A STUDY OF MUTATIONS IN EVOLUTION.

II. ONTOGENY IN THE EQUINE SKULL.

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(With Two Text-figures.)

If size is the only variable that is responsible for the change of form during the evolution of the equine skull, then the skull of a modern horse should manifest the primitive features of *Eohippus* when, and only when, it is of the same absolute magnitude. Likewise, the characteristic proportions of *Mesohippus* would be reproduced when, but neither before nor after, the horse has attained the corresponding size. Fortunately it has been possible to test this proposition and to find in its confirmation independent evidence for the conclusions of the previous paper.

A quantitative description of "continuous" evolution in the horse has been presented. In this family the amount of pre-optic or facial preponderance is readily given by the ratio of face length to post-optic length, termed the "facial index". The progressive advance of this index from about 1·2 in the four-toed species to nearly 1·8 in the one-toed species is a convenient measure of evolution.

To demonstrate the reappearance of the facial index of any given ancestor in the modern Equidae, one need do no more than select the skeleton of a domestic horse when it has arrived at a comparable size. Thus, for example, a young Percheron of the dimensions of *Eohippus resartus* happens to be a five months old foetus, and in each the facial index is exactly 1·2 as predicted.

Data concerning the development of extant species of wild and domestic horses were obtained from specimens in the American Museum of Natural History and are listed in Table I. The domestic animals of known age are so arranged, but the others are given in order of size. These data are shown in Fig. 1, where they are superimposed upon the graph representing ancestral and related prehistoric forms. It is obvious that all points, both ancient and modern, lie along a straight line and are indistinguishable. Their homogeneity is further attested by a coefficient of variability sensibly unaltered during ninety-five million years.

Since the two series are algebraically identical the burden of proof lies upon him who would consider them dissimilar.

Discussion.

During the growth of the individual, change of form is quantitatively dependent upon change of size in a vast number of cases, as witnessed by the growing literature on relative growth (Huxley, 1932). Now it has been demonstrated that during the growth of the race change of form is a function of the independent variable change of size. Moreover, with

TABLE I.

Progressive facial preponderance in the foetal and post-natal development of the horse. (Mature specimens arranged in order of size.)

Specimen	Museum No.	Skull length cm.	Face length cm.	"Cranium length" cm.	Facial index (face/ cranium)
Foetus, 5–6 months	2	15·2	7·9	7·3	1·08
		*16·3	*9·0	7·3	*1·23
Foetus, 10 months	1	26·4	15·4	11·0	1·36
(Zebra foal)	—	26·7	15·1	11·6	1·30
New-born "trotter"	66	33·0	19·2	13·8	1·39
(Shetland pony, live weight 170 lb.)	—	33·0	20·0	13·0	1·54
New-born work-horse	35	33·8	20·5	13·3	1·54
4–6 weeks old colt	34	36·7	21·7	15·0	1·45
9 months old colt	36	44·4	27·0	17·4	1·55
11 months old colt	38	48·2	29·3	18·9	1·55
(*Equus zebra*)	169	49·3	30·5	18·8	1·63
2 years old horse	43	50·0	30·7	19·3	1·59
3½ years old horse	146	51·7	31·3	20·4	1·54
(Arab stallion "Nimr")	59	52·0	32·0	20·0	1·60
(Trotter "Elmer Wilkes")	74	54·0	35·0	19·0	1·85
(Thoroughbred "Sysonby")	61	56·0	35·0	21·0	1·67
4½ years old horse	37	56·0	(35·0)†	(21·0)	(1·67)
(Yellow Dunn)	159	56·5	36·0	20·5	1·76
25 years old horse	50	59·5	36·5	23·0	1·59
(Gelding truck-horse)	14,132	62·0	39·5	22·5	1·76
(Percheron, live weight 2370 lb.)	62	69·0	43·0	26·0	1·66

* Measurement includes unossified cartilage of premaxilla.
† Bracketed numerals are approximations.

respect to facial preponderance, ontogeny in the horse both repeats and outruns phylogeny, in that living varieties are in some instances larger than any predecessor.

It is still too soon to raise the subject of "recapitulation". This partial study of evolution will be supplemented by other data showing that foot development in the horse does not repeat phylogeny. As briefly intimated (Robb, 1932), discontinuous evolution is manifested in these structures by a single, abrupt reduction in the size of the anlagen of the second and fourth toes. The old maxim "Ontogeny repeats phylogeny" is a partial truth; the processes are identical only if evolution has been continuous, they are not identical if any mutation has intervened.

These data do seem to suggest orthogenesis, if by that is implied a continuity of change, in a direction predictable from the first two or three members of the series, without reference to the mechanism involved. This definition precludes interruption by random mutations in various directions and of diverse magnitudes. No mutation of pattern

Ontogeny of the equine face

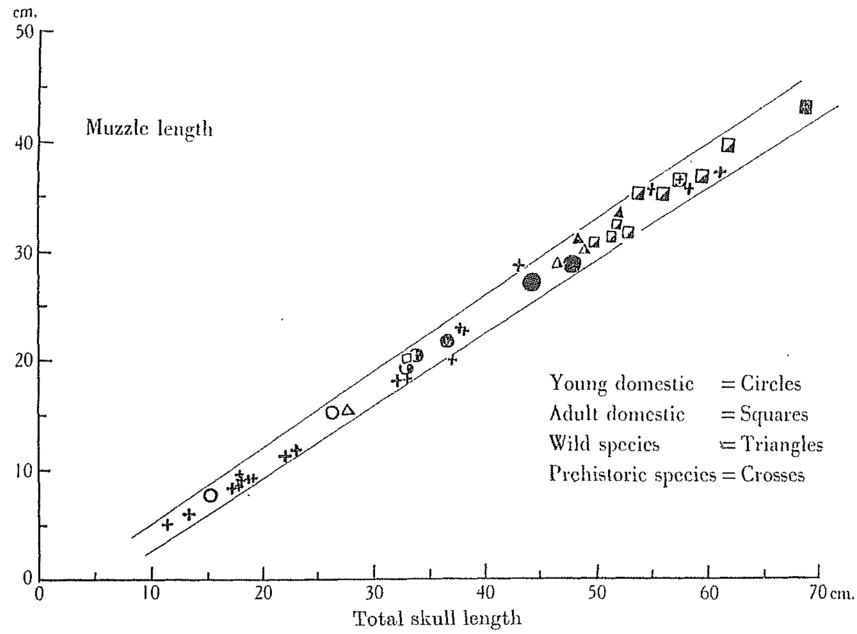

Fig. 1. Face length in relation to total skull length, representing foetal and post-natal development of the modern horse, superimposed upon points (crosses) for ancestral and prehistoric species. Circles: young domestic horses; open circles are prenatal, shaded at birth, solid for colts. Squares: adult domestic; open for Shetland, shaded for Arab, thoroughbred, etc., solid for Percheron. Triangles: modern wild species; open for zebra colt, shaded for adult zebra species, solid for Kiang.

has been discovered in this material. The form of the skull is an identical function of its total length whether we compare growing individuals or the same species or adults of ancient and modern species. This algebraic analysis excludes also the possibility that evolution has taken place through the accumulation of numerous small mutations of form. Continuous evolution is in this case adequately described as the result of a sequence of changes in total size.

Why does change of size alter form? This occurs inevitably whenever, as in Fig. 1, the linear regression line of the graph fails to pass through the origin (where both ordinate and abscissa equal zero). This raises the question whether, in Fig. 1, the regression line, if projected downward, would actually intercept the base-line, or would trail over to the zero point. In the former case a first degree equation would suffice, otherwise an equation of an higher order might be required to describe the data. Other one-dimensional studies of skull development are available for comparison, but are subject to the same limitation, except in cattle.

Titanotherium (Osborn):	Face = 0·47	skull length,	plus 4·0 cm.
Cattle ontogeny (Robb, unpublished):	,, = 0·53	,,	plus 0·0 ,,
Sheep-dog ontogeny (Becher):	,, = 0·54	,,	less 1·5 ,,
Horse (phylogeny and ontogeny)	,, = 0·66	,,	less 2·3 ,,

If for theoretical reasons one prefers to use the more general equation, for which a physiological basis may be assumed (Robb, 1929), the same data can be described thus, without recourse to an x or y intercept constant.

Titanotherium:	Face length	$= 0{\cdot}60$ (skull length)$^{0{\cdot}9}$
Domestic cattle:	,,	$= 0{\cdot}53$ (,,)$^{1{\cdot}00}$
Horse:	,,	$= 0{\cdot}30$ (,,)$^{1{\cdot}23}$
Dog:	,,	$= 0{\cdot}28$ (,,)$^{1{\cdot}50}$

Since most of the known examples of relative growth are exponential in character the second group of equations are perhaps more complete. The issue can be settled only by the examination of much younger embryos than are at present available at the American Museum of Natural History.

If size is the only variable responsible for changes of skull shape during the evolution of the horse, to what cause may we attribute this serial increase of total size? If *Eohippus* had been as large as the draft horse, or if *Eotitanops* had approximated the bulk of its distant offspring *Brontotherium* (Fig. 2), the concept of orthogenesis could not have been

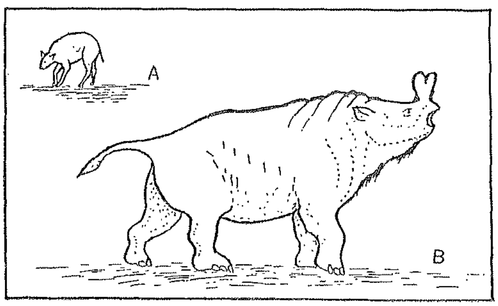

Fig. 2. *A*, *Eotitanops borealis*, ancestor to *B*, *Brontotherium gigas*. (Each to same scale, 1/200, after Osborn.) Note importance of size changes in the evolution of form.

derived from these mammals. The geological records do confirm an evolution toward greater size, but the enlargement has been very erratic. Even at the present time the size range within a single species is extensive. The following observations by Chubb will emphasise that point:

Measurement	Shetland pony	Giant draft horse
Weight in life	170 lb.	2370 lb.
Height at shoulder	2 ft. $9\frac{3}{8}$ in.	6 ft. 1 in.
Bulk of humerus	$9\frac{1}{2}$ cu. in.	119 cu. in.
Bulk of femur	$13\frac{1}{2}$ cu. in.	188 cu. in.

It will be noted that the draft horse weighed fourteen times as much as the adult Shetland; the latter may have been over 100 lb. heavier than its four-toed ancestor but it coexists with members of its own species that outweigh it by 2200 lb. Its facial index is comparable to that of the three-toed *Merychippus* rather than to its contemporaries. It is therefore entirely possible to conclude that the occurrence of apparently progressive size augmentation in certain families is partly illusory and wholly fortuitous. Some type of selection may have acted to eliminate the lesser forms but we may accept the so-called "orthogenetic" trend in the evolution of the horse as in entire conformity with the law of maximum probability.

SUMMARY.

1. Very extensive changes of form appear during foetal and post-natal development in the horse as quantitative functions of increase in total size.

2. These developmental changes of skull shape correspond precisely, if comparison be made between specimens of the same absolute magnitude, to those shape transformations arising during the evolution of the horse.

3. Since progressive pre-optic preponderance in the individual and in the race is algebraically the same function of total size, one may analyse the form of any horse's skull, either ancient or modern, as the manifestation of the characteristic equine skull pattern modified only by the absolute extent of growth. The post-optic extension of *Hyracotherium* and the pre-optic preponderance of *Equus* are believed to represent a single embryological pattern, of which diverse manifestations occur as a function of total size.

4. The appearance of an "orthogenetic" trend in the evolution of the equine skull is due to the attainment of successively greater adult sizes by the more recent genera.

5. One may interpret the progressive augmentation of racial size as

a fortuitous occurrence, possibly aided by some natural selection, perhaps chemically determined by the mutation tendencies of certain size genes, but not inconsistent with the nature of probability.

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