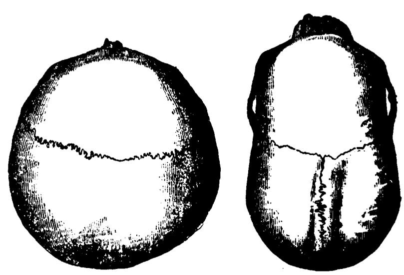
Article VII.—DOLICHOCEPHALY AND BRACHYCEPHALY IN THE LOWER MAMMALS.[1]

By HENRY FAIRFIELD OSBORN.

Skulls are classified according to their cephalic indices into three groups: dolichocephalic, mesaticephalic, and brachycephalic.—*Nature*, XXXIII, 4.

Dolichocephaly and brachycephaly are familiar terms in anthropology. The cephalic index, or ratio of breadth to length, marks a profound distinction between different races of man; it is one of the most stable of all racial characters, although no satisfactory theory or explanation of what it signifies has thus far found general acceptance among anthropologists.[2]

These facts render it all the more surprising that *skull* proportion, distinguished from *cranial* or brain-case proportion in man, has not been considered more generally by students of the lower mammals as of great value in the separation of races, as well as of profound morphological significance. It is true that certain mammals have been described as short- or broad-skulled, others as long- and narrow-skulled. As early as 1873 Kowalevsky demonstrated the elongation of the face in Ungulates for the accommodation of long-crowned teeth, but this does not explain the long free space or diastema in front of these teeth; the studies of Nathusuis (1864) on the proportions of the skull in races of pigs,



A. B.

Fig. 1. Human Crania of dolichocephalic and brachycephalic type. After Huxley.

[1] Presented in Abstract before the New York Academy of Sciences, Nov. 8, 1901, and before the National Academy of Sciences, Nov. 13, 1901.

[2] I make this statement on the authority of Dr. A. Hrdlička of the American Museum of Natural History.

are well known; in 1895 Nehring referred to the long- and short-skulled races of dogs associated with early races of man; quite recently also Wortman (1899) has distinguished between short- and long-jawed races of Tertiary dogs, and Matthew (1901) has distinguished between the long- and short-skulled races of Oreodonts, as a basis of classification. These are a few examples, among many which might be found, of attention directed to such facts; but I am not aware of any general application of *dolichocephaly and brachycephaly as factors in cranial and dental evolution, and as correlated with the proportions of the limbs and habits of feeding.*

At all events the principle has not found its way into palæontological literature, with which I am fairly familiar, and was reached by myself independently and purely inductively while engaged upon the phylogeny of the Rhinoceroses (1900). After accumulating a great number of facts on the evolution of this baffling group the correlation of long limbs with long skulls (dolichopody and dolichocephaly) and short limbs with short skulls (brachypody and brachycephaly) suddenly appeared as a key, and was expressed in the following statement:

"It [the classification adopted] sets aside several homoplastic parallel characters heretofore employed in Rhinoceros evolution and attempts to establish a firmer basis *in the fundamental proportions of the skull, whether dolichocephalic or brachycephalic, in the correlated proportions of the body, and in the location of the horn cores.* These characters are found to be more distinctive of phyla than the pattern of the molar teeth."

The full bearings of the principle were only partly perceived at this time, and singularly enough I turned to the study of the Titanotheres for the Geological Survey Monograph without reference to my previous work on the Rhinoceroses and wholly unbiassed by any theory. Aided by Mr. W. K. Gregory about eighty-five skulls were measured and studied, hundreds of facts were noted which seemed to have no particular significance; finally all these data were put together and the conclusion was reached again, inductively, that *dolichocephaly and brachycephaly are among the dominat-*

ing factors in the skull of the Titanotheres, and that they are probably correlated with similar proportions in the trunk and limbs. This result, as in the case of the Rhinoceroses, placed the whole evolution of the family from its beginning in the Eocene period in a new light and directly contradicted the phylogenetic conclusions I had reached in 1896.

Considering the principle, however, as only a working hypothesis I read through various memoirs of Cope, Marsh, Earle, and others on the structure of the skull in the Rhinoceroses and Titanotheres and was delighted to find that dolichocephaly and brachycephaly explained a vast number of detailed facts which had been recorded abstractly by these authors without reference to their significance, not only in all parts of the skull but in the teeth. In many respects the teeth were proved to conform to the skull rather than the skull to the teeth.

In brief, the proportions of the skull were found to involve, as one might anticipate, every bone in the skull, but more particularly nasals, horns, zygomatic arches, palate, relations of the foramina in the base and side of the skull, the occiput, the mastoid and other bones around the auditory meatus, the premaxillary and mandibular symphyses, the jaw, the diastemata between and behind the teeth, the number and shape of the teeth, the shape, number, and relations of the cusps, and even, it would appear, the cingulum around the teeth. In other words all these characters were found correlated in many animals with the proportions of the skull, and consequently with the structure of the limbs and feet,— a quite unlooked for illustration of Cuvier's famous law of correlation.

This gratifying result suggested a superficial review of the mammals in general in respect to the same factors. The conclusions reached in this paper are therefore of a preliminary character.

We may first consider the skull in itself, then the correlation of its proportions with similar proportions in other parts of the body, the exceptions to such correlation and special reasons for them, some of the apparent causes of dolichocephaly and brachycephaly, and finally some of the facts which await explanation.

In applying these terms to the lower mammals we refer to the *skull as a whole*, whereas in man the reference is only to the *cranium*.

The Long and the Broad Skull.

The three skulls photographed below from the American Museum collection (Fig. 2) are three nearly contemporary species of Eocene Titanotheres which illustrate admirably dolichocephaly, brachycephaly, and the neutral or inter-

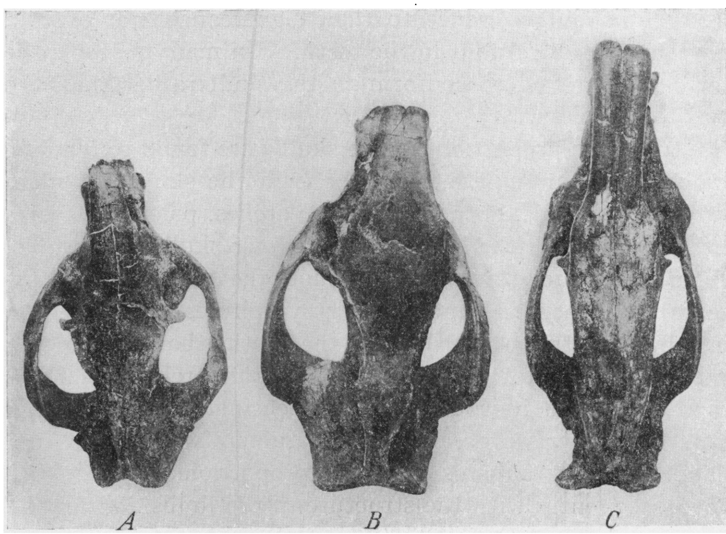


Fig. 2. Eocene Titanotheres. *A*, Brachycephalic, *Palæosyops paludosus*. *B*, Mesaticephalic, *Limnohyops manteoceras*. *C*, Dolichocephalic, *Telmatotherium cornutum*.

mediate condition of mesaticephaly. The species are the classic *Palæosyops paludosus*, the extremely long and narrow *Telmatotherium cornutum*, and the moderately broad *Limnohyops manteoceras*. The first and second species are believed to belong to side lines which became extinct; the third, more generalized, form is now believed to have given origin to the Oligocene Titanotheres, although this inference awaits confirmation. The skulls of these Titanothere species differ from those of man and of Rhinoceroses in the fact that the cranium, or skull proper, does not vary in width so widely as the cheek arches or zygomata. It is chiefly the enormous expansion of the latter bones in *Brontotherium elatum* which makes the skull actually as broad as it is long. But while mainly a zygomatic expansion, that there is a very pronounced cranial and facial expansion is attested by the broad palate, relatively short and crowded dental series, transversely expanded horns, abbreviated nasals, short malar bridge in front of the orbit, abbreviated mastoid and paroccipital portion behind the external auditory meatus, transversely expanded occiput and occipital condyles, broad exoccipital and postglenoid processes, short, deep, and thick lower jaw with less prominent angle. There is no mistaking a typical brachycephalic for a dolichocephalic jaw, every contour and proportion is different. Analogous differences are observed among the Rhinoceroses.

The above are only a few of the correlated effects of skull proportion. In the comparison of all the Titanotheres from the beginning to the end of their remarkable history it is found that the primitive and central types are mesaticephalic, and the divergence is into brachycephaly and dolichocephaly. The following table presents the extremes of structure as observed especially in the Titanotheres.

Correlated Skull Characters.

	BRACHYCEPHALY.	DOLICHOCEPHALY.
	Teeth.	
Dental series.......	Crowded...........	Elongate.
Diastemata.........	Closed..............	Increased.
Anterior premolars, pm $\frac{1}{1}$	Suppressed. One fang suppressed.	Persistent and spaced. Two fangs retained.
Intermediate tubercles of molars.....	Persistent..........	Reduced.
Opposite dental series..............	Convergent or arched	More parallel.

	BRACHYCEPHALY.	DOLICHOCEPHALY.
	Teeth.	
Grinding teeth......	Shortened and widened.	Lengthened and narrowed.
Cingula between teeth............	Suppressed.........	Persistent.
Canine teeth........	Rounded and broadened............	Elongate compressed.
Incisor series.......	Placed transversely..	Converging anteriorly.
	Skull.	
Whole skull........	Shortened and broadened.	Lengthened and narrowed.
Most of the constituent bones.	Shortened and broadened.	Lengthened and narrowed.
Palate.............	Broadened and flattened.	Narrowed and transversely arched.
Nasals.............	Shortened and spreading.	Long with incurving or straight sides.
Malar and maxillary bridge over infra-orbital foramen.	Narrowed..........	Broadened.
Infra-orbital foramen.	Not seen on side of face.	Conspicuous on side of face.
Lachrymal bone....	Crowded into orbit..	Exposed on side of face.
Lachrymal canal....	Crowded into orbit..	Seen on edge of orbit.
Zygomata..........	Broadened, especially in the "buccal plates"; in section broad rather than deep.	Elongate and vertically deepened; in section deep rather than broad.
Areas of insertion of masseteric and temporal muscles.	Increased.........	Balanced or retained.
Mastoid portion of periotic..........	Abbreviated.......	Exposure persistent.
Exoccipital, post-glenoid, and post-tympanic processes.	Broadened........	Deepened and narrowed.
Post-glenoid and post-tympanic processes.	Approximated, especially below, enclosing the external auditory meatus.	External auditory meatus not closed below.

	BRACHYCEPHALY.	DOLICHOCEPHALY.
	Skull.	
Tympanic bulla.....	Thrust inward......	Exposed laterally.
Foramen ovale and f. lacerum medius...	Approximated......	Separated by a bridge of bone.
Foramen lacerum medius and f. lacerum posterius....	Approximated......	Separated by periotic.
Alisphenoid canal...	Abbreviated........	Elongate.
Presphenoid........	Abbreviated........	Elongate.
Vomer.............	Thrust backward....	
Premaxillary symphysis...........	Abbreviated.......	Elongate.
Horns............	Transversely expanded...............	Not so expanded.
	Jaw.	
Jaw...............	Shortened, thickened, deepened.	Elongate, with straight lower border and backwardly produced angle.
Area of insertion for temporal muscle..	Reduced...........	Balance maintained.
Coronoid process....	Reduced...........	Lengthened antero-posteriorly.
Mandibular symphysis.............	Abbreviated.........	Elongate.

The above characters are chiefly observed in the Titanotheres, in which the most careful comparison of dolichocephalic and brachycephalic skulls has been made.

Many characters in the first column apply with equal force to the Primates which are progressively brachycephalic, marking the passage from the more dolichocephalic Lemurs and Baboons to the more brachycephalic Lemurs, Monkeys, and Apes.

On the other hand many characters in the second column apply also among the Horses, which are progressively dolichocephalic.

Many of these characters also distinguish the brachycephalic from the dolichocephalic Rhinoceroses.

There are, however, notable exceptions, as shown below.

Unequal Elongation of Face and Cranium.

When we compare a long-skulled with a short-skulled Rhinoceros the skull of the latter appears compressed antero-posteriorly, as if composed of india-rubber, all the parts being affected alike (Fig. 3). But although both the face and the cranium in the Rhinoceroses and Horses appear to be affected, this is by no means a general principle. In the Titanotheres the face is shortened and the cranium greatly elongated, so

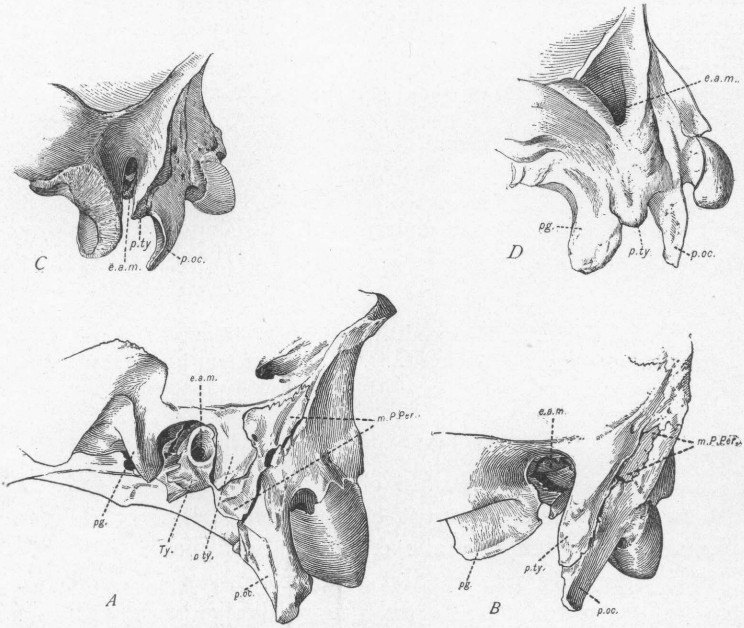


Fig. 3. Influence of progressive brachycephaly upon the ear region of Perissodactyla. *A*, Dolichocephalic, *Equus caballus*. *B*, Mesaticephalic, *Tapirus*. *C*, Dolichocephalic, *Ceratorhinus sumatrensis*. *D*, Brachycephalic, *Rhinoceros sondaicus*. Disappearance of mastoid portion of periotic, *m. P. Per*, and enclosure of auditory meatus, *e. a. m.*, inferiorly.

that the distance between the orbit and the external auditory meatus is very great, the molar teeth extending back beneath the orbit. In the Horses, on the other hand, the face is greatly elongated and the cranium only moderately so, and this is true of by far the greater number of long-skulled Ungulates. Such unequal elongation of different regions of the skull will no doubt be found by examination in every family of mammals.

But every exception has some special adaptive significance. For example, the nasals in the Tapirs and the Proboscidea are abbreviated not as an expression of brachycephaly but in correlation with a prehensile upper lip or proboscis. The mastoid portion of the periotic, generally exposed in dolichocephalic types such as the Horses, persists also in the brachycephalic Primates, for the insertion of one of the most important muscles of the neck. The contrasts of brachycephalic with dolichocephalic characters, brought out in the above table, therefore are limited in the various mammalian families by special adaptive conditions.

SIGNIFICANCE OF DOLICHOCEPHALY.

The earliest known Ungulates have moderately elongate or mesaticephalic skulls, from which it follows that brachycephaly and dolichocephaly are for the most part secondary.

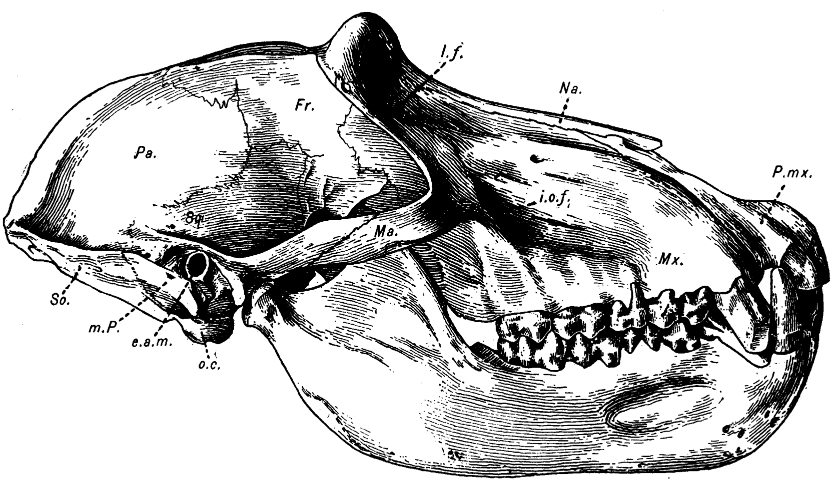


Fig. 4. Dolichocephalic skull of Baboon, *Cynocephalus olivaceus.*

In Titanotheres and Rhinoceroses they are definitely progressive characters. The earliest horses (*Protorohippus, Hyracotherium*) are already specialized in the direction of dolichocephaly, which, it is important to note, is here accompanied by progressive lengthening of limb.

In fact, dolichopody, in the broad sense of lengthening of limb, is in general an adaptation to cursorial habits and speed, associated with life on the plains, cropping front teeth, absence of defensive weapons.

The lengthening of the limb for the purpose of speed appears in fact to have been the prime correlate of the lengthening of the skull. There are numerous cases where the elongation of the limbs and of the skull have developed *pari passu*, notably in the case of the long-limbed Rhinoceroses as well as in the Horses. It is also very characteristic of the long-limbed Elotheres, which have extraordinarily long skulls, in contrast with the remotely related Pigs. We reach the conclusion that both dolichocephaly and lengthening of neck, in order to enable grazing animals to reach the ground, may be primarily due to lengthening of limb.

Exceptions to the Correlation of Dolichocephaly with Dolichopody and of Brachycephaly with Brachypody.

There are, however, many exceptions to the correlation of long limbs and long skulls. Among the races of men, although there are notable cases of such correlation, there are also notable exceptions; the bipedal Primates generally offering an exception to quadrupedal mammals.

Again, the cursorial long-limbed Hyracodonts are a family of Rhinoceroses with very long limbs and short skulls. Here, however, brachycephaly is compensated for in a measure by length of neck, possibly also by a substitution of browsing for grazing habits. The most remarkable elongation of the limbs and neck, in connection with an only moderately elongate skull, is in the Giraffes, which are typical tree-browsers. The opposite combination of long limbs with very long head and short neck is exemplified in the Moose (*Alces*), habitually a browser, which, like the giraffe, extends its mouth to the ground with great difficulty. Whenever an animal acquires the shrub- or tree-browsing habit, therefore, as in the case of *Rhinoceros bicornis*, a new factor is introduced. Other families in which the browsing habit appears to have been acquired secondarily are the Chalicotheriidæ, Agriochœridæ, and Anoplotheriidæ.

Again, among the Carnivora the Dogs are typically long-skulled and long-limbed or cursorial animals. A dog feeds in a standing position, the food held upon the ground by the fore feet, the limbs being somewhat flexed. In this family the skull and limb correlation seems to hold good. Moreover, the short-faced dogs are generally short limbed. Cats, on the other hand, present a decided exception, because they are brachycephalic and dolichopodal, the Cheetah, for example, having an exceptionally short skull and elongate limbs. We should recall, however, that cats always feed in the recumbent or semirecumbent position, crouching or lying down. Thus the abbreviation of the Cat skull is correlated with the functions of the teeth and not with those of the limbs, because the Cats have a special position in feeding. Similarly the Proboscidea are extremely brachycephalic and long-limbed, but the exceptional elongation of the limbs is compensated for by the development of a proboscis.

To sum up, the numerous exceptions to the correlation of skull and limb proportions are mostly capable of special adaptive explanations, and, as we shall see below, when correlation does occur it is probably adaptive also. In brief, there is no innate, invariable law of correlation; skull and limbs may or may not be dependent upon each other.

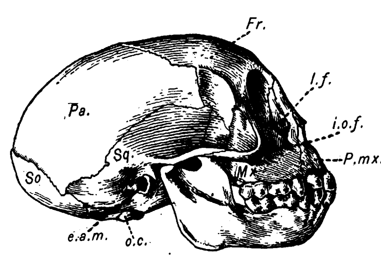


Fig. 5. Brachycephalic skull of Monkey, *Maccacus* sp., juv.

But when such correlation does occur, as in *Telmatotherium* or *Hyopotamus* on the one hand, or in *Teleoceras* on the other, it is likely to affect the whole skeleton: length of the cervical and dorsal vertebræ, form of the scapula and ilium, length of the metapodials. So complete is the correlation that we can, for example, immediately distinguish between the elements of the pes of a long-skulled and of a short-skulled Rhinoceros.

Eliminating all the exceptions, there appear to have been two general causes for the elongation of the skull. First, the elongation of the face for the accommodation of very long hypsodont grinding teeth in front of the orbit, as observed by Kowalevsky. Second, the elongation of the skull as a whole, correlated with the elongation of the limbs, an adaptation to grazing and cursorial habit.

No Adequate Theory of Brachycephaly.

It is much more difficult to account for progressive brachycephaly. An adequate theory of its causes is still wanting, as shown by the following examples:

Among Primates the shortening of the skull takes place *pari passu* with the increasing use of the manus in conveying food to the mouth; this is well illustrated by the contrast between the quadrupedal, long-skulled baboons and the more bi-pedal short-skulled monkeys.

We are especially at a loss to offer any adequate explanation of the causes of progressive brachycephaly in mammals which seem to suffer thereby a reduction and compression of the dental series. In certain Titanotheres and Rhinoceroses the shortening of the skull seems to crowd and diminish the usefulness of the teeth, an apparently inadaptive process.

The observations of Nathusius led him to the conclusion that among the Suidæ abundant food tended to shorten and broaden the head and the face. Darwin observes that domestication tends to shorten the bones of the face in many animals.

Among Carnivores, and among the long-horned Titanotheres, abbreviation of the skull favors the effective use of the canine tusks and of the paired horns respectively. But brachycephaly also develops to an extreme in certain defenceless types, such as *Cyclopidius* among the Oreodonts.

Further investigation and comparison may produce some general law.

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