RELATIVE GROWTH AND VERTEBRATE PHYLOGENY.

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ABSTRACT. A statistical analysis is made of the measurements of some Recent and Pleistocene feld skulls with particular reference to the relative growth method. The use of this method is demonstrated and its implications are discussed. Its application as a phylogenetic tool is tested on the Merycoidodontidae, a recently monographed family of Tertiary mammals. The chief use of this method is shown to be as a tool for making comparisons between parts which cannot be observed directly. Possible clues concerning causes of extinction in certain genetic lines are obtained by comparing the relative growth coefficients. The relative variation in species, genera, and a family are indicated by computed values for the Pearson coefficient of variation.

INTRODUCTION.

In attempting a taxonomic study of any group of fossil animals data are usually accumulated which are difficult to digest and correlate. This applies particularly to measurements. Several methods are used to aid in placing material in frequency groups, but these are only partially satisfactory. Any proper taxonomy should be founded upon an understanding of the evolution of the group being considered. A method of handling numerical data from the viewpoint of phylogenetic change should be of value if it can be demonstrated that it can be applied successfully.

The presentation adopted in the following discussion is to describe the method here discussed as a possibility and indicate its apparent implications. Its application has been checked on the type of vertebrate material most readily available for this kind of study, on Recent and Pleistocene mammal skulls. Its use as a phylogenetic tool has been applied to a group of recently monographed fossil mammals, and the conclusions presented by this method are compared with those reached on strictly morphological grounds.

The writer is grateful to Prof. O. C. Glaser of Amherst College for many helpful suggestions and criticisms, and to Prof. P. E. Raymond of Harvard University for a critical reading of the manuscript. Dr. G. G. Simpson of the American Museum of Natural History has been especially helpful in offering valuable suggestions, mainly through his recent book, "Quantitative Zoology" (1939).
THE RELATIVE GROWTH METHOD AND ITS IMPLICATIONS.

Studies in growth by Huxley (1932) and others have demonstrated that in the growth of certain forms the relative growth rate of some of the parts has a constant ratio to the relative growth rate of the rest of the body. This relationship can be expressed by the following simple formula:

\[ y = bx^k \]

in which \( y \) = the weight or linear measurement of the part, \( x \) = that for the rest of the organism, and \( b \) and \( k \) are constants. According to Huxley, (1932, p. 6) "the value of \( k \) implies that for the range over which the formula holds the ratio of the relative growth-rates of the body remain constant, the ratio itself being denoted by the value of \( k \). By relative growth-rate is meant the weight of growth per unit weight (or size), i.e., the actual absolute growth-rate at any instant divided by the actual size at that instant."

If measurements obtained from different size groups of the same species are averaged and plotted logarithmically the resulting curve is a straight line in many forms, at least between the beginning of sex maturity and senescence. The value of \( k \) (the slope of the line) is then constant in the species. Theoretically, in growth every part of the organism should have a constant differential growth-ratio to every other part.

This method probably can be applied to discovering relationships between members of a phylogenetic series provided specimens of varying sizes of each member are available. In analyzing such a series actual growth, as applied to the individual or the race, is not recorded, but the specimens are simply measured at some size in the adult stage. This simulates the studies made on single species by Huxley (1932) in which size stages in a considerable number of individuals are measured rather than following the growth stages in one individual. It is then a correlation between animals which differ in size.

Relative phylogenetic growth-ratios are expected to be constant if it is assumed that the ratios are based upon genetic factors. Some genetic basis appears to be the inescapable conclusion since it is the combination of the ratios between parts which gives an animal its form. The method here used is therefore a method of analyzing details (ordinarily difficult to observe and compare directly) of the correlation of parts in related animals. The more closely related phyletic stocks
should show closer agreement of some of their relative growth-ratios, etc.

It may be true that each taxonomic unit in a related group of units, for example, has its own constant differential growth-ratio for certain diagnostic ratios. A comparative study of the constants in related groups should give a clue to the manner in which they are related. This mechanism may also have an important bearing upon the problem of extinction. According to Huxley (1932, p. 16), “the existence of an organ with a high growth-ratio tends to limit the extreme size attainable by the type in question during evolution, for with very large absolute size, the relative size of the organ will tend to become so huge that it becomes unwieldy or even deleterious.”

In analyzing the data in the present paper the constants of $b$ and $k$ of the relative growth formula, and the position of the line in logarithmic plotting, have been obtained by the least squares method. The coefficients of correlation, $r$ and $z$, have been calculated better to indicate the intensity of the relationships, and therefore the degree to which the relative growth formula holds in certain cases. To check the degree of reliability of the computed values for $k$, the standard error of the regression coefficient also has been calculated according to the formula

$$\sigma_{b_{RX}} = \frac{\sigma_y}{\sigma_x} \sqrt{\frac{1-r^2}{N-2}}$$

($b_{RX}$ of the regression formula is equal to $k$ of the relative growth formula.)

The Pearson coefficient of variation, $V = \frac{100\sigma}{M}$, has been calculated to indicate the relative variability of the various groups discussed. The values of these constants and coefficients are listed in tables I to IV. These statistical techniques and some of their biological implications are adequately explained by Simpson and Roe (1939).

There is some doubt in the mind of the present writer as to the necessity of calculating the position of the line on the logarithmic plot, and the values of $k$ and $b$, by the least squares method. Originally, the positions of the lines and the values of the relative growth constants in all the present cases were obtained by inspection. A comparison of the values for $k$
obtained by inspection and those obtained by least squares calculation shows an average difference of no more than 10 percent.

Hersh (1934), in his analysis of the Titanotheria by this method found that the constant differential growth-ratio in the horn-core-length relationship is approximately 9.0, which indicates a tremendously accelerated growth-rate for this part of the skull. This clearly indicates a relative-growth mechanism as one important factor in causing extinction of the group. Hersh draws the following conclusions (1934, pp. 539-540):

“If we accept the viewpoint that evolution was preceded by the selection of mutations, then it may be said that the mutations which become incorporated into the genus with the passage of time, and which the paleontologist recognizes as species, are mutations for increase in size without changes in b and k. So these constants of the relative growth functions may be considered genetic constants descriptive of the various genera in regard to the characters under consideration. . . . Within the genus, b and k are constant. Genera are distinguished by differences in b and k.”

Robb (1935) has made a relative-growth analysis of muzzle length against total skull length in a phylogenetic series of the horse. He shows that the differential growth-ratio is approximately the same in the three groups, i.e., four-toed horses, three-toed horses, and one-toed horses. This demonstrates that the change in facial proportion in the evolution of the horse is a function of increase in size, and that the constant differential growth-ratio was not affected by mutation in equine evolution. Quoting Robb (pp. 45-46), “Within a narrow range of variability, all specimens of the same size exhibit the same facial index, irrespective of phylogenetic status.

“Although it is permissible to assume the occurrence, from time to time, of mutations affecting general body size, which may be in large measure responsible for differences of stature characterizing the several genera, there is yet no evidence for the belief that specific mutations governing differences of form (in animals of equal stature) have played any significant part in the facial evolution of the equine skull.”

The analysis of Smilodon californicus, Felis atrox, the jaguar, and the Merycoidodontidae made in the present paper suggests that Hersh’s conclusions hold for the forms here considered in respect to at least the constant k. In logarithmic
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plotting of presumably well-established genera and species it is observed by inspection that the points in many cases fall in a band with more or less parallel sides, as has been pointed out by Hersh (1934, p. 553). This would indicate that the constant $b$ in some of the cases here analyzed may be of no definite value in taxonomy. This conclusion is based upon the assumption that these species and genera established by ordinary morphological methods are valid. The width of the band in these regression plots must certainly indicate slightly different genetic lines, but their taxonomic importance is in most cases doubtful. The one important conclusion which this coincidence in plotting appears to indicate is that these taxonomic groups have no sharp delineation but show transitional phases in one or more directions. This is probably a normal expectation. The arrangement of the points in a band occurs in the excellent analysis by Brody (1937) of the ratio between the chest girth and weight of dairy cattle. In Sinnott's work on the relative growth of bottle gourds (1935) the points occur in a band, and also in Robb's analysis of the horse series (1935). This scatter in some cases may be due in part to faulty preservation of fossil material.

One of the difficulties inherent in fossil specimens is their generally faulty preservation. Since work of this kind is statistical in nature large numbers of good specimens are to be desired. Linear measurements must be used, and even these can be only approximations in many cases. Another difficulty is that association of parts as belonging to the same individual is rarely certain, and this is especially true of fossil vertebrate skeletons. It is only in the skull that any number of measurable parts with definite association can be obtained.

Studies in the relative growth of modern mammal skeletons, although comparatively rare, are known. Huxley (1932; 1927) has plotted the growth of the facial region relative to the cranial region in baboons and sheep. The same author has plotted tail length against total length in growth in the mouse Phenacomys. In all these cases Huxley finds a constant differential growth-ratio to hold. Donaldson (1897) noted that in frogs of different sizes tibia and foot exhibit a constant specific relationship to the entire length of the animal.

Green (1933) has shown that the relative growth formula applies to skull measurements of Mus bactrianus and Mus musculus, and that the relative growth coefficient "describes fairly
satisfactorily the increase in the several cranial dimensions in relation to skull length." Also, "The relatively more narrow interorbital region and lesser rostral height of \textit{Mus bactrianus} as contrasted with \textit{Mus musculus} seem to be specific characters and not functions of absolute size"; their relative growth coefficients are different.

The system here used differs from the majority of relative growth studies in one important respect. Most workers on living material have separated large numbers of specimens into size classes. Averages have been taken of the measurements and each average has been plotted. This procedure has a statistical advantage. The disadvantage is that it does not represent individual or small group eccentricities since these disappear in the averages taken. The individuals taken for analysis in this paper have been taken more or less at random, the only decisive factor being the quality of preservation as an aid to accurate measurement. In fossil material choice is in most cases quite limited.

\textbf{ANALYSIS OF THREE FELID SPECIES.}

Merriam and Stock (1932) have recorded some very complete measurements of the skeletal remains of some Pleistocene and Recent Felids. From that material data on the skulls of \textit{Smilodon californicus}, \textit{Felis atrox}, and some Recent jaguars, have been calculated and plotted by the present writer according to the relative growth formula, and the coefficients of correlation and variation have been obtained. The authors list measurements of 32 skulls of \textit{S. californicus} which range from 283 to 377 millimeters in maximum length. Of these six are young specimens with the permanent teeth not yet completely erupted. These are measurements of individuals taken from about 1600 specimens from Rancho la Brea. The skulls of \textit{F. atrox} vary in length from 310 to 467 millimeters, and all are adult specimens from the Rancho la Brea deposits. The measurement of 12 of the 18 skulls listed by Merriam and Stock are included in the calculations.

For direct comparison with a modern felid the measurements of 12 modern jaguar skulls are used. These are at least two different species (\textit{Felis onca} and \textit{F. hernandezii}) and were collected over a very large area (three specimens from Brazil, two specimens from Costa Rica, three specimens from Arizona, one from Tehuantepec, one from Venezuela, one from Mexico, and one from Guatemala). The choice of such an apparently
Fig. 1. Skull measurements of *Smilodon californicus* plotted logarithmically.
A. Length from anterior end of premaxillary to anterior end of posterior nasal opening/maximum skull length.
B. Posterior palatal width between inner roots of superior carnassials/maximum skull length.
All measurements in millimeters. The dotted lines are the calculated positions of the regression lines.

Fig. 2. Skull measurements of *Felis atrox* plotted logarithmically.
A. Anterior palatal width between superior canines/maximum skull length.
B. Length of palate from anterior end of premaxillary to a line tangent to the posterior surfaces of maxillary parapets/maximum skull length.
heterogeneous group of modern cats for analysis was made
because the data were available. Although they do not provide
an entirely satisfactory basis for comparison with the Rancho
la Brea material, the group is not as variable as expected.
This suggests interesting implications, discussed below.

A series of interesting observations can be made from the
logarithmic plots of this material. The points in plotting are
not grouped in a single straight line but are in the form of a
band, in most of the graphs, which has essentially parallel sides,
and some of which are approximately parallel to the regression
line obtained by the least squares formula. In most cases a
straight line can be drawn by inspection between and parallel
to the sides of the band about which a large percentage (in
many cases the majority) of the points are grouped. In other
cases the points are aligned in a series of parallel lines with
no line coinciding with a very large percentage of the points.
The essentially parallel arrangement of these lines indicates
that the differential growth-ratio is constant for the charac-
ter under examination, although their separation indicates
that there are differences in the value of b within any one char-
acter comparison.

The calculated values for the coefficients and constants of
these fields are listed in tables I to III. The various measure-
ments listed in these tables have been compared against the
length of the skull from the anterior end of the premaxillary
to the posterior end of the inion in all three groups. The coeffi-
cients of correlation (r and z) are uniformly high enough to
be significant, as shown by the standard error of z being .33 in
the jaguar and Felis atrox and .19 in Smilodon californicus.
This demonstrates a rather uniformly intense correlation be-
tween the measurements listed and the skull length (with one
exception). This gives a relative idea of the degree of scatter
of the points in plotting, and thus the fitness (in a sense) of
applying the relative growth formula to each comparison. It
must be remembered that the degree of correlation is affected
by imperfect preservation of fossil material and thus unavoid-
able errors of measurement. This, however, is not so important
a factor in these recent skulls and in the Rancho la Brea skulls
as in older Tertiary mammal skulls. A more direct check on
the validity of the constant k is obtained by the standard error
of k (σk). In all but two cases this error is small enough to
be ignored.
TABLE I.

Constants and Coefficients for the Jaguar.

\( x \) equals the length from the anterior end of the premaxillary to the posterior end of the inion.

<table>
<thead>
<tr>
<th>Character</th>
<th>( k )</th>
<th>( b )</th>
<th>( r )</th>
<th>( z )</th>
<th>( \sigma k )</th>
<th>( V )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length from anterior end of premaxillary to a line tangent to posterior surfaces of maxillary parapets</td>
<td>.8</td>
<td>1.09</td>
<td>.862</td>
<td>1.3</td>
<td>.044</td>
<td>8.56</td>
</tr>
<tr>
<td>Length from posterior end of glenoid cavity to posterior end of condyles</td>
<td>.723</td>
<td>1.13</td>
<td>.934</td>
<td>1.68</td>
<td>.021</td>
<td>8.73</td>
</tr>
<tr>
<td>Antero-posterior diameter of nasals</td>
<td>.82</td>
<td>.634</td>
<td>.913</td>
<td>1.55</td>
<td>.027</td>
<td>9.93</td>
</tr>
<tr>
<td>Width of anterior nares</td>
<td>.8</td>
<td>.449</td>
<td>.941</td>
<td>1.75</td>
<td>.013</td>
<td>9.32</td>
</tr>
<tr>
<td>Greatest width across muzzle at canines</td>
<td>.85</td>
<td>.634</td>
<td>.956</td>
<td>1.90</td>
<td>.073</td>
<td>10.0</td>
</tr>
<tr>
<td>Least width between superior borders of orbits</td>
<td>.84</td>
<td>.443</td>
<td>.903</td>
<td>1.49</td>
<td>.018</td>
<td>10.4</td>
</tr>
<tr>
<td>Width across postorbital process</td>
<td>.96</td>
<td>.360</td>
<td>.88</td>
<td>1.38</td>
<td>.045</td>
<td>11.7</td>
</tr>
<tr>
<td>Least width of postorbital constriction</td>
<td>.423</td>
<td>4.42</td>
<td>.801</td>
<td>1.08</td>
<td>.019</td>
<td>6.07</td>
</tr>
<tr>
<td>Greatest width across zygomatic arches</td>
<td>.87</td>
<td>1.40</td>
<td>.974</td>
<td>2.17</td>
<td>.042</td>
<td>9.67</td>
</tr>
<tr>
<td>Anterior palatal width between superior canines</td>
<td>.966</td>
<td>.167</td>
<td>.924</td>
<td>1.61</td>
<td>.017</td>
<td>11.3</td>
</tr>
<tr>
<td>Posterior palatal width between inner roots of superior carnassials</td>
<td>.674</td>
<td>1.36</td>
<td>.914</td>
<td>1.55</td>
<td>.021</td>
<td>8.21</td>
</tr>
<tr>
<td>Greatest transverse diameter across auditory bulla</td>
<td>.7</td>
<td>.532</td>
<td>.936</td>
<td>1.7</td>
<td>.009</td>
<td>8.56</td>
</tr>
<tr>
<td>Greatest width across mastoid process</td>
<td>.85</td>
<td>.964</td>
<td>.752</td>
<td>.97</td>
<td>.112</td>
<td>15.6</td>
</tr>
<tr>
<td>Greatest diameter across condyles</td>
<td>.314</td>
<td>8.26</td>
<td>.851</td>
<td>1.26</td>
<td>.014</td>
<td>5.15</td>
</tr>
</tbody>
</table>

TABLE II.

Constants and Coefficients for *Smilodon californicus*.

\( x \) equals the length from the anterior end of the premaxillary to the posterior end of the inion.

<table>
<thead>
<tr>
<th>Character</th>
<th>( k )</th>
<th>( b )</th>
<th>( r )</th>
<th>( z )</th>
<th>( \sigma k )</th>
<th>( V )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of palate from anterior end of premaxillary to posterior surfaces of maxillary parapets</td>
<td>.846</td>
<td>1.02</td>
<td>.90</td>
<td>1.47</td>
<td>.033</td>
<td>7.7</td>
</tr>
<tr>
<td>Length from posterior end of glenoid cavity to posterior end of condyles</td>
<td>1.38</td>
<td>.032</td>
<td>.896</td>
<td>1.45</td>
<td>.038</td>
<td>12.9</td>
</tr>
<tr>
<td>Width of anterior nares</td>
<td>.604</td>
<td>1.63</td>
<td>.74</td>
<td>.95</td>
<td>.018</td>
<td>7.15</td>
</tr>
<tr>
<td>Greatest width across muzzle at canines</td>
<td>.726</td>
<td>1.56</td>
<td>.90</td>
<td>1.47</td>
<td>.02</td>
<td>6.42</td>
</tr>
<tr>
<td>Least width between superior borders of orbits</td>
<td>.672</td>
<td>1.88</td>
<td>.82</td>
<td>1.16</td>
<td>.028</td>
<td>7.54</td>
</tr>
<tr>
<td>Least width of postorbital constriction</td>
<td>.55</td>
<td>2.48</td>
<td>.463</td>
<td>.50</td>
<td>.026</td>
<td>7.29</td>
</tr>
<tr>
<td>Greatest width across zygomatic arches</td>
<td>1.02</td>
<td>.552</td>
<td>.917</td>
<td>1.57</td>
<td>.048</td>
<td>8.39</td>
</tr>
<tr>
<td>Anterior palatal width between superior canines</td>
<td>1.07</td>
<td>.112</td>
<td>.86</td>
<td>1.29</td>
<td>.017</td>
<td>9.0</td>
</tr>
</tbody>
</table>
(Table II cont’d)

<table>
<thead>
<tr>
<th>y character</th>
<th>k</th>
<th>b</th>
<th>r</th>
<th>z</th>
<th>(\sigma k)</th>
<th>V</th>
</tr>
</thead>
<tbody>
<tr>
<td>Posterior palatal width between inner roots of superior carnassials .......</td>
<td>.824</td>
<td>.849</td>
<td>.836</td>
<td>1.22</td>
<td>.029</td>
<td>7.65</td>
</tr>
<tr>
<td>Width across palate between posterior alveoli of superior carnassials ....</td>
<td>.658</td>
<td>2.77</td>
<td>.748</td>
<td>.96</td>
<td>.037</td>
<td>6.35</td>
</tr>
<tr>
<td>Greatest transverse diameter across auditory bulla ..........................</td>
<td>1.17</td>
<td>.596</td>
<td>.885</td>
<td>1.4</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Greatest transverse diameter across condyles ..................................</td>
<td>.524</td>
<td>3.09</td>
<td>.83</td>
<td>1.2</td>
<td>.014</td>
<td>5.73</td>
</tr>
<tr>
<td>Height of anterior zygomatic pedicle ........................................</td>
<td>1.13</td>
<td>.871</td>
<td>.707</td>
<td>.88</td>
<td>.028</td>
<td>10.4</td>
</tr>
<tr>
<td>Length of anterior zygomatic pedicle .........................................</td>
<td>.59</td>
<td>1.06</td>
<td>.754</td>
<td>.97</td>
<td>.017</td>
<td>6.39</td>
</tr>
</tbody>
</table>

Table III.

Constants and Coefficients for *Felis atrox*.

x equals length from anterior end of premaxillary to the posterior end of the inion.

<table>
<thead>
<tr>
<th>y character</th>
<th>k</th>
<th>b</th>
<th>r</th>
<th>z</th>
<th>(\sigma k)</th>
<th>V</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of palate from anterior end of premaxillary to posterior surface of maxillary paraepats ..................</td>
<td>.52</td>
<td>6.34</td>
<td>.885</td>
<td>1.4</td>
<td>.038</td>
<td>7.98</td>
</tr>
<tr>
<td>Length from posterior end of glenoid cavity to posterior end of condyles.</td>
<td>.767</td>
<td>.991</td>
<td>.942</td>
<td>1.75</td>
<td>.024</td>
<td>10.1</td>
</tr>
<tr>
<td>Width of anterior nares .......................................................</td>
<td>.807</td>
<td>.497</td>
<td>.903</td>
<td>1.49</td>
<td>.019</td>
<td>9.59</td>
</tr>
<tr>
<td>Greatest width across muzzle at canines ....................................</td>
<td>.791</td>
<td>1.03</td>
<td>.872</td>
<td>1.34</td>
<td>.059</td>
<td>13.07</td>
</tr>
<tr>
<td>Least width of postorbital constriction ...................................</td>
<td>.564</td>
<td>2.67</td>
<td>.894</td>
<td>1.44</td>
<td>.016</td>
<td>6.41</td>
</tr>
<tr>
<td>Anterior palatal width between superior canines ............................</td>
<td>.624</td>
<td>1.45</td>
<td>.964</td>
<td>2.0</td>
<td>.012</td>
<td>9.98</td>
</tr>
<tr>
<td>Posterior palatal width between inner roots of superior carnassials ....</td>
<td>.79</td>
<td>.807</td>
<td>.91</td>
<td>1.53</td>
<td>...</td>
<td>13.9</td>
</tr>
<tr>
<td>Width across palate between posterior alveoli of superior carnassials ....</td>
<td>.49</td>
<td>6.93</td>
<td>.854</td>
<td>1.27</td>
<td>.036</td>
<td>7.51</td>
</tr>
<tr>
<td>Greatest transverse diameter across auditory bulla .........................</td>
<td>.932</td>
<td>1.02</td>
<td>.881</td>
<td>1.38</td>
<td>.014</td>
<td>15.4</td>
</tr>
<tr>
<td>Greatest width across mastoid process .......................................</td>
<td>.70</td>
<td>2.21</td>
<td>.921</td>
<td>1.59</td>
<td>.046</td>
<td>10.9</td>
</tr>
<tr>
<td>Greatest diameter across condyles .............................................</td>
<td>.702</td>
<td>1.05</td>
<td>.913</td>
<td>1.54</td>
<td>.018</td>
<td>8.86</td>
</tr>
<tr>
<td>Height of anterior zygomatic pedicle .......................................</td>
<td>.57</td>
<td>2.43</td>
<td>.916</td>
<td>1.56</td>
<td>.024</td>
<td>11.1</td>
</tr>
<tr>
<td>Length of anterior zygomatic pedicle .......................................</td>
<td>.835</td>
<td>.305</td>
<td>.895</td>
<td>1.45</td>
<td>.017</td>
<td>11.9</td>
</tr>
<tr>
<td>Length from anterior end of canine alveolus to posterior end of P4 .......</td>
<td>.437</td>
<td>6.97</td>
<td>.763</td>
<td>.98</td>
<td>.042</td>
<td>7.64</td>
</tr>
<tr>
<td>Length from anterior end of alveolus for P2 to posterior end of alveolus for P4 ..................................</td>
<td>.58</td>
<td>2.53</td>
<td>.905</td>
<td>1.5</td>
<td>.017</td>
<td>6.87</td>
</tr>
<tr>
<td>P4 anteroposterior diameter ..................................................</td>
<td>.436</td>
<td>2.96</td>
<td>.955</td>
<td>1.89</td>
<td>.001</td>
<td>5.4</td>
</tr>
</tbody>
</table>

The values of b obtained by calculation probably represent an approximate mean of a series of true values in many cases, because of the occurrence of the plots in a band in many plots.

The question naturally arises concerning the relative homogeneity of the three groups. This can be measured by the
Relative Growth and Vertebrate Phylogeny.

Coefficient of variation, $V$. The means for all the coefficients of variation obtained in each of the three groups are as follows:

- Jaguar 8.82
- Smilodon californicus 8.04
- Felis atrox 9.51

To obtain a more accurate comparison of variation the mean of the values of $V$ in the same measurements only have been obtained. There are eight measurements which are the same in all three feline groups, and the means of $V$ for these are as follows:

- Jaguar 8.21
- Smilodon californicus 7.99
- Felis atrox 9.55

The results of the two means check closely, particularly in the two fossil species. Their close agreement with the mean of $V$ in the jaguar, a group composed of two species and from widely separated localities, indicates that the fossil species are not so closely delineated as the modern ones. This is usually the case, especially where characters of parts other than the skeleton are used in diagnosis of modern forms. The variation in *Felis atrox* is appreciably more than in *Smilodon californicus*. A possible explanation of this may be that the specimens of *F. atrox* represent deposition over a longer period of time and thus have more accumulated variations.

A direct comparison of the values for $k$ in the three groups shows significant differences in most of the comparisons. A detailed analysis of these is beyond the scope of the present paper. It is proposed at a later date to analyze the growth gradients in the two Rancho La Brea species.

**Evolution of the Merycoidodontidae.**

In the following section various measurements of the skulls and rami of the Merycoidodontidae listed by Thorpe (1937) are analyzed by the relative growth method. These represent specimens of various species and they are analyzed according to genera. Only such measurements have been used as those about which there is no published doubt concerning their validity. These are 54 of the 114 described species, or about half of the family. The present writer has assumed that the species are valid ones and that the measurements are correct.

The main purpose of applying this technique to an already monographed family of extinct vertebrates is to determine
whether any independent conclusions can be made concerning the relationships and evolution within the family. These conclusions can then be compared with those reached on the basis of morphology and thus a good test of the phylogenetic application of this method of analysis is obtained. It is to be regretted that the measurements of more individual specimens are not available. All measurements are in millimeters.

The differential growth-ratios in the family as a whole have been determined by the least squares method for seven character comparisons. It has been possible to use the least squares method for determining the constants for two genera within the family, *Eporateodon* and *Promerychochoerus*. In the other genera the number of points (5 or less) is insufficient to
use this method and the positions of the lines have been determined by inspection fitting. The values for \( k \) in the latter cases have been taken as the tangent of the angle of the regression line with the horizontal. The values for \( k \) for these genera must therefore be taken as the best approximations which could be made with the data available to the writer. The results below are intended to be more suggestive than final. It is the hope of the writer that the data can be supplemented with additional measurements on large numbers of specimens at some future date.

In the following section three of the eight character comparisons made are illustrated in logarithmic plots and their apparent phylogenetic significance discussed. In addition table IV gives constants and coefficients obtained by calculation.

**MAXIMUM LENGTH OF RAMUS/MAXIMUM SKULL LENGTH.**

*Fig. 4.*

A considerable number of merycoidodont skulls have the ramus in place, being held in that position by the matrix. The following analysis is based upon the assumption that Thorpe's measurements have been taken from such specimens, or that the association of the two parts in each individual has been verified by other methods.

This plot shows the closest correlation of any of those attempted by the writer. Most of the points occur in a relatively narrow band; the differential growth-ratio in the family is \( .92 \pm .19 \). This indicates that the growth functions within the family as a whole are fairly well organized in respect to this relationship. The jaw should lengthen at the same rate as the relative increase in skull length to provide proper tooth occlusion if the dental series remains complete, and the demonstration of this is normally expected.

Within the individual genera the occurrence of the points in a straight line is remarkable in most cases. Certain relationships between genera are clearly shown by the comparative values of the differential growth-ratios, and probably also to a lesser extent by the size group occurrence. The relationships suggested by them agree very closely with the phylogeny presented by Thorpe on the basis of comparative morphology and geologic sequence (see Fig. 3). The central stock of Thorpe's phylogeny, called the "**Ticholeptus-Metoreodon** phylum" by
that author, and containing also the genera *Merycoidodon* and *Eporeodon*, is shown to be closely interrelated by having constants essentially equal. The relative increase in absolute size in progressively younger species, geologically, is noticeable in this group. In regard to *Protoreodon*, the earliest genus of the family (Upper Eocene), Thorpe concluded that "The

![Graph](image)

Fig. 4. Logarithmic plotting of maximum length of ramus against maximum skull length in the Merycoidodontidae.

The numbers on all the plots of the Merycoidodontidae indicate the genera as follows:
1. *Protoreodon*.
2. *Merycoidodon*.
3. *Eporeodon*.
4. *Ticholeptus*.
5. *Promerycochoerus*.
7. *Promotherium*.
8. *Merycoidodon*.
9. *Cyclopidius*.
10. *Merychys*.

molars possess a protoconule and the feet are longer than we should expect them to be, if this genus is the direct ancestor of the Oligocene forms. As a consequence I believe that it stands a little to one side of the unknown stem stock." (1937, p. 25.) This conclusion by Thorpe is clearly brought out by the relative growth graph, and such a phylogenetic position for this genus holds in the ratio of other characters in the family. Thus the same result is reached in the analysis of a
Relative Growth and Vertebrate Phylogeny.

relationship not usually considered as that reached from a purely morphological point of view. The close relationship of Protoreodon with the Ticholeptus-Metoreodon phylum is attested by the agreement of the differential growth-ratios.

The divergence of the Merychys stock from the central stem, already surmised on other grounds by Thorpe, is seen in the divergence of the value of \( k \) (0.75) as compared with that for the Ticholeptus-Metoreodon stock. Thorpe states that in his opinion Merychys is derived from "some form, perhaps like Merycoidodon gracilis." It is interesting in this connection to note the close association of the two genera in plotting. If Merychys were derived directly from M. gracilis, however, a considerable mutation for increase in size would have been necessary: M. gracilis can be identified on the graphs as the smallest species in the genus.

The differential growth-ratio for Promerycochoerus suggests that it is closely related to the Eporeodon-Metoreodon line, but a distinct divergence is recorded in other comparisons. This may indicate that the genus represents a transition phase to Merycochoerus, as suggested by Thorpe's phylogenetic chart. Merycochoerus differs sharply from either Promerycochoerus or the central line in possessing a differential growth-ratio of 0.33. This indicates that the relative growth increase of the ramus was much slower than that of skull length, and may suggest a possible reason for extinction of Merycochoerus. Any mutation which brought about increase in size would have tended to decrease the efficiency of dental occlusion because of this obvious disharmony in the development of two important length features. Such an arrangement might have become deleterious in making the individuals less able to compete for food during time of shortage due to drought, plant disease, or over-population of feeding areas. It certainly limits the maximum skull size attainable. The low growth ratio holds also for three other characters which were analyzed in Merycochoerus. It appears from this that the real genetic difficulty in this genus was a disproportionately large increase in length of the skull causing the form of the head, vital for survival mainly in feeding, to develop in a manner not suited to its mechanical requirements.

Pronomotherium, on the other hand, has a differential growth-ratio for this comparison of 4.0. This indicates a genetic constitution in which the maximum skull length did not
grow at a sufficient relative rate to develop a head compatible with the developmental tendencies present in the ramus.

The facts just cited suggest that in the geological history of certain groups the mutations affecting the relative growth rate accumulate in such a way that certain of them are in ratios which become mutually incompatible at some stage in size increase. When a certain size limit is reached they react to produce disorganization in the sense that the group becomes less fitted for important mechanical functions. In some cases this might cause a limitation of the maximum size attainable, even though the germinal organization for extreme size be present. A race may develop in this manner to the point of structural inefficiency and natural selection then brings about its extinction. Such a genetic association may suggest that most mutations are essentially accidental and therefore tend to accumulate in as many phylogenetically lethal as advantageous ratios.

**LENGTH OF SUPERIOR DENTITION WITH CANINE/MAXIMUM SKULL LENGTH.**

**Fig. 5.**

The size measurements of the dentition may not be important in themselves. But complication in tooth pattern may in some cases develop synchronously with increased relative anterior-posterior length, and in the increase of the relative length of the skull the rate of increase in length of the dental series is of considerable importance. The average differential growth-ratio for this character for the family is 1.07, and for the central stem about the same.

The ratio for *Merychys* (3.66) indicates a tendency for the growth of the upper tooth series to be much greater than the relative increase in skull length; serious crowding of the teeth might be expected, at least in some of the later species. On this point it may be noted that Thorpe says in his description of this genus, . . . "lower premolars less crowded in earlier than in later species . . . molars increasing very gradually in length in earlier forms and more rapidly in later ones." A relatively large ratio for this genus is seen also in the length of the superior molar series/maximum skull length; in this case the constant is 1.5, whereas, the constant for the family is only .96. Thus a possible extinction factor for this genus is sug-
gested by the lack of correlation in relative growth in length between the skull and dental series. Such a mechanism of growth could conceivably lead to serious dental inefficiency when skull length reached a certain point.

It is interesting to observe that *Cyclopidius* has a ratio of 1.0 for this comparison and also for the length of superior molars/maximum skull length. In this respect it adheres closely to the trend of the main stem of the family. The con-

![Graph](https://via.placeholder.com/150)

**Fig. 5.** Logarithmic plotting of length of superior dentition with Canine against maximum skull length in the Merycoidodontidae.

stant of *Ticholeptus* of 0.6 varies considerably from those of *Merycoidodon* and *Eaporeodon*. The significance of this is not certain, unless the following statement by Thorpe is the explanation: “It seems as if there were too many species in this genus, especially as a majority of them were collected in Montana. . . . This genus was derived from *Eaporeodon*, or at least, from some branch of the stem stock of that genus.” (1937, pp. 186-187; Thorpe’s italics.)

*Promerycacochoerus* has a relative growth constant of .925 and essentially the same as seen in the ratio of length of ramus compared to maximum skull length, further indicating the
close relationship of this genus to the central stem and therefore transitional to *Merycochoerus*.

**LENGTH SUPERIOR MOLAR SERIES/MAXIMUM SKULL LENGTH.**

Fig. 6.

The band enclosing the points obtained in plotting this ratio is somewhat wider than in the plot of the superior dentition, but the relationships between the genera shown by the constants are essentially similar. The growth ratio for the family is near unity (.96). The crowding of the teeth in *Merychius*, mentioned above, appears to be mostly in the premolars and not so much in the molar series, since the constant for the molars is only 1.5 and for the whole tooth series is 3.66.

**VARIATION.**

It has not been possible to make a complete study of the variation within and between the groups here considered. The coefficient of variation has been calculated, however, where a sufficient number of cases is available to make it worthwhile. Three different taxonomic groups are represented; coefficients
Relative Growth and Vertebrate Phylogeny.

Table IV.

Constants and Coefficients for the Merycoidodontidae.

<table>
<thead>
<tr>
<th>x equals maximum length of skull.</th>
<th>y measurement</th>
<th>k</th>
<th>b</th>
<th>r</th>
<th>z</th>
<th>σk</th>
<th>V</th>
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<tbody>
<tr>
<td>Bizygomatic diameter</td>
<td></td>
<td>.97</td>
<td>.752</td>
<td>.81</td>
<td>1.13</td>
<td>.071</td>
<td>31.6</td>
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<tr>
<td>Postorbital constriction diameter</td>
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<td>.877</td>
<td>.385</td>
<td>.87</td>
<td>1.33</td>
<td>.015</td>
<td>33.5</td>
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<tr>
<td>Anteroposterior diameter of orbits</td>
<td></td>
<td>.873</td>
<td>.471</td>
<td>.91</td>
<td>1.5</td>
<td>.006</td>
<td>23.7</td>
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<tr>
<td>Braincase diameter</td>
<td></td>
<td>.758</td>
<td>1.05</td>
<td>.70</td>
<td>.87</td>
<td>.032</td>
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<td>1.13</td>
<td>.989</td>
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<td>.019</td>
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<tr>
<td>Superior dentition with canine</td>
<td></td>
<td>1.07</td>
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<td>1.8</td>
<td>.028</td>
<td>37.8</td>
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<td>Superior molar series</td>
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<td>.96</td>
<td>.3</td>
<td>.863</td>
<td>1.31</td>
<td>.022</td>
<td>39.4</td>
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Constants and Coefficients for Eporeodon.

<table>
<thead>
<tr>
<th>x equals maximum length of skull.</th>
<th>y measurement</th>
<th>k</th>
<th>b</th>
<th>r</th>
<th>z</th>
<th>σk</th>
<th>V</th>
</tr>
</thead>
<tbody>
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<td></td>
<td>.87</td>
<td>1.46</td>
<td>.537</td>
<td>.6</td>
<td>...</td>
<td>9.03</td>
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<tr>
<td>Postorbital constriction diameter</td>
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<td>.76</td>
<td>.571</td>
<td>.62</td>
<td>.73</td>
<td>.061</td>
<td>15.1</td>
</tr>
<tr>
<td>Anteroposterior diameter of orbits</td>
<td></td>
<td>.574</td>
<td>9.95</td>
<td>.396</td>
<td>.41</td>
<td>.028</td>
<td>8.64</td>
</tr>
<tr>
<td>Braincase diameter</td>
<td></td>
<td>.69</td>
<td>1.43</td>
<td>.927</td>
<td>1.62</td>
<td>.028</td>
<td>8.64</td>
</tr>
<tr>
<td>Maximum length of ramus</td>
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<td>.911</td>
<td>1.25</td>
<td>.80</td>
<td>1.1</td>
<td>.016</td>
<td>11.2</td>
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<tr>
<td>Superior dentition with canine</td>
<td></td>
<td>.826</td>
<td>1.20</td>
<td>.928</td>
<td>1.64</td>
<td>...</td>
<td>13.1</td>
</tr>
<tr>
<td>Superior molar series</td>
<td></td>
<td>.71</td>
<td>1.05</td>
<td>.794</td>
<td>1.05</td>
<td>...</td>
<td>13.1</td>
</tr>
</tbody>
</table>

Constants and Coefficients for Promerychoerus.

<table>
<thead>
<tr>
<th>x equals maximum length of skull.</th>
<th>y measurement</th>
<th>k</th>
<th>b</th>
<th>r</th>
<th>z</th>
<th>σk</th>
<th>V</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bizygomatic diameter</td>
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<td>.628</td>
<td>...</td>
<td>...</td>
<td>...</td>
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<tr>
<td>Postorbital constriction diameter</td>
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<td>1.52</td>
<td>.082</td>
<td>.45</td>
<td>.48</td>
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<td>15.1</td>
</tr>
<tr>
<td>Anteroposterior diameter of orbits</td>
<td></td>
<td>.98</td>
<td>1.21</td>
<td>.783</td>
<td>1.05</td>
<td>.028</td>
<td>8.64</td>
</tr>
<tr>
<td>Braincase diameter</td>
<td></td>
<td>.908</td>
<td>.395</td>
<td>.3</td>
<td>.31</td>
<td>...</td>
<td>10.3</td>
</tr>
<tr>
<td>Maximum length of ramus</td>
<td></td>
<td>.89</td>
<td>1.47</td>
<td>.976</td>
<td>2.2</td>
<td>.016</td>
<td>11.2</td>
</tr>
<tr>
<td>Superior dentition with canine</td>
<td></td>
<td>.925</td>
<td>.785</td>
<td>.97</td>
<td>2.09</td>
<td>...</td>
<td>13.1</td>
</tr>
<tr>
<td>Superior molar series</td>
<td></td>
<td>.89</td>
<td>.444</td>
<td>.868</td>
<td>1.32</td>
<td>...</td>
<td>13.0</td>
</tr>
</tbody>
</table>

Of variation are shown in fossil species of felids, and are listed and discussed above, within fossil genera in Eporeodon and Promerychoerus, and in the family Merycoidodontidae. All these are based upon length measurements of comparable parts of the skull. It seems worthwhile to list the means of V for comparison, and they are as follows:

- Smilodon Californicus 8.04
- Felis atrox 9.51
- Eporeodon 11.47
- Promerychoerus 13.63
- Merycoidodontidae 32.20

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Fred B. Phleger, Jr.

The different degrees of variability, measured in this manner, are quite striking.

CONCLUSIONS.

1. Logarithmic plotting and calculation of measurements of the skulls of Felis atrox, Smilodon californicus, and the Recent jaguar demonstrates the application of the relative growth formula to this type of material. Analysis of the measurements of the Merycoidodontidae demonstrates that different genera have different values for the constant k in the relative growth ratio of many characters. Phylogenetic relationships suggested by this method agree closely with conclusions reached by Thorpe on morphological grounds.

2. A constant differential growth-ratio of approximately unity appears to indicate that phyletic increase in size of a part in the Merycoidodontidae proceeded on a harmonious genetic basis. A ratio considerably more or less than unity is thought to produce an eventual disharmonious result, given sufficient increase in absolute size, and a point may be reached in the evolution of the group at which the correlation of parts becomes so discordant that extinction results.

3. This method is primarily of value in suggesting or verifying phylogenetic relationships by use of characters not otherwise easily compared. Small differences in the values of k are likely to be of no significance due to faulty preservation of specimens and insufficient reliable data.

REFERENCES.


Amherst College,
Amherst, Mass.