OBSERVATIONS ON
ALLOMETRY IN MAMMALIAN DENTITIONS;
ITS INTERPRETATION AND EVOLUTIONARY
SIGNIFICANCE

BY

BJÖRN KURTÉN.

GEOLOGICAL INSTITUTE OF HELSINGFORS UNIVERSITY

INTRODUCTION

The general shape of the mammalian tooth crown appears to be genetically determined in the form of a growth pattern that may or may not include a gradient. If there is no gradient, the shape of the tooth crown will be identical regardless of its absolute size (isometry). This is a special case of allometry *s.l.;* allometry *s.str.,* the presence of a gradient, will always result in differences in shape between teeth of unequal size. The allometry concept was formulated by HUXLEY (1932).

A large body of data has been sampled by the present author, mainly relating to the dentitions of carnivores. Some are being published elsewhere. In the present paper I intend to discuss some general principles in connexion with the study of allometry in mammalian dentitions, relating to biometric technique as well as to interpretation, and illustrated by means of selected examples showing the manner in which such studies may contribute to the theory of evolution. In an immediate sequel to this paper (1954) the method will be applied to a special case.

THE DESCRIPTION AND INTERPRETATION OF ALLOMETRY

It has been shown (SINNOT 1936) that an allometric pattern is genetically determined and may suffer a change through mutation. In order to obtain a basis for subsequent investigation, we shall initially discuss a case in which the allometry appears to be homogeneous for a population — that is, where biometric method cannot demonstrate any heterogeneity.

Fig. 1 represents the covariation between the length and the (talonid) width of the lower carnassial in *Meles meles* (data from DEGERBØL 1933: a sample of recent specimens from Denmark and elsewhere, and a sample of subfossil specimens from Denmark). It appears that there existed no difference in this allometry between the subfossil and recent populations, though there is a marked difference in average size (this is one of the rare instances when phyletic growth has occurred in postglacial time: see Degerbøl, op.cit. p. 635).
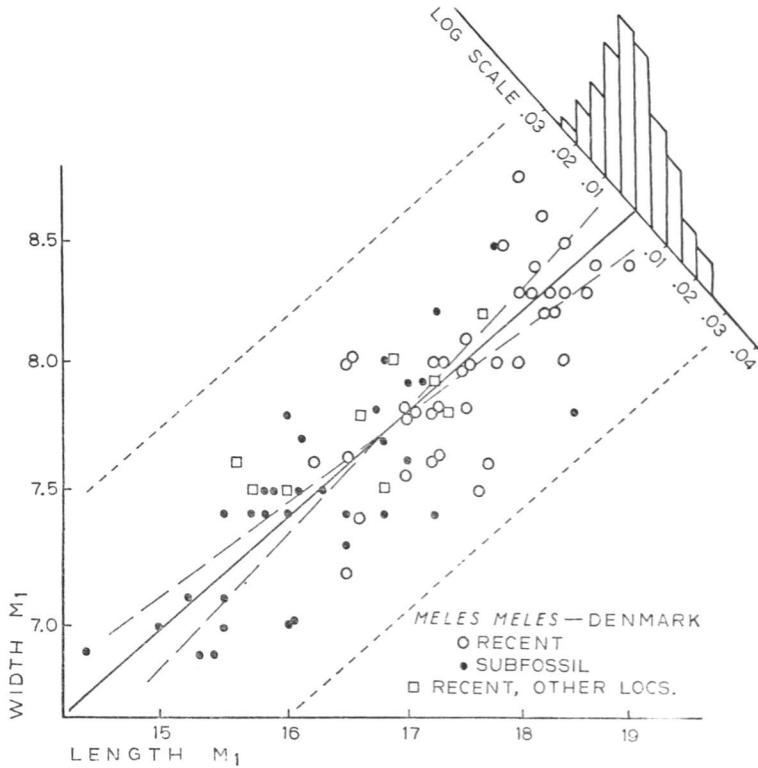
Fig. 1. Covariation of (talonid) width and length of M_1 in subfossil and recent badgers, as labelled; data from Degerbøl. Two least squares and one intermediate regression fitted to the data as described in the text. Histogram (top, right) shows distribution around intermediate regression; dashed lines indicate standard range of distribution.

Our primary task is now to formulate an accurate description of the relationship between length and width, expressing, in numerical terms, the genotypic correlation between the two variates.

Obviously the phenotypic correlation is not absolute: the variate pairs are not on a single curve. The correlation between the logarithms of the data is $r = .799$. We shall assume, as a working hypothesis, that the deviations are due to phenotypic modification only. We shall further assume that the genotypic correlation conforms to the principle of allometry. Hence the relationship may be expressed by a single curve with the equation

$$y = bx^k,$$

where y and x are the variates, b is the constant of integration, and k the constant of allometry. On a logarithmic grid this curve takes the form of a straight line.

If such a curve is to be fitted accurately, arithmetics must be employed; the scatter is too great to permit accurate fitting by eye. In such cases the method of least squares is commonly used. It gives two regression lines, the regression of y on x, and that of x on y (fig. 1); these will diverge, the more the lower the correlation. Either one of these regressions, however, is less likely to approximate to the actual genotypic regression than is an intermediate line. The genotypic regression being the subject of interest to us, we must therefore try to find a better approximation.

With absolute correlation the two least squares regressions coincide. This limit regression may, however, also be obtained by the simple formula

$$k = \frac{\sigma_{\log y}}{\sigma_{\log x}}$$

or, when convenient, any development of this formula, such as

$$k = \left[\frac{m^2_{\log y}}{m^2_{\log x}} \right]^{\frac{1}{2}}$$

where m^2 denotes the variance, or second moment around the mean. The resulting curve will be intermediate between the two least squares regressions when the correlation is not absolute; it is given as the main regression in fig. 1, where it evidently appears to approximate to the actual genotypic relationship better than the other curves. Hence this method — which has the additional merit of being much less laborious than the method of least squares — has been used throughout. Naturally caution is necessary in its use, since it will give a »regression» even where there is no correlation, and it does not discriminate between positive and negative slope. The results should always be checked by means of scatter diagrams, and, when necessary, by calculating the coefficient of correlation.

Returning now to the case represented in fig. 1, we may note that the width of the lower carnassial in *Meles meles* is negatively allometric to its length, but very slightly so ($k = .88$). On an average, larger teeth tend to be relatively more slender than smaller ones, but the difference is almost imperceptible for the present range of size, and is almost overshadowed by the deviations away from the regression.

These deviations were tentatively assumed to be due to modification only. The question may be further studied by investigating the pattern of deviation away from the line.

The frequency distribution of these deviations is summarized in the inserted histogram (fig. 1), which shows the distribution to conform excellently to the »normal» binomial type. This appears to support our assumption. If there had been two parallel and distinct regressions involved, our frequency distribution would have been bimodal; if the regressions had not been parallel, it would have been strongly platykurtic. Theoretically, the distribution may still result from intermediate polygenic inheritance comprising a number of distinct regressions close to each other, but there does not appear to be any necessity for this assumption, and it is made definitely improbable by other data.

It appears thus that we are justified in drawing the following inferences: 1) The subfossil and recent *Meles meles* exhibit the same allometry; 2) the deviations from the regression result from modification; and, hence, 3) there has been no genetic change, as regarding this character, in the *Meles meles* population from postglacial to recent time. The single genetic change to be deduced from the present data is that constituting size increase; this has caused the population to slide up the regression. There is more to be said about the allometry in this tooth, but this will be deferred to a later paragraph.

THE DETECTION OF MUTATION: SINGLE ABERRANTS

The detection of actual genetic changes in allometry is not always easy. As regarding single aberrant individuals in otherwise homogeneous populations, there is a possibility if the deviation is really great (in which case the difference is often, though by no means always, easily visible to the trained eye, even without biometric analysis). But judgment from morphological inspection only may be fallacious: aberrations may result also from strong allometry, if especially large or especially small variants happen to turn up. From the frequency distribution around the regression line we may be able to form a tentative judgment as to the significance of a deviation. SIMPSON (1941) considers the estimate of variation limits in a sample of 1,000 (which is = $M \pm 3.24\ \sigma$) to give reasonable security; this is called the standard range. In the present case, the standard deviation of the frequency distribution around the regression is $\sigma = .01015$, in terms of logarithms. The standard range would, then, be indicated by lines parallel to the regression and at a distance of .033 (logs) from it (fig. 1). Observations at a greater distance from the regression may be considered to indicate genetic change. Actually, this is valid only in the vicinity of the means for the two variates, x and y; the standard error of the regression coefficient is not taken into account. This may, however, be allowed for if the necessity arises; but in doubtful cases it is better to try and find other allometry relations and see how they behave.

POLYMORPHISM

The standard deviation of the present distribution, in logs, was $\sigma = .01015$. A number of such standard deviations have been studied in order to form an estimate of the average magnitude of the log deviation for genetically homogeneous populations. It was found that the values, for functional teeth, were fairly constant and varied between .010 and .015 (these data relate to mensuration in different planes, such as length and width; much higher correlations, i.e. lower sigmas, may be found in, for instance, the covariation of two length dimensions). For vestigial teeth, where the shape is less rigidly determined, the deviations were often much greater; this can hardly be due to genetic diversity in general, for it would be peculiar if all vestigial teeth were controlled by several allometry genes, when most functional ones, apparently, are not.[1]

In a few instances, however, functional teeth showed deviations greatly exceeding the usual values. Some instances are being published by me (1954) and will not here be discussed in detail. It was found that the homologous tooth, in other populations, exhibited »normal» scatter, and it was inferred that the great increase in variation resulted from the presence of different allometry alleles. In some instances the alleles could be tentatively homologized, respectively, with genes present in other populations. The best instances (KURTÉN, unpublished) were found in the first upper molar of recent and fossil bears, where two types of allometry are in evidence, in different proportions, in various populations.

INTERGROUP DIFFERENCE

Clear evidence of genetic change is found when the allometry is decidedly different in related populations. This appears to be a very common state of matter in closely related but distinct species. One instance is given in fig. 2; this is the covariation of paraconid height and crown length in the lower carnassial of small cats, after data from DEGERBØL (op.cit.).

In the wildcat (*Felis silvestris*, a series of subfossil specimens from Denmark) paraconid height is positively allometric to crown length (k = 1.39). The distribution around the regression line (inserted histogram) does not indicate heterogeneity; $\sigma = .015$. In the domestic cat (*Felis catus*), the allo-

---

[1] There is, however, a possibility. Changes in allometry may be brought about by pleiotropic genes that are selected for in conjunction with other qualities. Balanced polymorphism for some other quality may, thus, be reflected in polymorphism for allometry; the latter may not be of sufficient functional disadvantage, when appearing in a vestigial tooth, to bring about adverse selection, or to be eliminated by modifiers.
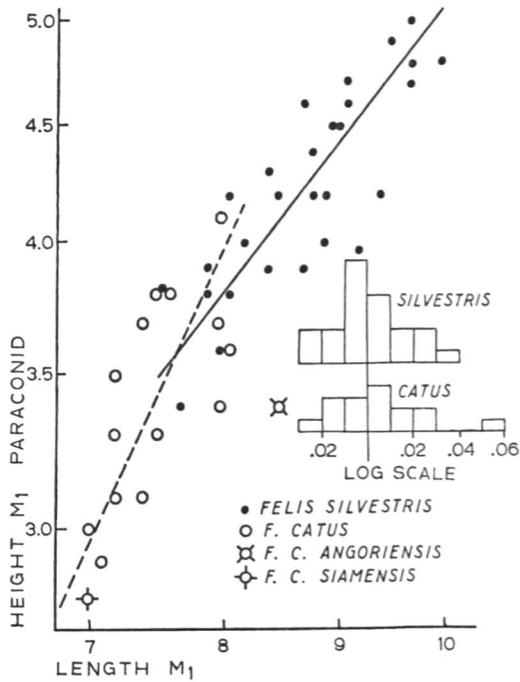
Fig. 2. Covariation of paraconid height and length of M_1 in subfossil *Felis silvestris* and recent *F. catus*, as labelled; data from Degerbøl. Inserted histograms show distributions around regression for each sample.

metry is also positive and much stronger (k = 2.17, one of the highest values I have found in mammalian dentitions). The Siamese appears to be on the same regression; *angoriensis* is probably not, and was left out in calculation. The distribution, then, has the parameter σ = .014. We may infer that the domestic cat and the European wildcat differ genetically in this respect; and that the wildcat population is »pure» for one allele and the domestic form for another, with the tentative exclusion of *angoriensis*.

OBSERVATIONS ON HYPSODONTY

In this case, as, for instance, with the bear M_2, to be discussed below, height is positively allometric to length, and therefore larger teeth tend to be more hypsodont. It is, perhaps, superfluous to add that this relation is not universal for mammalian tooth crowns; all sorts of allometry have been found, and the trends may be of bewildering variety in closely related species (KURTÉN 1954). It may, however, happen that there is a direct intrapopulation correlation between hypsodonty and gross

size. As this is contrary to earlier statements by SIMPSON (1944) and myself (1953), some further remarks are necessary. On the basis of studies on horse teeth, SIMPSON (op.cit. p. 7—8) stated: »Hypsodonty, the relationship between vertical and horizontal dimensions, is positively correlated with size and with most linear dimensions among successive populations, but shows no such correlations among individuals or among contemporaneous populations . . . The stated independence is an evident and, I believe, incontrovertible biological fact.» In 1953 I followed Simpson without entering on analysis of this special question. From the data in the previous paragraph (and also in the next paragraph; and from a number of unpublished data sampled by me) it is, however, clear, that the notion of independence as a general principle is erroneous.

This does not reflect on SIMPSON's main thesis, which is that genetic changes have occurred in horse history affecting the length-height relation of the cheek teeth. The manner in which these changes were realized was probably analogous to the instances illustrated in the present paper; as the raw data are not given, detailed allometry analysis is not possible.

ALLOMETRY AND SELECTION

What is the biological function of allometry, as opposed to isometry, in a tooth crown? As far as I can judge, almost none at all. Of course the greater hypsodonty of a large individual, when crown height is positively allometric, may be useful, under certain circumstances; but in that case the corresponding brachyodonty of a small variant would seem to be harmful[1]. I do not think that the allometric trend *per se* has any biological function (except, perhaps, a preadaptive one in exceptional instances); what is important is, I think, the *average relation* between two dimensions (say, length and width) that is conditioned by a certain regression and a certain average size. What is selected for appears to be a certain average proportion, regardless of the resulting shape and proportions of distal variants, except perhaps where these latter become biologically *untragbar* as a result of excessive growth gradients. The average proportion is realized by means of the available genetic material, and this, in turn, may be isometric or allometric.

This is especially clear in cases where related populations show differences in allometry. The necessity for a change in allometry with change in average size is easily appreciated if we imagine the allometry of one population projected into the gross size of the other. Thus, for instance, it is evident

---

[1] There is evidently more to be said on this topic. I have, however, but scant data for herbivores, and shall not enter into detail.

that the pattern of *Felis catus* (fig. 2) cannot persist unchanged with phyletic growth or phyletic dwarfing. In the former case, the trend would lead to an enormously hypsodont carnassial; in the latter case, the carnassial would grow very low. Both changes would apparently be inadaptive. Accordingly, the larger species, *Felis silvestris*, is on a different regression, and is much less hypsodont than it would have been with the allometry of *catus*.

    Fig. 3 shows another case, the covariation between protoconid height and crown length of M_2 in *Ursus spelaeus* (original data: the von Nordmann collection from Odessa, at the Geological Institute of Helsingfors University) and *U. arctos* (original data: recent Finnish population, collections at the Zoological and Anatomical Institutes of Helsingfors University). In both species there is a positive allometry of height on length; yet the average relation between the two dimensions is identical, as will appear from the mean indices:
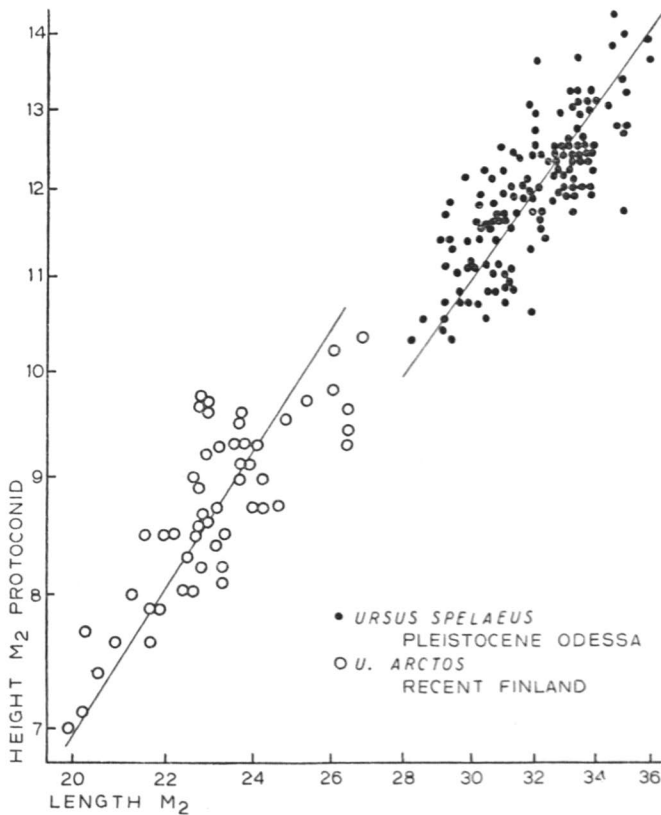

Fig. 3. Covariation of protoconid height and length of M_2 in *Ursus spelaeus* (Pleistocene, Odessa) and *U. arctos* (recent, Finland); original data.

| | Mean | | Index |
	Length	Height	100 height/length
U. arctos ...	23.2	8.3	37
U. spelaeus .	31.9	11.9	37

This relation is apparently optimal for the tooth crown in question, but its realization has necessitated a genetic change somewhere in the ancestry of either species, or both. The actual history of this change may be mapped in some detail and is essentially similar to that of M^1, where stability in average proportions is similarly brought about by the interplay of two different regressions (KURTÉN, unpubl'shed). Suffice it for the moment to note the important fact that *similarity*, in the present case, *has sprung from genetic change, where stability* (except for size) *would have produced dissimilarity*. And this, again, delivers a *coup de grace* to *all studies trying to evaluate relationships by means of indices or ratios* without previous analysis of allometry.

Instances such as this may be called micro-evolutionary examples of converge, in the almost literal sense of the word — convergence in ratios, that is, shape. Studies utilizing relative values — indices — will, in all such instances, give a completely misleading picture of what actually has happened, and of the true genetic affinity of populations; whereas the study of allometry means a new and important tool for the detailed mapping of microevolutionary events, and for the evaluation of actual genetic relationships of extinct forms where no experiments can be performed.

TEMPORAL SUBSPECIFIC DIFFERENTIATION

Let us finally consider a case in which a subspecific advance during a geologically short period has been detected by more orthodox methods. We return to the M_1 of *Meles meles*, the length-width relation of which was illustrated in fig. 1. DEGERBØL (op.cit.), when making a subspecific distinction between the oldest subfossil badgers and the recent Danish ones, pointed not only to the difference in size, but also to the difference in relative size between trigonid (the anterior shearing part) and talonid (the posterior crushing part). The trigonid is relatively smaller, and the talonid relatively larger, in the recent form, which is thence more specialized for the particular mode of life of this species. Does this difference result from simple allometry, or has there been a genetic change?

The answer appears to be perfectly clear and definite: there has been a genetic change, and the subspecific distinction is justified beyond dispute. Fig. 4 shows the covariation between trigonid length (measured internally, from anterior end to metaconid) and crown length. It shows two distinct
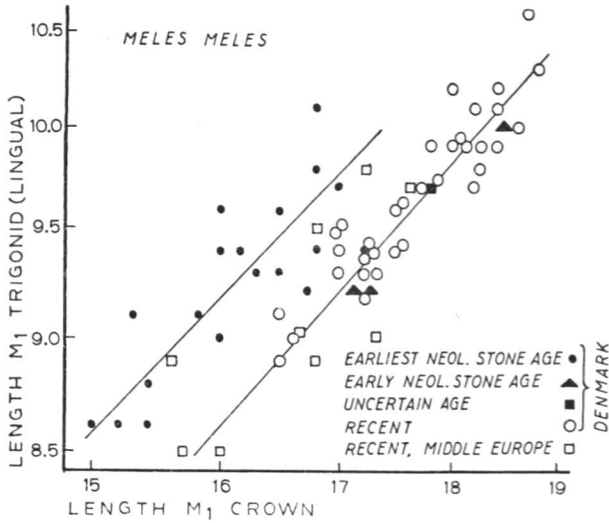
Fig. 4. Covariation of trigonid length (lingual, to metaconid) and crown length of M_1 in subfossil and recent badgers, as labelled; data from Degerbøl.

regressions, one for the oldest subfossil sample with persistently longer trigonid, and another for the others, with shorter trigonid[1]. In spite of the difficulties of accurate mensuration, pointed out by Degerbøl, the scatter is not very great. It may be noted that the actual change occurred between the periods labelled »earliest» and »early neolithic stone age», that is, the population was completely saturated by the new gene in a very short time, and has been stable since then. The recent Danish population has evidently lost the »long trigonid» gene completely, whereas it may persist in some Middle European populations. The rapidity of the change may have been made possible by the fact that the Zealand population evidently was isolated during the period in question (DEGERBØL, op.cit.) and thus would have permitted a relatively short *Anlaufzeit* of the new gene.

CONCLUSIONS

It has been shown that the study of allometry permits the actual mapping of microevolutionary events in geologic time. Thus we may, for good, reject the claim repeatedly stated by neozoologists (e.g. HUXLEY 1942), that data of a paleontological nature cannot give evidence on the mechanism of evolu-

---

[1] The difference appears also from other data published by DEGERBØL, though not in all possible combinations.

tion. Data of this sort shed light on selection and indicate the essentially »opportunistic» nature of evolution (SIMPSON 1949). They are throughout definitely in favour of Neodarwinism, and flatly incompatible with »orthogenetic», finalist, and Lamarckist theories of evolution. *No other interpretation than that of random mutation and selection is consonant with these data, which are essentially paleontological in nature.*

REFERENCES

DEGERBØL, M. 1933. Danmarks pattedyr i fortiden i sammenligning med recente former. I. Vid. Med. Dansk Naturh. For. 96, Festskr. II.

HUXLEY, J. S. 1932. Problems of relative growth. London.

—»— 1942. Evolution. The modern synthesis. London.

KURTÉN, B. 1953. On the variation and population dynamics of fossil and recent mammal populations. Acta Zool. Fennica, 76.

—»— 1954 The type collection of *Ictitherium robustum* (Gervais, ex Nordmann) and the radiation of the ictitheres. Acta Zool. Fennica 86.

SIMPSON, G. G. 1941. Range as a zoological character. Amer. Jour. Sci. 239.

—»— 1944. Tempo and mode in evolution. Columbia Biol. Ser. 15.

—»— 1949. The meaning of evolution. Yale Univ. Press, New Haven.

SINNOT, E. W. 1936. A developmental analysis of inherited shape differences in cucurbit fruits. Amer. Nat. 70.