ANALYSIS OF MERYCOIDODON SKULLS.

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ABSTRACT. Statistical analyses have been made of 12 linear measurements taken from 155 specimens of *Merycoidodon* skulls. Studies of relative and absolute variation indicate that the species are relatively homogeneous assemblages. Relative growth and variation analyses suggest that the major differences in skull form between species are functions of size. Evolution within the genus may have occurred mainly by mutations for increase in size and secondarily by mutations of relative growth rates.

INTRODUCTION.

RECENTLY a few workers have made an effort to analyze fossil vertebrate material by quantitative methods. A summary of the methods which can be used and some of the probable implications of the results are discussed by Simpson and Roe (1939). In a recent paper by Phleger (1940), the application of various statistical methods to fossil material was tested, and a portion of this analysis was devoted to an examination of the various genera of the Merycoidodontidae. The present paper is an extension of these methods to the species of the genus *Merycoidodon*. The main purposes of the present study are as follows: (1) to analyze the degree and direction of variation in a fairly homogeneous group of fossil mammals (i. e. the species of one genus), (2) to apply these results in determining what constitutes a valid fossil species in this type of material, and (3) further to apply the results in understanding some of the details of evolution within the genus, if this is possible. It is hoped that a more exact delimitation of the species in question can be formulated and that this type of analysis might be usefully applied to other groups of fossil mammals.

Fossil specimens of *Merycoidodon* are particularly useful for a statistical study of this kind because of their relative abundance. The most recent morphological opinion as set forth in Thorpe's monograph (1937) on the family Merycoidodontidae assigns six species to the genus *Merycoidodon*. Two species, *Merycoidodon platycephalus* and *M. macrorhinus* are known only from their type specimens and are not used in the present analysis. The other four species, *M. culbertsonii*, *M. periculorum*, *M. affinis*, and *M. gracilis*, are among the most

abundant mammalian fossils of the middle Oligocene. There is little doubt that the four species studied are valid ones, but their exact delimitation by ordinary methods in many cases is rather difficult.

For their kind coöperation in making available the collections of their respective institutions the writers are deeply indebted to the following: Dr. G. E. Lewis of the Peabody Museum of Yale University, Dr. G. G. Simpson of the American Museum of Natural History, Drs. A. S. Romer and T. White of the Museum of Comparative Zoölogy of Harvard University, and Dr. E. C. Olson of the University of Chicago.

METHOD OF STUDY.

The material studied was selected from approximately five hundred *Merycoidodon* skulls at present in several collections at various museums. Of this total number of specimens examined one hundred and fifty-five specimens were sufficiently well preserved to be suitable for measurements and these specimens are grouped as follows: eighty-five specimens of *M. culbertsonii*; thirty-three specimens of *M. gracilis*; twenty-four specimens of *M. affinis*; twelve specimens of *M. periculorum*; and one specimen of *M. platycephalus.*

The limitations of fossil material as a subject for statistical study are well known and are discussed by Simpson and Roe (1939) and Phleger (1940). The question of association of parts as belonging to one individual is an important practical limitation, and this difficulty has been avoided in the present study by restricting study to the skulls. Under this restriction there can be no doubt that all parts measured belonged to the individual in question. The detection of small geographical and geological variations within the species is not possible with the data available to the authors. Such a study demands very accurate records of stratigraphic and geographic occurrences and most of the specimens examined lack detailed recorded information of this type. The factor of distortion of specimens has been eliminated as far as possible by omitting the obviously distorted skulls from any consideration. In general, the width measurements are less reliable than the length measurements, for the skulls are more liable to suffer lateral rather than longitudinal distortion. A study such as this is also limited by the

loss of protruding portions of the skull; the zygomatic arches, the tips of the nasals, and the wings of the supraoccipital crest are missing in many specimens. For this reason it has been found convenient to devise a set of measurements unconventional in many respects but well suited to skulls in this state of preservation. Twenty-four different measurements were made of each skull where degree of preservation permitted. Twelve of these measurements were eliminated as being unreliable or containing insufficient data. It is with the analysis of the twelve remaining series of measurements that this paper is concerned. The following uniform measurements were made in units of millimeters:

Width Measurements.

1. Width of the palate between the first premolars.
2. Width of the palate between the third molars.
3. Width of the skull across the posterior edge of the orbits.
4. Width of the post-orbital constriction.

Tooth Length Measurements.

5. Length of the cheek teeth (from the posterior edge of the third molar to the anterior edge of the first premolar).
6. Length of the molar series.
7. Length of the premolar series.

Skull Length Measurements.

8. Length of the skull from the anterior edge of the second premolar to the upper edge of the foramen magnum.
9. Length of skull from anterior surface of canine to the bottom of the occipital condyle.
10. Distance from the palatonarial border to the bottom of the occipital condyle.
11. Distance from the inner edge of the incisors to the palatonarial border.

Ramus Length.

12. Ramus length from symphysis to the most posterior point of the jaw.

The measurements were analyzed as follows: (1) The direct measurements were plotted in frequency curves to make clearly apparent the overlapping variation ranges of measurements in the various species. (2) The coefficient of variation (Pearson, $V=\frac{100\sigma}{M}$) was calculated for each species and for the genus for

each series of measurements. (3) The series of uniform measurements were paired in different combinations and subjected to a relative growth analysis. The b and $\propto$ values were calculated according to the relative growth formula $y = bx^{\propto}$. The significance of the relative growth method is discussed by Huxley (1932), by Phleger (1940), and by Simpson and Roe (1939). The trend lines in logarithmic plotting were calculated and fitted by means of the method of least squares. b and $\propto$ values were calculated for the genus and where possible for the species, and the degree of validity of these has been partially checked by calculating the coefficient of correlation, r.

RELATIVE VARIATION.

The Pearson Coefficient of Variation is a partial measure of the relative homogeneity or heterogeneity of the material studied. Morphological variations not easily detected by direct observation may be revealed and analyzed by calculation of these coefficients. A high degree of variation suggests that the population was subjected to considerable environmental differences or that the genic constitution of the population was quite heterogeneous, or that both conditions existed. The values obtained for the Pearson Coefficient of Variation are listed in Table I.

It can be observed that the measurements of width have, on the average, slightly greater variation than have the length measurements, the most variable character in every case being the width of the palate at P^1. This slight differential is probably due to greater lateral distortion of the skull.

The validity of each of the species analyzed appears to be supported by the variation coefficients which have been obtained. The coefficients are only slightly greater than those listed by Simpson and Roe (1939, p. 124) as characteristic of a modern species, and they are in the same order of magnitude as those obtained by Phleger (1940, pp. 651-652) in his analysis of the modern jaguar, *Felis atrox*, and *Smilodon californicus*. The discrepancy is probably due to two factors. The modern material can be more rigorously selected and it will show no distortion. The average values obtained by Phleger (op. cit.) for variation in skull characters in the three felids

TABLE I.

Pearson Coefficient of Variation in the Species of Merycoidodon.

Character	Merycoidodon No.	Merycoidodon V	M. culbertsonii No.	M. culbertsonii V	M. periculorum No.	M. periculorum V	M. affinis No.	M. affinis V	M. gracilis No.	M. gracilis V
Width palate at P^1	72	23.31±1.94	37	10.22±1.2	7	12.37±3.31	13	14.65±2.87	15	10.80±1.97
Width palate at M^3	79	14.84±1.18	44	8.34± .9	8	5.60±1.4	11	11.27±2.4	16	4.04± .71
Width across posterior edge of orbits	78	16.47±1.33	36	6.00± .71	8	4.40±1.4	14	7.72±1.46	20	8.10±1.28
Width post-orbital constriction	113	14.00± .97	61	4.02± .36	10	7.81±1.75	18	9.42±1.57	24	7.82±1.13
Length cheek teeth	123	16.28±1.04	70	5.40± .46	11	4.86±1.04	17	8.15±1.4	25	7.47±1.05
Length molar series	128	13.50± .84	74	5.55± .46	8	4.89±1.22	21	7.89±1.22	25	9.96±1.41
Length premolar series	125	19.58±1.23	70	6.48± .55	10	7.97±1.8	19	8.51±1.38	26	7.71±1.07
Length ant. end of P^2 to foramen mag.	118	17.37±1.13	65	5.79± .51	10	6.11±1.4	19	7.53±1.22	24	5.57± .8
Length ant. of canine to occ. condyle	108	18.99±1.29	60	5.62± .52	9	7.17±1.7	14	5.48±1.04	25	7.17±1.01
Length palatonarial border to occ. cond.	90	19.09±1.42	49	6.35± .64	9	9.79±2.3	16	9.82±1.74	16	9.72±1.7
Length inner edge of incisors to palatonarial border	83	16.11±1.25	45	5.76± .6	9	5.94±1.4	16	6.87±1.21	13	7.96±1.5
Mean of V's		17.23		6.32		6.99		8.85		7.85

mentioned above are about the same as those here obtained, and are as follows:

Jaguar	8.82
Smilodon californicus	8.04
Felis atrox	9.51

Smilodon californicus and *Felis atrox* are both fossil species, but the conditions of their preservation in the Rancho la Brea tar pits have protected them from appreciable distortion. It appears evident that the species of *Merycoidodon* are relatively homogeneous assemblages.

The mean values for V indicate that *Merycoidodon culbertsonii* and *M. periculorum* are the least variable species; *M. affinis* is the most variable, and *M. gracilis* is approximately between the two extremes. This is in apparent contradiction with the conclusions of Bump and Loomis (1930) which were that *M. gracilis* and *M. periculorum* were "the most stable species and *M. affinis* and *M. culbertsonii* were the more variable." However, it should be pointed out that those authors were considering absolute rather than relative variation. Since *M. culbertsonii* is the largest species it would naturally tend to show the greatest absolute variation. This point will be further illustrated in the next section.

In the series of width measurements *M. gracilis* shows the least variation of the palatal width of M^3 as well as one of the lowest variations for palatal width at P^1. The variation of the length from the inner edge of the incisors to the palatonarial border in *M. gracilis* is high relative to other species. This suggests that variations in muzzle shape in *M. gracilis* are primarily due to variations in length rather than width. In the other three species the converse appears to be true, the average variation of the width of the palate being greater than the variation in the length.

M. affinis and *M. gracilis* show greater variation in the dental series than do the other two species. It is perhaps significant that in no case is the coefficient of variation for the entire cheek teeth series as great as the mean of the V values for the length of the molar series together with that of the premolar series. It would appear evident that molar and premolar teeth vary independently, at least to a certain extent. A long molar series is not necessarily associated with a long premolar series. Of the two series the molar series is less variable in every species except in *M. gracilis*.

TABLE II.

Constants of the relative growth formula for species of *Merycoidodon.*

Characters		Merycoidodon		M. culbertsonii		M. periculorum		M. affinis		M. gracilis	
Y	*X*	$\propto$	*b*	$\propto$	*b*	$\propto$	*b*	$\propto$	*b*	$\propto$	*b*
Ramus length	Ant P^2 to foramen magnum	.94	1.33 r = .98 $\sigma\propto$ = .018	.99	1.02	...	...	...	...	1.1	.131
Width across posterior edge of orbits	Ant P^2 to foramen magnum	.88	1.14 r = .90 $\sigma\propto$ = .086	.96	.128	.91	1.01	1.12	2.72	.96	.129
Post orbital constr. (width)	Ant P^2 to foramen magnum	.62	1.34 r = .77 $\sigma\propto$ = .17	1.00	.522	.87	.245	.64	1.19	.70	.108
Width palate at M^3	Width palate at P^1	.55	5.63 r = .64 $\sigma\propto$ = .126	.48	7.15	...	...	.85	2.32	.15	16.81
Inner edge of incisor to palatonarial b.	L. palatonarial b. to O. condyle	.75	3.80 r = .97 $\sigma\propto$ = .026	.76	3.74	.43	14.45	.53	9.47	.63	6.02
Length premolar series	Length molar series	1.34	.404 r = .81 $\sigma\propto$ = .13	.90	1.36	1.46	.638	.98	.116	.64	2.83

In examining the coefficients of variation of the length measurements one striking fact is apparent. Each species shows greater variation of the posterior or cranial portion of the skull than it does in palatal length. A comparison of the V values obtained for the distance from the palatonarial border to the bottom of the occipital condyle with those obtained for the distance from the inner edge of the incisors to the palatonarial border clearly illustrates this.

If the mean variation for the genus *Merycoidodon* is compared with those obtained by Phleger (1940, p. 661) for *Promerycochoerus* and *Eporeodon*, *Merycoidodon* is seen to have a greater variation than either of these two genera. Coefficients of variation, as listed by Phleger (op. cit.), are as follows:

Eporeodon	11.47
Promerycochoerus	13.63

The mean coefficient of variation for *Merycoidodon*, as determined in the present analysis, is 17.23. Phleger's data were taken from Thorpe (1937, pp. 279-291) and consist of one series of measurements for each species; thus each species was of equal weight in the calculations. In the present analysis the data are unequally weighted for the species, as indicated above. A frequency graph of most of the characters here considered would yield a bimodal curve due to the larger numbers of the two extreme species. This naturally tends to give a high V value, for the standard deviation (σ) on which it depends is based on the assumption of a normal distribution.

ABSOLUTE VARIATION.

Having considered the relative variation in the species of *Merycoidodon* it would seem instructive to examine the absolute variation in the same group of species. The absolute range of variation is best comprehended by means of frequency curves. To that end the appended graphs have been constructed (Fig. 1).

In nearly every case, with the exception of the dental measurements, *Merycoidodon culbertsonii* shows the greatest abso-

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M. culbertsonii ————————
M. periculorum .....
M. affinis — - — - — -
M. gracilis — — —

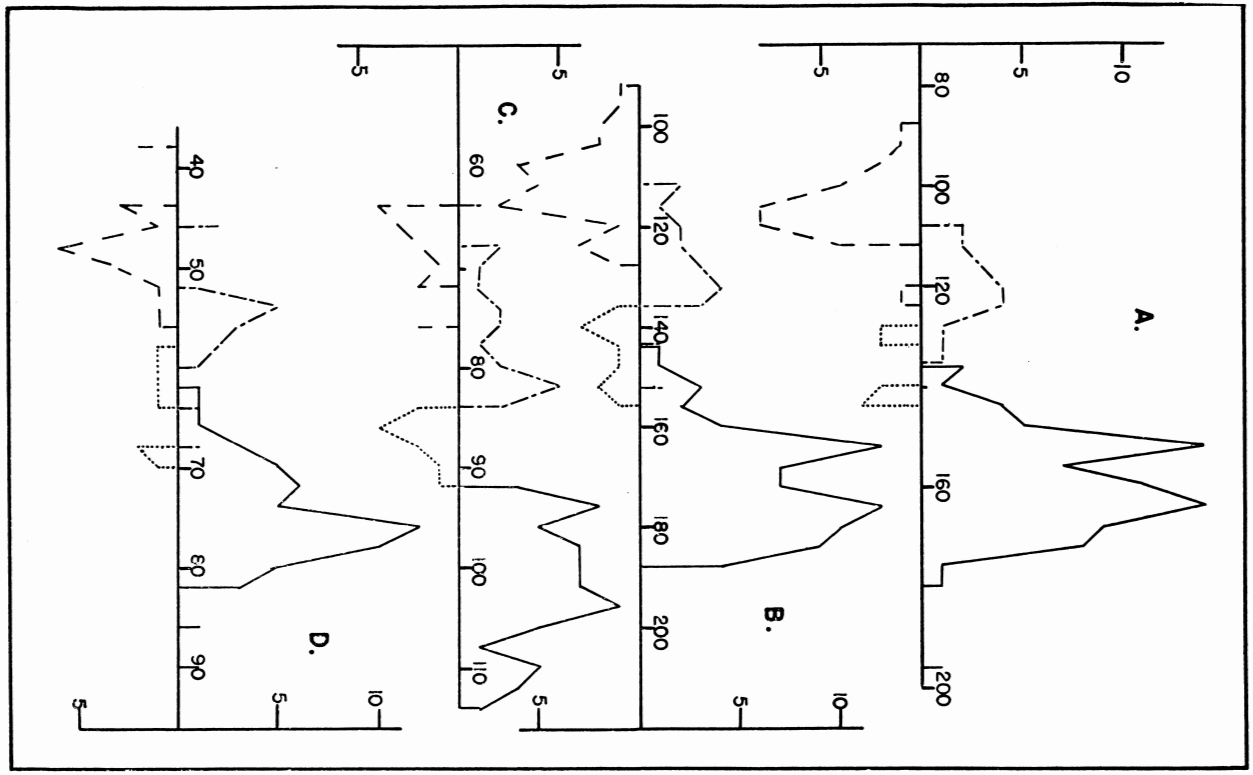

FIG. 1. Frequency curves of measurements of skull length.

A. Length of skull from anterior of second premolar to top of foramen magnum.
B. Length of skull from anterior surface of canine to the bottom of the occipital condyle.
C. Distance from the inner edge of the incisors to the palatonarial border.
D. Distance from the palatonarial border to the bottom of the occipital condyle.

Horizontal axes are the sizes in millimeters; vertical axes are the numbers of specimens.

lute variation, with *M. affinis* in most cases having the next greatest spread. This is in complete accord with the conclusions of Bump and Loomis (1930, p. 21), which have been indicated above.

A most significant fact clearly shown by these graphs is the degree to which the measurements of the species overlap in range. Not one of the various measurements which have been charted by the writers shows a clear demarcation between the various species. Even the two extremes in size, *Merycoidodon gracilis* and *M. culbertsonii*, show overlapping ranges in many of the width and dental measurements.

Dr. G. G. Simpson has pointed out to us that none of these data and analyses actually prove the existence of the four species which are indicated as belonging to the genus, and moreover that there is at present no reliable and objective way in which some specific separations can be made in *Merycoidodon*. This is particularly true in the separation of *M. culbertsonii* and *M. periculorum*; Thorpe has suggested that *M. periculorum* is a geographic variant of *M. culbertsonii*. The difference in size between the two species (or varieties) is the only significant difference yet demonstrated. It is true also that the frequency curves constructed from the present measurement data are bimodal for the genus, strongly suggesting the existence of two *Merycoidodon* "groups"—the *M. gracilis* "group" and the *M. culbertsonii* "group." This bimodal nature of the graphs for the genus is in part due to the fact that more specimens were examined belonging to *M. culbertsonii* and *M. gracilis* (the two extremes in size). The curves also are quadrimodal to a certain extent and might be more clearly so if the numbers of specimens in each group were equalized. These may be specific, varietal, geographic, or sex-linked variations in size. The fact remains that there are few important morphological differences other than size. It should be pointed out that absolute variation is of slight taxonomic use unless accompanied by other information, since it is largely dependent upon the number of specimens available.

RELATIVE GROWTH ANALYSIS.

The fact that the genus contains a fairly large number of specimens which significantly vary in size (and despite the number of species it may embrace) permits analysis by the

relative growth method. Huxley's formula, $y=bx^{\alpha}$, is based on the assumption, which can be demonstrated in many cases, that the growth rate of a part of an organism bears a constant ratio to the growth rate of the whole organism or to other parts of the organism. It is another and more definite way of stating that there is a correlation between the parts of an organism, and of analyzing that correlation. The α value indicates the relative growth ratio between the characters designated as x and y; where the α value is 1 the growth rate is the same. The b value is the initial difference between x and y; that is, $b=y$ when $x=1$. Animals which differ in form should have different relative growth ratios (constant or not) in both their ontogenetic and phylogenetic development. If this is true, then these ratios must have a genetic basis; in phylogenetic development mutations might occur for differences in size or differences in relative growth ratios, or both.

If x and y measurements are plotted logarithmically the points occur in a straight line where the relative growth formula holds and the correlation is perfect. The α value (relative growth coefficient) is expressed by the tangent of the angle between the regression line and the horizontal; where the angle is 45 degrees, α equals 1.

Discussions of the technique and significance of the relative growth method may be obtained from the following sources: Huxley (1932), Hersh (1934), Simpson and Roe (1939), and Phleger (1940). The generic coefficient of correlation (r) has been calculated for each of the relative growth calculations made in the present study. The short method of calculation (Simpson and Roe) was used. The coefficient, r, is designed to measure straight line relationships. Its use in this instance is justified by the fact that when the actual data, instead of the logarithms, are plotted only a slight degree of curvature is obtained. Presumably if sufficient young specimens were obtainable a more typical sigmoid growth curve would result and r could not be used for the logarithmic plots. The following section is a discussion of the relative growth analyses which have been made on the specimens of *Merycoidodon* and their apparent implications.

Ramus length from symphysis to most posterior point of jaw / Length of skull from the anterior edge of the second premolar to the upper edge of the foramen magnum.

A comparison of ramus length with this measure of skull length yields a differential growth ratio of .94 for the genus. This is very close to an isogonic ($\propto = 1$) relationship and agrees very well with the results obtained by Phleger (1940, p. 665) for similar measurements in the family Merycoidodontidae. It

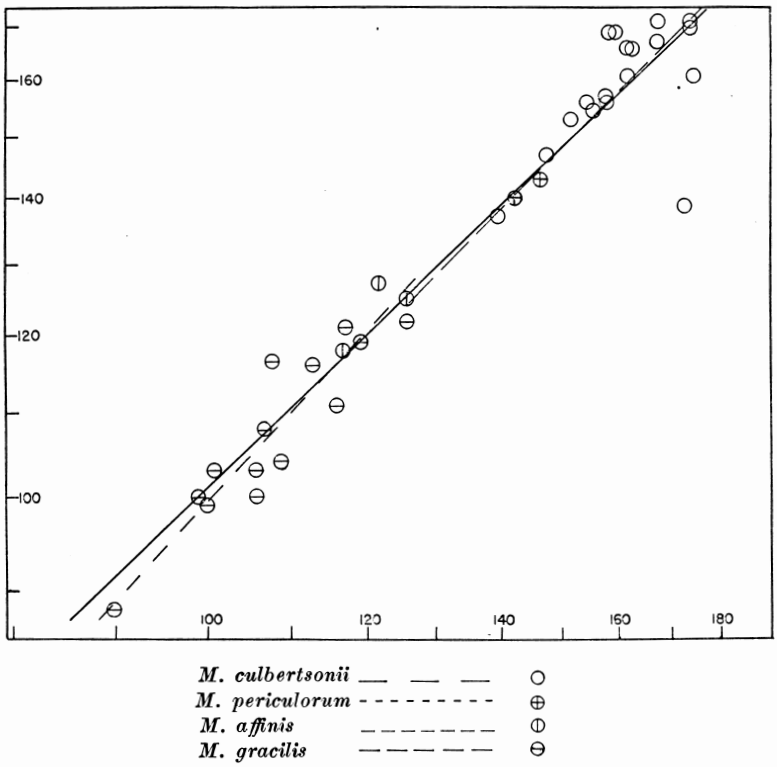

FIG. 2. A logarithmic plot of ramus length from symphysis to most posterior point of jaw (y) against the length of skull from anterior border of the second premolar to the upper edge of the foramen magnum (x). Measurements in millimeters.

also confirms the accuracy of his plot of the genus *Merycoidodon* which was based on only one individual of each species. The high coefficient of correlation obtained indicates how closely the ratio holds. The $\propto$ values obtained for the two species calculated do not differ significantly from that obtained for the genus. This analysis substantiates Thorpe's suggestion that *Merycoidodon* is on the main evolutionary stem of the

family Merycoidodontidae. Without compensating mutations, a high degree of heterogony for this comparison could not exist in the stem of stock of a family which shows considerable increase in size during evolution. Larger members of the family would be subject to adverse selection due to increasingly poor dental occlusion. The only essential difference between the species *in this character relationship* is a difference in size.

Width of skull across posterior edge of orbits / Length of skull from anterior edge of second premolar to upper edge of foramen magnum.

In this comparison the relative growth coefficient for the

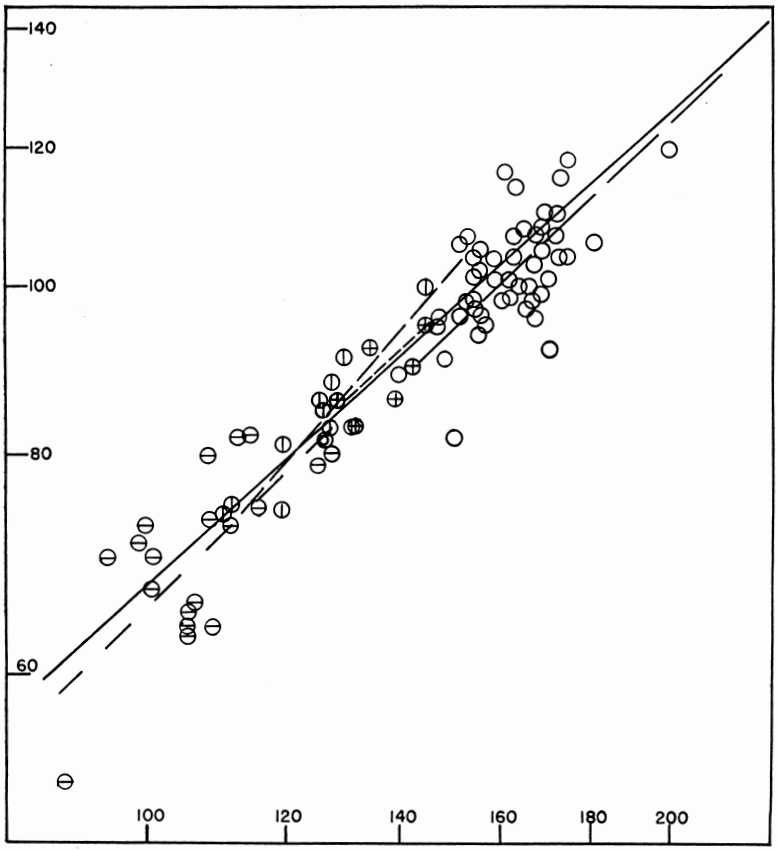

FIG. 3. A logarithmic plot of the width of the skull across the posterior edge of the orbits (y) against the length of the skull from the anterior of the second premolar to the upper edge of the foramen magnum (x). Measurements in millimeters.

genus is .88, indicating that the width of the skull increased a little more slowly than its length. The coincidence of the points does not so nearly approximate a straight line, but falls in a band instead. The directions of the lines for the species are not significantly different from the direction of the line for the genus *Merycoidodon*; this suggests, again, that in this character comparison the only significant difference between the species is one of size, and that in the evolution of the genus this width-length relationship remained constant.

Width of post-orbital constriction / Length of skull from anterior edge of second premolar to upper edge of foramen magnum.

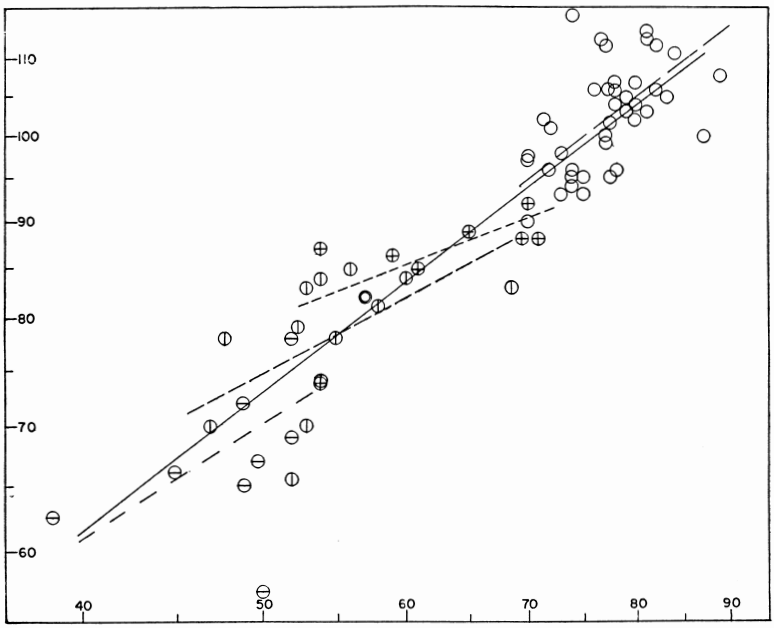

FIG. 4. A logarithmic plot of the distance from the inner edge of the incisors to the palatonarial border (y) against the distance from the palatonarial border to the bottom of the occipital condyle (x). Measurements in millimeters.

The frequency curves suggested that the width of the post-orbital constriction varies, to a considerable extent, independently of skull size. The coefficient of correlation (.77) here obtained supports this. The relative growth ratio obtained for the genus (.62) and those obtained for *Merycoidodon affinis* and *M. gracilis* indicate that increase in skull length is

not accompanied by a corresponding increase in the width of the post-orbital constriction. *M. culbertsonii* differs from the other species with a ratio of 1.00. If we assume that growth ratios are under genic control, *M. culbertsonii* must have different genes controlling this character than are found in *M. affinis* and *M. gracilis.*

Width of palate between third molars / Width of palate between first premolars.

The high variation of the palatal width at the first premolar is largely responsible for the spread in the data observed in this plot. The coefficient of correlation is .64. The low $\propto$ value indicates a considerable degree of heterogony. The palate at the first premolar is relatively more narrow in small specimens than it is in large. Thus with increase in size the jaw tends to change from a V shape to a U shape. This is especially true for *Merycoidodon gracilis.*

Distance from inner edge of incisors to palatonarial border / Distance from palatonarial border to bottom of occipital condyle.

This plot was undertaken to ascertain whether the genus *Merycoidodon* has any tendency for increasing preponderance of the anterior or posterior portion of the skull such as Robb (1935) found in the horse. Interestingly enough, as the differential growth-ratio (.75) indicates there is considerable heterogony in this comparison, but in this case it is the posterior part of the skull which becomes preponderant with increase in total size. This relationship holds for the individual species, as their $\propto$ values indicate. This heterogony may be due to selection against variations in the palatal region because of the adverse effect which these variations might have upon the grazing abilities of the affected animals. It should be borne in mind that the results of this plot do not necessarily indicate that *Merycoidodon* follows a different evolutionary trend from that of the horse. In Robb's data on the horse the orbit is used as a reference point and in the present case the palatonarial border is the reference point. These two points do not always have the same positions relative to one another.

Length of molar series / Length of premolar series.

A relative growth analysis of the relationship between the lengths of the molar series and the premolars indicates that

for the genus the premolars tend to form a longer series relative to the molars in the large skulls than they do in the smaller specimens. There is a suggestion that this tendency is even more extreme in the species *Merycoidodon periculorum* ($\propto = 1.46$). However, the number of specimens of *M. periculorum* was too small in this instance to place great reliance on the validity of this calculated value of $\propto$. *M. gracilis*, with a differential growth-ratio of .64, shows the opposite tendency.

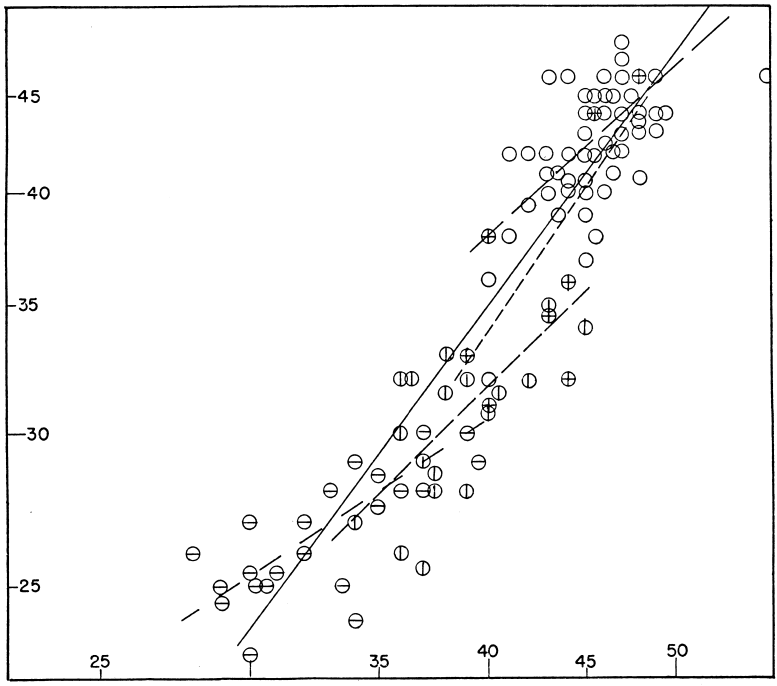

FIG. 5. A logarithmic plot of the length of the molar series (y) against the length of the premolar series (x). Measurements in millimeters.

With increase in skull size the molar series shows a greater relative increase in length than the premolars.

It should be noted that *M. platycephalus* falls very near the genus trend line in every case which has been analyzed.

In Fig. 5 the lines indicating the relative growth coefficients for each of the species are more askew from the trend of the line for the genus than in Figs. 2 and 3. This suggests a relative growth ratio which is different for each species in the genus in this character relationship, from a lower one in

M. gracilis, through two higher ones, and back to a lower one in *M. culbertsonii.* In this graph, however, the points are quite scattered and the correlation is relatively poor for the genus as a whole. This fact presents the possibility that in this case the differences in the relative growth ratios between the genus as a whole and the species may not be significant. Fig. 4 shows a similar difference in trend between the genus and the species.

PHYLOGENY OF THE GENUS.

The relative growth analyses indicate that the differences in skull form of at least the two terminal species of *Merycoidodon* are mainly functions of size. It is true that in some cases there are apparently significant differences in relative growth ratios from one species to another. If the growth ratios are under genic control, as Hersh (1934) and Robb (1935) have suggested, one of the chief differences between the various species is in those genes controlling size, although there are secondary genic differences in relative growth proportions. Inasmuch as the evolution of the main stem of the family Merycoidodontidae shows a fairly constant tendency for increase in size, it might be instructive to consider whether the same condition exists in *Merycoidodon* which is near the base of the main evolutionary stem of the family.

Each of the species of *Merycoidodon* is found in the lower Brule (middle Oligocene) while *M. gracilis* and *M. culbertsonii* have been reported from the Chadron (lower Oligocene). Thus on purely stratigraphic criteria either of these species can be suggested as the original stem member of the genus. As the relative growth analyses indicate, *M. gracilis* may be closer to the main stem than *M. culbertsonii* since it is the smallest species of the genus.

The foregoing suggestion receives support from various additional sources. Thorpe (1937) suggests that *M. gracilis* is closely related to the *Eporeodon* stock by reason of its bullae which are proportionally larger than in any other of the *Merycoidodon* species. It is generally accepted that the members of two related phyletic stocks resemble one another more closely as an approach is made to the common ancestor. Scott's contention that the presence of large bullae is a primitive condition gives added support to this line of reasoning.

A comparison of *M. gracilis* with a very young specimen of *M. culbertsonii* also seems to indicate that the former is more primitive. W. B. Scott (1940, p. 672) lists the following characters as distinguishing *M. gracilis* from *M. culbertsonii*:

"1. The very much smaller size.
2. The much shorter and inconspicuous occipital wings.
3. The shallow antorbital fossa.
4. The articulations of the premaxillaries with the nasals.
5. The more closely set premolars often with overlapping of the anterior ones."

The skull of a very young *M. culbertsonii* (Rapid City Museum, No. 311) which is figured by both Thorpe (1937) and Scott (1940) displays most of these characters to a greater degree than does the adult *M. gracilis*. There are no occipital wings, the antorbital fossa is very shallow, and the premaxillaries articulate with the nasals. There are other striking similarities between young *M. culbertsonii* and *M. gracilis*. Both have short, relatively wide nasals. In addition to this the young *M. culbertsonii* shows little trace of a post-orbital constriction. As previously indicated, the relative growth analysis shows that *M. gracilis* is proportionately much wider in this region than are the other species.

It should be pointed out that one of the relative growth analyses indicates an apparent exception to the similarities between *M. gracilis* and the young *M. culbertsonii*. The analysis of palatal length against the distance from the palatonarial border to the bottom of the occipital condyle indicates that the posterior portion of the skull increases at a greater rate than the palatal portion. However, the young *M. culbertsonii* has the short muzzle characteristic of young mammals. The seeming discrepancy between these two facts is due to the use of different points of reference in the two cases. In an estimate of muzzle length the region of the orbits is the usual point of reference. If the relative lengths of the pre-orbital region in *M. gracilis* and in young and mature *M. culbertsonii* are compared, it is seen that *M. gracilis* is again intermediate. *M. affinis* and *M. periculorum* are in this respect, as in most others, intermediate between *M. gracilis* and *M. culbertsonii*. Thus on purely observational grounds it is suggested that *Merycoidodon* has a tendency for preorbital preponderance such as Robb found in the horse. It is, however, proceeding at a less rapid

rate and never approaches the extreme condition found in the horse.

The foregoing evidence strongly supports the hypothesis that *M. gracilis* is the stem member of the genus. It is suggested that from it, or from some form much like it, the other species of *Merycoidodon* have evolved chiefly by accumulative mutations for increase in size. The frequency graphs suggest that the individual mutations were of slight effect and the change from one form to the next a gradual one. Mutations in growth ratios probably also occurred during the evolution of the various species. However, these mutations must have been few in number and of only minor consequence. This is indicated by the fact that, in general, relative growth-ratios for the species vary within a limited range around those for the genus and family. These limits may be imposed by selection or possibly by some other genic control.

SUMMARY OF CONCLUSIONS.

About 150 skulls of *Merycoidodon* have been studied with the following results:

1. By calculation of the Pearson coefficient of variation for various dimensions of the skulls of four species of the genus *Merycoidodon*, it has been found that these fossil species show only slightly greater variation than modern species. Some of the evidence indicates that various portions of the skull can, within limits, vary independently of the rest of the skull.

2. The absolute variation of the skull characters of *Merycoidodon culbertsonii*, *M. periculorum*, *M. affinis*, and *M. gracilis* have been studied by means of frequency curves of the measurements. The extent to which each species overlaps the next in various dimensions has been illustrated.

3. A relative growth analysis indicates that in many cases the growth coefficients for the species are essentially the same as the coefficient for the genus in the same comparison. In other cases different coefficients for the species suggest different genic constitution.

4. On the basis of evidence from morphological observations and from relative growth analysis it is suggested that *Merycoidodon gracilis* is the stem stock of the genus. The other species of the genus may have evolved from it, or from a similar form by accumulation of mutations for increase in size, and also by mutations for change in relative growth ratios.

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