

ALLOMETRY AND SIZE IN ONTOGENY AND PHYLOGENY

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I. INTRODUCTION: THE CORRELATION OF SIZE AND SHAPE

The term 'allometry' will be used in this article in its broadest sense, to designate the differences in proportions correlated with changes in absolute magnitude of the total organism or of the specific parts under consideration. The term will be used thus: (1) whether the variates be morphological, physiological or chemical; (2) whether the size differences occur in ontogeny, phylogeny, or arise merely from the static comparison of related forms at one growth stage (usually the adult); and (3) regardless of the form of the mathematical expression used to abstract the general trend of variate correlation.

Allometry then is the study of size and its consequences. Since size is a variable in allometric analyses, this statement may at first seem trivial. I am, however, interested

in probing beyond statistical relations towards an assessment of the role of absolute magnitude as a cause of trends in form alteration. As a palaeontologist, I acknowledge a nearly complete bias for seeking causes framed in terms of adaptation; yet I recognize that explanations of allometry in terms of physiological efficient causes are of strictly equal validity. Such a vast subject could, and should, be approached in many ways, but coherence demands a synthetic theme. The theme must be accurate and fruitful; it must not be twisted to encompass more than it can explain; it must not claim exclusive rights as a unifying approach.

An artificial distinction between two types of size-correlated change in shape seems justified, at least in a heuristic sense. Certain shape alterations are mechanically required by size increase.* Other regular allometric trends not causally related to absolute magnitude are nonetheless size-dependent in the sense that any variation in absolute magnitude implies a different shape. This is particularly important in phylogenetic size increase where extrapolation of ancestral trends into widened size ranges produces new shapes and corresponding new functions. In the first case, size increase *requires* form change; in the second, size increase *permits* the expression of new potentiality. Cases of the second type predominate in the published literature on allometry.

Since the role of size in allometry is most unambiguously seen in examples of the first type, these shall be explored at some length as a prelude to discussion and application of quantitative allometric methods.

II. SIZE-REQUIRED ALLOMETRY

'It is a truism in engineering', writes von Bertalanffy (1964, p. 21), 'that any machine requires changes in proportion to remain functional if it is built in different size.' The organism-machine analogy has been as misused and over-extended as opposite contentions of complete organic uniqueness; still, it is not without merit.

If geometrical similarity is maintained with size increase, any series of objects will exhibit continually decreasing ratios of surface area to volume. This is a simple consequence of elementary geometry: area increases as the square of linear dimensions, volume as the cube. Constant area-to-volume ratios, an adaptive necessity for many organic relationships, can only be maintained by altering shape. To obtain the necessary surface area an initial sphere will, upon size increase, be subdivided, convoluted, flattened or attenuated.

(i) *Area-to-volume relationships: the elaboration of structure*

In Galileo's *Dialogue of the second day* in the *Discorsi e dimostrazioni matematiche* (English translation by H. Crew and A. Del Salvio as *Dialogues concerning two new sciences*), two students and a professor deduce the biological consequences of decreasing A/V ratios from a consideration of the breaking strengths of prisms and

* This is a short-cut mode of expression and should not be taken as implying that size increase is the efficient cause of shape alteration. In phylogeny that role is, of course, played by natural selection. Given the truism that any organism must be well adapted to survive, size increase does become a formal cause of adaptation in determining a specific direction in which natural selection *must* operate in order to produce adequate adaptation in the expanded size range.

cylinders. Further elaboration, however, awaited the attention of such leading nineteenth-century scholars as Herbert Spencer (1868, pp. 121–9) and C. Bergmann.*

It is in D'Arcy Thompson's *On growth and form* (1942, first edition, 1917) that the principle was given its finest explication. The notion that smallest animals have the greatest relative surface forms the basis for Thompson's elucidation of protist form by analogy to surface-tension models: 'The form of all very small organisms is independent of gravity, and largely if not mainly due to the force of surface tension' (Thompson, 1942, p. 57).

With the continually greater demands placed by size increase upon such surface-dependent functions as respiration and ciliary locomotion (which must serve the volumetrically expanding total body bulk), even protists may reach an adaptive impasse. It has therefore long been suspected (see, for example, Ryder, 1893) that the continually decreasing surface-area/volume ratio may serve as a formal cause of cell division.

Subdivision of the total body bulk is one 'mode of escape' (Ryder, 1893, p. 16) from decreasing A/V ratios, but not an adequate one for metazoa. Three general solutions which preserve the integrity of the organism are commonly observed:

(a) The differential increase of surfaces by complication of structure—branching, convolution, etc.

(b) The differential increase of surfaces by change in shape without complication of structure—attenuation, flattening, etc.

(c) The incorporation of inactive organic matter within the volume occupied.

Large platyhelminths have taken the second solution. Increase in bulk imposes extreme relative flattening since all body parts must be in intimate contact with the external surface which, in the absence of internal differentiation (solution *a*), must perform respiratory and other functions serving total body bulk. Such extremes in size-required shape are not adaptively flexible and must be regarded as evolutionary dead ends.

The third solution, that adopted by coelenterates and some higher plants (Bonner, 1952, p. 16), represents another means of avoiding extensive complication of structure. Most of the volume of these organisms is occupied by inert, non-respiring matter (jelly and wood, respectively). Although total bulk increases as the cube of length, that active part which is served by surface-dependent functions does not increase faster than the surfaces themselves.

Among animals at least, the second and third solutions are confined to 'lower' phyla. More advanced groups solve A/V problems by increased complication of (internal) structure. It is, in fact, the genetic potentiality for solving A/V problems in this way that defines the advanced groupings.

In general, the smallest animals of the advanced phyla possess the simplest internal structures. The minute gastropod *Caecum glabrum* has no gills since skin respiration supplies sufficient oxygen; the intestinal glands consist simply of two tubules (Rensch,

* Bergmann's famous ecological rule relating size to latitude in homiotherms is also explained by the area/volume relationship. Within a related group, larger animals occur in high latitudes because the lower external-surface/volume ratio relative to smaller forms in warmer climates is favourable for the retention of heat.

1960, p. 171). Increase beyond these very small sizes necessitates structural elaboration of area-dependent functions, most notably locomotory, respiratory and digestive.

Locomotory. Since cilia number is proportional to body surface (and locomotory force is proportional to cilia number), ciliary locomotion is only possible in small organisms with very high relative surface (Adolph, 1931). Larger echinoderm larvae which approach the limiting size for ciliary locomotion possess enormously complicated and coiled cilia bands (Rensch, 1960). Rhabdocoel worms longer than 3 mm. are creepers; smaller species use cilia in swimming (Adolph, 1931). The differentiation of muscular systems by so many advanced groups probably represents a parallel solution developed by natural selection to escape the size-limitations of ciliary locomotion. Speculative literature on the invertebrate-vertebrate transition, for example, has attributed an important role to size increase in the development of muscular from ciliary systems. Garstang (1928), who favoured vertebrate origin from a neotenized deuterostome larva, traced the development of muscular locomotion to body enlargement beyond weights capable of being propelled by cilia. Further bulk increase might lead to efficient systems of muscular segmentation (Whithead, 1957). Branchial musculature, replacing cilia as producers of gill motion, would develop at these larger sizes (Young, 1950, p. 133).

Respiratory. Since it must function to support, to protect and to insulate, the external surface itself is strictly limited in its possibilities for differential increase with increasing size. It cannot convolute like a brain or dichotomize like a circulatory system. External surface respiration, common among small forms and probably an initial stage in the phylogeny of most higher phyla, cannot persist beyond a definite size, and the differentiation of more efficient structures (lungs or gills), that can differentially increase surface to keep pace with the body volume it must serve, is inevitable. Sattel (1956) found a constant trachea-surface to body-volume ratio with size increase in the silkworm, *Bombyx mori*. This A/V constancy implies that the tracheae become geometrically more complicated (differentially lengthened, branched, etc.) with size increase.

Amphibians employing skin respiration are among the smallest of their class (Rensch, 1960). As an initial attempt at compensation, amphibians increase the ratio of meshes per square millimetre skin in order to keep a constant respiratory surface to volume ratio. *Salamandra salamandra* increases the mesh ratio from 12·25 in the young larva to 43·10 just before metamorphosis; in *Rana esculenta* it increases from 15·7 to 80·9 (Szarski, 1964). Lungs offer far greater potentiality for differentially increasing surface area. A freshly metamorphosed *Rana pipiens* has no lung folds. *Hyla arborea* at 2·56 g. possesses 6·3 cm.² of lung surface; at 6·8 g. lung surface has increased to 46 cm.² (Szarski, 1964).

Nutritive. The absorption of digested food is another major function performed by body surfaces. Intestines of larger mammals are relatively longer than those of related smaller species (Rensch, 1948). Alternatively, intestinal surface area can be extended by internal complication; villi increase surface area on the bath-towel model (Thompson, 1942, p. 56).

The direction of shape change (differentiation of organ systems and increase in their

complexity) with increasing size is that of anagenetic evolutionary improvement (Huxley, 1958). Some of the most important steps in the evolution of complex organisms may be attributed to mechanical requirements of size increase. This should not obscure the importance of such steps as biological improvements; for whatever reason complex organ systems may have been originally developed, the expanded potential for further progress thus conferred upon organisms bearing them is a true and most significant phylogenetic advance. The pre-adaptive possibilities of complexity are vast.

The following examples, illustrating phylogenetic compensation in feeding, respiratory and locomotory systems, exactly parallel previously cited ontogenetic cases and demonstrate how absolute magnitude can serve as a synthetic theme to unite conceptually the varied phenomena classed together as allometry.

Nutritive. Increased looping and folding of the brachiopod lophophore (a food-gathering structure) has generally been treated as an independent criterion of evolutionary advance. In many, if not most, cases it is more probably explained as a differential growth of surface to compensate size increase. Jurassic thecidelliniform brachiopods (maximum length 5 mm.) possess a simple bilobed lophophore (Elliott, 1948a). In the descendent thecidiforms 'the number of brachial lobes is increased from two up to a varying larger number, and the shell increases to about double the size' (Elliott, 1948a, p. 23). Since this sequence of events occurred more than once (Elliott, 1948b, 1953), an explanation in terms of size increase seems likely. Moreover, *Dielasma elongata*, which becomes progressively dwarfed through the upper part of Permian reef dolomites of Co. Durham (Westoll, 1950, p. 500), shows corresponding decrease of lophophore complexity.

Hypsodonty, a convergent feature among large mammals of many orders (Romer, 1945), is adaptive in increasing the life span at a given size (a matter of no small importance as many fossil mammal teeth, worn to the roots, indicate premature mortality) (Van Valen, 1960). Since size increase squares the tooth grinding surface, but cubes the amount of food required, 'simple mathematical considerations' (Romer, 1945, p. 428) require that large mammals compensate enlarged bulk by differentially expanding the grinding surface (molarization of premolars) or increasing the crown height (hypodonty). Molarization, hypodonty and complication of enamel ridge folding, the three major trends in equid dental evolution, are probably all required by size (Watson, 1949).

Respiratory. Progressive elaboration of the suture pattern (an expression of septal margin plication) is a major evolutionary trend in many independent lines of ammonites. Increased shell strength is often cited as an explanation for such trends, but Newell (1949), noting the usual correlation of pattern complexity with increased size, suggests an explanation involving the *A/V* principle. Suture elaboration reflects crenulation of the posterior fold of the cephalopod mantle. Since the mantle lining partly or completely assumes the respiratory function in many molluscs, suture elaboration may indicate differential expansion of respiratory surface area.

Locomotory. The echinoderm order Melonechinoidea steadily enlarges in maximum transverse diameter from 45 to 155 mm during the Mississippian. Corre-

sponding to this, the number of ambulacral plate columns bearing tube feet increases from ten to approximately forty. 'A large form must have more tube feet than a small one to function equally well' (Newell, 1949, p. 112).

'As the fusulines increased in size, they faced the problem of secreting a shell strong enough for protection but light enough to be transported by their feeble pseudopodia' (Dunbar, 1963, p. 30). The development of a complexly honeycombed alveolar wall among several independent lines of these late Palaeozoic foraminifera provided requisite strength without excessive gain in weight and allowed size increase from wheat-grain dimensions (solid wall) to 60 mm. (alveolar wall).

(2) *Other size-required shape changes*

Surfaces are not the only body structures which increase as the square of length. Since the strength of bones, muscles and stems is proportional to cross-sectional area, larger organisms in a series of geometrically similar bodies will possess relatively weaker weight supports. Relative thickening of limb bones in large vertebrates compensates size increase by keeping the enlargement of weight-supporting cross-sections proportional to that of body volume. Differential limb thickening is a phenomenon common to all types of allometry. It occurs in the ontogeny of individuals (Cock, 1963, p. 187, on fowls); between sexes of a species (Jolicoeur, 1963a, in *Martes americana* and man), among races of a species differing in absolute size (Schlabitzky, 1953, on the fowl) and within evolving phylogenies (Gould, 1966a, on the late Palaeozoic reptile *Dimetrodon*). Nor is this expression of compensation confined to vertebrate limbs; Ingold (1946) found that a mushroom stem thickens differentially so that its cross-sectional area may increase proportionately to the cap weight it must support.

The physical impetuses for shape changes are not restricted to consequences of decreasing area-to-volume ratios. Structures which must reach a certain size in order to function at all may gain little advantage from increase beyond this threshold. Thus, the vertebrate eye shows characteristic relative decrease in progressively larger animals of a related series: 'The rods and cones do not vary with the size of the animal, but have their dimensions optically limited by the interference patterns of the waves of light, which set bounds on the production of clear retinal images... The eye, in short, can never be very small and need never be very big; it has its own conditions and limitations apart from the size of the animal' (Thompson, 1942, pp. 53-54). Likewise mushroom caps must be sufficiently high above the ground to give spores a good chance of being blown away without landing in the immediate vicinity of the parental body. Since this minimal height need not be greatly exceeded by larger forms, smaller mushrooms are relatively taller (Ingold, 1946).

Other cases are more peculiar to individual organisms than illustrative of general principles. In the three following examples, flattening is correlated with size increase for three different reasons:

(a) Flattening of some large peneroplid foraminifera provides light access for symbiotic photosynthesizing zooxanthellae.

(b) Small Cretaceous orbitolinid foraminifera built successive test chambers as

continually enlarging complete disks (*loges entières*), giving the entire structure a conical form. Phylogenetic size increase occurred in several lines when the necessity for constructing and occupying the large central part of a complete chamber was removed by the development of ring-shaped test chambers (*loges annulaires*). Size increased from a few millimetres to 5 cm. (*Orbitolina concava* and *O. aperta* of the Cenomanian) as the form changed from a small conical stack of enlarging disks to a large plate of concentric rings (Rat, 1963).

(b) Among ovoviviparous siliquariid gastropods which carry developing young in a brood pouch, small protoconchs (*Siliquaria*—0·25 mm. diameter) are conical, while large protoconchs (*Stephopoma*, *Pyxipoma*—1 mm. diameter) are planispiral. Since many more disks than spheres of corresponding diameter can be fitted into a limited space (the parental brood pouch), this correlation of size and shape seems reasonable (Gould, 1966b).

Since the direction of ontogeny, and more often than not that of phylogeny also (Newell, 1949; Rensch, 1960), is towards increasing size, I have been primarily concerned with the allometric consequences of volumetric expansion. Many evolutionary lineages and even some ontogenetic sequences (metamorphosis of leptocephalus larvae) show decrease, however, and shape compensations must be made for size alteration in either direction. Since small mammals have relatively large heads* (relatively larger still as embryos), pelvic structures of the smallest mammals are altered to allow successful passage of the relatively enormous fetus. The symphysis of the pubic bones becomes incomplete in many small forms, replaced by an elastic ligament or cartilage, or reduced to a single point of contact so that the pubes may be moved aside for successful parturition (Rensch, 1960, pp. 173–175).

(3) Allometry and size limitation

Trends in compensation by differential increase (in complexity or size) of area-dependent structures cannot be continued indefinitely without producing structural absurdities. If leg cross-sectional area is expanding to compensate body volume (L^3), then leg width increases as the square root, or as $L^{1.5}$. With total body length growing simply as L , increased size leads to a continual increase of the leg-width to body-length ratio. One need only extrapolate to absurd situations (at which, for example, leg width is greater than body length), well beyond the observed size range to appreciate why ‘it is impossible to construct an efficient terrestrial animal much larger than an elephant’ (Huxley, 1958, p. 24). (The giant sauropods were semi-aquatic.) These limitations arise from the finite constructional potentialities of organic matter, an aspect of evolution well appreciated, but too rarely considered when primary emphasis is placed on species-divergence as a model for evolutionary events. In engineering theory, an elephant could grow two more legs and become larger; in actuality, it is far more likely to remain within physically imposed size limits for four-legged forms.

The importance of A/V phenomena as determinants of organic size and shape is

* Relative head decrease may also be a consequence of the A/V principle. The brain of a large mammal, since it innervates surfaces which do not increase as fast as the body bulk, can be as efficient as that of a smaller form at smaller relative size (Rensch, 1954).

further emphasized by noting that the lower size limit of homoiotherms, too, is attributable to one of its aspects. Increasing surface-area to volume ratios with decreasing size imposes severe heat-dissipation problems upon homoiotherms. The voracious eating habits of shrews reflect an attempt to balance dissipation with high heat production. 'A mammal smaller than this [2·5 g.] would be unable to gather enough food to support its infinitely rapid metabolism' (Pearson, 1948, p. 44).

Flight in birds is dependent on wing area. Besides wing surface, other important flight factors varying as the square of length are surface of the crista sterni and strength of flight feathers in resisting bending (Dinnendahl & Kramer, 1957). As birds increase in size, compensatory allometry can preserve flight capability up to a certain point. Limited by their structural plan, however, a critical boundary is finally reached. The upper weight limit of modern flying birds lies at approximately 15 kg. (species of *Pelecanus* and *Cygnus*), but ostriches reach 90 kg. and several flightless fossil genera (*Aepyornithes*, for example) were even heavier (Meunier, 1959a, p. 453). Moreover, in some size series of related birds, terminal forms (like the fossil goose *Cnemiornis calcitrans* and the giant auk *Pinguinus impennis*) are flightless.

III. THE QUANTIFICATION OF ALLOMETRY

(1) *The equation of simple allometry*

(a) *Applicability*

The form of mathematical expression implied by the deduction that leg thickness should increase as the 1·5 power of body length is a power equation of the form: leg width = (a constant) \times (body length)^{1·5} or, more generally, $y = bx^\alpha$, where y is a variable whose increase is considered relative to that of another variable, x , which may represent a different dimension of the same organ or, more commonly, a measure of total body size. The logarithmic transformation of this power function, $\log y = \alpha(\log x) + \log b$, indicates a rectilinear plot for original variables on logarithmic co-ordinates (or of logarithms of variates on rectangular co-ordinates). α is the slope of the rectilinear plot; b , as a convenience for calculation, may be read as the y value at $x = 1$. α is the ratio of specific growth rates of y and x . It serves as a criterion for the intensity of differential increase. α values greater than 1 (positive allometry) imply a differential increase of y relative to x ; α less than 1 (negative allometry) indicates that y/x ratios decrease with increasing absolute magnitude of x : the special case $\alpha = 1$ (isometry) represents the maintenance of geometrical similarity with size increase. The use of these criteria for allometry and isometry requires that the dimensions of x and y be the same. If, on the other hand, y is a surface (L^2) and x a length (L), then $\alpha = 2$ represents isometry. If y is a length (L) and x a volume (L^3), then $\alpha = 1/3$ indicates isometry.

Although a power function of this type may be predicted *a priori* for the size-required area to volume compensations discussed in the last section, I also emphasized in the Introduction that most examples of allometry, although dependent upon size variation for their expression, do not have their characteristics determined by the physical requirements of increasing bulk. In these cases the applicability of power

functions as an adequate description of trends in differential increase must be determined on empirical grounds. Using this empirical criterion, the power function has been successfully applied to such diverse phenomena as nuclei of rabbit nerve cells (Schadé, 1959), planarian epithelial cells (Abeloos & Lecamp, 1929), elephant organs (Quiring, 1938), slime moulds (Bonner & Dodd, 1962), gourds (Sinnott, 1936), citrus trees (Turrell, 1961) and even to the differential incorporation of chemical variables (J. Needham, 1934, 1950; Forbes, 1955)—a range which led Teissier (1948, p. 14) to call this function ‘l’instrument indispensable de toute étude sur la croissance relative’. This relation, first used to quantify brain-weight to body-weight relationships late in the nineteenth century (Snell, 1891; Dubois, 1897, 1898; Lapique, 1898), was extended by Klatt to other organ-weight to body-weight relationships (e.g. heart weight, 1919) and generalized by Huxley (1924, 1932)—whose *Problems of relative growth* is both a classic synthesis and a prime stimulus to further work—and by Teissier (1931). Given its wide applicability and long history of fruitful use, the power function $y = bx^\alpha$ is generally known to biologists as the equation of simple allometry.

The special biological designation of this equation should not obscure its recognition as the power function used in all empirical sciences. It is, for example, the major descriptive tool of fluvial geomorphologists (Strahler, 1958, on stream lengths; Allen, 1963, on ripple shapes). It has also been applied to such non-allometric biological phenomena (proportion differences unrelated to variation in absolute magnitude) as the correlation of lift *v.* transverse speed in sharks (Alexander, 1965). In studies combining non-biological size differences and biological perception, Stevens & Girao (1963) and Teghtsoonian (1965) have related size as judged by an observer to physical size. The conclusion, derived from α values less than one, that perceived areal and volumetric increases of geometrically similar bodies are less than the actual values (and this not wholly due to the mistaken procedure of using L rather than L^2 or L^3 as an increase estimator—Teghtsoonian, 1965) has practical applications. A cartographer wishing to indicate by two geometrically similar symbols that one country’s rice production is twice that of another’s should make the area ratio of his two symbols greater than 2 to 1 (Stevens & Girao, 1963).

Moreover, the power function is not the only, or even necessarily the simplest, means of describing allometric trends. Since any linear relationship of the form $y = mx$ implies no change in shape with size increase, it is often forgotten that linear regressions in which the y -intercept is significantly different from zero indicate allometry. Allometry described by the power function results from continually increasing (or decreasing) y/x values for each unit increment of x . y/x for each unit increment of x is constant in a linear relationship, but allometry may arise from the addition of such increments to an initial shape of different proportions. A constant $2/1 = y/x$ for each millimetre increase of x will quickly transform a 1 mm.² square to a rectangle nearly twice as high as wide.

D’Arcy Thompson (1942) was unimpressed with Huxley’s power function because he felt that many allometric trends described by it were equally well rendered by linear regressions (see also Olson & Miller, 1951). Linear functions have often been used in allometric studies (Robb, 1935*a, b*; McIntosh, 1955; Mosimann, 1956;

Mount, 1965). Expressions more complex than simple linear or power functions have been applied to obtain closer fits to point scatters. Robb (1929) suggested the addition of a constant to the power function. Count (1947) fitted a second-degree parabola to brain-weight to body-weight relationships; A. Needham (1950) used successively higher polynomials (up to quartic) to express progressively finer details of abdominal growth in the female pea crab, *Pinnotheres pisum* Leach.

Closer fits can always be obtained by adding further terms to a power series $y = a_0 + a_1x + a_2x^2 + \dots$ (Bertalanffy, 1964, p. 22), but this method of data abstraction offers little hope of increasing biological understanding. The possibility of interpreting parameters is here sacrificed for details of fit applying only to the particular case under consideration—detail which may, moreover, be only the random effects of small sample sizes. Adequate statistical fit, while certainly the most important consideration in choosing a mathematical expression for data trends, is not the only attribute of a ‘good’ formula (see Teissier’s criteria for a *bonne formule* in Boucquet, 1953, p. 221). Sholl (1954, p. 225) emphasized the importance of choosing ‘a reasonably simple functional expression involving the minimum of non-interpretable parameters’. It is for all these reasons—adequate statistical fit in a great number of cases, simplicity, and interpretability—that the power function $y = bx^\alpha$ has enjoyed almost exclusive use in allometric studies.

(b) Interpretation of parameters

Constancy of the exponent α indicates that the variables y and x are increasing at different rates of self-multiplication and that the ratio of these rates is constant. The coefficient b , however, presents two important problems which have hindered its interpretation.

(1) Its mathematical correspondence to the value of y at $x = 1$ has often been given a spurious biological interpretation. Brett (1962, p. 1032), for example, plotted metabolism against body weight in salmon, interpreting b as ‘the rate of oxygen uptake for unit weight’. More often than not, however, measurement units are chosen to be much smaller than objects measured; $x = 1$ therefore introduces a distant extrapolation into a size range not only unrepresented in the data, but also often biologically absurd (brain weight of a 1 mm. long human being, for example). Allometric regressions are empirically determined and apply only to size ranges represented by actual data.

(2) The mathematical interdependence of b and α has not been sufficiently appreciated. The correlation between b and α for any two allometric regressions is determined by their point of intersection; if the intersection is at $x = 1$, b values are equal regardless of α ; at $x > 1$, b varies inversely with α ; at $x < 1$, directly with α (White & Gould, 1965, fig. 1). Since points of intersection can be varied by arbitrary change in the unit of measurement, observed correlations can have no biological meaning. Unaware of the mathematical artifact of correlation, many authors have assumed independence of the two parameters. Parker & Larkin (1959, p. 742) suggest that α measures ‘the complex of physiological processes’ while b indicates ‘ecological opportunity’. Any variation in physiology would then automatically influence ecology

and that influence would be in different directions according to whether body weight (as reference base for physiological processes) was measured in milligrams or kilograms. For regressions differing in α , an unambiguous biological interpretation for b will not be available until methods are devised to separate out that aspect of b value variation due to differences in α . A preliminary step in this direction has been made by Cock (1963, appendix).

At the moment, biological interpretations can only be offered for those special cases, fortunately quite numerous, in which regressions of the same slope (parallel lines on log-log paper) differ in b . For any two regressions of equal α , the ratio of y values at any x is equal and b_1/b_2 is an index of differences in proportions at any significant common x value (e.g. at the outset of allometric growth). For these cases, White and I (1965) have proposed a general meaning of b in terms of a 'scale ratio', $s_2/s_1 = (b_2/b_1)^{1/(1-\alpha)}$, a criterion of geometric similarity whose dimensionless value is the ratio of x values (i.e. usually of absolute body magnitudes) at which y/x for the two regressions is the same. Thus, using Jerison's (1961) data, a Recent mammal weighs 80 times as much as an Eocene mammal of the same brain-weight/body-weight ratio. Since decreasing brain-weight/body-weight relations with increasing size is the rule in ontogeny and static comparison of related adults living at one time, the preservation of geometric similarity through an 80-fold increase in size would represent a significant phylogenetic increase in relative brain size at a given body weight.

(c) Status

Medawar (1945) has delineated two approaches to the quantification of growth phenomena: the empirical and the deductive. An allometric equation of the second type, deduced from axioms concerning the nature of growth, claims 'a range of application that is wider than the sum of its known instances' (Medawar, 1945, p. 159), but must stand or fall on axioms which, 20 years after Medawar's article, are still far from general acceptance. An empirical fit is a model, neither true nor false, whose criterion is utility: 'It summarizes and makes explicit the information otherwise diffusely concealed in two bald columns of figures' (Medawar, 1945).

Early works on the equation of simple allometry tried to find a theoretical justification for its use—Robb (1929) by analogy to partition of a substance between two immiscible solvents; Teissier (1931; 1960, p. 543) by nutrition and the unequal appetites of organs; Huxley (1932) by the multiplicative nature of growth. More recently, Serra (1958) has, with some simplifying assumptions, deduced the power function from exponential and sigmoidal absolute growth curves. His claim that the equation of simple allometry is therefore 'a necessary relation' (Serra, 1958, p. 309) is unfounded since it just casts the search for a rational basis one step further back, through some very dubious simplifications, to equations of absolute growth which are no better established than those of allometry (relative growth).

Haldane's objection (Huxley, 1932, p. 81), that the sum of two power functions cannot be a function of exactly the same sort, dimmed the hopes of those searching for a rational basis (for how then could total limb length obey the equation if two limb segments did). Since these deduced deviations from simple allometry are very slight,

usually within the limits of measurement error, this objection does not threaten the empirical view which has gained favour in the last two decades. Huxley (in Reeve & Huxley, 1945, p. 134) abandoned his earlier attempts and adopted the empirical position: 'The "axioms" of growth which were put forward to justify the general use of the formula are far from self-evident, and should perhaps be considered as no more than consequences of simple allometry.' This view is also expressed by Brody (1945, p. 641), Waddington (1950, p. 511), Medawar (1950, p. 476), Bonner (1952, p. 138), Simpson (1953, p. 26), Hersh (1955, p. 487), and Kidwell & Williams (1956, p. 279).

(d) Difficulties

(i) *Deviations from simple allometry.* Reeve & Huxley (1945) specified three types of departure from simple allometry: curvilinear trends, critical points and rhythmic fluctuations. Data plots yielding smooth curves on log-log paper indicate continuous change of the parameter α , whose constancy, at least over short intervals, is usually taken as the criterion for fitting a power function to allometric data. David Thompson's (1934) smooth curve for rostral growth of the spoonbill, *Polyodon spathula*, is most often cited. Hamai (1937), in an excellent but unfortunately neglected work, systematically analysed curvilinear departures from simple allometry in terms of differential decline of specific growth rates in the two variables. Smooth log-log curvature was further noted by Weymouth & MacKay (1936) in *Cancer magister*; A. Needham (1950, p. 115) for abdominal growth in *Pinnotheres pisum*; Kidwell, Gregory & Guilbert (1952) for heart girth in cattle; and Wilson (1953, p. 147) in ants.

More often, varying numbers of simple allometry lines have been fitted to obviously curved data. Day (1935) used up to six lines to describe abdominal width growth in *Carcinus maenas*. Martin (1949) fitted five linear segments to various bivariate plots in salmon. He interpreted inflexions in terms of significant physiological stages (eyed egg, hatching, ossification and sexual maturity) but used no statistical tests to analyse the data, which seem to indicate complex curvature (see fig. 8, p. 19). To thickness $v.$ diameter relationships of the ammonite *Desmoceras kossmati* Matsumoto, Obata (1959) fitted four lines, said to represent four definite stages of growth rather than a regular fluctuating trend. Again, no statistical tests were made; some of these 'stages' are based upon only two points. Huggins & David Thompson (1942, p. 168) found smooth curvature with constantly diminishing α in longest anal fin $v.$ standard length regressions for the short-nosed garfish, but fitted three lines to the scatter.

Smooth curves have most often been fitted with two straight lines. A supposed point of inflection is chosen (usually by inspection) and parameters determined for scatter above and below this critical x value. Large sudden breaks in α are the spurious results of averaging lower and upper parts of the curve separately. Examples of this sort are the following: Nomura (1926–27a, b) and Sasaki (1926–27) on molluscs; Miller & Hoy (1939)—reanalysed as curvilinear by Richards & Kavanagh (1945)—on the isopod *Asellus californicus*; Kienle & Ludwig (1956) on length-width relationships in snails; Veevers (1959, p. 895) and Parkinson (1952, 1954, 1960, 1961) on Palaeozoic brachiopods. This method was criticized by Lumer (1937), Reeve & Huxley (1945, p. 140), Richards & Kavanagh (1945) and McIntosh (1955, pp. 19–20).

The large literature on allometry in mouse and rat skeletal ontogeny best illustrates this common misuse of power function plotting. Green & Fekete (1933, calculating b and α to five significant figures), MacArthur & Chiasson (1945), Moss & Baer (1956), and Rosenthal & Doljanski (1961) fit varying numbers of straight lines to wide curvilinear scatter. 'Critical points' were chosen by inspection, or imposed upon the data from external knowledge of average x values at such significant stages as time of weaning.* Ford & Horn (1959), adopting different methods, calculated α for each successive pair of points and demonstrated constantly diminishing α values (i.e. smooth log-log curvature) for data plots similar to those formerly fitted by several straight lines. For basisphenoid $v.$ basioccipital length, for example, α declines evenly from 2.5 to 0.7 during the first 80 days of growth. King & Eleftheriou (1960, pp. 185, 189) found curvature in several deer mouse skull relationships.

This discussion of spurious breaks in allometric trends should not obscure the fact that true sharp transitions between two well-fitted power functions do occur. Discontinuous growth by moulting is most compatible with sharp breaks in allometry. Consequently, the concept of critical points has been most fruitfully used by students of crustacean growth (review in Teissier, 1960). Breaks are usually associated with sexual maturity and lead to the definition of maturity and pre-maturity moults. MacKay's (1942, 1943a, b) extensive studies on *Cancer pagurus*, in which the treatment of several thousand specimens removes fluctuations caused by random variation in small samples, define sharp α alterations at sexual maturity (6.7–8.3 cm. carapace length) in several relationships.

The concept of critical breaks is also tenable when such transitions can be definitely related to equally sharp physiological events such as tadpole metamorphosis (Davison, 1955). Schadé (1959, p. 164) correlated a sharp break in nuclear volume $v.$ body weight in rabbit nerve cells with a series of morphological changes in the nucleus.

Departures from simple allometry more complex than smooth curves or sharp breaks are occasionally observed. Sigmoidal log-log trends have been noted by Kaiser (1935) in fruits of the pepper and by Huggins, Huggins & Hellwig (1943) in the wren. Rhythmic fluctuations were discussed by Huxley (1932, p. 203), and by A. Needham (1937) for thoracic segments and abdomen of *Asellus aquaticus*.

(ii) *Inadequate statistical methods.* Appropriate methods for fitting power functions depend upon the purposes of investigation. Whereas visual estimation may suffice if scatter is very small and no implications are drawn from allometric parameter values, taxonomic studies in which discrimination is determined by differences in b and α require careful statistical fits. The few early workers concerned with adequate statistical testing (notably Reeve, 1940, on ant-eaters) fitted least squares regressions to the data. In most allometric bivariate plots, however, neither variable can be regarded as independent and a method considering variation in both may be preferable. The 'reduced major axis' or 'line of organic correlation' (Teissier, 1948; Kermack & Haldane, 1950) has therefore been used by many authors (Kermack, 1954; Cock,

* I do not mean to suggest that rates of change in allometric relations are not more rapid at important physiological transitions: sharpness of curvature around these stages indicates that they are. I object to the fallacious implication, derived from fitting straight line segments to curved data, that such changes are sudden.

1963). When correlation between the variates is high, least squares regressions and reduced major axes give almost identical results (Röhrs, 1961; Cock, 1963; Misra & Reeve, 1964).

A reduced major axis can be mechanically fitted to any scatter of points; the observer must then judge whether the parameters thus obtained have any meaning. Too often the same misplaced *a priori* faith in the equation's validity that led to fitting lines to curves has resulted in simple allometric fits to an almost random array of points (e.g. in Bohlken, 1964). As a purely visual technique illustrating best guesses at data trends, this may be defensible; to use obtained b and α values for drawing further conclusions is unwarranted. Even rather high values of α may not be statistically different from 1 (no allometry). For parietal bone thickness *v.* skull length in the late Palaeozoic amphibian *Diplocaulus magnicornis* an α of 1.79 ($N = 10$) was not significantly different from 1 despite the high correlation coefficient $r = 0.88$ (Olson, 1952). Moreover, even 'best' guesses for wide scatter may be misleading. Bohlken (1962) demonstrated how spuriously high α values result from fitting power functions to a restricted part of the total size range when scatter is great.

Dubious results may also arise when the effects of random scatter are not considered. The plotting of class means, while considerably narrowing the scatter ellipse, does not eliminate the effects of small sample size and random variation. Bernardis & Skelton (1963) simply joined the points of nine class means with straight lines; seven breaks were found in the pattern. This point-joining can be justified as a visual-descriptive technique, but when the implication is then made that 'changes in α are associated with crucial developmental events in the body' (Bernardis & Skelton, 1963, p. 280), lack of statistical testing becomes a serious omission.

Maximum retrieval of information contained in bivariate data can only be obtained when adequate statistical methods are used in the determination of allometric parameters. Subtle differences, useful in taxonomic distinction, can be discerned (Kermack, 1954, on Cretaceous echinoids) and, in special cases, genetic estimates of α -value heritability can be made (Misra & Reeve, 1964, on the water boatman *Notonecta undulata*).

(2) *The terminology of allometry*

Despite numerous pleas for a unification of terminology (Huxley & Teissier, 1936; Huxley, J. Needham & Lerner, 1941) a mire of non-substantive disagreement and confusion lies scattered within the literature. Even the general phenomenon of size-correlated shape change lacks an accepted name. 'Relative growth' has been popular, but its primary emphasis is upon the method of measuring increase of one part against that of another morphological dimension rather than against time in its Newtonian absolute sense. 'Differential growth' more definitely implies change of shape with size increase. Since static comparisons of related adults constitute much of the data of allometry, yet cannot strictly be termed growth (though they result from it), neither term is applicable to all allometric phenomena. 'Allometry' has been used in the general sense adopted here (Röhrs, 1959, 1961; Mosimann, 1956; Corbet, 1964), but other authors have applied it only to those size-correlated form changes fitted by power

functions (Hersh, 1955, p. 404). Neither definition is 'true'; both are in use. I only hope that this procedure generates less confusion than would the coining of a new term.

'Allometry', as defined here (p. 1), includes a remarkably heterogeneous group of phenomena sharing the one common characteristic, hence the theme of this article, of relation to absolute magnitude.

I shall adopt Röhrs' (1961) classification with some modifications from Simpson (1953). Five major types of allometry may be discerned (terminology of several authors is summarized in Table 1):

Table 1. *An epitome of allometric terminology*

Röhrs, 1961	Simpson, 1953	Huxley, Needham & Lerner, 1941	Röhrs, 1961	Teissier, 1960	Meunier, 1959 ^a
ontogenetic allometry <i>a</i>) longitudinal data	heterauxesis	heterauxesis	Proportions-änderungen	allometrie de croissance	Wachstums-allometrie-Allotrophie
<i>b</i>) mass data				—	—
evolutionary allometry	lineage allomorphosis	allomorphosis	Proportions-änderungen	—	—
intraspecific allometry	individual allomorphosis	allomorphosis	Proportions-unterschiede	allometrie de taille	Ordnungs-allometrie-Allotaxis
interspecific allometry	race allomorphosis	allomorphosis	Proportions-unterschiede	—	—
interspecific (generic, c.) allometry	species (genus, etc.)—form allomorphosis	allomorphosis	Proportions-unterschiede	—	—

(a) *Ontogenetic allometry*. Two methods, direct and indirect, are used to define differential growth in individual ontogeny. In the direct approach, obviously preferable but not always possible (especially in palaeontology), each bivariate plot represents data for a single individual taken at different growth stages—'longitudinal' data (Cock, 1963). The more usual and often criticized method (see Lerner, 1938, p. 139; Scholl, 1950, p. 473; Yates, 1950, p. 482; Medawar, 1950; Scholl, 1954, p. 226, for criticisms) estimates individual growth from a mass sample of individuals in various growth stages. Any sudden spurt occurring at varying sizes in different individuals will be damped to a more gently curved transition in the mass data regression. In palaeontological data, individuals representing the lower end of the size scale died naturally when young. If strong natural selection is occurring, these individuals will be systematically different from young stages of organisms reaching the adult stage (and therefore unrepresented in the fossil record). The mass curve, in this case, is not an adequate approach to individual ontogeny.

(b) *Evolutionary allometry*. Allometry among members (usually adult) of a single direct (or at least approximate) line of descent.

(c) *Intraspecific allometry: individual allomorphosis*. Allometry among members of a single population at the same growth stage (usually the adult) but, of different size.

(d) *Intraspecific allometry: race allomorphosis.* Allometry among races or subspecies of a single species at the same growth stage (usually the adult), but of different sizes.

(e) *Interspecific (generic, etc.) allometry.* Allometry among species of a single genus (genera of a family, etc.) at the same growth stage (usually the adult), but of different sizes.

Two broader schemes of division encompass the five major types of allometry. First, and most important, a distinction is to be made between allometric trends occurring during growth of an individual (category *a*) and those arising from the static comparison of many individuals at a single growth stage but differing in size (categories *b–e*). The two types have been called, respectively, heterauxesis and allomorphosis; *allometrie de croissance* and *allometrie de taille*; *Wachstumsallometrie* and *Ordnungsallometrie*. Secondly, ontogenetic and evolutionary allometry (categories *a, b*) represent true temporal changes of proportion (*Proportionsänderungen* of Röhrs within a genetic continuity of relationship, while intra- and interspecific allometry (categories *c–e*) are a static comparison of proportion differences (*Proportionsunterschiede*) in which each successive point represents, not the temporal successor and linear descendant of the former, but rather a larger organism with a different onto- or phylogenetic history.

Recent German articles (Röhrs, 1958, 1959, 1961; Meunier, 1951, 1959*a, b*; Bohlken, 1961, 1962, 1964; Bährens, 1960) have made clear distinctions among the types and have emphasized that allometric parameter values for similar relationships in different types need not be the same (mammalian brain-weight/body-weight α -values are low (0·15–0·30) in intraspecific comparisons; characteristically 0·66 in interspecific allometry and often approaching 1·0 in phylogeny).* Since ontogeny does not recapitulate phylogeny and since smaller adults of a population are not merely arrested ontogenetic stages of larger adults, this lack of correspondence is not unexpected. Still, failure to distinguish differing types of allometry has often led to erroneous conclusions. Count (1947), for example, held that mammals must have evolved from very small reptiles since the interspecific curves for living reptile and mammal brain-weight *v.* body-weight relationships intersect near the lower end of the size range; yet the most progressive known therapsids are far larger. Röhrs (1961, p. 306) has cautioned that: 'es ist nicht gerechtfertig, Grossenreihen rezenter Tiere näher Verwandtschaft als Modelle phylogenetischer Grossenreihen zu benützen'.

A major theme of this article, that similar form requirements are imposed by size increase whether it occur in ontogeny or phylogeny, by no means implies that specific allometric patterns of attaining well-adapted forms at adult sizes must correspond. Meunier (1959*a*, p. 451) has emphasized that interspecific allometry, which represents 'die erbliche Zuordnung bestimmter Proportionen zu bestimmten Endgrößen', is most likely to illustrate predicted parameters of size-required trends. In feather growth,

* These values are not capricious. Since surface innervation is a major brain function, interspecific $\alpha = 0\cdot66$ represents the surface dependency of brain growth (Rensch, 1954). Higher values in certain progressive phylogenies represent evolutionary increase of relative brain weight (White & Gould, 1965). Low ontogenetic and intraspecific values result from the need for only small enlargement of relatively enormous initial brain weight (at birth)—related to the fact that neurons do not multiply in post-embryonic development (Bertalanffy, 1960).

each point of an interspecific curve represents an adult organism whose wings are well adapted to support the body bulk. Ontogenetic curves, on the other hand, show extremely strong wing allometry since feather growth, which does not begin until the body has reached a good size, must be completed before wings are functionally required for flight. Allometric parameters for this 'preparatory growth' (*Vorbereitungswachstum* of Kramer, 1959) will not correspond to those mechanically required by size increase in a series of organisms functioning in the same manner. Other size-required allometric trends—for example, differential leg thickening—are more likely to correspond in ontogeny and phylogeny since the allometric organ performs the same function at all postnatal sizes in both series.

(3) Quantification and explanation

Although the value of quantification in general need hardly be emphasized here, some increased interpretative potentialities arising from the quantification of allometry should be mentioned. The primary value of a more adequate description is not increased rigor in description, but rather the explanatory insight transcending description that may be given by such precision. Quantitative precision in allometry studies is an aid to explanatory analysis in several areas:

(i) *Environmental and phenotypic variations as an explanation of parameter changes: experimental alteration of parameters.* Problems of the extent to which specific allometric patterns are precisely determined or phenotypically alterable within the genetic system can be approached by correlating parameter variation with changing environmental conditions. Rosenthal & Doljanski (1961) found general similarity of α values in normal, diet controlled, and thyroidectomized rats. They conclude (1961, p. 362) that 'the mechanism controlling the maintenance of proportions is a very stable genetic character, unaffected by diet or hormonal variation'. Many allometric parameters, on the other hand, are very plastic. Brooks (1947) demonstrated a positive correlation between water turbulence and α for head length $v.$ carapace length in *Daphnia*. The effects of temperature on allometric parameters have been studied by Vernberg (1959) in *Uca*, Krüger (1964) in *Arenicola*, and Newell & Northcroft (1965) in *Balanus*. Other instances of experimental alteration are reviewed by Bertalanffy (1964).

(ii) *Absolute magnitude as an explanation of parameter values and changes.* As discussed in § II, the direction, form and intensity of certain allometric trends can be said to have absolute magnitude as a formal cause. To test the proposition of magnitude determination, observed parameter values can be compared with models deduced from theoretical considerations. Values of α near 1.5 often indicate differential growth of surfaces to keep pace with volumetric body enlargement. Departure from $\alpha = 1.5$ in area-dependent structures serving total volume may suggest that other types of compensation are occurring. The value of α for leg thickness $v.$ total length, while almost always significantly greater than 1, rarely reaches the predicted value of 1.5. Structural strengthening is an alternative to differential thickening, as recognized by Galileo in 1638.

Parameter values for allometric trends not predictable *a priori* may also indicate the role of absolute magnitude in the adaptive explanation of proportion variation. Extra-

pulation of parameter values obtained for small ancestral species or early stages of an ontogeny into larger size ranges may lead to inadaptive proportions. Increasing absolute magnitude then requires that parameters of the function quantifying the same relationship at larger sizes be different, and the direction of this difference is often predictable. Size increase, a cause of definite parameter *values* in the former case, here becomes a cause of definite parameter *changes*.

(iii) *The adaptive explanation of shapes not correlated with size.* It may seem initially curious that allometric analysis is often the best approach to understanding those aspects of form which are not correlated with size and hence non-allometric. The deviation of an animal's organ-size to body-size ratio from that normally expected for its body size first suggests lack of size determination. Moreover, the direction and magnitude of deviation, together with knowledge of mode of life, may suggest an adaptive explanation for the deviation. This type of analysis first requires that the general direction of size dependence for the relationship under consideration be determined by allometric methods. The human brain, for example, is absolutely smaller than an elephant's and relatively smaller than a shrew's. Its superiority in bulk is indicated by pronounced upward deviation from the average mammalian brain-weight to body-weight curve.

IV. SIZE AND SHAPE IN ONTOGENETIC AND STATIC ALLOMETRY

(1) *Size-required parameter values*

Having separately treated the allometric requirements of size increase and the quantification of allometric phenomena, a synthesis can now be sought in the quantitative verification of trends predicted from theoretical considerations of absolute magnitude variation. The power function provides an excellent tool for testing size dependence since it removes time as a variable and relates form alteration to a measure of magnitude (Reeve & Huxley, 1945, p. 125).

Respiratory. Sattel's (1956) demonstration of differential trachea-surface elaboration with increasing size in *Bombyx mori* results from simple allometric analysis. The value of α is 2.75 for the volume $v.$ length relation and 2.88 for the tracheal inner surface $v.$ length regression. The resulting tracheal surface $v.$ volume relation is nearly isometric (surface actually increasing a little faster— $\alpha = 1.05$ —though the difference from $\alpha = 1$ is not significant). Since external surface \propto length², tracheal surface, in order to maintain physiological constancy in respiration, must increase with strong positive morphological allometry to external body surface ($\alpha = 1.44$, near the predicted $\alpha = 1.50$ for surface/volume compensations).*

* This information may be deduced from the two equations given by Sattel, where L = length, V = volume, ES = external surface, TS = tracheal surface:

given $TS \propto L^{2.88};$ (1)

given $V \propto L^{2.75};$ (2)

$(V)^{1.05} \propto (L^{2.75})^{1.05};$ (3)

$V^{1.05} \propto L^{2.88};$ (4)

$TS = bV^{1.05};$ (5)

$ES \propto L^{2.00};$ (6)

$(ES)^{1.44} \propto (L^{2.00})^{1.44};$ (7)

$TS = bES^{1.44}.$ (8)

assumed

Positive allometry of surfaces occurs for the same reason in gills and lungs. Although the gill-filament number to weight ratio declines sharply during ontogeny of the crayfish *Austropotamobius pallipes*, the gill-surface to body-weight ratio remains relatively constant (Curra, 1965). Since the compensating surface area is only partly provided by filament number proliferation, it must result largely from differential size increase and/or elaboration (i.e. positive allometry) of the filaments.

Digestive. Studies on the ontogeny of intestinal systems of teleost fish [Al-Hussaini, 1949, on *Cyprinus carpio*; Szarski (in Parker & Larkin, 1959) on *Abramis carpio*] have demonstrated that the gut infolds differentially with positive allometry sufficiently strong to keep the gut-absorptive-area to body-weight ratio constant. For intra-specific plots of intestinal length *v.* body weight in 154 species of birds and 52 species of mammals, Rensch (1948) found average α values of 0.52 for birds and 0.49 for mammals. (Since $L^3 \propto V$, $\alpha = 0.33$ is a criterion of isometry in a length *v.* volume plot; $\alpha = 0.50$, equivalent to $\alpha = 1.50$ of a length/length regression, is a criterion of A/V compensation.)

Although head-length *v.* body-length relationships almost always show negative allometry due to relatively decreasing brain size, α for head length (snout to blowhole) *v.* body length in the blue whale, *Balaenoptera musculus*, is 1.55—probably reflecting differential increase of baleen surface to compensate body bulk (data from Huxley, 1932, pp. 135–7). The deduced value for compensation can be calculated as follows (where L = body length, V = body volume, BS = baleen surface and BL = length of baleen, the prime determinant of head length):

$$L^3 \propto V, \quad (1)$$

if surface increases differentially to keep pace with volume

$$BS \propto V, \quad (2)$$

since

$$BL^2 \propto BS, \quad (3)$$

then from (2)

$$BL^2 \propto V, \quad (4)$$

from (1)

$$BL^2 \propto L^3 \quad (5)$$

or

$$BL \propto L^{1.5}. \quad (6)$$

The observed value of 1.55 is not significantly different from that predicted. (Data plotted in figure 1, from Huxley, 1932, p. 137).

Locomotion and support. Differential thickening of fowl legs in ontogeny (Cock, 1963) and static intraspecific comparison (Schlabritzky, 1953) has been determined by power-function fitting. In gulls, the sum of leg bone lengths *v.* body length is isometric ($\alpha = 0.97$) in interspecific plots, but α for cross-sectional area of femur *v.* body length is 2.55, significantly exceeding the surface *v.* length isometric value of 2.00 (Dinnendahl & Kramer, 1957). Since bird bones are hollow, a better measure of support is the breaking strength $(D^4 - d^4)/(L^2)$, where D is the outer diameter of the bone ring, d the inner diameter and L the bone length. This number has dimensions of L^2 and will increase with $\alpha = 0.66$ when plotted against a measure of mass (L^3) if geometrical similarity is maintained. For femur breaking strength *v.* body bulk in gulls, however, $\alpha = 1.00$ and mechanical similarity is assured by systematic departure from geometric similarity (Dinnendahl & Kramer, 1957).

Rashevsky (1944, 1961) demonstrated that if quadrupeds be considered as uniform bars supported at the ends, then maximum resistance to sagging with weight increase is attained by differential widening of the trunk such that trunk width \propto trunk length^{1.5}. Although environmental adaptation produces numerous exceptions (weasels relatively longer than shrews), the general tendency of heavier animals to shorten trunks relative to width (at $\alpha = 1.5$) is confirmed (Fig. 2). We can at least rest assured that

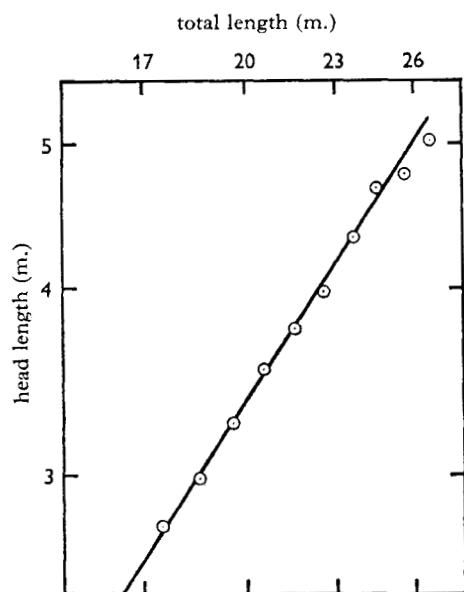


Fig. 1

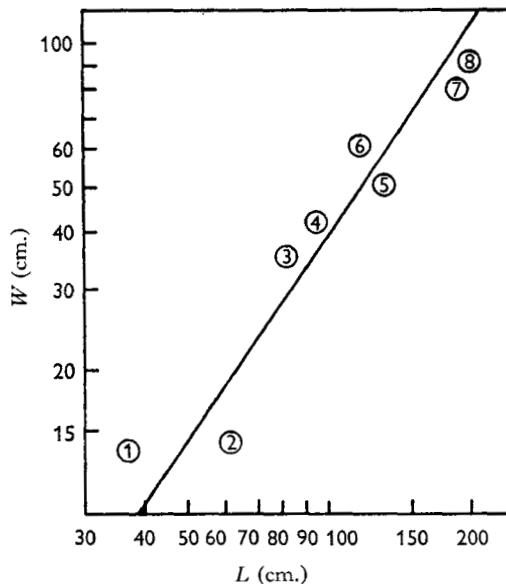


Fig. 2

Fig. 1. Ontogenetic allometry of head length *v.* total length in the whale *Balaenoptera musculus*. Log-log scales; slope = 1.55. (From Huxley, 1932.)

Fig. 2. Interspecific allometry of trunk width *v.* trunk length in selected mammals. Log-log scales; slope = 1.50. 1, cat; 2, dog; 3, dog; 4, goat; 5, ass; 6, sow; 7, elk; 8, ox. (From Rashevsky, 1944.)

a dachshund of elephant proportions is a physical impossibility. Rashevsky (1944, p. 17) has further noted that since the shape of both supporting extremities and trunk is related to absolute bulk, the general form of a quadruped is largely a function of size.

(2) Size-required changes in allometric parameters

Most α values, though not formally caused by absolute magnitude, are nonetheless adapted to a definite size range beyond which their maintenance would lead to inadaptive proportions. Major workers (soldiers) of the ant *Atta texana* show an intra-specific (individual allomorphic) α of 1.3 for head across occiput *v.* head across eyes. Extrapolation of this trend into the range of minor workers (whose α is 0.8) would lead to inviable microcephalic forms (Wilson, 1953, p. 142). The α value of each caste is adjusted to produce proportions adaptive in its size range.

In cases of positive allometry, the y/x ratio continually augments with size increase: the higher the α value, the faster the rate of augmentation. From this, a rule relating size and α may be deduced: high α values will either limit maximum size or become diminished to permit size increase. In general, then, α values high in small organisms will progressively decline for the same relationship in larger forms. Similarly, α values will be lowered during an individual's ontogeny if their maintenance would lead to inadaptive proportions at the adult size. This correlation of size and the direction of α alteration has absolute magnitude as a cause, even though the actual parameter values are not required by size. Since I have elsewhere discussed all examples of this rule known to me (Gould, 1966c), only two cases will be presented here.

Table 2. *Inverse correlation of α for height v. width and adult size in three species of the Bermudian pulmonate gastropod Poecilozonites*

	mean α	maximum adult radius (mm.)	mean radius end of 7th whorl (mm.)	no. of specimens
<i>P. nelsoni</i>	1.50	21	17.5	22
<i>P. bermudensis zonatus</i>	2.18	14	11.2	33
<i>P. cupula</i>	2.86	5	4.6	27

Intraspecific (individual allomorphosis). For mandible length *v.* body length in the stag beetle, *Lucanus mearesi* Hope, α declines from 1.83 among small animals to 1.12 among specimens above mean body length (Kuyten, 1964). If the high α value of small specimens were maintained in all size ranges, the mandible of the largest specimen (72 mm. long) would be longer than the rest of the body (with the observed α decrease, it is actually 64% rest-of-body length) and a theoretical individual 2.25 times the maximum size would present the impossible situation of a mandible length equal to total length (calculated from Kuyten's data). The observed inverse correlation of α and size permits an expanded size range.

Interspecific. For ontogenetic height *v.* width α is negatively correlated with adult size in three species of the Bermudian pulmonate gastropod *Poecilozonites* (Table 2). If the small *P. cupula* grew to twice its maximum width at the same α (2.86), it would be 6 times higher than wide, while extrapolation to the size of large *P. nelsoni* would produce a biological absurdity more than 20 times higher than wide (Gould, 1966c).

(3) Size-shape trends and the elucidation of special adaptations

The importance of considering absolute magnitude is also evident in studies which seek to explain specific environmental adaptations by assessing the departure of points representing such adaptations from curves expressing the normal correlation of the measured variables with size. This explanatory analysis of departure cannot be performed until both the trends of normal size-shape correlation are empirically established and the adaptive reasons for these general patterns determined.

(i) *Departure of points from general curves of size dependency.* Bernardis has studied (Bernardis, 1963; Bernardis & Floyd, 1964) abnormal growth in experimentally altered rats (adrenal enucleation and hypothalamus lesion) by comparing the deviation

of their organ-weight *v.* body-weight curves from those of normal rats. Wilber & Gilchrist (1965) generalize this approach by considering the normal organ-weight *v.* body-weight curve as a prediction equation. Their interest centres on the analysis of deviations from predicted values caused by experimental alterations of morphology and environment.

(ii) *Departure of parameter values and changes from the general rules of size-shape correlation.* Exceptions to expected patterns are often noted in the difference between observed and predicted curve parameters or to patterns of parameter change in series of curves. Departure from $\alpha = 1.50$ in volume-compensating surface increase indicates either that compensation is not the complete explanation of observed trends or that the problem of increasing bulk is being solved in another manner. For interspecific muscle weight *v.* body weight in the Felidae $\alpha = 1.03$. The lack of differential surface increase led Davis (1962, p. 510) to conclude that the locomotory efficiency of a lion "is certainly distinctly inferior to that of a domestic cat". This need not be so. Bulky extremities are disadvantageous in large animals dependent upon speed; such animals may compensate increasing volume by types of structural strengthening which avoid the necessity of massive, thick supports. Watson (1949, p. 50) maintains that the transition to monodactyly in horse evolution is a size-compensation, obviating the need for a differential thickening which would preclude agility: 'It seems reasonably clear that to replace three smaller bones by a single larger one is economical in material, a given increase in strength being attained by a smaller increase in weight.'

For relationships exhibiting strong allometry, ontogenetic α values should vary inversely with adult size. An exception to this normal pattern of parameter change required by size occurs in the Myrmecophagidae (New World ant-eaters) in which α for face length *v.* cranium length (a measure of snout elongation) correlates positively with size in three genera (Reeve, 1940).

V. ALLOMETRY AND TAXONOMY

It has been long recognized that absolute size measurements, so subject to environmentally induced phenotypic fluctuations, may be useless as taxonomic criteria. The common alternative of avoiding size altogether by the use of ratios or indices is equally misleading since it is a primary fact of allometric growth that ratios of original variates change continuously and in a regular manner with size. The dimensionless index $100H/L$ is 37 in the second lower molar of both *Ursus arctos* and *U. spelaeus*, but this value occurs at different sizes and results from two distinct patterns of allometry (Kurtén, 1954a, p. 11). The major trend in Trueman's (1922) temporal sequence of *Gryphaea* evolution is a progressive increase in coiling. But this trend is also related with positive allometry to size, and size increase is a parallel temporal tendency. The use of simple coiling to length ratios in progressively younger samples could show strong increase due only to body enlargement. If we consider *Gryphaea* coiling to length ratios at a standard radius of 20 mm., a reversed trend towards reduced coiling occurs through the *angulata* to *gmuendense-bucklandi* zones (Burnaby, 1965); however, since size increase also occurs in this sequence, comparison of the pro-

gressively increasing ratios taken at adult sizes would give a fallacious indication of increased coiling.

(1) *Shape as an aspect of size*

New shapes produced by continuation of an allometric relationship into new size ranges are not independent taxonomic criteria. Size increase itself may be a mark of taxonomic distinction, but failure to recognize the allometric consequences inter-

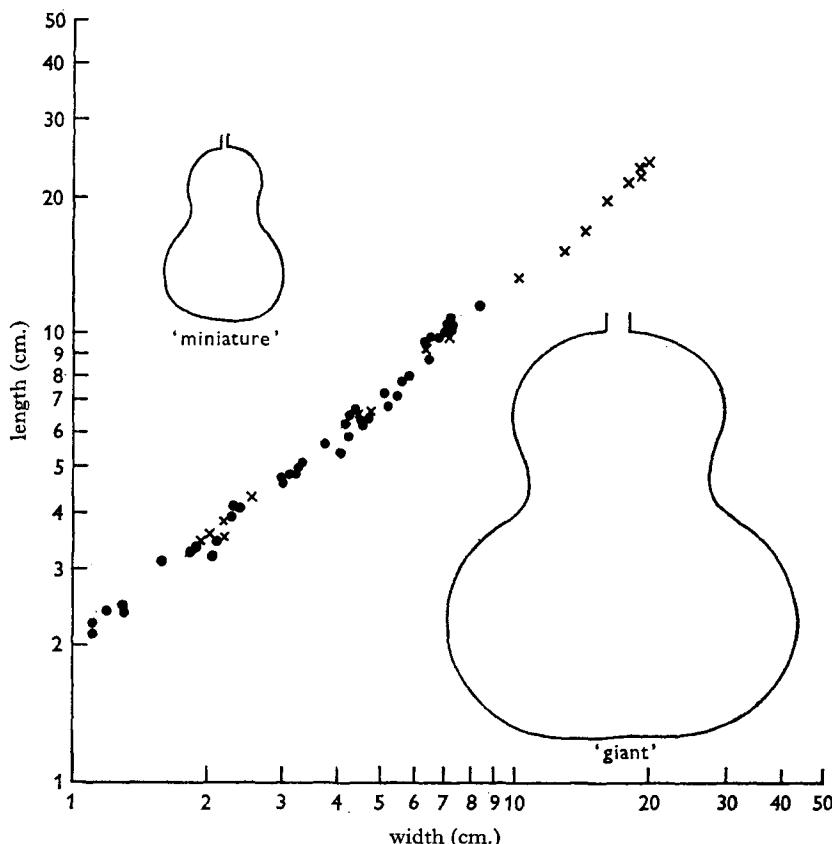


Fig. 3. Coincidence of ontogenetic and intraspecific allometry of length *v.* width in two races of the bottle gourd (*Lagenaria*); early primordia to maturity, log-log scales. Profiles of mature fruits show relative size and shape of the two races. (From Sinnott, 1936.)

dependent with such increase has often led to unwarranted taxon distinctions between organisms differing in only one characteristic whose complex effects were not appreciated.

Rowe's (1899) distinction of the Cretaceous echinoids *Micraster praecursor* and *M. cortestudinarium* on the basis of several shape criteria was ill-founded; a continuation of *M. praecursor*'s allometric trends to larger sizes produces a typical '*M. cortestudinarium*' (Kermack, 1954, p. 424). Regional skull proportion differences in island populations of the bank vole *Clethrionomys glareolus* are largely due to size variation; 'the number of independent characters distinguishing the island races is

very small' (Corbet, 1964, p. 191). Former hypotheses of relict distribution, deemed necessary from the supposed intensity of genetic divergence indicated by differences in skull shape, are not required and the pattern of variation is compatible with a hypothesis of recent accidental introduction from the mainland. Three 'subspecies' of the ant-eater *Tamandua tetradactyla* originally defined by differences in proportions lie on the same allometric regression and are distinguished only by size (Reeve, 1941). In botanical studies, Sinnott (1936, 1963) demonstrated the independence of genetic factors governing size and inherent shape (initial proportions at the outset of allometric growth and therefore not a result of observed allometry) in gourds. Width grows with positive allometry to length in bottle gourds. The larger of two races shown in Fig. 3 is relatively wider, but since both races lie along the same allometric regression, change in shape is attributed to differences in genetic factors for size only. In taxonomic categories above species, the ant-eater *Cyclopes* was distinguished from *Tamandua* and *Myrmecophaga* at the subfamily level, primarily on the basis of its relatively short and normal face. Since the snout grows with strong positive allometry in all genera, the short face of *Cyclopes* is the result of its small size. In fact, differences in α for face length $v.$ cranial length are not significant in *Cyclopes* and *Tamandua*, but are higher in *Myrmecophaga*. Other distinguishing features of *Cyclopes*, its relatively large brain and eyes, are also the effects of small size.

These examples of non-independence of shape and size characters may be supplemented by a case involving the usual negative correlation of α $v.$ size. Sayles (1931) distributed specimens of Bermudian pulmonate gastropods from one locality between the species *Poecilozonites dalli* (smaller and higher spired) and *P. cupula* (larger and lower spired). High α (height $v.$ width) will act as a size-limiting factor; since high spires indicate high α , the correlation of small size and high spires is expected. I determined α for the ontogeny of each specimen and found a mean α of 2.97 ($N = 15$) for '*P. dalli*' and 2.72 ($N = 12$) for '*P. cupula*'; the cumulative α distribution is unimodal (mean $\alpha = 2.86$). The '*P. dalli*' specimens do not constitute an independent taxonomic entity; theirs is an artificial category constructed for individuals at the upper end of the distribution of a parameter whose high value produces high spires and requires small size (Gould, 1966c).

(2) Allometric trends and taxonomic distinction

Several allometric methods have been used in the establishment of taxa.

(a) *Taxonomic discrimination by deviation of points from general trends.* The subspecies of *Mustela vison* Schreber arrange themselves along a single allometric trend for most regressions; shape differences are the result of size variation. Stronger divergence of some subspecies, involving genetic factors beyond those controlling size, is indicated by deviation from the general allometric trend in some relationships. Vancouver Island minks have especially massive teeth, while those from the Carolina coast possess narrow mastoids (Bährens, 1960). Relative size of the brain is similar in the squirrel monkey *Saimiri* and in man. It is the general interspecific trend of negative brain-weight $v.$ body-weight allometry in primates that indicates the value of relative brain weight as a taxonomic character. The brain of the squirrel monkey is

relatively large because the organism is small; that of man, showing strong positive deviation from the general primate curve at man's body weight, is unusual among primates and becomes an important character in the assessment of taxonomic status (Biegert, 1963). Deviation of points from general trends may also map evolutionary divergence. The fourth upper premolars of polar bears from the Yoldia Clay diverge so strongly from the allometric trend of Recent polar bears that the odds of drawing two such teeth from a recent sample are 1 in 500 (Kurtén, 1964). The divergence is in the direction of the presumed ancestor *Ursus arctos*.

(b) *Taxonomic discrimination by differences in α values.* Mitra (1958) used α value differences (width *v.* length) to distinguish French and English populations of the Jurassic brachiopod *Goniorhynchia boueti*. For Normandy, $\alpha = 1.05$; for Langton Heering, 1.26; Burton Bradstock, 1.27; and Eype Mouth, 1.45. Although not all the differences are significant, the values give some suggestion of a westward cline in α intensity. Using allometric regression differences, Bocquet (1953) distinguished six species of isopods previously lumped as *Jaera marina*. Populations of yellowfin tuna from Hawaii and the west coast of North America (Schaefer, 1951–53), species of the late Palaeozoic amphibian *Diplocaulus* (in Olson, 1952), subspecies of the deer mouse *Peromyscus maniculatus* (in King & Eleftheriou, 1960), and species of macaques (Lumer & Schultz, 1941) have been distinguished by significant differences in α . The last example is especially interesting since the curves of tail length *v.* trunk height in *Macaca philippensis* and *M. sinicus* converge at adult size; distinction can be made only by considering the pattern of ontogeny. It has been repeatedly emphasized that the dynamic morphology of ontogeny provides a more complete and satisfactory set of taxonomic characters than does the static form of adulthood. The parameters of ontogenetic allometry serve as excellent quantitative characters in the description of dynamic form.

(c) *Taxonomic discrimination by differences in b values.* Teissier (1936) and Chevais (1937) have compiled examples in which local races of a species whose regressions did not differ in α could be distinguished by values of b . In two races of *Homarus americanus*, for example, α values increase to the same value at the moult before maturity. In one race, this moult occurs at a larger size, producing differences in b (Teissier, 1936). Kermack (1954) found no significant α differences for seven relationships in *Micraster senonensis* and *M. coranguinum*. When mean pooled α is then used for both species, b differs significantly in five relationships. The interdependence of b and α requires that the use of b as an independent taxonomic indicator be attempted only when α is equal in the relationships considered.

VI. ALLOMETRY AND PHYSIOLOGY

(1) *Physiological constancy and morphological allometry*

Brody (1945, p. 580) remarked that 'the organism changes geometrically so as to remain the same physiologically'. The appeal to invariance as a final cause of change may seem enigmatic, but constant efficiency of many body functions can only be achieved by systematic size-correlated alteration of physical shape.

If physiological constancy is to be considered as a prime impetus for morphological allometry, we must know which physiological parameters remain constant over wide size ranges in related organisms. Some of these constancies, as repeatedly emphasized in A/V considerations, may be deduced from simple physical laws; others can be approached empirically. The development of an empirical method for determining dimensionless physiological constants from allometric data is an interesting recent development in allometric studies (Günther & Guerra, 1955; Guerra & Günther, 1957; Stahl, 1962, 1963, 1964). These derived constants may provide an adaptive explanation for the allometric parameter values from which they are extracted.

In Stahl's method, each variable is related to body weight by the allometric power function. Possible dimensionless terms are then located by inspection. Division of two simple allometric regressions with the same α value yields a number, dimensionless because the mass exponents are equal and invariant with change in body size. This number is the ratio of b values for the two regressions; since α is the same, it is also the ratio of y values at any x . As an example, for interspecific mammalian curves where X is body weight:

$$\text{lifetime} = 8.85 \times 10^3 X^{0.29}, \quad (1)$$

$$\text{breath time} = 4.7 \times 10^{-5} X^{0.28}, \quad (2)$$

$$\text{lifetime/breath time} = 2 \times 10^8 X^{0.01}. \quad (3)$$

The ratio is nearly dimensionless and indicates that, regardless of size, a mammal breathes an average of 200 million times during the course of its life. This implies that small mammals (which are usually short-lived) breathe absolutely more rapidly than large ones (Stahl, 1962). Regressions for duration of cardiac and respiratory cycles *v.* body weight have the same α . The breath-time to cardiac-beat-time ratio is 4.0 for all mammals: regardless of size, a mammal breathes once for every four heart beats (Günther & Guerra, 1955, p. 182).

Dimensionless numbers which must remain constant regardless of scale are known as *similarity criteria* in the engineering theory of models and prototypes. When an engineer scales a machine to function similarly at a larger size, the retention of these criteria often implies systematic alteration of shape. In hydrodynamics, the dimensionless Reynolds number must be maintained below a certain value to ensure laminar flow; yet this number will vary systematically if geometrical similarity is maintained with increasing sizes. Mammals of different sizes function in like ways; all are homoiotherms with a homologous set of internal organs performing similar tasks. The discovery of dimensionless numbers, constant throughout the Mammalia and capable of serving as scaling criteria, suggests that 'small mammals can be regarded as true physical models of large ones in the engineering sense of the term' (Stahl, 1964, p. 60). Once we discard the schoolman's faith in a perfect engineer, the analogy acquires severe limitations, which may, paradoxically, prove to be its greatest merit; for deviation from average mammalian performance can be analysed in terms of greater or lesser-than-average mechanical efficiency—a vital criterion, heretofore hard to measure, of relative evolutionary advance.

(2) *Physiological allometry; metabolism and size*

Most of the regressions which yielded constancy in combination were allometric power functions ($\alpha \neq 1$) which, taken separately, implied rate changes with size increase. Frequency of mammalian breathing and heart beat, and also of cirral beating in barnacles (Newell & Northcroft, 1965) are inversely correlated with size (negative α values). Most important of the physiological allometries, however, is the size dependence of metabolism.

A 12 g. clam releases a quantity of phosphorus equal to its total phosphorus content in 438 days, a 0.6 mg. amphipod in 31 hr., a 0.4×10^{-3} μg . ciliate in 14 min. (Johannes, 1964). A 600 kg. cow respires $\frac{1}{13}$ as intensely as a 21 g. mouse (Zeuthen, 1953). In 1839, Sarrus & Rameaux (see Kleiber, 1947) tried to quantify the systematic relative decrease of mammalian metabolism with increasing size by a hypothesis relating metabolism to surfaces. To balance surface-controlled heat dissipation, they argued, basal metabolism had to increase only as fast as body surfaces. Kleiber (1947, 1961) summarized as follows the reasons for surface dependency proposed during the last hundred years and found two of them 'basically sound' (1947, p. 538):

(i) The rate of heat transfer between animal and environment is proportional to external body surface area.

(ii) The supply rate of oxygen and oxidizable materials to tissues is a function of mean blood current intensity, which is proportional to blood vessel cross-sectional areas which are, in turn, proportional to body surfaces (Kleiber, 1947, p. 516).

The value of α for metabolism $v.$ weight varies among animal groups. It is characteristically low (0.55–0.70) in unicellular organisms; high (averaging 0.95) in small marine metazoa (< 1 mg. N) and in soil nematodes, close to 0.75 in larger poikilothermic metazoa and in homoiotherms (Zeuthen, 1953). In short, α varies between surface dependency (0.66) and weight dependency (1.00) with concentrations about each extreme and a general tendency for intermediate cases to fall nearer the former value.

The value of α for the interspecific mammalian 'mouse-to-elephant' curve is near 0.75 (Brody, 1945; Kleiber, 1947). This intermediate value, although closer to surface dependency, has been widely discussed as a potential difficulty for proposed surface-control explanations of allometric trends involving metabolism. Several attempts have been made to reconcile this α of 0.75 with the notion of surface dependency, as follows:

(a) Szarski (1964), accepting isometry between metabolism and surfaces, maintains that an α of 0.66 for metabolism $v.$ weight implies evolutionary change in body size with no accompanying compensatory surface allometry; an α of 1.00 indicates perfect compensation. That the average mammalian α is closer to 0.66 indicates that size-compensating modification of proportions in evolution is temporally retarded with respect to increase in size. Two objections may be raised:

(i) 'Perfect' compensation is impossible. The external body surface (Kleiber's first explanation for metabolic surface dependency) cannot increase proportionately with volume. This would imply a degree of complexity and convolution inconsistent with basic skin functions. If metabolism is largely controlled by the external body surface,

'perfection' in terms of maximally adapted skin configuration would imply an α significantly lower than 1.

(ii) Szarski is confusing various types of allometry. The interspecific mammalian curve is no model for temporal phyletic size increase. Some animals at the upper end—whales, for example—have existed at large sizes for as long as many smaller mammals have been small. Interspecific α significantly lower than 1 reflects progressive relative diminution of surface in a static series of well-adapted progressively larger forms, not imperfect surface adaptations to evolutionary increase in body weight.

(b) Davison (1955) drew a useful analogy to cell surfaces. If an animal grows solely by cell enlargement, then cell surfaces vary as the $2/3$ power of weight; if by formation of additional cells of fixed size (x cells added per x units of volumetric increase), then cell surfaces increase proportionately with weight. 'If metabolic rate were strictly a function of cell surface [he does not say that it is] one *a priori* would expect metabolic rate to vary directly as the body weight raised to some power between $\frac{2}{3}$ and 1 in accord with the manner in which the organism increases in mass' (Davison, 1955, p. 407). Although the dubious nature of an assumption relating metabolism to total cell surface precludes a general explanation of observed α values on this basis, recognition of the differing metabolic effects of cell enlargement *v.* cell number increase may explain puzzling specific cases. The observed clustering of protist α values near 0.66 (Zeuthen, 1953) reflects the limitation of growth type to that of enlargement. In this case, external cell surface and external body surface coincide. At metamorphosis, *Rana pipiens* undergoes a great (absolute and relative) increase in metabolic rate. Also associated with metamorphosis is the formation of new skeletal muscle elements with higher cell surface concentrations. Surface concentrations of dorsal myotomes in the tail of a mature tadpole is $350 \text{ cm.}^2/\text{cm.}^3$; in the reformed muscles of the new frog, $900 \text{ cm.}^2/\text{cm.}^3$ (Davison, 1955).

(c) An assessment of the relationship between metabolism and body surfaces requires that we define just which body surfaces influence metabolism. Kleiber mentioned two: external body surface and circulatory system cross-sections. It must be remembered that surface *v.* volume $\alpha = 0.66$ is a theoretical value applicable only to a set of objects maintaining geometric similarity with size increase. Many mammalian surfaces, as has been constantly emphasized throughout this article, cannot and do not maintain this geometric similarity; they increase with positive allometry to body bulk. The value of α for external body surface is fairly close to the theoretical 0.66, but circulatory cross-sectional areas must compensate volumetric increase since they serve the total body bulk. For total circulatory cross-sectional area *v.* weight, α is certainly higher than 0.66 and is probably closer to 1. If metabolism is dependent upon both external body surface and circulatory cross-sectional areas, then the observed metabolic α , intermediate between 0.66 and 1.00 but closer to the former, is expected because it reflects the rate at which the surfaces involved are increasing with respect to body weight. Brody (1945) suggested an explanation along these lines.

The generalized interspecific 'mouse-to-elephant' curve is valuable, not only because it quantitatively abstracts an important principle from raw data, but also because it may be further used to suggest explanations of related phenomena.

(i) As discussed in previous sections, the establishment of general size-correlated trends provides a criterion for the assessment of special adaptations. Scholander, Hock, Walters & Irving (1950) studied the metabolic patterns of arctic and tropical mammals. For arctic mammals, few significant deviations from the generalized curve were found; adaptation to cold temperature is achieved not by an increase of heat production at a given size, but rather by the control of dissipation (fur and skin insulation). Among tropical mammals, points for the sloth lie well below the general curve. Abnormally low metabolism suggests an explanation for lethargic habits and heavy fur coating.

(ii) That physiological phenomena may cause morphological allometry has been a major theme of this section. In mammalian interspecific regressions, most internal body organs increase with negative allometry to body weight; α values between 0.8 and 0.9 are common. A relationship between these values and body metabolism has often been proposed: 'Organs such as the kidneys, liver and heart will increase corresponding to the demands of metabolism including a safety factor, i.e. with an allometry exponent above 0.75' (Bertalanffy, 1960, p. 242).

VII. ALLOMETRY AND EVOLUTION

(1) Size variation in phylogeny

An analysis of size and shape correlations should not be limited to explanations of shape variation in terms of size. The causal chain leading from size to shape may be reversed; some important advantages of phyletic size increase are to be found in more adaptive proportions brought to expression by variation in size.

Size increase is a pervasive trend in many lineages of invertebrates (Newell, 1949) and vertebrates (Rensch, 1960). The very frequent repetition of any evolutionary event requires that similar strong selective pressures for its recurrence be operative. Many of these pressures arise simply because larger forms geometrically similar with smaller ancestors possess certain advantages. With larger brains, larger animals learn more, retain longer and perform more complicated tasks (though they may not learn faster) than related small animals (Rensch, 1956). Size increase may reduce predator attacks (Watson, 1949), increase locomotory stamina (Hill, 1950), and widen the size range of available food (larger starfish can successfully attack larger clams—Newell, 1949).

Other adaptive advantages of size increase, however, arise directly from the differences in physiological proportions between large and small forms. Metabolic efficiency is higher in large animals. 'In proportion to its weight, a mouse has to eat fifty times more than a horse, in order to maintain its basic activities and keep warm' (Hill, 1950, p. 226). Paloheimo & Dickie (1965, p. 539) express this metabolic relationship in terms of available food: 'The cost of use of energy units in the system, of maintaining a given weight of large fish, is less than the cost of maintaining the same weight of small ones.' Related to metabolism is 'the insulating effect' (Newell, 1949, p. 120) of large size; with low relative external surface, regulation of the internal environment

is more easily attained. Giant sauropods, by their sheer size, may have approached the homiothermal state (Kurtén, 1953, p. 114).

Weapons of attack and defence (horns and canines, for example) characteristically increase with positive allometry (Rensch, 1960). Size increase will continuously emphasize these structures, which are often more advantageous at larger relative size. Similarly, positive forebrain allometry is a trend established early in the size increase of many mammalian lineages (Rensch, 1954). Any further size increase will continually emphasize the forebrain provided that its allometric trend is unaltered at larger sizes. A large size range is favoured in ants, since the expression of proportion differences thus assured is an impetus to the development of polymorphism (Wilson, 1953).

Some non-morphological allometric trends further indicate the adaptive advantages of size increase. Among poikilotherms, progeny number per brood often increases with strong positive allometry to body length; $\alpha = 2.53-2.99$ in lycopsid spiders (Petersen, 1950) and is as high as 3.53 in the crustacean *Gammarus locusta* L. (Kurtén, 1953). Larger mammals tend to live longer: α for life in years *v.* body length ranges from 0.40 among the Bovidae to 0.73 among the Ursidae (Kurtén, 1953).

Although the repeated general trend towards phyletic size increase has been formulated as 'Cope's rule' (Rensch, 1960), exceptions occur with sufficient frequency to deprive the proposed rule of any universal significance. A catalogue of adaptive advantages for small sizes could also be established (Röhrs, 1961; Dinnendahl & Kramer, 1957). Size decrease is required for adaptation to many biotopes. As an extreme example, the smallest representatives of many phyla are found among the interstitial fauna of marine sand. Here metazoans attain protozoan dimensions, and the 2–3 mm. upper size limit is exceeded only by threadlike forms (Swedmark, 1964). Opposing adaptive advantages for large and small organisms guarantee a wide size range for the expression of allometric trends.

(2) Allometric consequences of evolutionary size variation

(a) Simple allometric trends; orthogenesis and recapitulation

Limb proportions of gibbon species (Lumer, 1939), several shape changes related to decreasing size in breeds of the domestic dog (Lumer, 1940) and facial proportions of baboon species (Freedman, 1962) can be ranked along a single simple allometric trend. Such a pattern may, but need not, indicate that alteration of size is alone responsible for observed proportion differences. The genetic basis for the allometric trend remains unmodified while selection alters the hereditary mechanism responsible for size determination. Selection for size increase alone will continuously emphasize structures expanding with positive allometry until the structure becomes sufficiently unwieldy to balance selective advantages of larger size. Since horns usually grow with strong positive allometry, the unidirectional differential enlargement of titanothere horns (Hersh, 1934) and 'Irish elk' antlers (Huxley, 1932), once cited as examples of non-material direction in evolution, is probably a simple concomitant of a phyletic trend

towards increasing body size. Simpson's explication of Irish Elk evolution (1953, p. 287) is worth noting: 'In early stages, selection was for both larger body and larger antlers, the allometric relation then accelerating the trend. When the point was reached where antler size ceased to be advantageous, selection against further increase in antlers was weaker than that for further increase in body size. The latter trend then continued, and therefore allometric increase in antler size continued, until the opposite selection pressures became equal. Body size was then somewhat under its optimum and antler size somewhat over this. That so specialized a creature might then be especially susceptible to extinction with environmental change is a different point, invoking no momentum effect.' When this unidirectional differential emphasis of structures occurs by a continuation of ancestral ontogenetic trends to larger sizes, the terminal adaptation will recapitulate ancestral configurations during its own ontogeny. This allometric explanation of recapitulation has been invoked by Hersh (1934) for titanotheres horn development and by Robb (1935a, b, p. 477) who spoke of 'algebraic identity of ontogeny and phylogeny in the equine skull'. 'Das Gehirnvolumen kleiner Insekten', writes Goossen (1949, p. 60), 'ist relativ grösser als das nahe verwandter grösserer Arten mit ähnlicher Lebensweise. Diese Regel kann als Auswirkung der ontogenetischen Wachstumsallometrie in der Phylogenetese angesehen werden.'

But while allometric analysis can often describe recapitulation when it does occur, it also illustrates that Haeckel's 'law' is an exception in phylogeny. The parameter values for most allometric trends change during phylogeny by selection for new proportions at all stages of a descendant's ontogeny (Kermack, 1954, p. 424, on ontogenetic and phylogenetic allometry within the *Micraster* stock). Many of these parameter changes are caused by size increase, as will be shown.

(b) Simple allometric trends; new functions and size

Size increase, especially in cases of strong allometry, leads to the expression of descendant proportions so different from those of ancestral forms that the development of new functions at large sizes becomes probable. Intense negative limb allometry in several lines of lizards eventually leads to serpentine locomotion (Rensch, 1960, p. 222). New functions then imply further morphological modifications. The elephant trunk developed when positive allometry of the second incisors made it impossible for the lips to take food directly. Meanwhile, negative brain allometry and consequent relative posterior skull reduction produced potential problems of insufficient insertion areas for neck and trunk muscles. This led to the 'lamellar inflation and enlargement of certain skull bones which is unique in the whole mammalian world' (Rensch, 1960, p. 231). Among ants, Wilson (1953, p. 138) has defined polymorphism as 'allometry occurring over a sufficient range of size variation within a normal mature colony to produce individuals of detectably different form at the extremes of the size ranges'. Once this expression is attained by phyletic widening of the size range, selection may operate in different directions upon forms at extreme sizes to further intensify caste formation. Positive jaw allometry in *Cataglyphis bombyana* Roger produces a caste of major workers whose greatly elongated mandibles work in conjunction with the maxillary palps in carrying large pellets of sand during

nest excavation. Allometric trends lead to shield-shaped or plug-shaped heads in majors of several *Paracrypcerus* and *Camponotus* species. These soldiers use their heads (literally) to block the nest entrance against invaders (Wilson, 1953).

(3) *Allometric adaptations to size increase*

(a) *Simple allometric trends*

There has been, in my opinion, mistaken emphasis on the non-adaptive nature of simple allometric trends in phylogeny. Proportions produced by constant α values need not be viewed as by-products of size increase brought to expression without selective modification of genetic shape factors; constant α may, rather, reflect an ordered set of proportions specifically selected to accommodate absolute magnitude at each step of phyletic size increase. The value of α for phyletic enlargement of the curious dorsal sail of *Dimetrodon* is 1.6 (Romer, 1948). If the sail is, as Romer suggests, an adaptation for heat regulation (large surface concentration to absorb heat when turned perpendicular to the sun's rays), then the observed α is reasonably interpreted as an example of volume-compensating positive allometry of surfaces. Since the pelycosaurs are direct mammalian ancestors, this would indicate an early attempt to deal with a problem later solved by the development of homoiothermy. Proportions at each stage of the sequence are adaptive. The simplicity of the allometric trend reflects a physical law relating surfaces and volumes, not necessarily a simplicity of genetic adaptation to its requirements. The allometric trend is an ordered sequence of adults; trends of ontogenetic allometry (for which we have no evidence) may have undergone complex genetic alteration to attain the adaptive adult proportion in each successively larger form.

The size range of Palaeocene–Oligocene Mesonychoidea is the widest of any known mammalian carnivore group. Tiny forms like *Hapalodectes* were active carnivores, while giant *Andrewsarchus*, which could scarcely live as an active predator, was probably omnivorous. Forms of intermediate sizes show a probable transition from active predation at smaller sizes to carrion feeding in larger forms. Connected with this size-correlated change in mode of life, the lower molar teeth become progressively wider as the long sharp tooth of an active carnivore is transformed to the broad, blunt crushing tooth of an omnivore or carrion feeder (Szalay & Gould, 1966). The value of α for width $v.$ length in $M/2$ is 1.18 as the W/L ratio declines from nearly 3/1 to less than 2/1 while tooth length increases from 5 to 35 mm. (Fig. 4). Again, tooth proportions are specifically adapted to mode of life (hence to body size) for each form.

(b) *Complex allometric trends*

Hersh (1934) and Phleger (1940) vitiated their material explanation of orthogenesis in terms of allometry with a concept of trend immutability leading to extinction: 'A size would finally be reached when the increased hazards at birth due to the larger horn would prevent successful parturition with consequently the sudden extinction of the stock' (Hersh, 1934, p. 550). Yet allometric trends are as subject to evolutionary alteration as are morphological features. If increasing size would lead to inadaptive

proportions, allometric parameters may be modified to allow further phyletic growth.

The usual negative correlation of size $v.$ α value holds for phylogeny as well as for ontogeny; requirements of absolute magnitude are the same in either case. The value of α is 2.17 for paraconid height $v.$ crown length in $M/1$ of the domestic cat and 1.39 in the larger related *Felis silvestris* (Kurtén, 1954a). Had the domestic cat regression continued to *F. silvestris* size, an 'enormously hypsodont carnassial' (Kurtén, 1954a, p. 10) would have been produced.

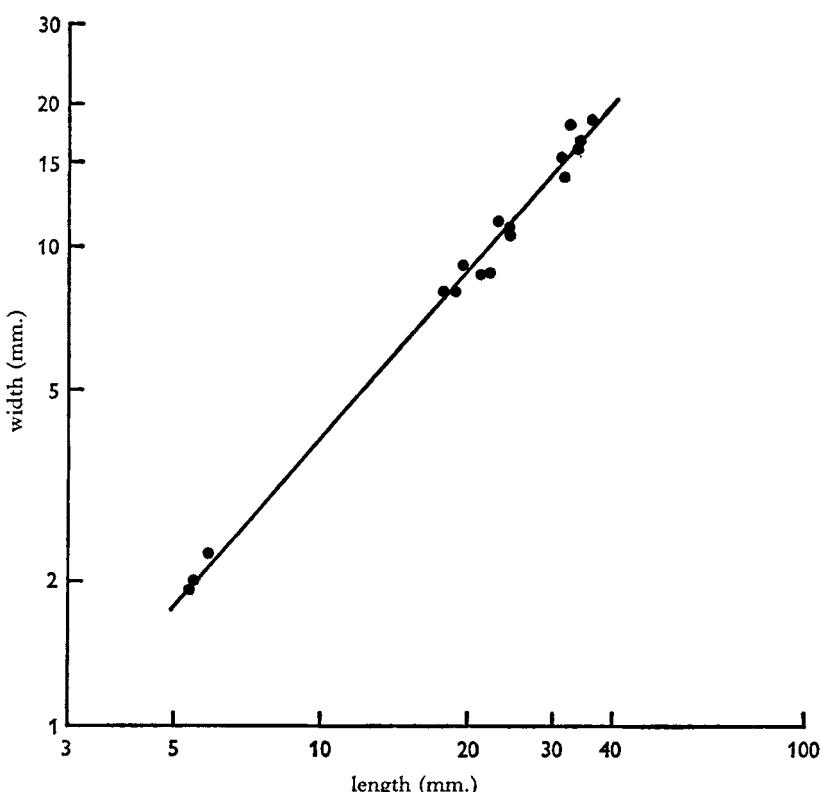


Fig. 4. Interspecific allometry of tooth width $v.$ tooth length for $M/2$ in the Mesonychoidea.
Log-log scales; slope = 1.18.

The hyaena *Ictitherium hyaenoides* may have evolved from the smaller *I. robustum*. Strong positive allometry ($\alpha = 1.72$) occurs for width $v.$ length in $M/1$ of *I. robustum*. Continuation of this trend to *I. hyaenoides* dimensions would lead to an inadaptively wide tooth. In *I. hyaenoides*, α is less than 1 (Kurtén, 1954b). Examples of α modification as an adaptation to size increase should evoke an attitude of caution towards Rensch's statement (1960, p. 136) that ' α is a growth coefficient from which, for example, one can calculate the size of a certain organ at a given body size. This is an important help to palaeontologists, as one can find out about the size of organs in animals of a body size exceeding that of the types known so far.'

Decreases in α are not the only parameter modifications noted as adaptations allowing expanded size ranges; shifts of the allometric regression effected largely by a change in b may also prevent the expression of inadaptive proportions. The value of α is approximately the same for positive allometry of paracone height $v.$ crown length in M_1 of the large fossil cave bear *Ursus spelaeus* and the smaller fossil and Recent brown bear *U. arctos*, but b values differ significantly as the *U. arctos* regression lies well to the left of that for *U. spelaeus*. The *U. arctos* trend extrapolated to *U. spelaeus* dimensions would produce a very hypodont tooth which, since enlargement of the

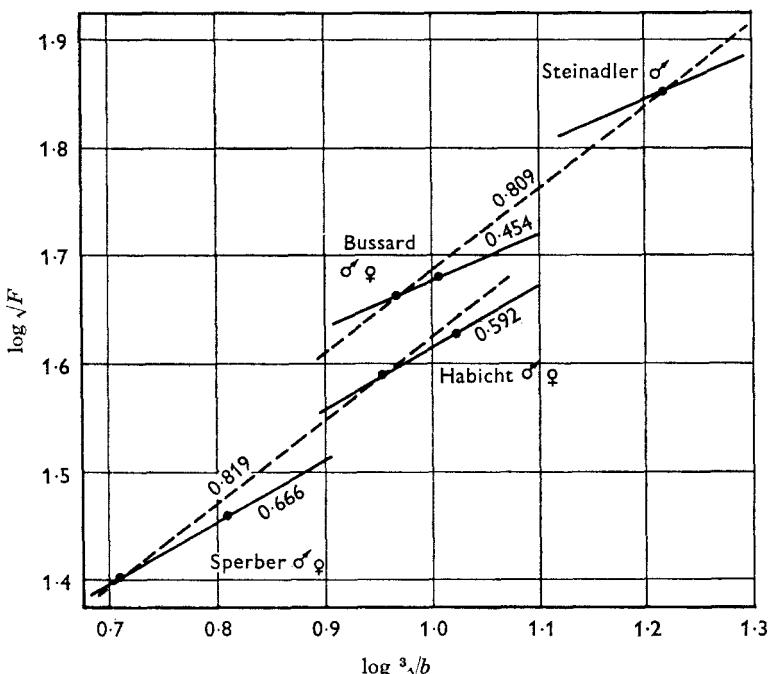


Fig. 5. Transpositions in birds of prey. Solid lines are intraspecific allometry regressions for $\log \sqrt{F}$ v. $\log \sqrt[3]{b}$; points are for male and female means. Points for individuals, though used to calculate α , have been omitted. Two transpositions are shown: *Accipiter nisus* (Sperber) to *A. gentilis* (Habicht) and buzzard (*Buteo buteo*) to golden eagle (Steinadler). The relationship of two regressions differing primarily in the b parameter is considered a transposition only if wings of the two forms are of the same aerodynamic type and compensation is for size alone. The shift in regressions from *A. gentilis* to *B. buteo* is not a transposition. The effect of transpositions in increasing wing length is indicated by the interspecific α values (dotted lines), which are significantly higher than the intraspecific α 's. Extrapolation of the intraspecific α values to larger sizes would produce disadvantageously short wings. (From Meunier, 1959a.)

succeeding M_2 is isometric, would project increasingly farther beyond the tooth row. Phyletic growth favours the *U. spelaeus* regression which, by a decrease in b (hence a decrease in y at any value of x , since α for the two regressions is the same), shortens the paracone to concordant proportions at larger sizes (Kurtén, 1955).

In birds, intraspecific (individual allomorphosis) trends for wing length $v.$ body length are generally negative. With the constantly increasing wing loading thus

implied, severe upper size limits for flight exist for each regression. Four gull species lie on a single regression. Extrapolated to albatross dimensions, wing loading is 15 kg./m.², too high for successful gliding. But the albatross intraspecific regression is shifted above that for the gull extrapolation, producing a longer wing and a wing loading of only 10 kg./m.² (Meunier, 1959a).

The concept of size-required allometric shifts has been generalized by Meunier (1959a, b) as 'transpositional allometry'. Allometric regressions are adaptive only within a limited size range; phyletic size increase or dwarfing beyond these limits requires a change in allometry which is usually effected by a shift, or transposition, of allometric regressions denoted primarily by alteration of the *b* parameter (Fig. 5). Meunier (1959b, p. 347) writes that 'das Vorhandsein von Transpositionen die logische Konsequenz des Vorhandsein von Allometrien ist'.

Returning to mammals, extrapolation of the ancestral *Ictitherium robustum*-*I. gaudryi* regression for width *v.* length of *P/4* to *I. hyaenoides* size would produce a disadvantageously narrow tooth, since negative allometry is strong (Kurtén, 1954b). A transposition therefore occurred during ictithere evolution allowing further size increase by shifting the regression for descendant *I. hyaenoides* upward (greater width at a given length).

(4) Size and phylogeny: the assessment of evolutionary adaptations

Explanation in terms of adaptation, specifically the role played by absolute magnitude in the determination of proportions, has been my principal concern. A satisfactory assessment of that role would lead to the formulation of a set of rules expressing general correlations between size and form. Such rules would then serve as criteria for the evaluation of evolutionary shape alteration. Adaptations arising as necessary correlates of size variation could be distinguished from other modifications indicating environmental adaptation or structural improvement. Our ultimate goal in the study of a phyletic lineage is the explanation of each morphological change in terms of its selective advantage, its purpose or final cause expressed materially without imputing conscious purposive activity either to the organism or to non-verifiable externals. 'Purpose', defined as the reason why a modification of form is advantageous to the organism, is an inescapable concept in evolutionary biology. The separation of a set of observed adaptations into categories reflecting similar purposes constitutes a major step in the evolutionary explanation of form. Thus Colbert (1948) used absolute magnitude as a criterion for the classification of morphological trends of ceratopsian dinosaurs in terms of adaptive purpose. Some adaptations—relative shortening of tail and limbs, for example—could be attributed to size increase; others could not. Among those that could not, constancy of relative head size is of special interest. The initial assumption of many evolutionists that no proportion change means no adaptation is not correct. Since relative head decrease is the normal correlate of size increase, maintenance of constant proportions is an adaptation requiring special explanation. In this case, the development of more complex offensive and defensive armament may have required a relatively large head.

I shall conclude this discussion with comments on two phenomena whose explana-

tion requires the distinction of trends caused by size from those that are adaptive for other reasons.

(i) *Convergence*. Limited possible solutions to similar problems is a central consideration in evolutionary convergences. The problems, however, are of several different types whose distinction and definition often constitute explanations for particular cases. The independent evolution of several pairs of marsupial-placental homeomorphs represents optimal adaptation, within the limitations of mammalian structure, to specific environmental situations. Other independent developments—eyes of cephalopods and chordates, forward migration of pelvic fins in several groups of fishes (Harris, 1938)—are general structural improvements related to environment only in the broadest sense and unrelated to body size. A third general class of convergences gives limited solutions to problems imposed by size increase. Compensation of increasing bulk requires modification of form in accordance with what D'Arcy Thompson (1942, p. 1095) called the 'comparatively few definite lines, or plain alternatives, of physicomathematical probability'. Thus, differential leg-thickening and secondary quadrupedalism occur independently in several lines of dinosaurs (Colbert, 1948). Hypsodonty in many groups of large mammals and size-correlated lophophore complexity in numerous independent brachiopod lineages are convergent bulk-compensating modifications of the feeding system. The situation becomes potentially complex when size-imposed convergences result either in similar adaptation to a specific environment or in structural improvement. The mesonychid creodont *Andrewsarchus* shows remarkable cranial and dental convergence upon later entelodonts. These features are probably related to similar omnivorous modes of life (Szalay & Gould, 1966). Yet *Andrewsarchus* is the giant of the Mesonychoidea (and the largest known creodont). It is the terminal member of a trend in size-related environmental adaptation, leading from light cursorial carnivores through large carrion feeders to giant omnivores. Size increase was the primary impetus for convergence. Moreover, size increase is a cause of many convergent structural improvements. One of the most important steps in the evolutionary history of animals, the (at least partially) independent development of complex internal organ systems in advanced metazoan phyla, is primarily a response of surface-dependent functions to problems of increasing bulk. These examples should emphasize the importance of considering the absolute magnitude of all forms in convergent series when attempts are made to derive adaptive explanations for specific evolutionary convergences.

(ii) *Evolution of the mammalian brain*. That certain mammalian lineages trace their success largely to improvement of the brain can scarcely be doubted, but the establishment of a criterion for assessing such improvement has been plagued with difficulties arising from lack of consideration for the morphological consequences of absolute brain size. Absolute brain size itself is clearly an inadequate criterion since super-human mental powers would then be imputed to whales, due to the positive correlation of brain and body weight. Determination of the interspecific mammalian brain-weight *v.* body-weight allometric regression demonstrates the further inadequacy of relative brain size. The value of α is close to 0.66 (denoting the surface-dependency of brain increase); relatively large brains may be a simple consequence of small size.

Other proposed criteria fail because supposedly independent trends towards improvement are simple correlates of brain size increase unrelated to any consideration of body size. Leboucq (see Clark, 1945) tried to use a criterion involving relative convolution. He compared actual brain surface area (s) with that of a sphere occupying the same volume as the brain (s_1). The ratio s/s_1 is 2.14 for 'the baboon', 2.28 for the chimpanzee and 2.75 for man. Clark (1945), however, noted that the cerebral cortex, a surface layer of grey matter, increases only by surface expansion, while the internal

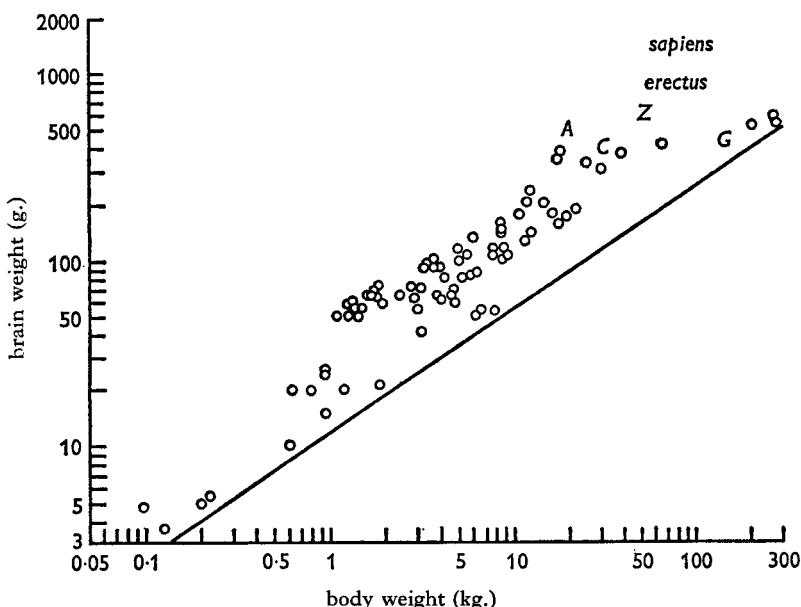


Fig. 6. Interspecific allometry of brain weight $v.$ body weight in primates compared with the mean mammalian brain weight $v.$ body weight regression (solid line, slope = 0.66). Primate superiority (in size) is indicated by upward deviation of points from the mean line at specific body weights. A = *Australopithecus africanus*; Z = '*Zinjanthropus*'; C = chimpanzee, and G = gorilla. (From Jerison, 1963.)

white matter expands volumetrically. 'Therefore, if the cerebrum, regarded as an approximately spherical body, increased its size without deformation of the surface, the expansion of the cortex would only be proportional to the square of the radius while that of the white matter would be proportional to the cube. As we have seen, however, the proportion of white matter to grey cortex remains approximately uniform, and to maintain this ratio the cortex must necessarily become folded' (Clark 1945, p. 2). Since folding is related to brain size, and brain size to body size, the high s/s_1 value of man may only reflect his larger body size. In fact, von Bonin (1941) plotted a folding index $v.$ weight for many mammals and found that the point for man falls *below* the general trend.

A valid criterion must employ both relative and absolute brain size. Such a combination permits the distinction of those aspects of brain development due only to absolute magnitude from those independent acquisitions indicative of evolutionary advance.

The degree of upward divergence from the general interspecific mammalian brain weight *v.* body weight curve is a measure of the divergent species' increased brain weight relative to that of a 'normal' mammal of the same body size. Relative brain weight at a given body weight is therefore the useful criterion. Points for primates, for example, fall well above the general mammalian curve (Fig. 6).

This criterion of relative brain weight at the same body weight has been widely applied to the analysis of brain evolution, beginning with the initial use of the allometric power function by Snell in 1891. Jerison (1961) plotted curves based upon adults of several genera of Eocene, Oligocene and Recent mammals. Where y = brain weight and x = body weight: Eocene, $y = 0.026x^{0.657}$; Oligocene; $y = 0.055x^{0.655}$ Recent; $y = 0.115x^{0.664}$. Since α values are nearly the same, a ratio of b values is the ratio of y 's (brain weights) at any x (body weight). Progressively higher b values in more recent mammals is an index of relative brain enlargement at all body weights during the course of mammalian evolution.

Among primates, Stephan & Andy (1964) compared the deviation of points for macroscelidid insectivores, *Tupaia*, prosimians and monkeys from general curves constructed from 'basal' insectivores (tenrecs, shrews and hedgehogs). Seven divisions of the telencephalon were analysed separately. The monkey neocortex is 21–24 times larger than that of 'basal' insectivores, at any common body weight, and this differential is more than 3 times greater than that of the structure (the striatum) making the second largest contribution to increased brain weight at specific body weights.

Jerison (1963) devised a method for estimating the number of cortical neurons from brain size. This number can be divided into a component accounted for by body weight and a number of 'extra' neurons expressing the deviation of a point from the curve of primitive mammals at the given body weight. This method plays an important role in Tobias's (1965) assignment of a morphologically intermediate position to *Homo habilis* between *Australopithecus* and later members of the genus *Homo*. Jerison's (1963) table of 'extra' neurons for hominids contains the values (in billions) of 4.4 for *Australopithecus africanus*, 4.7 for 'Zinjanthropus', 6.4 for a *Homo erectus* (brain weight 900 c.c.), 7.0 for a *H. erectus* of 1000 c.c., and 8.5 for *H. sapiens*. Tobias's *H. habilis* value of 5.3–5.4 nicely fills the largest gap in hominid brain evolution.

VIII. BEYOND BIVARIATE ALLOMETRY: THE ANALYSIS OF TRANSFORMATION PATTERNS

Bivariate plots, which constitute the data of almost all allometric studies, are paired abstractions from the total form of an organism. Models for total pattern analysis have been proposed, but difficulties in quantification of complex form alterations have generally precluded fruitful use. Three proposed approaches to the analysis of total form alteration may be delineated.

(1) *The transformed co-ordinate model*

D'Arcy Thompson (1942) showed that a Cartesian rectangular grid superimposed upon one organism could often, by suitable deformation, be made to yield the grid pattern of a related form. The grid of a great ape can be transformed to that of man

by bulging and stretching of grid elements in the cranial area and compression of those superimposed upon the jaw. Though Thompson applied his method primarily to form differences among related adults (allomorphosis), its potential for describing ontogenetic form alteration (heterauxesis) was utilized by Richards & Riley's (1937) study of amphibian larval development. Lull & Gray (1949) considered both ontogenetic (*Protoceratops andrewsi*) and phylogenetic transformation sets among the ceratopsian dinosaurs. Richards (1955) summarized the use of transformed co-ordinates in differential growth analysis.

Thompson's model has been criticized on two grounds: that it is 'purely descriptive' (Bonner, 1952, p. 135) and that it has not proved amenable to quantification. The first objection, while valid from our standpoint, is, in a sense, unfair to Thompson, whose conception of organic transformation rendered his proposed method as ideally explanatory. Direct deformation of structure by the operation of mechanical forces is a central theme in the Thompsonian analysis of growth and form. Cartesian grid lines are, to us, mere reference points; to Thompson, they represented actual force schemes whose deformation could give insight into the direction of operation of mechanical forces which actually produced the transformation. 'If', writes Thompson (1942, p. 1037), 'diverse and dissimilar fishes can be referred as a whole to identical functions of very different co-ordinate systems, this fact will of itself constitute a proof that variation has proceeded on definite and orderly lines, that a comprehensive "law of growth" has pervaded the whole structure in its integrity, and that some more or less simple and recognizable system of forces has been in control.'

Thompson's transformation diagrams are visually impressive, but their failure to yield quantitative information on shape transformation has greatly limited their utility. Medawar (1945, 1950) admitted that such a subtly complex concept as shape is not easily rendered numerically, but based a quantitative scheme on the notion that *change* in shape could be expressed in terms of rate and direction. This general approach, the establishment of a one-parameter abstraction to render shape as a whole, has been followed by Mosimann (1958) in his study of differential growth in turtles. Mosimann treats general turtle shape as the percentage of total volume occupied by the actual animal of an ideal rectangular prism of dimensions: turtle $L \times W \times H$. Thus, in *Sternotherus odoratus* the development during ontogeny of a roughly hemispherical cross-section from an initial triangular form results in an increase of the turtle-volume/prism-volume ratio of 46·2% at $L = 20$ mm. to 54·4% at $L = 107$ mm. These results cannot, however, be unambiguously reverted to actual shapes for many different forms will fill the same percentage of total volume. In *Chrysemys picta* and female *Graptemys geographica* the turtle-volume/box-volume ratio does not alter in ontogeny, although allometric trends in the three principal dimensions are noted (Mosimann, 1958, p. 210).

(2) Sets of allometric equations; growth gradients in ontogeny

An approach to total pattern analysis may be made by considering together the allometric regressions of many different body parts relative to a common standard adequately representing total body magnitude. Huxley found (1932) that α values are

generally distributed in an ordered fashion among body parts, with even spatial gradients radiating from centres of maximum differential growth. It is unfortunate that so little attention has been paid to the biochemical or physiological basis of these gradients which 'strongly suggest a graded distribution of some substance or process concerned with the regulation of relative growth rate' (Huxley, 1950, p. 468). It is (perhaps uniquely) in this area of growth centres and gradients that numerical values of allometric parameters may mirror actual efficient causes of growth. There is evidence, moreover, that the gradient itself may be inherited as a unit, indicating that it represents a specific set of potentialities under direct genetic control. Matsuda (1961, 1962, 1963) has noted a tendency for ordered variation of α values among homologous segments of closely related insect species. Magnitude differences occur in parallel fashion and the shape of the gradient remains unchanged. Selection seems to be operating upon the gradient as a whole. In femurs of three legs of the water boatman *Notonecta undulata*, significant differences for absolute α values, but none for the shape of the growth gradient, are found among individuals (Misra & Reeve, 1964).

Growth-gradient studies have been particularly successful in describing the ontogeny of sexual dimorphism among Crustacea (Teissier, 1960, for summary). In *Cancer pagurus* (MacKay, 1942, 1943) the relatively wide female abdomen, advantageous 'for the protection of extruded ova during the long period of attachment' (MacKay, 1943, p. 225), is correlated with a mid-abdominal growth centre stronger (higher α value) than that of the male. Among other growth-gradient patterns amenable to functional interpretation, high relative bill growth forms an exception to the postero-anterior α -value gradient in hatching to 8-day growth of the house wren, *Troglodytes domesticus baldwinii* (Huggins, 1940). A high specific growth rate early in ontogeny is requisite for an organ which, while possibly disadvantageous to the bird when in the egg, must reach useful proportions rapidly during a brief nest life.

Gradients are often altered during ontogeny. A. E. Needham (1937) divided the total size range of *Asellus aquaticus* into equal log-intervals and computed α for each segment in each interval. The resulting α matrix is plotted as a 'growth contour' with segment number on the abscissa and growth stage on the ordinate. 'Growth centres in space-time then appear as hills, gradients as the slope of the hills and centres of relative inhibition as valleys... The construction of the map is justified by the simplicity of the system revealed; isolated values of α marring a general scheme do not occur, but all may be combined in a simple hill and valley system' (A. E. Needham, 1937, p. 300). In another pictorial representation of complex temporal gradient changes, Richards & Kavanagh (1945) contoured specific growth-rate intensities (maximum considered as 100%) on developing tobacco leaves. The maximum rate in each of four developmental stages occurs in two areas symmetrically disposed about the midrib, a third of the distance from base to tip. The steep gradient running from the area of maximum specific growth rate to the leaf tip falls during ontogeny. With size increase, the originally narrow leaf differentially broadens in areas of maximum growth intensity.

(3) *Multivariate analysis*

The two models just presented try to encompass multivariate proportion changes without using multivariate analytical techniques. Medawar (1945) and Mosimann (1958) sought to abstract the complexity of total shape as a one-parameter entity; growth gradient studies consider several bivariate regressions together, but do not treat all parameters simultaneously to consider the complexities of interdependence. With electronic computers now available to handle the previously unmanageable volume of calculations required by many techniques long known in theory, the abstraction of simplifying patterns from a raw matrix of differential growth data becomes possible. The abstracted simplifying pattern is a model which, if useful, will mirror a causal scheme and suggest explanations for the correlations observed in raw data. Factor analysis (see Harman, 1960; Imbrie & Van Andel, 1964; Gould, 1966a) is one such technique and, to my knowledge, the only one so far applied to allometric studies.

Factor analysis resolves a set of samples (Q mode) or variables (R mode) into a series of end-members (reference axes) considerably fewer than the total sample or variable size. In the R mode used in relative growth studies, each variable is depicted as a vector in n -space. Vectors radiate from a common point and correlation between any pair is a function of the cosine of the angle separating them. Reference axes (sufficiently numerous to resolve a significant amount of information but few enough to produce a simple abstraction) are constructed within the vector swarm. Various positioning schemes for the reference axes can be used in the attempt to reach meaningful interpretations. In the principal components solution, the first reference axis is positioned within the space of data vectors as that axis which resolves the maximum possible information of the data vectors. Since the high positive correlation of most body parts in ontogeny (nearly overlapping vectors) is due primarily to the common factor of increasing body size, the first principal components axis has been interpreted as a general growth factor. It has been used by Teissier (1948, 1955) and Matsuda & Rohlf (1961) as the reference (x) dimension for allometric regressions with body parts. Jolicoeur & Mosimann (1960) used differences in vector projections of length, width and height on the first principal component axis to describe allometry in the ontogeny of sexual dimorphism in some turtles.

The equation for the first principal component of the covariance matrix of logarithmically transformed data constitutes a multivariate generalization of the allometric power function (Jolicoeur, 1963b, pp. 497-8). The association of any two variables in the system for which the principal component is derived yields a two-dimensional relationship equivalent to the simple allometric equation. An isometry hypothesis can be formulated for all variables simultaneously to test whether any significant departure from geometric similarity occurs during growth (Jolicoeur, 1963b, pp. 498-9.)

In another positioning scheme for reference vector axes, the oblique solution (Imbrie & Van Andel, 1964), actual data vectors lying at extreme positions in the vector swarm are used as reference axes. I have used this solution in a study of phylogenetic proportion changes among the Palaeozoic pelycosaurian reptiles (Gould, 1966a).

Measures of fourteen variables in twenty-two species were converted to logarithms. Since R-mode analysis assumes linear relationships among variables, this data transformation acknowledges the simple allometric nature of most of the bivariate regressions.

Table 3. *Matrix of vector projections upon oblique factor axes*

group	variable	femur, distal width	lumbar centrum, length	ilium, neck width	ilium, base width
I	femur distal width	1.000	0.000	0.000	0.000
	body weight	0.854	0.104	-0.160	0.208
	femur proximal width	0.839	0.060	0.152	-0.044
	dorsal centrum width	0.775	0.081	-0.161	0.312
	tibia width	0.587	0.180	0.191	0.053
	lumbar centrum height	0.480	0.308	0.006	0.221
II	lumbar centrum length	0.000	1.000	0.000	0.000
	dorsal centrum length	-0.424	0.918	0.209	0.309
	humerus length	-0.163	0.917	0.686	-0.422
	body length	-0.200	0.644	0.453	0.121
	humerus width	0.348	0.563	0.502	-0.395
	femur length	0.260	0.518	0.512	-0.270
III	ilium neck width	0.000	0.000	1.000	0.000
IV	ilium base width	0.000	0.000	0.000	1.000

The final step of an R-mode analysis is a matrix (Table 3) whose elements represent the projection of each variable on each selected reference axis. Each variable is grouped with the reference axis upon which its vector most strongly projects. A reference axis and its associated variables form a set which, with due regard to the *post hoc* fallacy, may delimit a functional complex of interdependent parameters mirroring an underlying common causal factor.

I had, *a priori*, expected bone lengths to sort in the same group as their width, but the two groups may be clearly defined as bone width-body weight and bone length-body length clusters. Only humerus width sorts with its length in the general length grouping, but even the force of this exception is vitiated since, of all measures in the length grouping, humerus width projects most highly on the width-grouping reference axis. Lengths of dorsal vertebrae, lumbar vertebrae, femur and tibia sort with body length, widths of the same variables with body weight. The conclusion that bone width measures are sufficiently independent of their own lengths to sort as a discrete group with body weight constitutes a multivariate confirmation of Galileo's observation that large terrestrial organisms compensate increasing bulk by disproportionate thickening of weight-supporting structures.

As primary justification for the labour involved in quantifying allometric phenomena, Huxley (1932, p. 2) wrote that 'it [the allometry formula] may suggest important ideas as to the underlying processes involved'. Multivariate techniques suited for the apprehension of causal influences may soon supersede the simple allometric equation as a major quantitative technique for explanatory analysis of the phenomena of allometry.

IX. CONCLUSION

Using size and its requirements as a point of departure, I have tried to explain some observed allometric patterns as adaptations which produce altered proportions leading to the maintenance or improvement of physiological and ecological efficiency in modified size ranges attained during the course of ontogeny and phylogeny. I chose this approach among numerous possible synthetic themes in the hope of demonstrating that the rigorous quantitative expression of changes in form is not merely a descriptive technique.

Waddington (1950, p. 513) characterized allometric quantification as 'an empirical description with no simple relation to the effective causal system whose nature and modifications constitute the biological problem which we have to understand'. Yet, if the determination of causal systems be 'the biological problem', then an assessment of the mirroring of causal influences by quantitative parameters requires that the semantic complexity of the term 'cause' be recognized. Primarily as a heritage from mechanical aspects of the Newtonian approach, we too often confine our explanatory attempts to immediate efficient causes; but, whereas the citation of efficient physiological mechanisms can explain the form of a wolf's dentition, the response 'all the better to eat you with my dear' answers the question 'why this specific form' in another, and equally valid, sense.

Quantitative data abstractions are descriptive devices which also serve to suggest explanations when derived mathematical parameters reflect a causal system not immediately explicit in raw data. Parameters of the simple allometric equation probably do not directly represent efficient physiological substances or processes (except perhaps in the study of growth gradients). They certainly do not when parameters are derived from static comparisons of adult forms (allomorphosis).

Allometric parameters may, however, directly reflect causes expressed in terms of adaptation. An α near 1.50 need delineate no efficient physiological cause, no differential concentration of enzyme or hormone; yet it may mirror a physical law relating surfaces and volumes—a formal cause of changes in proportions. Adequate adaptation in new situations and size ranges is the final cause of changes in proportions; absolute magnitude and the physical laws related to it are formal causes of specific adaptations brought to expression by the efficient phylogenetic mechanism of natural selection. Within the theme of adaptation, at least, the parameters of allometry may transcend sheer description and suggest reasons for changes in proportions by mirroring rules relating size and shape.

X. SUMMARY

1. *Definition.* Allometry is defined as the study of proportion changes correlated with variation in size of either the total organism or the part under consideration. The variates may be morphological, physiological or chemical; the size differences may arise in ontogeny, phylogeny or the static comparison of related forms differing in size; the term is not confined to any one form of mathematical expression, such as the power function.

2. *Size-required allometry.* (a) In organisms which maintain geometric similarity with growth, the surfaces increase as the square of length, volumes as the cube. Since many functions require that organ surfaces increase proportionately with total body volume in order to maintain adequate efficiency in expanded size ranges, departure from geometric similarity with smaller stages of ontogeny or phylogeny is inevitable in well-adapted larger forms. This departure involves a positive allometric increase of surfaces.

(b) Of the various possible modes of escape from decreasing area-to-volume ratios, higher metazoan phyla have achieved differential surface increase by complication of structure and the resultant development of elaborate internal organ systems. The genetic capacity for solving area-to-volume problems in this way is a primary definition of the advanced phyla.

(c) Differential increase of surfaces in phylogeny runs parallel with examples drawn from ontogeny for respiratory, digestive and locomotory structures. Absolute magnitude can serve as a synthetic theme in allometric studies. The shape modifications required by size increase are similar whether the small form used for comparison be an earlier ontogenetic stage or a phyletic ancestor.

(d) Other size-required allometric trends may involve further consequences of area-to-volume relations (relatively thick supporting structures of large terrestrial organisms) or be related to size for other reasons (flattening of large foraminifera to provide light access for symbiotic zooxanthellae).

(e) Positive allometric increase of area-dependent structures has physical limits which determine the maximum size of efficient flying and terrestrial animals.

3. *Quantification of allometry.* (a) The power function $y = bx^\alpha$ has been generally applied to bivariate allometric data. Other functions (linear with y intercept unequal to 0, various polynomials) are in less frequent use. The power function's popularity results more from the interpretability of its parameters (and the ease of their determination) than from its close approximation to most bivariate data trends.

(b) The power function's status in allometric analyses is empirical; it should not be forced upon curvilinear log-log data by the construction of several line segments to approximate to the curve.

(c) Interpretation of power-function plotting has often been hampered by inadequate statistical methods. The reduced major axis is recommended for most cases in which both variates are subject to error.

(d) Allometry encompasses a varied set of data types sharing the common characteristic of relationship to absolute magnitude. The major types are: ontogenetic, phylogenetic, intraspecific and interspecific. Only the first represents individual growth; the latter three constitute the comparison of related forms at a single growth stage (usually the adult), but of different sizes.

4. *Quantification of allometry; ontogeny and static comparison.* (a) Power-function parameters often delimit size-required allometric patterns. An α near 1.50 may imply proportionate growth of surfaces and volumes. Changes in parameter values may also be size-required. Since the y/x ratio augments continually with size increase when

allometry is positive, very high α values will either be size-limiting or will be reduced to permit an expanded size range.

(b) Special adaptations, causally unrelated to size, are often best elucidated by allometric methods. Evidence for such adaptations may be seen in the departure of points from general curves of size-dependency and in the departure of parameter values and changes from general rules of size-shape correlation.

5. *Taxonomy.* (a) Mistaken taxonomic distinctions have often been based upon the assumption that shape parameters in two related forms are independent of size differences. New shape patterns may result from a continuation of allometric trends to larger sizes and difference in magnitude may be the only character separating the two forms.

(b) Allometric parameter values are important characters in a taxonomy based upon the dynamics of ontogenetic development rather than only upon the statics of adult configuration.

6. *Physiology.* (a) If α values are equal, two expressions for the regression of physiological variates upon body weight may be combined to yield a dimensionless number which is invariant with change in size. These numbers may serve as scaling criteria whose constancy throughout the size range of a group implies systematic alteration of shape.

(b) Negative physiological allometry of metabolism *v.* body weight for most organisms is generally attributed to the relationship between metabolism and surfaces. Since some of the surfaces involved in metabolism increase with positive allometry, α for metabolism *v.* body weight in mammals is above the theoretical value of 0.66 for surface *v.* volume in a series of objects constituted in geometric similarity.

7. *Evolution.* (a) Many general adaptive advantages of size increase in phylogeny (metabolic and insulatory efficiency of large forms) result from differences in physiological proportions between large and small forms. Other advantages (emphasis of weapons of attack and defence) result from differences in morphological proportions.

(b) Selection for size increase with no alteration of allometric parameters produces orthogenetic and recapitulatory effects. Altered proportions produced in new size ranges imply modification of function.

(c) Undue emphasis has been placed upon supposedly non-adaptive allometric trends in phylogeny. Differential increase of respiratory, feeding and locomotory surfaces occurs in both phylogeny and ontogeny. In phylogeny, too, α near 1.50 may indicate surface compensations of volumetric increase. Allometric parameter changes in phylogeny are often size-required. Decreases of initially high α values and shifts involving the b parameter (transpositions) preserve adaptive proportions in expanded size ranges.

(d) A study of allometry in evolution could lead to the establishment of a set of rules expressing general trends of size-shape correlation. Changes of proportions due to size could then be distinguished from those adaptive for other reasons. Distinction and ordering of adaptations into categories related to and independent of size is useful in increasing understanding of two important evolutionary phenomena: convergence, and the development of the mammalian brain.

8. *Transformation patterns.* (a) Attempts have been made to extend the notion of bivariate allometry to the analysis of changes in total form. D'Arcy Thompson developed the method of transformed co-ordinates to describe shape differences in related organisms. Huxley plotted allometric regressions for several variables against a common standard and established ontogenetic gradients in α intensity.

(b) Multivariate methods which consider allometry in all variables simultaneously are needed. Factor analysis has shown much promise in this area and should be extended further.

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XII. ADDENDUM

Size-required allometry. The impossibility of ciliary swimming with large sizes has been proposed to explain a postulated swimming-to-crawling transition among ancestors of the Bilateria. 'There is an element of inevitability in the transition from a pelagic to a benthic life with increasing size' (Clark, 1964, p. 213). Alternatives to such inevitability are, however, available in the form of structural improvements—in this case in the development of muscular locomotory systems. It is in this sense that size increase may have provided the impetus for some major steps in the development of structural complexity among Metazoa. Clark (1964, p. 42) further mentioned that among the Turbellaria smaller species move by cilia, larger ones by muscular contraction.

Applicability of the simple allometric equation. Nordbeck (1965) and Woldenberg (1966) have applied the term 'allometry' to geographical and geomorphological relations fitted by power functions. Nordbeck equates the term 'law of allometric growth' to 'power function' and then proceeds to use the power function only for relations exhibiting isometry—i.e. no change of shape with size increase. Moreover, he proposes some improbable *ad hoc* assumptions to preserve isometry when fitted parameters indicate shape change. He tries to explain away $\alpha > 0.5$ for perimeter v .