A STUDY OF MUTATIONS IN EVOLUTION[1].

I. EVOLUTION IN THE EQUINE SKULL.

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(With Three Text-figures.)

> A change in the magnitude of a leaf is of little consequence, while a change in the form of a leaf (which is the same as saying a change in the established ratios of growth) is of great importance.
>
> HENRI BERGSON[2].

WHEREAS Mendelian genetics has found its most gratifying demonstration in the inheritance of qualitative differences, it is the quantitative character that has preoccupied the students of evolutionary remains. From such material there has arisen the concept of orthogenesis. Huxley (1924, 1932) has pointed out that the mechanism of relative growth could explain continuous aspects of evolution on a physiological basis, without recourse to teleological hypotheses. The data for Huxley's conclusion were not extensive, and in the case of antler growth in deer, presented the further complication that the linear relationship was applicable to adults but not to growing animals. The data now presented show a complete identity of curves for ontogeny and phylogeny, and demonstrate the contribution of relative growth to each.

MATERIAL AND DATA.

In fairness to the proponents of continuous evolution it is necessary to examine one of their most extensive series of fossils, such as that of the horse or the titanothere. In this material let us investigate the character that most adequately illustrates, without sensible interruption, the obviously progressive transformation of some one important structure. Let the pedigree selected be that of the horse because (as will presently appear) access to living specimens can illuminate our investigation. Let the character we select be one often treated by H. F. Osborn himself, *i.e.* the progressive pre-ocular preponderance manifest in the

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[1] Undertaken while Fellow of the National Research Council of Washington, D.C., in the department of Anatomy, College of Physicians and Surgeons, New York City.

[2] *Creative Evolution* (English translation, Henry Holt and Co., 1913), p. 67.

skull of the horse since Eohippus (Fig. 1) in contrast to a progressive post-optic elongation characteristic of the titanothere (Fig. 2).

Through the courtesy of the American Museum of Natural History[1], their most valuable specimens of fossil Equidae were made available for direct examination. Only the complete skulls were studied, partial reconstructions being of lesser validity. This specification reduced the collection to about twenty. Even among these were several that had suffered pressure distortion before petrification reinforced their outlines. Such questionable measurements are bracketed in the accompanying Table II. Since no better material than the horse exists, its analysis should provide significant evidence regarding the alleged continuity or fortuitous discontinuity of evolutionary trends, or whether any such trends exist.

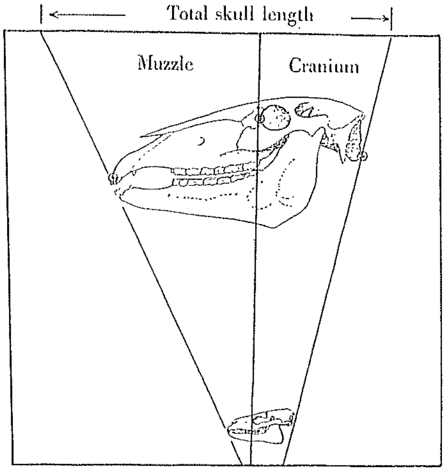

Fig. 1.

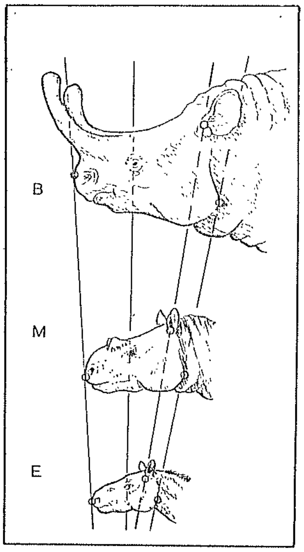

Fig. 2.

Fig. 1. Progressive pre-optic preponderance in the evolution of the horse skull; *Eohippus* below, *Equus* above.

Fig. 2. Progressive post-optic preponderance found in the evolution of the titanotheres; *Eotitanops* below, *M* = *Manteoceras*, *B* = *Brontotherium*.

The major features of evolution in the horse are most obvious in its extremities, the head and feet. The feet (to be reported at another time:

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abstract, Robb, 1932 *a*) present a characteristic specialisation of the third or "middle toe", with relative diminution of the other digits, suggesting to the Lamarckian mind "atrophy from disuse". The head presents for inspection an increasing elongation of the muzzle and complication of the grinding teeth, recorded by Osborn as follows:

> The progressive elongation of the skull in horses is apparently for two purposes; first, to facilitate reaching the ground with the row of incisor teeth; second, and no less important, to allow space in front of the eye sockets for the great rows of elongate, or hypsodont grinding teeth, the marvellous dental battery of the horse. We might assume from these facts that long-headedness is correlated with long teeth, but the giant pigs (elotheres) have still longer and narrower skulls than the horse, yet all the teeth are brachydont, or short-crowned. Again, the elephant has extremely long or hypsodont molar teeth, yet it possesses also the shortest, or most brachycephalic, skull known among the Mammalia. (Osborn, *Age of Mammals*, p. 18.)

Since teleological explanations for the direction of skull modifications in the horse are at variance with modern biology, their basis of fact will bear scrutiny.

To acquaint the reader with the phylogenetic relationship of the specimens here discussed a brief survey is unavoidable. The precursors of our domestic horse may be conveniently allocated to four successive levels of attainment, these being: (*a*) primitive animals with four toes, (*b*) three toes and primitive teeth, (*c*) three toes and modified grinding teeth, (*d*) one toe only on each foot.

The analytic procedure was very simple. Careful measurements were made of skull length and width, face length, the dimensions of the brain case, the size of the hard palate, the location of the teeth in the upper jaw, diastema length, etc. At the same time, each of the long bones of the skeleton was studied. The elongation of the head, the extension of the muzzle, and the apparent retreat of the eye sockets were thus subject to strictly quantitative treatment.

Total skull length was measured as the maximum distance from the caudal limit of the occipital condyles to the prosthion or centre point of the anterior margin of the upper alveolar arch (see Fig. 1).

The length of the muzzle was obtained as the minimum linear distance from the inner surface of the orbital margin of the lachrymal bone to the prosthion. This dimension in the horse corresponds closely to the nasion-prosthion interval used by anthropologists as a measure of face length in man. For this reason the same terms have been applied to the horse.

The index of facial preponderance is defined as the ratio of muzzle (face) length to cranium length, where the latter is conveniently derived as the difference between total skull length and muzzle length. (In the case of petrified crania it was not possible to measure the inside length of the brain-case.)

These data are given in Table II.

OBSERVATIONS.

The evolution of the horse has been characterised by a tremendous augmentation of adult size, progressing from *Hyracotherium* weighing perhaps 20 lb. to the modern Percheron which may exceed 2300 lb.

TABLE I.

Conspectus of fossil Equidae.

I. Eocene genera:
  Height: about 13 in. at shoulder, "cat-size".
  Head: relatively short muzzle; facial index = 0·85; teeth short-crowned and without cement.
  Feet: four digits on anterior limbs, three on posterior; all touching ground and functioning.
    (1) *Hyracotherium* and *Eohippus* (17 species).
    (2) *Orohippus* (10 species).
    (3) *Epihippus* (2 species).
II. Oligocene:
  Height: comparable to small sheep, or coyote.
  Head: facial index between 0·95 and 1·20; teeth short-crowned and without cement, last three premolars resemble molars.
  Feet: three toes on each foot, all functioning.
    (4) *Mesohippus* (18 species).
  Collateral line: *Anchitherium* to *Hypohippus*, the Miocene "forest-horse".
    (5) *Miohippus* (17 species).
III. Miocene and Pliocene:
  Height: about 36 in. at shoulder, like the Shetland pony.
  Head: facial index from 1·3 to 1·7 for tallest; teeth become long-crowned and with cement.
  Feet: three toes on each foot but 2nd and 4th digits do not reach the ground hence not functional.
    (6) *Parahippus* (18 species).
    (7) *Merychippus* (25 species).
    (8) *Pliohippus* (17 species, transitional genera with some one-toed forms).
  Collateral genera: { *Hippidium*;
    Hipparion and *Neohipparion*.
    (9) *Plesippus* (2 species).
IV. Pleistocene and recent:
  Height: both fossil and living species ranging up to 73 in.
  Head: facial index from 1·5 to 1·8; teeth long-crowned, with cement.
  Feet: digits II and IV reduced to "splints".
    (10) *Equus* (47 extinct and 7 living species).

Whereas the eocene face was shorter than its brain-case, the face (muzzle) of the modern horse is nearly twice as long as its brain-case (or cranium). Accordingly, in the jaws of the ancestor a diastema between the canine and premolar teeth is hardly discernible although in the modern specimens this toothless gap may exceed 7 cm. The eye-sockets have apparently receded from their primitive site near the nostrils to a locus nearer the ears. In all these details the head of *Eohippus* bore a greater resemblance to that of *Eotitanops* than to its modern representative (compare Figs. 1 and 2).

TABLE II.

Progressive facial preponderance in the evolution of the horse.

Specimen	Museum No.	Skull length cm.	Face length cm.	Cranium length cm.	Facial index (face/ cranium)
Group I (four-toed):					
Hyracotherium (Cope)	(15,431*)	11·5	5·2	6·3	0·82
Eohippus venticolus	4,832	13·5	6·1	7·4	0·82
E. resartus	15,428	(17·8)	(9·7)	8·1	(1·20)
Group II (three toes):					
Mesohippus bairdi (Leidy)	1,492	(17·2)	(8·5)	8·7	0·98
M. bairdi	11,862	17·8	8·7	9·1	0·96
M. bairdi	12,454	(18·0)	(9·2)	8·8	1·05
M. bairdi	1,477	18·8	9·3	9·5	0·98
M. bairdi	12,456	19·0	9·4	9·6	0·98
M. intermedius	1,196	22·0	11·3	10·7	1·06
M. intermedius (Osborn and Wortman)	1,218	23·0	12·0	11·0	1·09
Group IIA:					
Hypohippus osborni	9,407	37·0	20·0	17·0	1·18
Group III (three toes and long teeth):					
Merychippus sejunctus (Cope)	8,291*	32·1	19·2	12·9	1·49
M. sejunctus	8,347	32·9	18·5	14·4	1·29
Pliohippus lullianus (Young)	17,225	38·0	22·8	15·2	1·50
P. leidyanus (Osborn)	17,224	43·4	(29·3)	—	(2·00)
Group IIIA:					
Neohipparion whitneyi (Gidley)	9,815	37·7	23·0	14·7	1·57
Hippidium neogaeum (Lund)	11,872	57·5	36·2	21·3	1·71
Group IV (one-toed):					
Plesippus simplicidens (Cope)	20,077	55·0	35·5	19·5	1·82
Equus scotti (Gidley)	10,606	57·7	36·0	21·7	1·66
E. scotti (Gidley) (extinct)	—	61·0	37·0	24·0	1·54
E. granti (a zebra)	142	46·5	28·8	17·7	1·63
E. hemionus (kiang)	97	48·5	31·0	17·5	1·77
E. chapmani (zebra)	166	48·7	30·0	18·7	1·61
E. zebra	169	48·3	30·5	17·8	1·72
E. przewalsky	32,686	52·0	33·0	19·0	1·74
E. gregori	172	56·3	36·0	20·3	1·78
E. caballus typicus (horse)	163	53·0	31·5	21·5	1·46
E. caballus (common horse)	14,132	62·0	39·5	22·5	1·76

* Specimens incomplete and partially reconstructed.

The outstanding feature of these observations is expressed by progressive changes in the facial index (face length/cranium length) which is a direct function of total size. If the animal be small, as was *Hyracotherium*, the index approximates 0·8. If the animal becomes somewhat larger as in the case of *Merychippus*, the index is found to have values between 1·3 and 1·5, which magnitude is exemplified in its present day descendant of almost the same elfin dimensions—the Shetland pony weighing 170 lb. and with an index of 1·54. The largest prehistoric horses, such as *Hippidium*, *Plesippus* and *Equus scotti*, were as tall as a modern draught horse (*e.g.* A.M. No. 14,132) and achieved indices as great as 1·71, 1·82 and 1·66 in comparison to the draught animal with 1·76.

These data are presented in graphic form in Fig. 3 to show the straight line relation of face length to total skull length. One hundred million years of facial evolution may be summed up in the expression: Slope $m = 0{\cdot}66$.

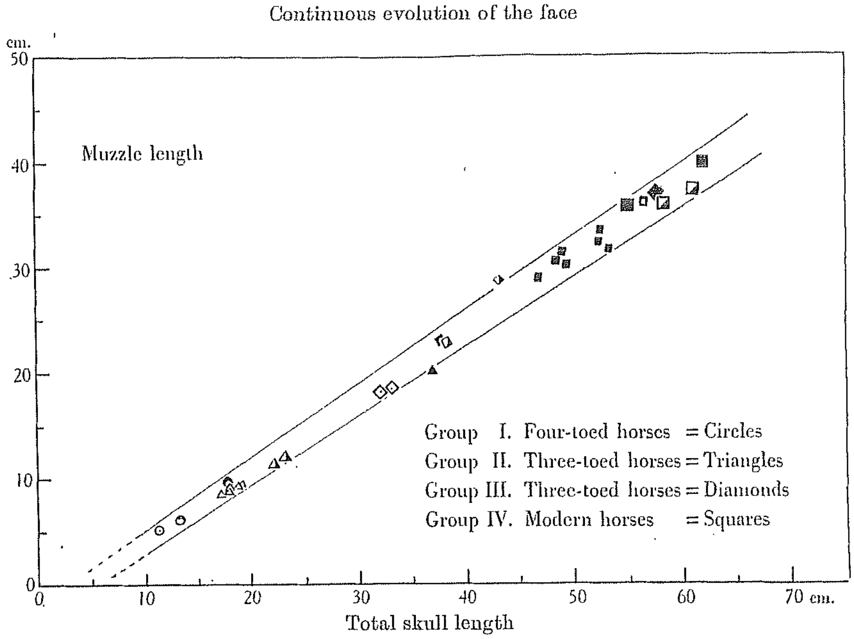

Fig. 3. Evolution of the horse skull (face length/total skull length) showing consistent change of form with evolution in size. Group 1, circles: open, *Hyracotherium*; shaded, *Eohippus venticolus*; solid, *Eohippus resartus*. Group 2, triangles: open, *Mesohippus bairdi*; shaded, *M. intermedius*; solid, *Hypohippus*, "the forest horse". Group 3, diamonds: open, *Merychippus*; shaded, *Pliohippus*; solid, *Neohipparion* and *Hippidium*. Group 4, squares: open, *Plesippus*; shaded, extinct wild species of Equidae; solid, modern wild and domestic species of Equidae.

CONCLUSIONS.

Continuous evolution in the shape of the horse skull did not occur except as a concomitant of the one hundred-fold increase in total mass. Given that size is in large measure genetically determined, it is possible to describe the evolution of *form* in terms of genes augmenting total *size*.

Progressive pre-optic preponderance in the horse is a by-product of whatever factors have permitted size increase in the progeny of *Eohippus*. Conversely, had there been no evolution of size, there would have been little if any "orthogenetic" evolution of form.

It is also evident that the physiological mechanism known as "relative growth" is of major significance in the analysis of evolution. When we learned that acquired variations were not transmitted it became necessary to attribute to the germplasm a gene for every character, and to postulate a mutation for every minute innovation in the evolutionary tree. Such a multiplicity of modifying factors has become a concept too cumbersome for many to receive, especially when these modifiers seemed to accumulate in an orthogenetic fashion. Now we are aware of the manifold changes in every body tissue that may result from a single increment to total size (Robb, 1928, 1929 *b*, 1932 *b*). In Fig. 3 the evolution of *size* is visualised as a shift from left to right, of *form* as a shift upwards. If one size mutation can modify form in many organs because of their relative growth, this mechanism must assume part of the burden of evolution, thus effecting a vast economy in the number of local mutations hitherto believed involved. In this respect the evolution of form is algebraically linear and predictable.

"Natural selection" cannot be given any immediate rôle in the evaluation of certain characters for survival. The gene for "horns" is of no apparent value to the titanotheres, for example, until racial size has increased sufficiently so that the horns also have magnitude (see Fig. 2; also Hersh, 1932). The survival value of structures affected by relative growth is highly uncertain, depending upon individual and racial magnitudes and the duration of each phase in geologic time (Hersh, 1934).

SUMMARY.

1. A quantitative study has been made of the successive changes of skull proportion associated with evolution in the horse.

2. The ratio of face length to cranium length has been doubled, increasing by insensible gradations from 0·85 in the cat-sized *Hyracotherium* to 1·70 or more in the largest living horses. This trend, in contrast to the progressive post-optic preponderance of titanothere evolution, has been described as a progressive pre-optic preponderance.

3. This aspect of evolution is strictly related to increase in total body size. Within a narrow range of variability, all specimens of the same size exhibit the same facial index, irrespective of phylogenetic status.

4. 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 characterising 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.

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