and *Society* (Wiley-Interscience, New York, (1971); *Sci. Amer.* **224**, 224 (Sept. 1971).
7. A. Coale, *Science* **170**, 132 (1970).
8. I. Taeuber [in *Man's Place in the Island Ecosystems*, F. R. Fosberg, Ed. (Univ. of Hawaii Press, Honolulu, 1961), pp. 226–262] analyzes how absorption into expanding societies affects the age and sex composition of populations in formerly isolated social systems.
9. O. D. Duncan, *Handbook for Modern Sociology*, R. E. L. Faris, Ed. (Rand McNally, Chicago, 1964), pp. 36–82.
10. K. Boulding describes the human ecosystem as the "totality of human organizations" [*The Organizational Revolution* (Quadrangle, Chicago, 1952), p. xxii] and O. D. Duncan notes that the cycling of information is a unique feature of the human ecosystem (9, pp. 40–42).
11. R. Freedman, *Pop. Index* **31**, 417 (1965).
12. S. S. Kuznets, *Proc. Amer. Philos. Soc.* **111**, 170 (1967).
13. M. Abramowitz, *Amer. Econ. Rev.* **46**, 8 (1965).
14. J. Krebs and J. Spengler, in *Technology and the American Economy* (Report of the National Commission on Technology, Automation, and Economic Progress) (Government Printing Office, Washington, D.C., 1966), vol. 2, pp. 359–360.

Size and Shape in Biology

Elastic criteria impose limits on biological proportions, and consequently on metabolic rates.

Thomas McMahon

Observers of living organisms since Galileo have recognized that metabolic activities must somehow be limited by surface areas, rather than body volumes. Rubner (*1*) observed that heat production rate divided by total body surface area was nearly constant in dogs of various sizes, and proposed the explanation that metabolically produced heat was limited by an animal's ability to lose heat, and thus total body surface area. When more precise methods of measurement became available, Kleiber (*2*) noticed that when rate of heat production is plotted against body weight on logarithmic scales for animals over a size range from rats to steers, the points fall extremely close to a straight line with slope 0.75 (Fig. 1). The result has since been confirmed for animals as different in size as the mouse and the elephant (*3–5*), and has been verified for other metabolically related variables, such as rate of oxygen consumption (*6*). Excellent reviews of the problem are available (*7–10*).

While it is often true that biological laws are not derivable from physical laws in any simple sense, Kleiber's rule may be one of those fortuitous exceptions which D'Arcy Thompson (*11*) suggests lie at the basis of a fundamental "science of form." Plants as well as animals must be built strongly enough to stand under their own weight. In the following, a general rule is derived for the changing proportions of idealized trees as a function of scale, and later the results are applied to animals.

Buckling

Consider a tall, slender cylindrical column of length l and diameter d loaded by the force P, representing the total weight of the column, acting at the center of mass. Such a column will fail in compression if the applied stress P/A, where $A = \pi d^2/4$, exceeds the maximum compressive stress, $\sigma_{\max}$. Provided that the column is slender enough, it may also fail in what is known as elastic buckling, whereby a small lateral displacement (caused, for example, by the smallest gust of wind), allows the weight P to apply a toppling moment which the elastic forces of the bent column below are not sufficient to resist. In this case, "slender enough" means that l/d is greater than 25, a range which includes virtually all trees (*12*). The critical length for buckling is related to the diameter by:

$$l_{\mathrm{cr}} = 0.851 \left| \frac{E}{\rho} \right|^{1/3} d^{2/3} \qquad (1)$$

where ρ is the weight per unit volume and E is the elastic modulus of the material. The mathematician Greenhill (*13*) showed that when the force due to weight is distributed over the total extent of the column instead of being taken as acting at the center of mass, the critical height becomes:

$$l_{\mathrm{cr}} = 0.792 \left| \frac{E}{\rho} \right|^{1/3} d^{2/3} \qquad (2)$$

This result is identical to Eq. 1, with only a change in the numerical constant. It may be demonstrated that another change in the constant occurs when the solid cylinder is made hollow, provided that the thickness of the wall is proportional to the diameter. Greenhill further showed that if the shape of the column is taken as a cone, or a paraboloid of revolution, the result is again only to change the numerical constant. Recently, Keller and Niordson (*14*) have derived that the tallest self-supporting homogeneous tapering column is 2.034 times as tall as a cylindrical column made of the same volume of the same material, and that the distance to the top of such a tapering column above any cross section is proportional to the diameter of that cross section raised to the ⅔ power. The rule requiring height to go as diameter to the ⅔ power is thus independent of many details of the model proposed for the elastic stability of tree trunks.

Bending

The limbs of trees must also be proportioned to endure the bending forces produced by their own weight. If a branch is considered to be a cantilever beam built into the trunk, there exists a particular beam length l_{cr} for which the tip of the branch extends the greatest horizontal distance away from the trunk (*15*). Branches longer than l_{cr} droop so much that their tips actually come closer to the trunk. Suppose that the purpose of branches is to carry their leaves out of the shadow of higher branches, and therefore to achieve a maximum lateral displacement from

---

The author is assistant professor of applied mechanics in the division of engineering and applied physics, Harvard University, Cambridge, Massachusetts 02138.

the trunk. Then the limb should grow no longer than l_{cr}, where

$$l_{cr} = C\left|\frac{E}{\rho}\right|^{1/3} d^{2/3} \qquad (3)$$

and C depends only on the droop angle θ_D, which in turn depends only on the angle at which the limb leaves the trunk (*15*). The result may be made general for a tapered or hollow limb exactly as was done for the buckling problem. Comparing Eqs. 1, 2, and 3, it is apparent that elastic criteria set length proportional to the ⅔ power of diameter in both the trunk and the branches.

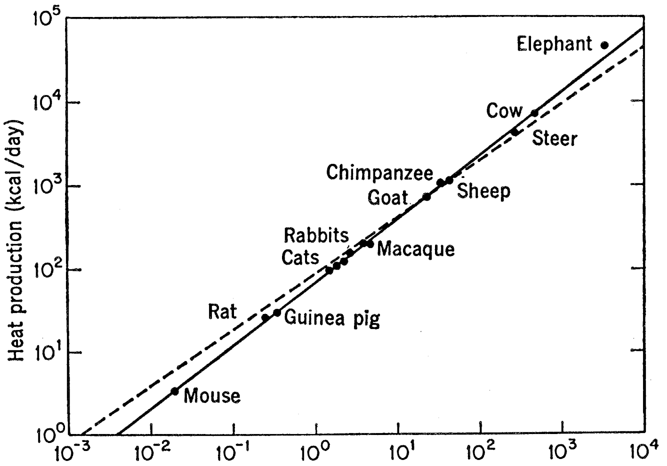
It should be possible to check the validity of these results by measuring the proportions of trees of different scale. Such a check would be arduous if it were necessary to know E and ρ for each species; fortunately, the ratio E/ρ is quite accurately constant in green woods (*16, 17*). In Fig. 2, the trunk diameter 1.525 meters from the ground is plotted against the total height for 576 individual trees, representing nearly every species found in the United States. The data, taken primarily from the American Forestry Association's "Social register of big trees" (*18*), include specimens both very slender and very stout, since trees are eligible for this list according to their bigness, an index depending on the sum of their circumference and height (*19*). A solid line representing Eq. 2 is also shown in Fig. 2; it was calculated for $E = 1.05 \times 10^5$ kilograms per square meter and $\rho = 6.18 \times 10^2$ kilograms per cubic meter (*16*). The broken line, which fits near the center of the data points, has the same slope as the solid line but represents a sequence of trees whose height in each case is only one-fourth of the critical buckling height. The conclusion seems to be that the proportions of trees are limited by elastic criteria, since there are no data points to the left of the solid line.

Animal Proportions

Just as trees must assume thicker proportions with increasing size, so must animals adjust their shape with scale. The argument has long been offered that animals could not remain geometrically similar from the small to the large because their limbs, whose cross-sectional area increases as the square of characteristic body dimension L, must then support a weight which increases as L^3 (*7*). The difficulty with these arguments based on strength criteria is the inevitable conclusion that animals may grow no larger than a size which makes the applied stress equal to the yield stress of their materials. Animals larger than this size would have to increase supporting areas directly with weight, so that no increases in height could be tolerated, only increases in width. If yield stress were the only criterion, an animal with slender proportions like the bobcat should be capable of attaining the same absolute height as the lion. In fact, it is widely found that some animals grow larger than others, and animals of small scale are relatively more slender than those of large scale (see cover). Perhaps this transformation occurs, as in differently sized trees, for reasons based on elastic rather than strength criteria.

In the following, we consider comparisons between animals of the same family, so that their shape is grossly similar. The only change in shape permitted is for lengths to bear a specified relationship to diameters: all lengths will be proportional to one another, as will be all diameters. Each limb, bone, or muscle will thus have a length l and diameter d, where length will be taken as a measurement parallel to the direction of tension or compression and diameter will be measured perpendicular to this direction. Thus, the length of the trunk is the distance between shoulder and hip whether the animal is bipedal or quadrapedal (Fig. 3a, bottom).

When a quadruped is standing at rest, the four limbs will be exposed primarily to buckling loads, but the vertebral column and its musculature must withstand bending loads. When the same animal runs, the situation is substantially reversed in those phases of the motion where the limbs are providing their maximum propulsive effort. At these moments, the limbs are supporting bending loads, while the vertebral column is receiving an end thrust and thus a buckling load. The fact that the loads are dynamic rather than static is not a consideration: the maximum deflection of a structure suddenly loaded under its own weight is



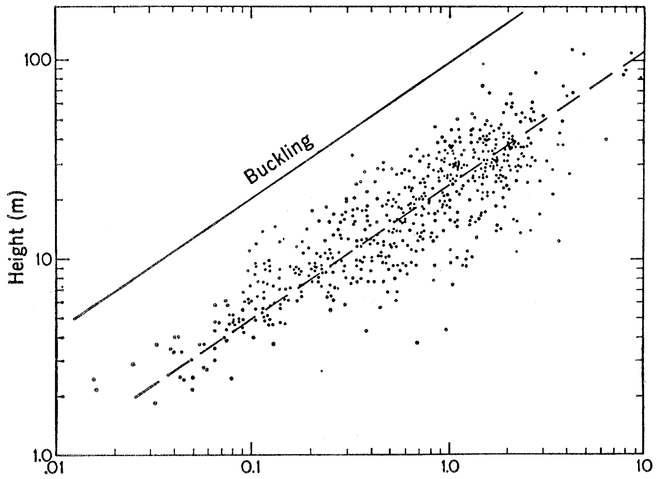


Fig. 1 (left). Metabolic heat production plotted against body weight on logarithmic scales. The solid line has slope ¾. The broken line, which does not fit the data, has slope ⅔ and represents the way surface area increases with weight for geometrically similar shapes [adapted from (*2*)]. Fig. 2 (right). Tree height plotted against trunk base diameter on logarithmic scales for record trees representing nearly every American species. The trunk proportions are limited by elastic buckling criteria, since no points lie to the left of the solid line. Data from (*18, 19*).

just twice the static deflection when the load is gradually applied (*12*). The true instantaneous loading condition for each of the quasi-cylindrical elements is thus some complicated sum of buckling, bending, and torsional loads, but fortunately the elastic criteria predict the same result independently of the type of gravitational self-loading, namely that every l should be proportional to the ⅔ power of the equivalent d.

Rashevsky (*20*) assumed that the trunk of an animal was a uniformly loaded beam, and used the linearized theory of beam bending to calculate the same result, that trunk length should go as diameter to the ⅔. Rashevsky's model additionally required the cross-sectional area of the animal's limbs to be proportional to the weight of the trunk, leading to a different set of rules for determining limb proportions from those for trunk proportions. In the present model all the proportions of an animal would change with size in the same way. If W is the total body weight, the weight of any limb is a specified fraction of W, and:

$$W \propto ld^2 \qquad (4)$$

but if l^3 is proportional to d^2, then

$$l \propto W^{1/4}; \quad d \propto W^{3/8} \qquad (5)$$

Comparative zoologists have long been aware that the gross dimensions of many species bear a power law relation to body weight. Brody (*4*) measured the chest girth G and the height at withers H of more than 3000 Holstein cattle. His data fit the present model well: he empirically found G proportional to $W^{0.36}$ ($W^{0.375}$ predicted), while H goes as $W^{0.24}$ ($W^{0.25}$ predicted).

In a study of primates whose weights ranged from 0.28 to 22 kg, Stahl and Gummerson (*21*) reported many of the important somatic and skeletal dimensions, x, as power functions of body weight, $x = aW^b$. Figure 3a, reproduced from their paper, shows that chest circumference in primates is proportional to $W^{0.37}$ with a correlation of .995. Agreement with the proposed model is excellent for most of his measurements: b is 0.28 for trunk height (0.25 predicted) and 0.38 for maximum thigh girth (0.375 predicted).

Let us return to the question of external body surface area. If the surface area of each of the quasi-cylindrical elements that make up the whole animal in the proposed model is calculated, we find

$$\text{surface area} \propto ld + d^2/2 \qquad (6)$$

where the second term is due to the ends of each cylindrical element, so that it is absent or halved in the case of many of the elements. For most limbs and many of the trunks under consideration, l/d is approximately 10, so that the second term is only 5 percent of the first and may be neglected. In this case, total body surface area is proportional to ld and thus to $W^{1/4}W^{3/8}$, or $W^{5/8}$. Hemmingsen (*8*) presented a plot of body surface area against weight for animals in a weight range of 1 to 10^6 grams, and he also included points representing defoliated beech trees. In his figure, only one solid line appears, that appropriate to the surface area of a sphere of density 1.0 g/cm^3. His figure is reproduced in Fig. 3b, with an additional line representing the proposed model of a cylinder whose surface area is three times the sphere area when both sphere and model weigh close to 8 g, but only twice the sphere area when both weigh about 70 kg. The slope of the line for this stretched cylinder is 0.63, while the slope of the line for the sphere, and thus all geometrically similar structures, is 0.67. Although Hemmingsen argues that the data points are well fitted by an imaginary line running parallel to that of the sphere, it is apparent that a good fit is obtained by the present model. In data spanning the range from rats to humans, Stahl (*22*) found that surface area increases as the 0.65 power of body weight. Thus, the present model agrees with experimental observations of body surface area as well as body proportions.

Metabolic Rate

Our ideas describing how size determines shape are now complete, and we may return to the original question concerning metabolism and Kleiber's law. Suppose a muscle, whose cross-

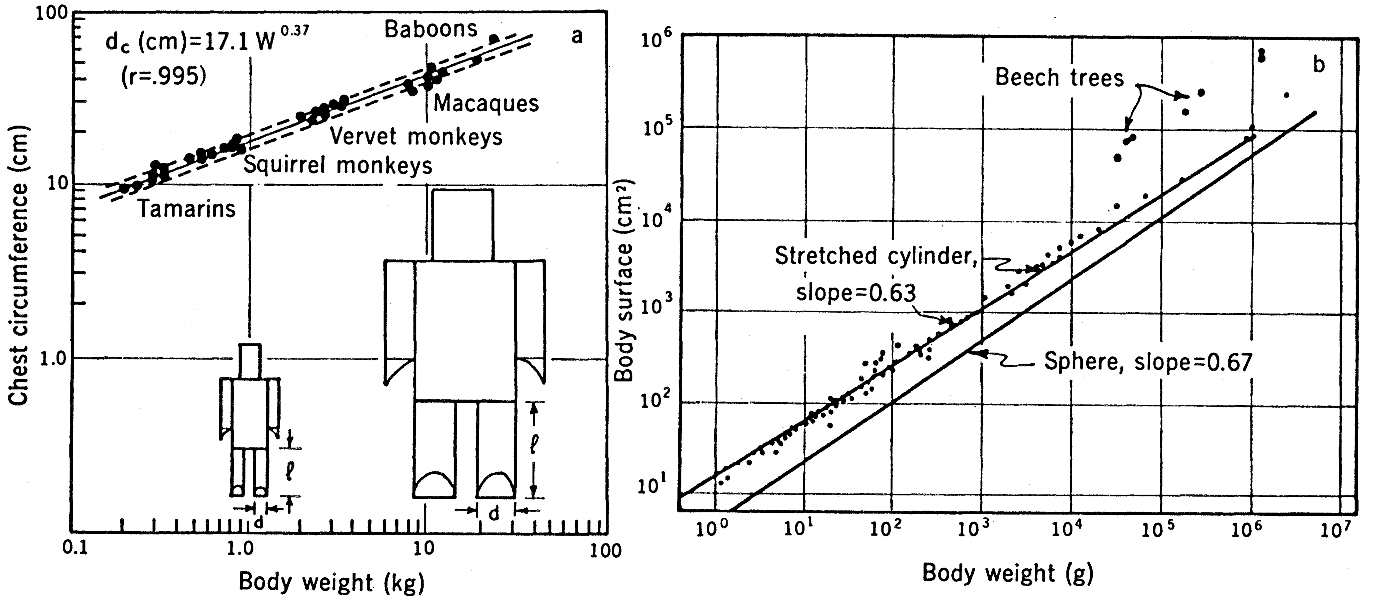


Fig. 3. (a) Chest circumference, d_c, plotted against body weight, W, for five species of primates. The broken lines represent the standard error in this least-squares fit [adapted from (*21*)]. The model proposed here, whereby each length, l, increases as the ⅔ power of diameter, d, is illustrated for two weights differing by a factor of 16. (b) Body surface area plotted against weight for vertebrates. The animal data are reasonably well fitted by the stretched cylinder model [adapted from (*8*)].

sectional area is A, shortens a length Δl against force σA in time Δt. The power this muscle expends is $\sigma A \Delta l / \Delta t$, where σ is the tensile stress developed, and is in general a function of the shortening velocity $\Delta l / \Delta t$. Hill (*23*) reported that "the inherent strength of a contracting voluntary muscle fiber is roughly constant, being of the order of a few kilograms per square centimeter of cross-section." He also presented arguments and experimental data to prove that the speed of shortening, $\Delta l / \Delta t$, is a constant in any particular muscle from species to species. If we understand from the work of Hill and others that both σ and $\Delta l / \Delta t$ may be taken as constant, then the power output of a particular muscle and hence all the metabolic variables involved in maintaining the flow of energy to that muscle depend only on its cross-sectional area. But this area is proportional to d^2, and hence

$$\text{maximal power output} \propto (W^{3/8})^2 = W^{0.75} \tag{7}$$

This is precisely the statement of Kleiber's law we were looking for, provided we have some confidence that maximal energy metabolism exceeds basal metabolic rate by a factor, the metabolic "scope," which is invariant with respect to scale. Hemmingsen (*8*) has presented evidence to this effect.

According to the model proposed here, if lung volume goes as W (*4, 21*) but alveolar ventilation goes as $W^{0.75}$, then respiratory frequency must scale as $W^{-0.25}$. The identical argument may be made for ventricular stroke volume, cardiac output, and heart rate. In fact, Adolph (*24*) reported that b for respiratory frequency in mammals is -0.28 [Tenney (*10*) independently gave the same number]. For heart rate, b has been reported as -0.27 (*25*) and -0.25 (*22*). Stahl (*9*) observed that the ratio of many physiological periods to one another is found to be nearly constant, independent of scale. Thus, the ratio of gut pulsation time to pulse time is nearly the same in all mammals, and each animal lives for approximately the same number of heartbeats or breath cycles. Other authors have discussed the importance of this conclusion in arriving at the "physiological age" of living organisms.

Summary and Conclusions

Arguments based on elastic stability and flexure, as opposed to the more conventional ones based on yield strength, require that living organisms adopt forms whereby lengths increase as the ⅔ power of diameter. The somatic dimensions of several species of animals and of a wide variety of trees fit this rule well.

It is a simple matter to show that energy metabolism during maximal sustained work depends on body cross-sectional area, not total body surface area as proposed by Rubner (*1*) and many after him. This result and the result requiring animal proportions to change with size amount to a derivation of Kleiber's law, a statement only empirical until now, correlating the metabolically related variables with body weight raised to the ¾ power. In the present model, biological frequencies are predicted to go inversely as body weight to the ¼ power, and total body surface areas should correlate with body weight to the ⅝ power. All predictions of the proposed model are tested by comparison with existing data, and the fit is considered satisfactory.

In *The Fire of Life*, Kleiber (*5*) wrote "When the concepts concerned with the relation of body size and metabolic rate are clarified, . . . then compartive physiology of metabolism will be of great help in solving one of the most intricate and interesting problems in biology, namely the regulation of the rate of cell metabolism." Although Hill (*23*) realized that "the essential point about a large animal is that its structure should be capable of bearing its own weight and this leaves less play for other factors," he was forced to use an oversimplified "geometric similarity" hypothesis in his important work on animal locomotion and muscular dynamics. It is my hope that the model proposed here promises useful answers in comparisons of living things on both the microscopic and the gross scale, as part of the growing science of form, which asks precisely how organisms are diverse and yet again how they are alike.

References and Notes

1. M. Rubner, *Z. Biol. Munich* **19**, 535 (1883).
2. M. Kleiber, *Hilgardia* **6**, 315 (1932).
3. F. G. Benedict, *Vital Energetics: A Study in Comparative Basal Metabolism* (Carnegie Institution of Washington, Washington, D.C., 1938).
4. S. Brody, *Bioenergetics and Growth* (Reinhold, New York, 1945).
5. M. Kleiber, *The Fire of Life* (Wiley, New York, 1961).
6. S. M. Tenney and J. E. Remners, *Nature* **197**, 54 (1963); A. C. Guyton, *Amer. J. Physiol.* **150**, 70 (1947); E. Zeuthen, *Quart. Rev. Biol.* **28** (No. 1), 1 (1953).
7. K. Schmidt-Nielsen, *Proc. Amer. Physiol. Soc.* **29**, 1524 (1970); A. M. Hemmingsen, *Rep. Steno Mem. Hosp. Nord. Insulin Lab.* **4**, 1 (1950); S. J. Gould, *Amer. Natur.* **105**, 113 (1971); W. R. Stahl, *Science* **137**, 205 (1962).
8. A. M. Hemmingsen, *Rep. Steno Mem. Hosp. Nord. Insulin Lab.* **9**, 1 (1960).
9. W. R. Stahl, *Advan. Biol. Med. Phys.* **9**, 355 (1963).
10. S. M. Tenney, *Circ. Res.* **20-21** (Suppl. I), **I-7** (1967).
11. D. W. Thompson, *On Growth and Form* (Cambridge Univ. Press, London, 1917).
12. S. Timoshenko, *Elements of Strength of Materials* (Van Nostrand, Princeton, N.J., 1962).
13. G. Greenhill, *Proc. Cambridge Phil. Soc.* **4**, 65 (1881).
14. J. B. Keller and F. I. Niordson, *J. Math. Mech.* **16** (No. 5), 433 (1966).
15. T. A. McMahon, in preparation.
16. T. A. McElhanney and R. S. Perry, *Forest Service Bulletin No. 78* (Forest Products Laboratories of Canada, Ottawa, 1927).
17. G. A. Garratt, *The Mechanical Properties of Wood* (Wiley, New York, 1931).
18. "Social register of big trees," *Amer. Forests* **72**, 16 (May 1966); *ibid.* **77**, 25 (January 1971).
19. Other data used in Fig. 2 are from the following books: Royal Horticultural Society, *Conifers in Cultivation* (Royal Horticultural Society, London, 1932), p. 316; W. Fry and J. R. White, *Big Trees* (Stanford Univ. Press, Stanford, Calif., 1930).
20. N. Rashevsky, *Mathematical Biophysics* (Dover, New York, 1960), vol. 2.
21. W. R. Stahl and J. Y. Gummerson, *Growth* **37**, 21 (1967).
22. W. R. Stahl, *J. Appl. Physiol.* **22**, 453 (1967).
23. A. V. Hill, *Sci. Progr. London* **38** (No. 150), 209 (1950).
24. E. F. Adolph, *Science* **109**, 579 (1949).
25. A. J. Clark, *Comparative Physiology of the Heart* (Cambridge Univ. Press, Cambridge, 1927).
26. The author is grateful to B. Budiansky, R. E. Kronauer, S. J. Gould, C. R. Taylor, and G. P. DeWolf for assistance through helpful discussions.