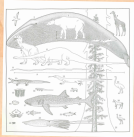

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Stefan-Boltzmann law: (⊞)

- $$\frac{\mathrm{d}E}{\mathrm{d}t} = \sigma S T^4$$

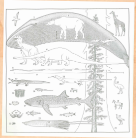
  where S is surface and T is temperature.

- Very rough estimate of prefactor based on scaling of normal mammalian body temperature and surface area S:

  $$B \simeq 10^5 M^{2/3} \text{erg/sec}.$$

- Measured for $M \leq 10$ kg:

  $$B = 2.57 \times 10^5 M^{2/3} \text{erg/sec}.$$



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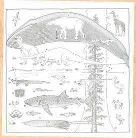

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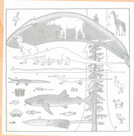

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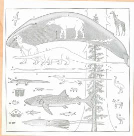
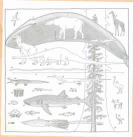


River networks

- View river networks as collection networks.
- Many sources and one sink.
- Assume ρ is constant over time:

$$V_{\mathrm{net}} \propto \rho V^{(d+1)/d} = \text{constant} \times V^{3/2}$$

- Network volume grows faster than basin 'volume' (really area).
- It's all okay:
  Landscapes are d=2 surfaces living in D=3 dimensions.
- Streams can grow not just in width but in depth...



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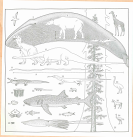

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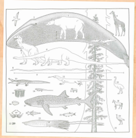

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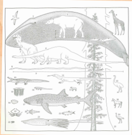

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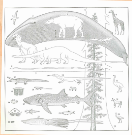

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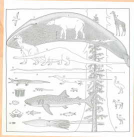


Hack's law

- Volume of water in river network can be calculated by adding up basin areas
- Flows sum in such a way that

$$V_{\mathrm{net}} = \sum_{\text{all pixels}} a_{\text{pixel } i}$$

- Hack's law again:

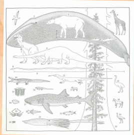
$$\ell \sim a^h$$

- Can argue

$$V_{\mathrm{net}} \propto V_{\mathrm{basin}}^{1+h} = a_{\mathrm{basin}}^{1+h}$$

where h is Hack's exponent.
- $\therefore$ minimal volume calculations gives

$$\boxed{h = 1/2}$$



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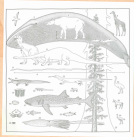

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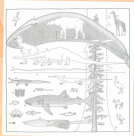

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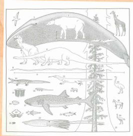

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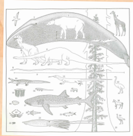

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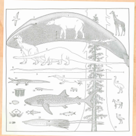

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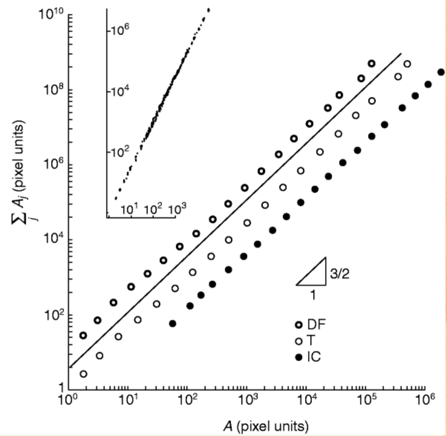

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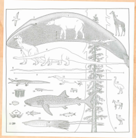

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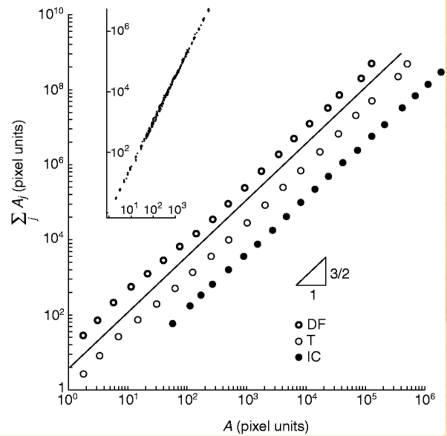

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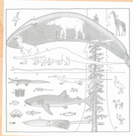

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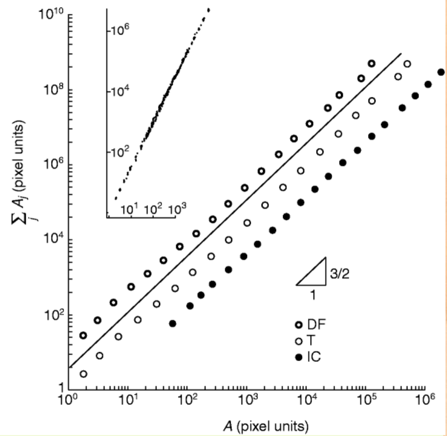

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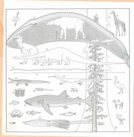

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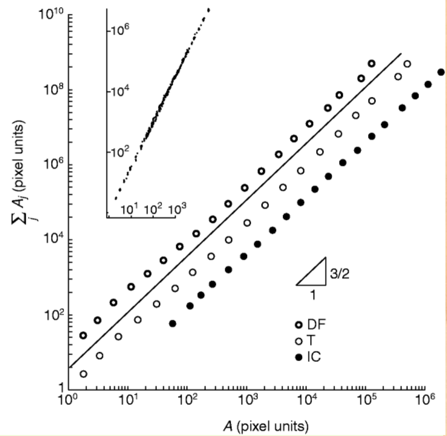

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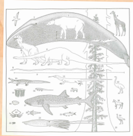
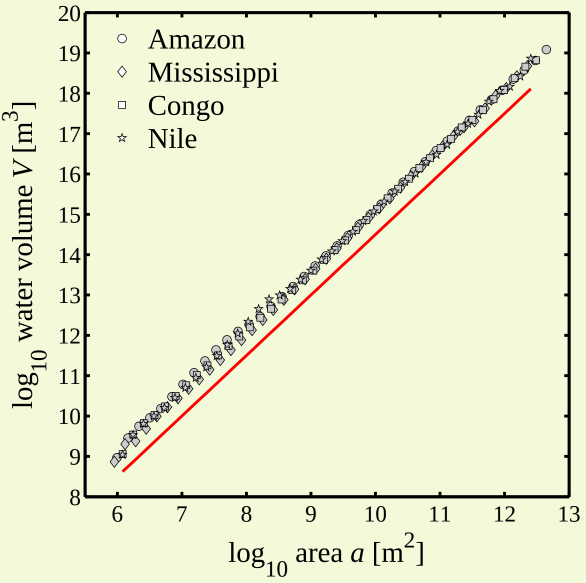
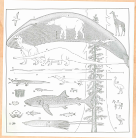


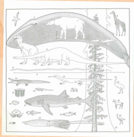
Even better—prefactors match up:





Yet more theoretical madness from the Quarterologists:

- Banavar et al., 2010, PNAS:
  "A general basis for quarter-power scaling in animals." [2]
- "It has been known for decades that the metabolic rate of animals scales with body mass with an exponent that is almost always < 1, $> 2/3$, and often very close to $3/4$."
- Cough, cough, cough, hack, wheeze, cough.



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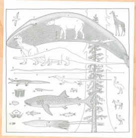

Yet more theoretical madness from the Quarterologists:

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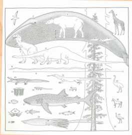
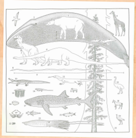
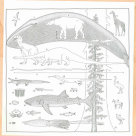


Outline



Conclusion

- Supply network story consistent with dimensional analysis.
- Isometrically growing regions can be more efficiently supplied than allometrically growing ones.
- Ambient and region dimensions matter ($D = d$ versus $D > d$).
- Deviations from optimal scaling suggest inefficiency (e.g., gravity for organisms, geological boundaries).
- Actual details of branching networks not that important.
- Exact nature of self-similarity varies.



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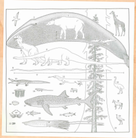

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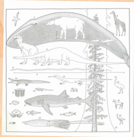

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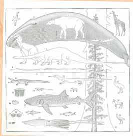

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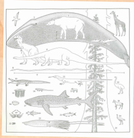

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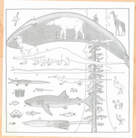

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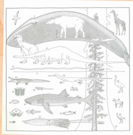

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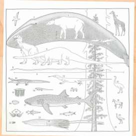

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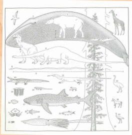

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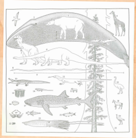

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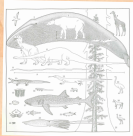

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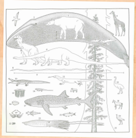

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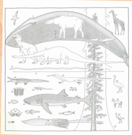

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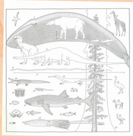

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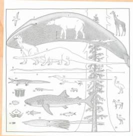

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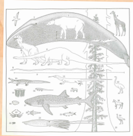

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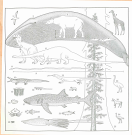

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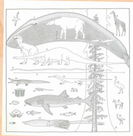

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