JOURNAL OF MAMMALOGY

Published Quarterly by the American Society of Mammalogists

VOL. 12 | FEBRUARY, 1931 | No. 1

NEW CONCEPTIONS OF SPECIES AND GENERA, AND OF CLASSIFICATION, DISCOVERED IN THE EVOLUTION OF THE TITANOTHERES[1]

By HENRY FAIRFIELD OSBORN

It is interesting to observe the bearing of palaeontology on the development of various branches of biology, especially upon the science of mammalogy.

Osborn began intensive palaeontological research in the year 1890. In June, 1900, he succeeded Marsh in the United States Geological Survey and at once began a most intensive geological, anatomical, and biological research on the evolution of the family of odd-toed ungulates, known as Titanotheres, from a name applied by Joseph Leidy to the jaw bone of *Menodus*, discovered in 1846. The monograph[2] covered twenty-nine years of research and exploration in New Mexico, Colorado, Utah, Wyoming, South Dakota, Montana, the Gobi Desert, Burma, and the Balkans. The evolution of the titanothere heredity germ was followed over a period estimated by geologists at ten million years, beginning with the *Eotitanops*, only a few inches in height, and ending with *Brontops*. Comparison is made with the family tree of the odd-toed ungulates known as Perissodactyls, showing the adaptive radiation of nine families and thirty-five sub-families as compared with the Titanotheres which, within a single family, include twelve

[1] Presented at the Twelfth Annual Stated Meeting of the American Society of Mammalogists, American Museum of Natural History, May 21, 1930.

[2] Osborn, Henry Fairfield: "The Titanotheres of Ancient Wyoming, Dakota and Nebraska." United States Geological Survey, Monograph 55. Washington, D. C., 1929.

sub-families, twenty-six genera, and one hundred and six species, many of which are arrayed in close phylogenetic order.

This affords an unprecedented opportunity to contrast the zoological concept of Linnaeus of contemporaneous species with the modern palaeontological concept of the origin of species, sub-families and families, observed in close detail through long periods of time. With the aid of very able colleagues, such as William K. Gregory, each minute part of many organs has been examined and precisely measured from its origin in the germ plasm to its increasing importance into what may become an absolutely dominating character of the organism. This progression or retrogression is absolutely continuous and invariably definite and determinate rather than fortuitous. Characters rise and fall under thirteen principles, four of which have been absolutely confirmed in the course of preparation of this monograph. The close analysis of thousands of separate characters gives us an entirely new concept of the origin of what has been called in palaeontology the "ascending mutation"[3] of a species and genus. The concept first put forward by Waagen in 1869 is that such mutations are so inconspicuous that we would not notice them were it not for their more distinct appearance in the next higher geological step.

Inasmuch as every single one of the thousands of characters in the dental and skeletal mechanism is independently evolving, although constantly interrelated with all the other characters, *a species is defined by one or more characters which reach a conspicuous stage either of progression or of retrogression.* This is as true of palaeontologic as of zoologic species, although in the latter case our definition is according to the eyes of Linnaeus and of Darwin, whereas in this palaeontologic monograph we trace back to their origin the inconspicuous antecedents of each specific character.

Characters of two kinds. It happens in the odd-toed ungulates, such as horses, rhinoceroses and Titanotheres, as well as in all other fossil mammals, that conspicuous characters mostly are of two kinds: first, *allometrons*, or changes of proportion, such as are seen in the changes of proportion of the skull and in the reproduction or enlargement of parts of the limbs; second, *rectigradations*, adaptively arising as new characters. In Miller's splendid work, "Mammals of Western Europe," can be found all the species defined by what may be called either "recti-

[3] This term of Waagen refers to the continuous progressive movement in a single character and is quite distinct from the sudden saltatory "mutations" of DeVries.

gradations" or "allometrons," that is, either by single characters or by changes of proportion. Also, Leidy, Cope and Marsh independently divided Eocene and Miocene horses by their successive "rectigradations" or "allometrons."

Characters of different velocities. In the Titanotheres we enjoy an unparalleled opportunity of discovery that *a genus consists not only of its visible generic characters but of invisible potential characters in the germ which may lie dormant for hundreds or thousands of years until they emerge.* Moreover, each genus is characterized by different rates or velocities in the progression or retrogression of the thousands of characters which are embraced in its hereditary germ. We see this illustrated for example in the horns of mammals; a horn is a rectigradation. The horn and teeth rectigradations are hurried forward in one generic or sub-family phylum, while they are closely guarded within the germ plasm of another generic or sub-family line dwelling in the same geographic region. These origins of rectigradations are controlled by ancestral or potential heredity, whereas the origins of allometrons or changes of proportion respond directly to adaptive changes in environment.

Thus it may be claimed without exaggeration that the Titanothere Monograph solves all the principles of all the hard parts involved in the origin of "ascending mutations" of species, of genera, of sub-families, and so forth. There is a firm and undeviating orthogenetic order in the entire animal mechanism, but the underlying causes of this order are only partly known.

The above is a very concise and condensed statement of changes which are illustrated in great detail in the Monograph, not only as they occur among Titanotheres but among other quadrupeds, both odd-toed and even-toed.

As shown graphically in illustrations in the Monograph, the family tree of the Titanotheres runs over a period estimated at 10,000,000 years, beginning with *Lambdotherium*, progressing into *Eotitanops* and finally into *Brontops*, and then branching out. These facts were obscure until twenty-one geologic life zones of lower Tertiary time were specifically and remarkably analyzed by Dr. William D. Matthew, aided by Walter Granger, through Osborn's work on a group with which he was especially familiar. Through Dr. William K. Gregory's skillful analysis of the musculature of *Brontops robustus*—a research of three or four years' length—the late Erwin Christman succeeded in producing a marvelous restoration of this animal, giving us the first complete musculature of an extinct mammal.

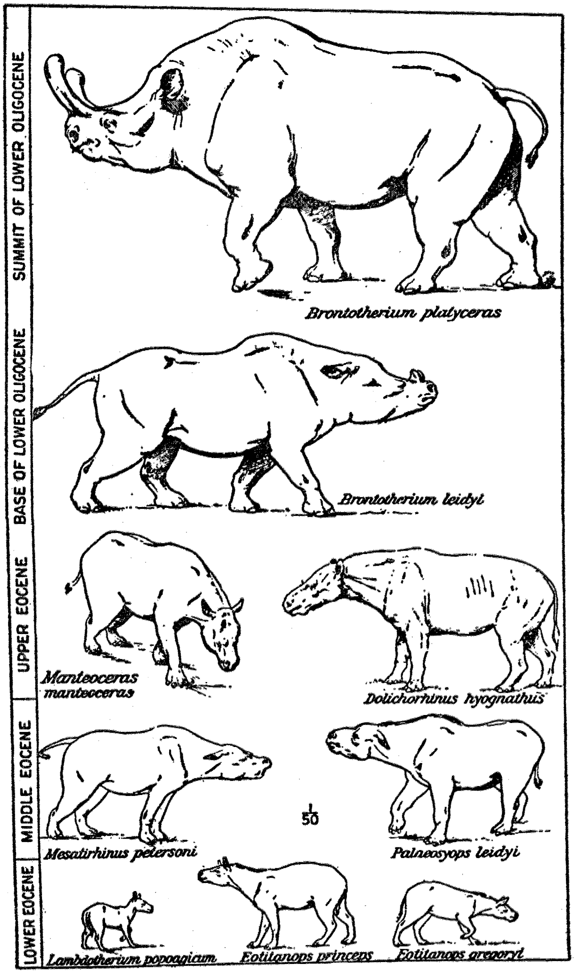

FIG. 1. RESTORATIONS OF NINE SPECIES OF TITANOTHERES FROM THE LOWER, MIDDLE AND UPPER EOCENE AND THE LOWER OLIGOCENE

Drawn by Mrs. E. M. Fulda. About one-fiftieth natural size

Osborn's analysis of the family tree of the Perissodactyls, or odd-toed ungulates, illustrates the principle of "adaptive radiation" and of "parallelism" in foot and dental structures brought about by similarity in environment. The Perissodactyls are divided into "cursorial," "forest-

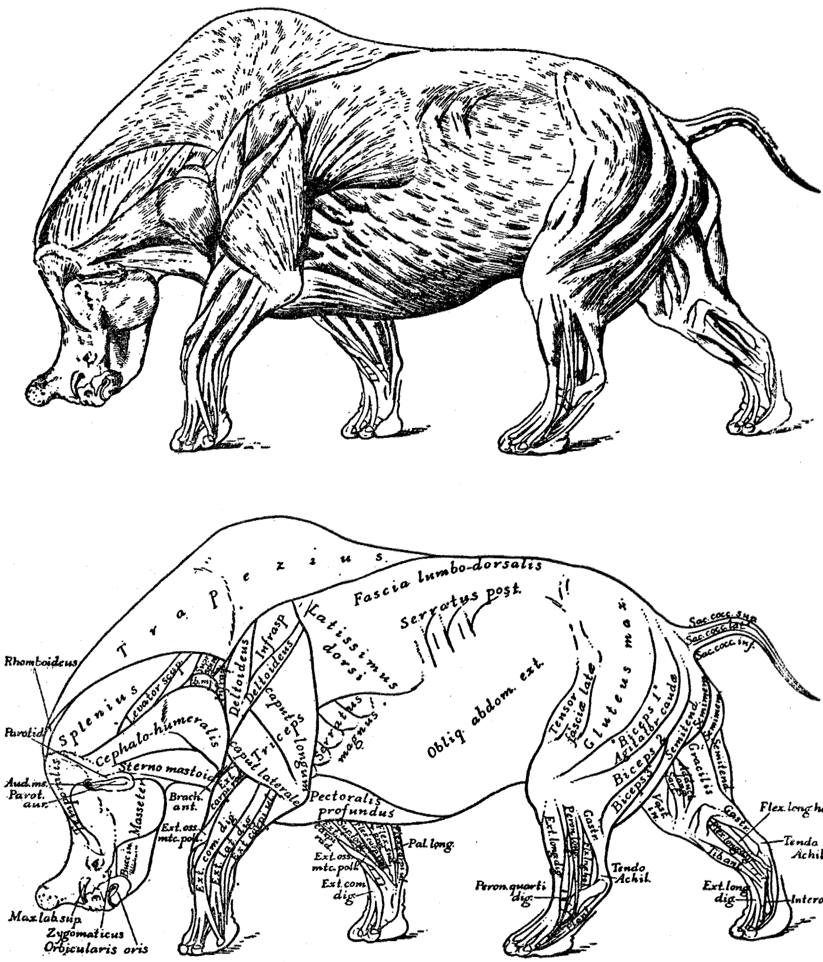

Fig. 2. Restoration of the Superficial Muscles of the Body of an Oligocene Titanothere (Brontops cf. B. robustus) after the Removal of the Panniculus

Drawn by Erwin S. Christman. About one twenty-fifth natural size

living," "aquatic," "mediportal" and "graviportal" types, all of which assume similar characters under the law of parallelism, although they

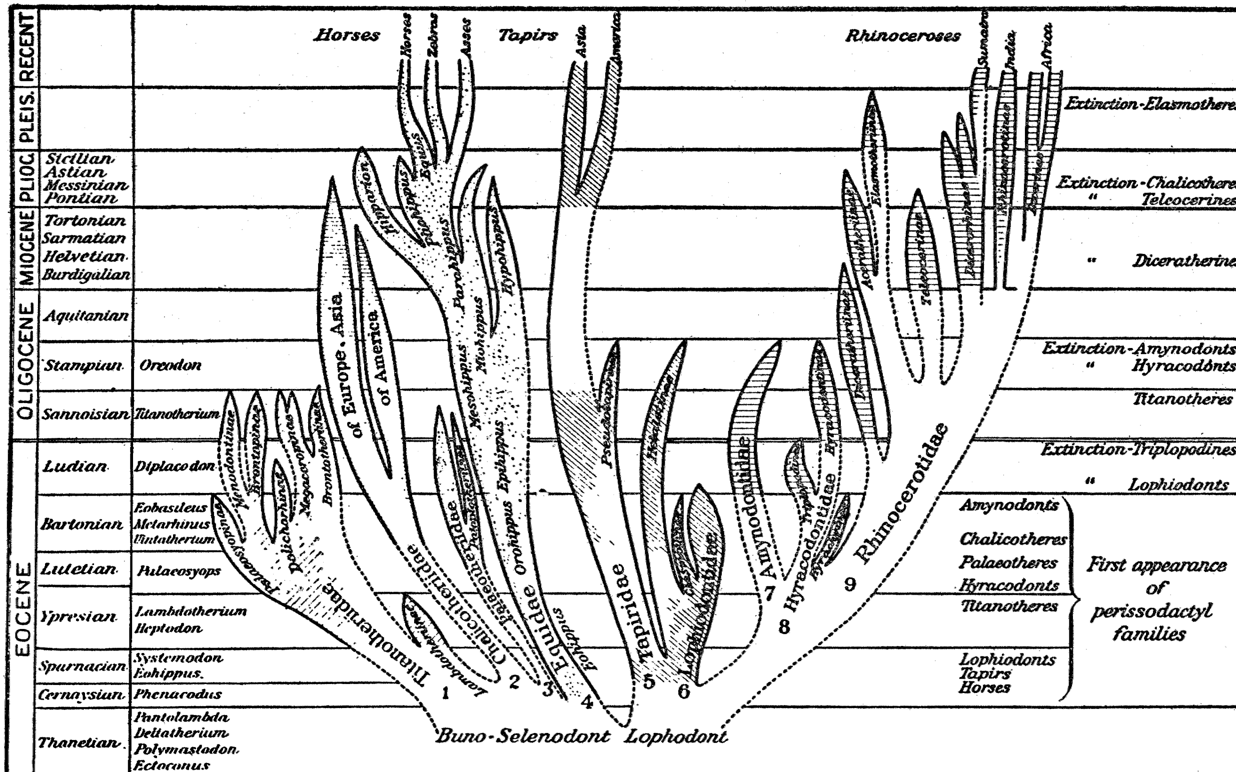

FIG. 3. THE FAMILY TREE OF THE PERISSODACTYLA. SUCCESSIVE APPEARANCE IN LATITUDE 40° OF REPRESENTATIVES OF THE NINE FAMILIES. SUCCESSIVE EXTINCTION OF SIX FAMILIES. SURVIVAL OF THE THREE EXISTING FAMILIES—THE HORSES, TAPIRS, AND RHINOCEROSES

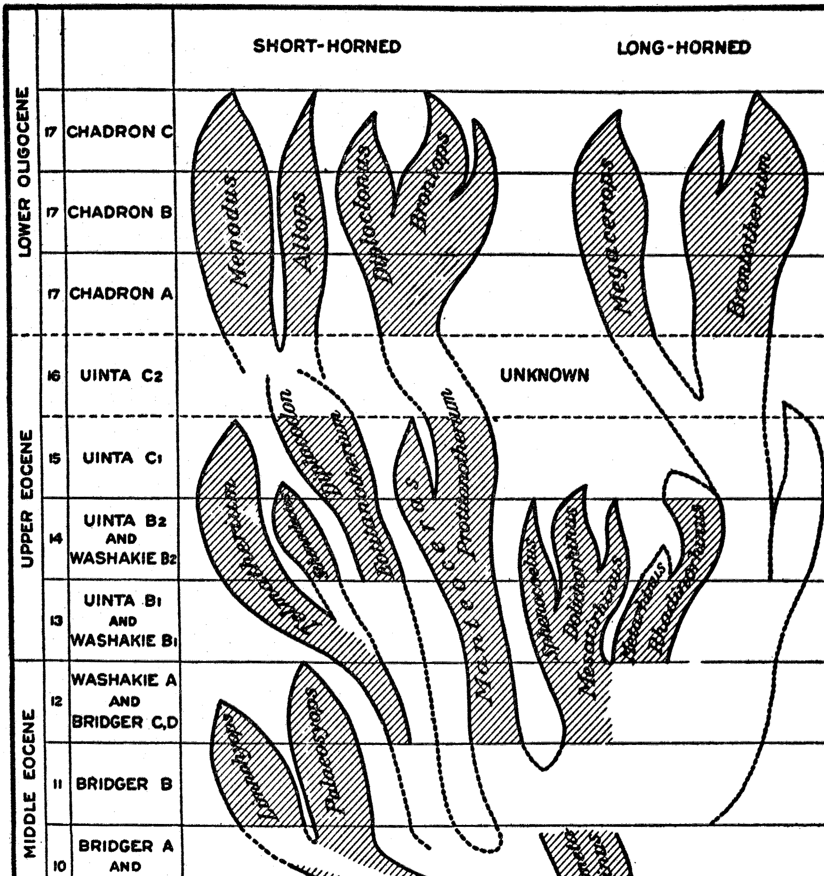

FIG. 4. THE FAMILY TREE OF THE TITANOTHERES, SHOWING THE RELATION BETWEEN THE BRANCHES (PHYLA), SUB-FAMILIES, AND GENERA, AS KNOWN TO SCIENCE IN 1919. THE SHADED AREAS SHOW CONNECTIONS THAT ARE WELL ESTABLISHED; THE DOTTED LINES SHOW GAPS THAT REMAIN TO BE FILLED BY FUTURE DISCOVERY, ESPECIALLY IN THE UINTA FORMATION OF UTAH

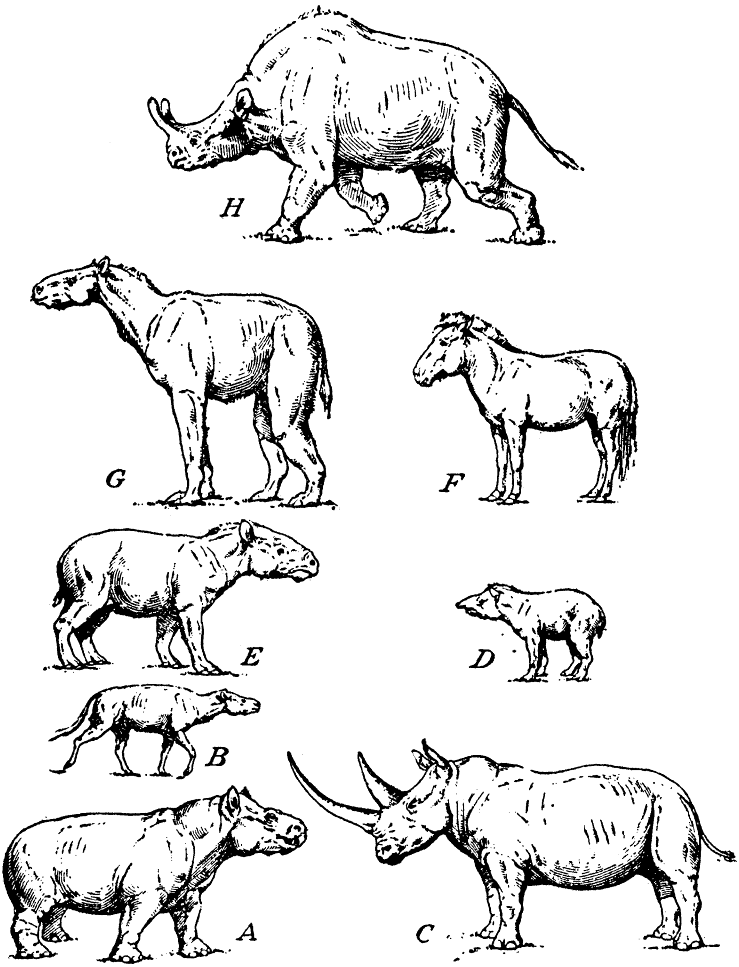

FIG. 5. OUTLINES OF THE BODY FORM OF THE PERISSODACTYLS, DRAWN TO THE SAME SCALE. THE LARGEST KNOWN MEMBER OF EACH FAMILY IS SELECTED FOR COMPARISON. THE ANIMALS ARE GROUPED ACCORDING TO THEIR NATURAL RELATIONSHIPS, AS INDICATED ESPECIALLY BY THE PATTERN OF THE MOLAR TEETH, AS FOLLOWS:

RHINOCEROTOID GROUP: *A*, *Metamynodon*; FAMILY AMYNODONTIDAE; GRAVIPORTAL; AQUATIC; LOWER OLIGOCENE. *B*, *Hyracodon*, FAMILY HYRACODONTIDAE; CURSORIAL; MIDDLE OLIGOCENE. *C*, *Ceratotherium simum*; LIVING WHITE RHINOCEROS; FAMILY RHINOCEROTIDAE; GRAVIPORTAL

TAPIROID GROUP: *D*, *Tapirus terrestris*; EXISTING TAPIR; FAMILY TAPIRIDAE; MEDIPORTAL

HIPPOID GROUP: *E*, *Palaeotherium*; FAMILY PALAEOTHERIIDAE; LOWER EOCENE; MEDIPORTAL. *F*, *Equus przewalskii*; EXISTING HORSE; FAMILY EQUIDAE; CURSORIAL

CHALICOTHEROID GROUP: *G*, *Moropus*; FAMILY CHALICOTHERIIDAE; CLAWED PERISSODACTYL; LOWER MIOCENE

TITANOTHEROID GROUP: *H*, *Brontotherium platyceras*; FAMILY BRONTOTHERIIDAE; GRAVIPORTAL; LOWER OLIGOCENE

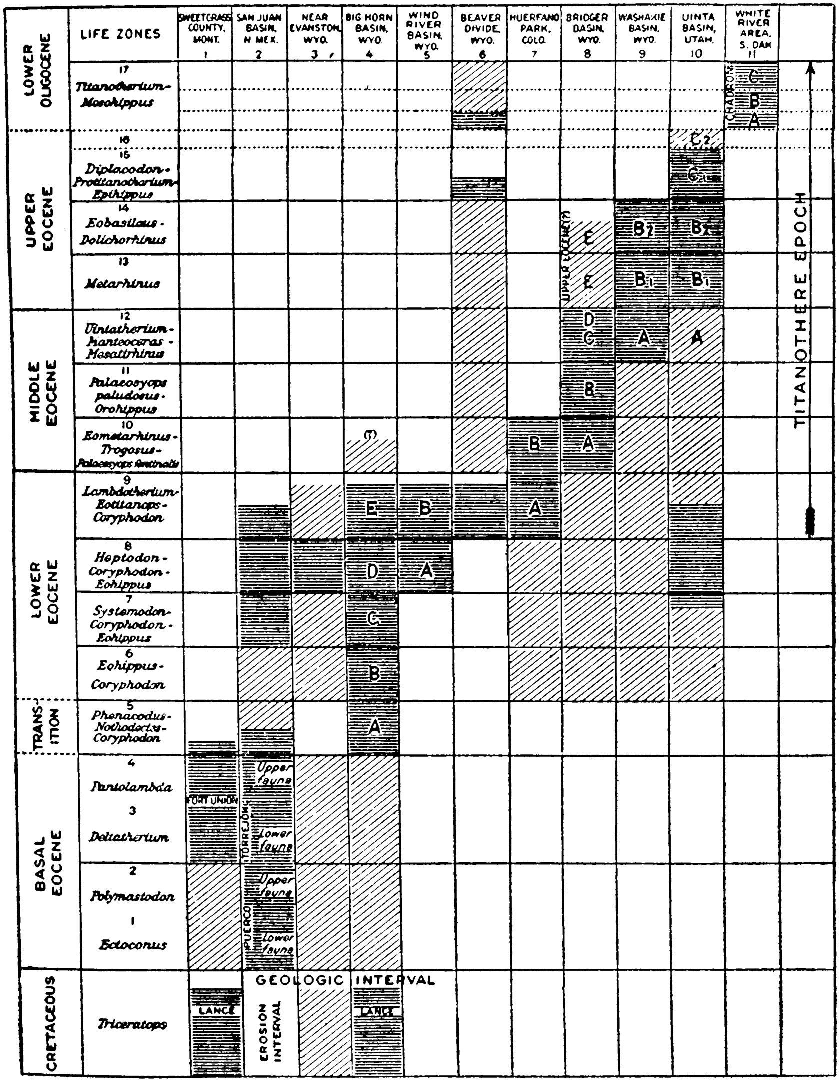

FIG. 6. EOCENE AND LOWER OLIGOCENE MAMMALIAN LIFE ZONES IN ELEVEN TYPICAL CORRELATED AREAS IN NEW MEXICO, COLORADO, UTAH, WYOMING, SOUTH DAKOTA, AND MONTANA. ARRANGED BY OSBORN (1919) AFTER ORIGINAL STUDIES MADE IN THE FIELD, CHIEFLY BY GRANGER, BUT ALSO BY HATCHER (OLIGOCENE), HILLS, PETERSON, AND GIDLEY (EOCENE). THE 16 KNOWN LIFE ZONES NUMBERED 1 TO 15 AND 17 ARE INDICATED IN THE DIAGRAM BY DARK HORIZONTAL LINES. THE NONFOSSILIFEROUS AREAS ARE INDICATED BY LIGHT OBLIQUE LINES. THE UNITED STATES GEOLOGICAL SURVEY CLASSIFIES THE LANCE FORMATION AS TERTIARY (?), EOCENE (?). THE AUTHOR REGARDS IT AS CRETACEOUS

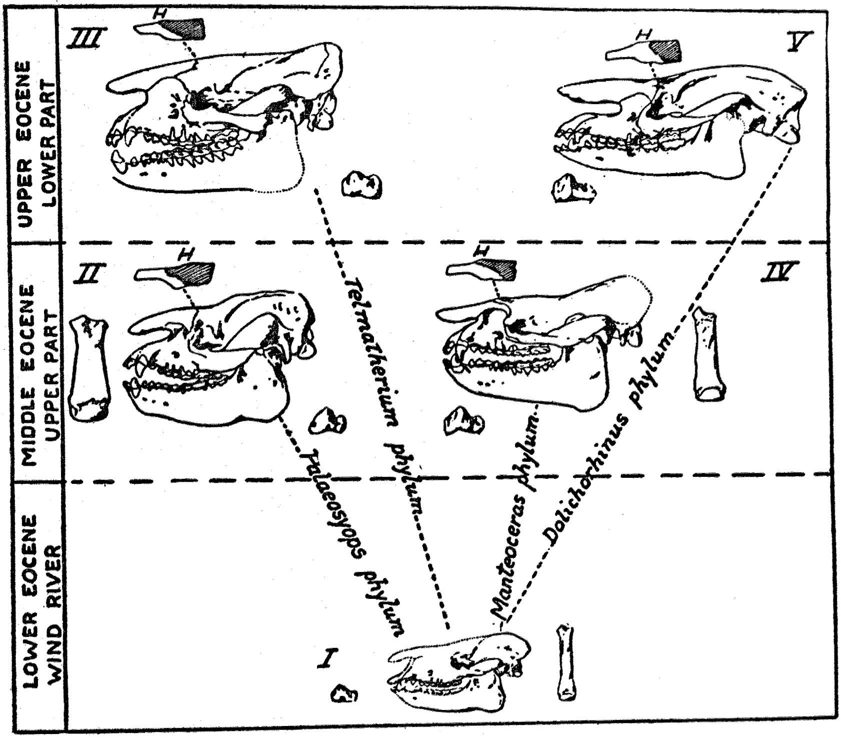

FIG. 7. RECTIGRADATIONS AND ALLOMETRONS IN THE SKULLS, TEETH, AND FEET OF TITANOTHERES. RECTIGRADATIONS ARE SHOWN ON THE CUSPULES OF THE LOWER SECOND PREMOLAR TEETH; ALLOMETRONS ARE SHOWN IN THE PROPORTIONS OF THE HEAD (BRACHYCEPHALIC, MESATICEPHALIC, DOLICHOCEPHALIC); ALLOMETRONS ARE SHOWN IN THE PROPORTIONS OF THE MEDIAN METACARPAL (DOLICHOPODAL, MESATIPODAL, BRACHYPODAL). I, *Eotitanops*, AN ANCESTRAL LOWER EOCENE MESATICEPHALIC, DOLICHOPODAL TITANOTHERE; II, *Palaeosyops*, A BROAD-HEADED (BRACHYCEPHALIC), BROAD-FOOTED (BRACHYPODAL) UPPER MIDDLE EOCENE TITANOTHERE; III, *Telmatherium*, A MEDIUM-HEADED (MESATICEPHALIC) UPPER EOCENE TITANOTHERE; IV, *Manteoceras*, A MEDIUM-HEADED (MESATICEPHALIC), MEDIUM-FOOTED (MESATIPODAL), MIDDLE EOCENE TITANOTHERE; V, *Dolichorhinus*, A LONG-HEADED (DOLICHOCEPHALIC) SHORT-FOOTED (BRACHYPODAL) UPPER EOCENE TITANOTHERE. II–V REPRESENT FOUR INDEPENDENT PHYLA OF EOCENE TITANOTHERES WHICH ARE WIDELY DIVERGENT IN THE ALLOMETRIC EVOLUTION OF THE HEAD AND OF THE FEET BUT ARE CONVERGENT IN THE INDEPENDENT EVOLUTION OF SIMILAR CUSP RECTIGRADATIONS ON THE TEETH AND SIMILAR HORN RUDIMENTS (H) ON THE SKULL

are descended from different ancestors. This family tree, when worked out with a greater degree of fineness, demonstrates that the Titanotheres are simply an early episode in the evolution of this great order, and that the maximum adaptive radiation of Perissodactyls occurred at the close of Oligocene time, and was followed by the extinction of numerous types and by the survival of only the three great existing types—the rhinoceros, the tapir and the horse.

Our knowledge of the external appearance and character of the Titanotheres is illustrated in the long-headed type, the *Dolichorhinus*, the relatively primitive horn-tipped *Manteoceras*, and the broad-headed type, *Palaeosyops*, constituting three separate generic phyla, all including a number of ascending types of species. *Dolichorhinus* presents a contrast to its ancestor, *Mesatirhinus*. Every line of Titanotheres originates with a form very much of the type of *Eotitanops*, in which the face and cranium are equal in length. There are many illustrations of rectigradations; from a hornless ancestor appear horned descendants, arising independently in entirely different phyla: there are a broad-headed phylum in which the horn appears very late, a precocious phylum in which the horn appears very early, a phylum in which the horn seems never to develop beyond a mere thickening of the nasal junction, and a long headed phylum in which the horn appears relatively early. Involved in these rectigradations is the idea of the potentiality of development of horns at different periods of geologic time, perhaps 100,000, 200,000 or 300,000 years apart. It is interesting to observe how from a face and cranium of equal size there evolves the elongated cranium of *Brontotherium*, the abbreviated face and the dolichocephalic condition. In time the horn becomes the dominating character of the organism and all parts are subsidiary to it.

A parallel study of the ontogeny of the horn in cattle, as worked out by Mr. S. H. Chubb of the American Museum, leads to the thought of the probability that all members of the family Bovidae had this general potentiality for developing horns; thus from the old concept that all horned animals are descended from animals with more or less developed horns we get the new concept that horned animals are descended from ancestors which had the potentiality for developing horns in a certain part of the cranium.

In the working out of the subject of allometrons, or changes of proportions, in the Titanotheres, most interesting results were demonstrated by living animals through modification by amputation of limbs, the influence of hormones, arrested growth of one or another bone, etc., as well as through the principle of natural selection.

The author of the Titanothere Monograph welcomes this opportunity to pay his tribute of appreciation to the large number of men and women who helped in the preparation of the great work, also to the liberality and large-mindedness of the United States Geological Survey in devoting no less than nine years to putting it on the press and, finally, to the genius of Roy Chapman Andrews, who in the Desert of Gobi fulfilled the prediction made in the early chapters of the work that the center of dispersal of the Titanotheres would be found, not in North America, but in central Asia. The author's parting word to Andrews was, "I hope you will find the Titanotheres;" Andrews' first message from Asia announced, remarkably, "I have found the Titanotheres" (the expedition's first fossil was an Upper Eocene *Protitanotherium*)! It is a coincidence that the first fossil mammal seen by the author as a youthful explorer at the age of nineteen was a Titanothere of the Bridger Beds of Wyoming.

THE LOUISIANA MUSKRAT

By Arthur Svihla and Ruth Dowell Svihla

[Plates 1–2]

This paper aims to record those data of scientific significance obtained while we were investigating the life history and habits of the Louisiana muskrat, *Ondatra rivalicia* Bangs,[1] during the years 1925–1927. The work was performed under the general supervision of the Louisiana Department of Conservation along lines suggested by the U. S. Biological Survey. A group of Louisiana men, interested in the muskrat industry and organized as the Louisiana Fur Industries, Incorporated, bore a portion of the expense for this investigation. Some of the more practical results of these studies have been given publicity from time to time by the Department of Conservation. The authors here wish to acknowledge their indebtedness to E. W. Nelson and Vernon Bailey of the Biological Survey, and to Julius P. Hebert of Morgan City, Louisiana, for many courtesies.

Apparently the first mention of muskrats in literature, according to Hollister, was made by Captain John Smith in 1612, when he described the commodities of Virginia.[2] From data compiled by H. B. Lotz, 1700 appears to be the earliest date of mention of the muskrat in Louisiana.[4] In the account by Father Gravier of the Society of Jesus of his