

A REVIEW OF THE RHINOCEROSES WITH A
DESCRIPTION OF APHELOPS MATERIAL
FROM THE PLIOCENE OF TEXAS

BY

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[A posthumous paper edited by R. A. STIRTON]

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FOREWORD

This revision of the rhinoceroses was the last paleontological work done by William Diller Matthew at the University of California. Fortunately the manuscript was nearly completed before his death, and its original form has been kept except for details of arrangement.

In accordance with Dr. Matthew's wishes I have prepared this paper for the press. Special acknowledgments are made to Barnum Brown, of the American Museum of Natural History, for measurements of *Aphelops mutilus*, *A. megalodus*, *Peraceras superciliosus*, and *Teleoceras fossiger*, all type specimens; to O. A. Peterson, of the Pittsburgh Museum, for measurements of *Aphelops ceratorhinus*, also a type, and to V. L. Vander Hoof for assistance in obtaining measurements from the specimens at the University of California. The photographs were taken by W. C. Matthews, University photographer, and the drawings were made by Owen J. Poe.

R. A. STIRTON.

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INTRODUCTION

This is the fourth of a series of articles¹ dealing with the Pliocene formations and mammals of northern Texas, chiefly based upon collections made in or near Hemphill County.

It is intended to deal with the Artiodactyla, Proboscidea, and the remaining carnivora and rodents in subsequent contributions, the entire series presenting a typical Lower Pliocene plains fauna with a critical study of the taxonomic and ecologic relations of the principal groups included.

The collections described and figured are chiefly in the Museum of Paleontology, University of California, but comparative studies of collections from Hemphill County and other localities made by the Colorado Museum of Natural History, the American Museum of Natural History, the museums of the University of Kansas, and the University of Nebraska have been of great aid in these researches. I take pleasure in expressing my appreciation of the friendly cooperation of the staffs of these institutions, who have given the freest access to their collections, published and unpublished, and facilitated study and comparison of material in every way possible.

The present contribution aims primarily to describe a series of rhinoceros skulls and skeleton material. For an adequate understanding of these it has been necessary to review the general relations of the American rhinoceroses, especially of the later Tertiary. No comprehensive revision of the Tertiary and modern Rhinocerotidae has been undertaken, but some attempt is made to reconcile the diverse

¹ Preceding papers are: Osteology and Affinities of *Borophagus*, Matthew and Stirton, Univ. of Calif. Publ., Bull. Dept. Geol. Sci., vol. 19, pp. 171-216, plates 21-34, 2 figures in text, 1930; Equidae of the Pliocene of Texas, Matthew and Stirton, *ibid.*, pp. 349-396, plates 45-58, 1930. Osteology and Affinities of *Machaerodus*, Burt, *ibid.*, pp. 261-292, plates 43-50, 1931. Reed and Longnecker have in preparation a paper on the Physiography and Geology of Hemphill County, Texas.

views of various European and American authorities with the many important additions that have been made in recent years to our knowledge of later Tertiary rhinoceroses. These later discoveries, giving a far more complete and more broadly based knowledge of the osteology of various Tertiary rhinoceroses, have served to confirm some and to modify or disprove other views and conclusions of earlier writers which have been adopted in most textbooks and are thoroughly imbedded in the literature of the subject. Some of these early conclusions have been revised and partly corrected by recent writers; for others it is necessary to go back to the direct evidence of the material as now known.

GENERAL RELATIONS OF AMERICAN RHINOCEROTOIDEA

The rhinocerotoid genera of the American Tertiary fall into three well defined evolutionary stages:

A. EOCENE RHINOCEROSSES. All small or medium sized with the rhinocerotoid pattern more or less distinct in the cheek teeth, but the front teeth maintaining much of the primitive perissodactyl construction. Incisors unspecialized, small, spatulate, uniform, canines moderately enlarged and laniary. Premolars mostly primitive, non-molariform. Molars brachyodont, the rhinoceros pattern either perfected or grading into the lophiodont or primitive tapiroid pattern. Four toes usually well developed on manus, three on pes. *Hyrachyus* is the best known. In *Amynodon* (Upper Eocene) the canines are much enlarged, in *Triplopus* (Upper Eocene) they are reduced and incisiform, in both, the molars are higher crowned with more decisively rhinocerotoid pattern, premolars progressively molariform in pattern, the anterior ones reduced. Four subequal toes on manus of *Amynodon*, three in *Triplopus*. These two genera lead up into the aberrant families of *Amynodontidae* and *Hyracodontidae*. None of the American Eocene rhinoceroses so far as known foreshadow the specializations of the front teeth peculiar to the Rhinocerotidae proper, nor do any Old World Eocene types except certain species of *Caenolophus* from Mongolia.²

² While this genus is probably a composite as was suggested by Matthew and Granger in describing it, it does not seem advisable, by splitting it up into its probable elements, to burden the literature with doubtful or possibly misleading names based upon insufficiently known types. Rhinoceros literature and especially that of the Eocene rhinocerotoids is already heavily encumbered with superfluous and confusing nomenclature.

Eotrigonias recently described by Dr. H. E. Wood is based upon upper cheek teeth from the Uinta Eocene and regarded by the author as a pro-rhinocerotid. He does not, however, point out any rhinocerotid as against hyracodontid characters in these teeth. They agree with hyracodonts and differ from all known rhinocerotids in the character of M^3 and conform quite closely to some species of *Hyracodon* in the premolar pattern. Until evidence is brought forward that *Eotrigonias* had front teeth foreshadowing or agreeing with the rhinocerotid specialization, and that the forefoot was really of the type assumed by Dr. Wood, it appears necessary to place it in the group with which it conforms on its known characters. That the ancestor of *Trigonias* had cheek teeth much of this pattern is wholly probable. So did the ancestor of *Hyracodon*. But it had certain other characters that would serve to distinguish it from *Hyracodon*, and there is not the slightest evidence that *Eotrigonias* had these characters. The probabilities on present knowledge are in favor of placing this species with the hyracodonts which it approaches more nearly and which are known to occur in the Uinta.

In a subsequent contribution Wood takes occasion to register his disapproval of Matthew's views in regard to the phylogeny of rhinoceroses as indicated on a general chart representing the phylogeny of the perissodactyla as a whole. I hope to present the evidence in support of this phylogeny in a later paper; much of it has never been adequately brought together in print. For the present it is enough to say that Wood's interpretation of my diagram is not wholly accurate, and that neither here nor elsewhere has he adduced any real evidence in support of his criticism.

B. OLIGOCENE AND LOWER MIOCENE RHINOCEROSSES include three distinct families—*Amyndontidae*, *Hyracodontidae*,³ *Rhinocerotidae*, primarily distinguished by the characters of the front teeth and of the muzzle. The Oligocene amyndonts have greatly enlarged canine tusks, vestigial incisors, broad muzzles, reduced premolars, very oblique molar crests, convex foreheads, stout limbs with four subequal digits on manus, three on pes. The Oligocene hyracodonts have cropping front teeth with small incisiform canines, rounded rather delicate muzzles, molariform premolars, moderately oblique molar crests, convex foreheads, slender limbs with three digits on manus and pes, the

³ *Hyracodontidae* is regarded by some authors as a subfamily of *Amyndontidae* but this is not supported by comparison of the characters of teeth, skull and feet in the two groups.

lateral digits considerably reduced. The true rhinoceroses have $I\frac{1}{2}$ enlarged as tusks, the remaining front teeth vestigial or absent, a very characteristic wedge-shaped skull,⁴ pointed muzzles, progressively molariform premolars, moderately oblique molar crests, ectoloph of M^2 confluent with metaloph, concave forehead, moderately proportioned limbs, three toed feet with small or vestigial fifth digit preserved on some. Hyracodonts and amynodonts disappear before the end of the Oligocene, the Rhinocerotidae continuing on into the Lower Miocene. All these mid-Tertiary rhinocerotoids have retained much of the primitive proportions of carpus and tarsus, more like a modern tapir than a modern rhinoceros. All the Rhinocerotidae have short-crowned teeth with little or nothing of the supplementary crests of the molars. In the other two families there is a precocious heightening of the crown, but not carried to any great extreme before their extinction.

C. LATER TERTIARY RHINOCEROSSES (MIDDLE MIOCENE AND PLIOCENE) are distinguished by a marked broadening of the carpal and tarsal elements, short stout metapodials, massive limbs. They are mostly of large size compared with the mid-Tertiary genera, the premolars are more molariform in pattern, all the cheek teeth higher crowned, the tusks more specialized with complete disappearance of the vestigial front teeth. Although the Palaeartic and Nearctic Rhinocerotidae run on parallel lines of evolution and succession, they appear to be generically different in the later Tertiary stages; their status in the middle Tertiary is not yet clear. Whether the American genera of the later Tertiary are descended directly from Nearctic or Palaeartic ancestry has not been shown by any adequate critical comparison of the mid-Tertiary genera.

The American later Tertiary rhinoceroses are customarily divided into three genera, distinguished as follows:

Aphelops. Cheek teeth relatively brachyodont, premolars un-reduced, upper incisors vestigial (or absent), skull long to medium, occiput narrow, narial notch extended far backward, nasals hornless and pointed or retracted and reduced, limbs and feet proportioned as in modern rhinoceroses.

⁴ This peculiar type of skull is not seen in any of the Eocene rhinocerotoids. *Hyrachyus* is erroneously represented by Osborn as having a skull of this type; the true form of the skull in this genus is much as in other Eocene rhinocerotoids. The skull figured by Osborn was reconstructed from fragments on the model of a *Caenopus* skull.

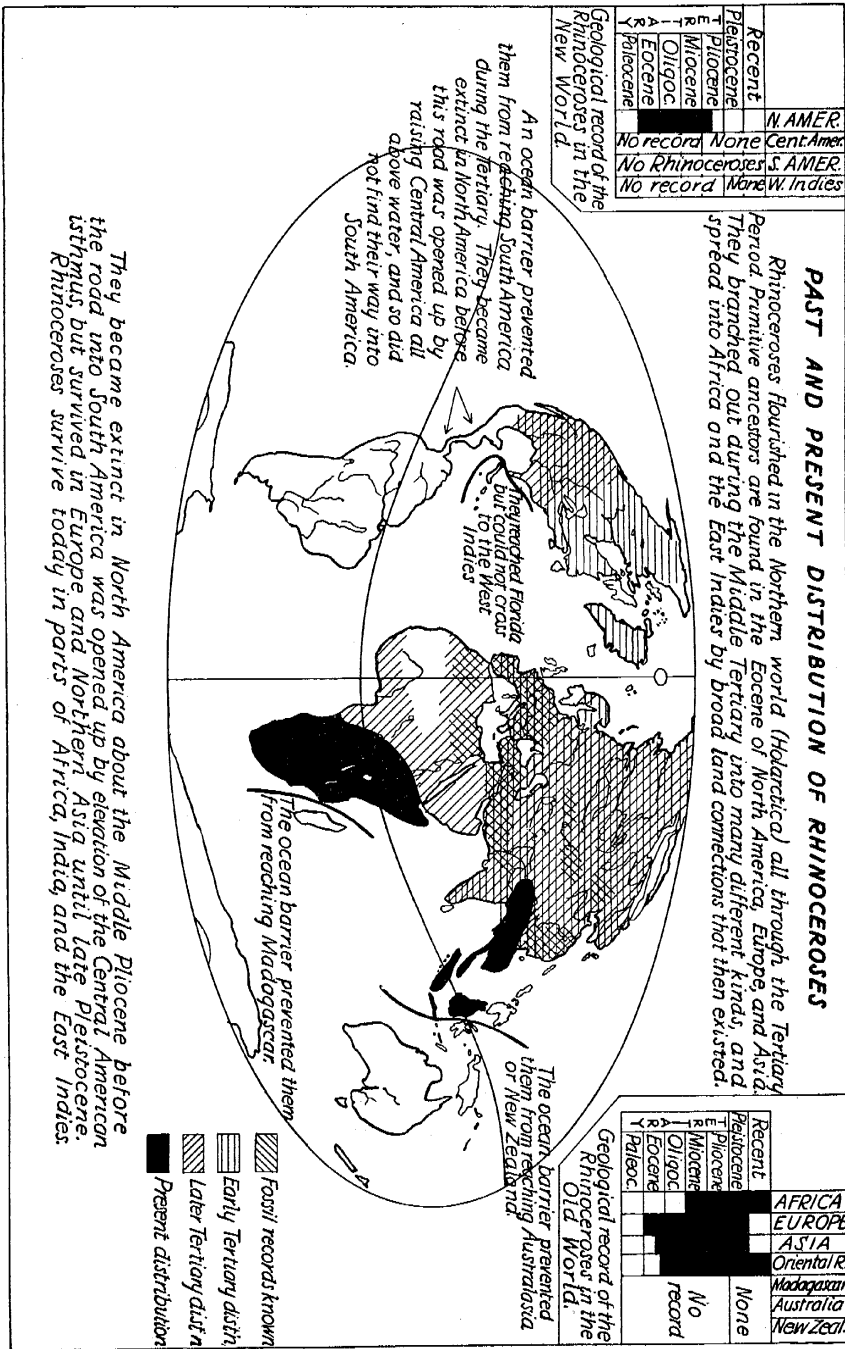


Fig. 1. (After Matthew, 1931.)

Peraceras. Cheek teeth much as in *Aphelops*, upper incisors absent (in the type), skull very short, occiput procumbent, broad at the base, narial notch as in *Aphelops*, nasals much retracted and reduced. Lower jaw and skeleton not positively known.

Teleoceras. Cheek teeth higher crowned, premolars reduced, upper incisors stout much as in *Rhinoceros*, skull moderately short, occiput vertical, broad at top as well as base, narial notch short, nasals unreduced and pointed with small horn on tip in male, limbs and feet much shortened and broadened.

These appear to represent three phyla not easily distinguished in the Middle Miocene, much more specialized in the Pliocene. The first two, however, are not as well distinguished, even in the Pliocene, and appear to intergrade more or less or to follow largely identical lines of diversification. *Peraceras*, indeed, is imperfectly known and more complete associated material might show it to be in reality as distinct from *Aphelops* as it appeared to Cope from the limited material available fifty years ago.

The geological occurrence of the various described species is shown in the following table (p. 418). The three species of the Middle Miocene (one undescribed) are each represented by one or more complete skulls which, while all are relatively small and primitive, seem to foreshadow the characteristics of the three genera.⁵ They resemble each other more closely than any of them resemble the specialized species of the Pliocene. A really logical arrangement would require that these three nearly related species should be referred to the genus *Aphelops*, of which the type is Middle Miocene, while the Pliocene species should be made typical of the three distinct genera which they represent. The Upper Miocene species, except probably the imperfectly known *meridianus* and *jemezianus*, would fall into the three specialized genera. This would make it necessary to give a generic name to the group of Pliocene species hitherto included under *Aphelops*.⁶ Singularly enough, in view of the multitudinous superfluous names in rhinoceros nomenclature, there is no published name available for this group of species. *Paraphelops* recently proposed by H. H. Lane for a lower jaw from the Pliocene of Kansas, and *Eusyodon* Leidy 1886 based upon part of a tusk from the Alachua clays of Florida need critical consideration in this connection.

⁵ Unpublished observations of W. D. Matthew on American Museum material.

⁶ A necessity already intimated by Douglass in his discussion of the affinities of *A. montanus* and *ceratorhinus*.

Leidy's type was found associated with cheek teeth, foot bones, etc., of both *Teleoceras* and "*Aphelops*." It has been positively referred to the former genus by Osborn and made a synonym of *T. fossiger*, but it is really indeterminate both as to genus and species. As being indeterminate, it does not preoccupy *Teleoceras* Hatcher 1894; but also it cannot be used for the "*Aphelops*" *malacorhinus* group unless it can be definitely proved to belong with Leidy's *Rhinoceros longipes* and not with his *proterus*. As the type is a short piece of tusk badly shattered such proof is beyond reasonable probability.

As for *Paraphelops*, Lane has distinguished it from *Teleoceras* and *Aphelops* by a very considerable series of characters, but most of these on examination prove to be age or individual variations. The jaw is not narrower than the *Teleoceras* jaw herein figured, the teeth are well worn, but the molars, although described by Lane as brachydont, appear to me to have been about as hypsodont as in *Teleoceras*; the form and spacing of the anterior part of the jaw, reduction of the premolars, proportions of coronoid, condyle, and angle agree rather nearly with *Teleoceras*; the backward extension of the symphysis is a variable feature in both genera, tending to increase with age. I regard *Paraphelops rooksensis* as a species of *Teleoceras*, not at present satisfactorily distinguished from *T. fossiger*.⁷

A third generic name that might be applied to these advanced species of "*Aphelops*" is *Chilotherium* Ringström; but as will be seen in later pages this Old World group, while partly parallel and nearly related, differs too much from the American Pliocene *Aphelops* to transfer them to it.

In view of the unsatisfactory situation as respects the Pliocene "*Aphelops*" and of the partly intermediate character of the Upper Miocene species, especially, of the Montana skulls described by Douglass, it appears better to retain them all in the genus *Aphelops* as a progressive group B (Type *A. malacorhinus* Cope).

⁷ Dr. Lane refers to *P. rooksensis* a lower jaw, No. 10878, in the American Museum, which he states accords with the Kansas type jaw except for smaller canines, thus confirming the validity of the genus. This characterization of No. 10878 is difficult to reconcile with Osborn's characterization as distinguished by (a) large canines (b) forward pitch or inclination of the condyle and coronoid region; the latter so far as I recall was the chief argument for Osborn's reference of this jaw to *Peraceras* rather than *Aphelops*. Moreover, Osborn's reference of No. 10878 to either *Peraceras* or *Aphelops* would involve brachydont molars and unreduced premolars. In view of these apparent discrepancies of observation some confusion of specimen number or record seems probable. I can hardly suppose that Lane and Osborn were discussing the same jaw.

GEOLOGICAL AGE OF SPECIES OF LATER TERTIARY RHINOCEROSSES

	Aphelops	Peraceras	Teleoceras	
LOWER PLIOCENE	Thousand Creek, Nevada.....	?	?	"fossiger"
	Hemphill Beds, Texas.....	mutilus, var.		"sp. indet."
	Clarendon Beds, Texas.....	? sp.		"sp. indet."
	Alachua Clays, Florida.....	longipes		proterus
	Rattlesnake, Oregon.....	? sp.	? sp.	"sp. indet."
	Upper Snake Creek, Nebraska	mutilus	troxelli	
	Ricardo, California.....	sp.	sp.	
Republican R., Nebraska.....	malacorhinus	superciliosus	fossiger	
UP. MIOCENE	Valentine Beds, Nebraska.....	crassus	"superciliosus"	
	Madison R., Montana.....	ceratorhinus		"sp. indet."
	-----	montanus		
	Santa Fe, New Mexico.....	jemezianus		

Navasota Beds, Texas.....	meridianus			
MID. MIOCENE	Pawnee Creek, Colorado.....	megalodus		medicornutus
	-----	profectus		
	Deep River, Montana.....	sp. indet.		
	Middle Snake Creek, Neb.....	megalodus	sp. indesc.	medicornutus
	Mascall, Oregon.....	sp. indet.		oregonensis?
Sheep Creek, Nebraska.....	sp. indet.			

"*Aphelops*" *planiceps* is a probable synonym of *Teleoceras medicornutus*.

The status of "*Caenopus*" *persisteus* Osborn from the Valentine is not clear. It appears to be too primitive in skull characters to fall into any of the above genera, but it is wholly improbable that it is *Caenopus*. Possibly it might be compared with "*Diceratherium*" *palaeosinense* of the Chinese Pliocene, which is not *Diceratherium* but not readily referable to any described genus.

Exact comparison with the rhinoceroses of the Alachua clays (Williston, Florida) and the Thousand Creek beds in northwestern Nevada, is not practicable, as these species are imperfectly known. The Thousand Creek fauna appears to be a very late phase of the Lower Pliocene and may prove to be later than the Hemphill beds. The Alachua fauna may be older but is insufficient for exact comparison.

Rhinoceros oregonensis Marsh 1873 is stated to be from "Pliocene deposits of Oregon," presumably Mascall or Rattlesnake. The type is an imperfect upper molar. It was referred by Matthew to "*Acera-*

therium" in 1899; to *Diceratherium* by Loomis in 1908. Peterson remarks that it may equally well belong to *Teleoceras* and regards it as indeterminate. It seems obvious enough that it is not *Diceratherium*. It agrees with *Teleoceras* and differs from *Aphelops* or *Pera-ceras* in the presence of medifossette (provided Peterson's identification of the tooth as M² is correct). It would be reasonably safe to refer topotypes and validate the species if it were certain whether it is Mascall or Rattlesnake.

CHARACTERS OF THE GENUS APHELOPS AND DIAGNOSIS OF THE SPECIES

TYPE, *Aceratherium megalodum* Cope, 1870 from the Middle Miocene (Pawnee Creek beds) of Colorado.

GENERIC CHARACTERS. Skull long to medium. Occiput narrow and high. Nasals long, slender, decurved and pointed, hornless, or more or less retracted and shortened; narial notch above P⁴, cheek teeth moderately brachydont, premolars unreduced, about equalling the molars in length and size; the three molars subequal in size and height of crown. Accessory crests not greatly developed, crochet present, anterochet mostly weak and crista absent; transverse valleys usually open, blocked only in premolars of the most progressive species. Upper incisors vestigial or absent, lower incisor tusks somewhat less curved than in *Teleoceras* and usually wearing on somewhat rounded planes to a progressively blunter point. Limbs and feet normally proportioned as in modern rhinoceroses, or slightly elongate, not shortened as in *Teleoceras*.

[Group A] Nasals unreduced, teeth sub-brachydont, accessory crests absent or little developed on molars and premolars.

[Group B] Nasals reduced. Teeth higher crowned, accessory crests more developed on premolars and molars. Type, *Aphelops malacorhinus* Cope.

SPECIFIC DIAGNOSIS—

1. Skull length 18 inches, width 12 inches. Nasals unreduced, narial notch narrow. Valleys open on molars and premolars. No crochet or crista, a weak anterochet on molars only. *A. megalodus*.

2. Skull unknown. Valleys open, weak crochets on molars and premolars. Size larger than *megalodus*. *A. jemezianus*.⁸

⁸ Including *A. "meridianus"* Cope 1877 not of Leidy 1869.

3. Skull length 22 inches, width 13 inches. Nasals unreduced, narial notch wide, valleys open, crochets developed on molars and premolars. *A. montanus*.⁹

4. Skull length 25 inches, width 14 inches. Nasals retracted narial notch wide. Valleys open on molars and premolars. Strong crochet, weak antecrochet, no crista. *A. malacorhinus*.

5. Skull length 25 inches, width 15 inches. Nasals retracted and reduced, narial notch broad. Valleys open on molars. Crochet strong on all teeth, united with ectoloph on premolars. *A. mutilus*.

6. Skull unknown. Isolated teeth resemble those of *A. mutilus*. *A. longipes*.

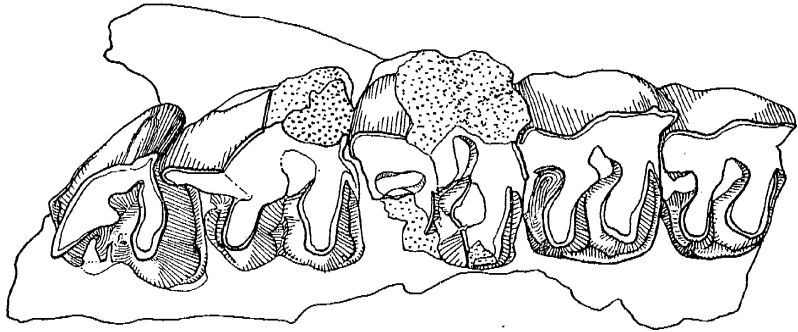


Fig. 2. *Aphelops meridianus* (Leidy), right upper jaw with P_2^3 to M_3^3 , U. C. No. 31043, from Jas. Fietsam's farm, $\frac{1}{2}$ mi. E. of Armandville, 9 mi. NW. of Weimar, Colorado County, Texas. $\times \frac{1}{2}$.

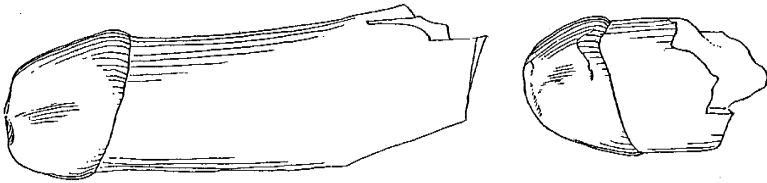
The two remaining species, *crassus* and *meridianus*, are indeterminate until adequate topotypes are known. If they belong to the *Aphelops* series they would probably fall between *megalodus* and *montanus*. Cope has referred to *meridianus* specimens from the Santa Fé Miocene which may or may not belong with the type molar; they are far from being topotypes. A specimen recently received from the Rio Bravo Oil Company, coming from a locality much nearer to the Navasota beds, more probably represents Leidy's species. It is a well preserved right upper jaw with P_3^3 - M_3^3 , and agrees quite closely with Leidy's type, also with the Santa Fé upper jaw and with *A. megalodus*. It is hardly possible to specify any distinctions except such as are known to vary with individuals and sex. Cope distinguished the Santa Fé jaws from *megalodus* by their small tusks—a well known sex difference in this group. He distinguished both from *jemezianus* of the Santa Fé by the position and form of the coronoid process; but the characters of his *jemezianus* are simply those that go with greater age, and the type is an old individual with heavily

⁹ *A. ceratorhinus* is regarded as probably the male, *montanus* the female, of the same species. *Ceratorhinus* is the earlier name but based on a very fragmentary skull.

worn molars. It is wholly probable that *megalodus*, *jemezianus* and *meridianus* are really distinct species, but it needs comparison of larger series of more complete specimens to prove this.

OSTEOLOGY OF APHELOPS MUTILUS¹⁰

Four finely preserved skulls, a palate, a number of upper and lower jaws, numerous teeth and skeleton bones are referred to this species (described as a sub-species). They agree, though not closely, with each other and with the type skull and are nearly related to *A. malacorhinus* Cope, but distinguished by the shorter broader skull, more reduced nasals, higher crowned, more progressive cheek teeth, in which the premolars usually have the crochet united to the ectoloph, separating a medifossette from the main transverse valley. As these characters, except the last, run constant through all the Hemphill specimens, they are regarded as valid specific characters. The skull is shorter and more robust than Cope's type, the occiput less elevated and more massive, the nasals apparently shorter although in none of our specimens are they preserved complete.



Figs. 3-4. *Aphelops mutilus* Matthew, two small tusks probably upper canines, U.C. No. 30263, Locality 20, Coffee Ranch, Hemphill County, Texas. Natural size.

DENTITION—

The upper tusks are not certainly known in any species of *Aphelops*, at least they are not preserved on any skulls referred to the genus. The reduction of the basal portion of the premaxilla preserved in *A. megalodus* suggests that even in that species the upper tusks were vestigial or absent. With the material from Locality 20 were preserved two small tusks (U. C. No. 30263) of peculiar form which cannot be otherwise identified than as vestigial upper tusks of a rhinoceros. These little tusks have a small oval convex crown, slightly divided on the inner side and with obscurely crested margins; and a long, straight, heavy root almost cylindrical in cross section, largest

¹⁰ Matthew, W. D. Third Contribution to the Snake Creek Fauna, Bull. Am. Mus. Nat. Hist., fig. 41, p. 151, 1924.

toward the middle of its length. They are quite suggestive in a general way of the vestigial front teeth seen in other Rhinocerotidae. They are certainly not *Teleoceras*, and this genus is not found at Locality 20. A similar tusk was figured by H. J. Cook from the Pliocene of Yuma County, Colorado, also associated with a skull and other material of *Aphelops ?mutilus*. Nothing resembling them is known in any proboscidean, tapiroid, carnivore or artiodactyl of the later Tertiary, and it seems reasonably safe to conclude that they are vestigial upper incisors, I_1^2 , of *Aphelops mutilus*.

Little is known about the upper tusks in any of this group of rhinoceroses. They were certainly absent in the type skull of *Peraceras superciliosus*, which however may be a female. They are figured by Ringström as absent in *Chilotherium*, upon the evidence of a number of skulls. No known skull of *Aphelops* has the premaxilla complete, but as the portions of the premaxilla preserved suggest reduction or absence of the tusk, unlike *Teleoceras* in which the large and characteristic upper tusk, or its alveolus, are not infrequently preserved on the skull or associated with skulls of this genus, it is a probable inference that all species of the genus *Aphelops* were characterized by vestigial I_1^2 , very likely absent in the female, or individually variable.

The lower tusks, I_2 , fall into two groups. In some jaws they are very large massive, moderately upcurved, but distinctly less so than in *Teleoceras*. When unworn, the form is elongate lanceolate, moderately convex longitudinally on the under side; in cross section a little convex on the supero-internal face, strongly convex on the infra-external face and with quite sharp edges. The enamel extends nearly halfway down on the length of the unworn tusk, but is thin, perhaps not wholly continuous, on the supero-internal face, which is the face of wear. In *Chilotherium*, the enamel is absent on this face of the tusk, auct. Ringström (*l. c.*, p. 98). With continued wear the nearly plane wearing surface takes a continually blunter angle, but it remains nearly plane. Ringström has discussed the method of wear that could produce these plane surfaces of wear on the lower tusk in *Chilotherium* in absence of upper tusks, and concludes that it must be through wear against the mobile pointed 'lip' that projects forward and downward from the muzzle. The action is partly analogous to the cropping of grass and leaves by ruminants, in which a convex row of lower incisors is worn to a flat oblique surface by the upper lip. It is necessarily true also of *Aphelops* in which the diminutive upper tusk could not produce any such heavy wear in the lower, nor does it show any signs

of having done so. But the precisely similar character of the wear in the lower tusk of other rhinoceroses makes it probable that this is the real method of wear in all of them, and that the upper tusk when present plays but a minor part in the wearing down of the lower tusk.

These large tusks have a considerable upward curve, somewhat less perhaps than in *T. fossiger*, but it is very doubtful whether the two genera can be distinguished by any difference in curvature of the lower tusks. Certainly they cannot be said to be procumbent as they appear to be in *Aceratherium*. As they wear down the curve partly disappears, so that heavily worn tusks appear nearly straight, but are set in the jaw at an upward angle of at least thirty-five degrees.

The smaller tusks assumed to belong to females are in place in several jaws with well worn adult dentition. They have about half the diameter and length of the large male tusks, and are similar in form of crown except for a more rounded oval cross section and almost entire absence of curvature save in unworn or slightly worn teeth. The root is nearly circular. Like the male tusks they are not procumbent but project upward almost as much as forward. They are more numerous than the larger tusks, the proportion 12 to 7 suggesting that these animals, like so many large ungulates, traveled in herds or small groups in which females were more numerous than males. Much more evidence, however, is needed to validate this suggestion based upon less than a score of specimens of *Aphelops* and upon a general impression with regard to the series of *Teleoceras* skulls, etc., that have been secured from the "Long Island Quarry" in Phillips County, Kansas.

The cheek teeth are moderately hypsodont, about as much so as in the black rhinoceros or *Chilotherium*, less than in *T. fossiger*, more than in *Peraceras* or *A. malacorhinus*. The premolars are unreduced in number except for absence of P_1 (presumably relegated to the milk series, but none of our specimens represent milk dentition except for a few isolated teeth). They are also unreduced in size, P_3^3 and P_4^4 as large as M_1^1 , M_2^2 and P_2^2 not much smaller, P^2 about equalling M^2 in size. P^1 appears to be always present,¹¹ the tooth or its alveolus appearing in well worn dentitions, but is of small size and simple

¹¹ Ringström interprets this tooth in *Chilotherium*, in accord with the common textbook identification of it as DP^1 . This, however, seems very improbable. The first of the premolar series in most mammals appears earlier than the other premolars, but usually later than the following milk molars, and is retained after these are succeeded by the true premolars. The first milk premolar appears, if at all, earlier than the succeeding deciduous teeth, but it is very generally suppressed.

construction, the remaining premolars being molariform and P_{3-4}^{3-4} hardly distinguishable from the molars. The crochet is well developed on all the upper molars and premolars except P^1 and usually united with the crista on premolars but not on the molars. Exceptions to this, however, are scarce among the specimens; in No. 30300 P^4 (right), P^{2-4} (left) are not united. The antecrochet is moderately developed in the molars toward the base of the protoloph, but not as much so as in *Chilotherium*.

SKULL AND JAWS—

A very large skull (U.C. Mus. Pal. No. 30252) was found by Mr. Vander Hoof at the Coffee Ranch Quarry, and within a couple of feet a pair of lower jaws lacking the posterior part. The wear corresponds so closely in upper and lower cheek teeth that there is no doubt that they belonged to the same individual. Other parts of the skeleton found close by may also belong to this individual judging from their size, but there is no way of proving it. They represent one of the largest of American rhinoceroses, apparently the largest skull on record, if the general robustness be taken into consideration. Other more fragmentary specimens, a palate No. 30253, jaws 30254-7, tusks and cheek teeth, from the same quarry, indicate that the size was not exceptional.

At another locality, Higgins Quarry A, about one mile southeast of Higgins, Lipscomb County, Texas, Dr. Camp, Mr. Reed, and Mr. Vander Hoof found three well preserved skulls (Nos. 30300-30302). These appear to be of the same species but are of smaller size, hardly exceeding large individuals of *T. fossiger* in bulk of skull, and present several other points of difference in proportions of skull and construction of teeth, which I do not at present regard as valid specific distinctions.

The skull resembles *A. malacorhinus* in the sharp upward pitch of the occipital region coupled with a much elevated basicranium, the occipital face of the skull nearly vertical with respect to the palatal plane. The orbits are elevated more than in *Teleoceras*, the position of the anterior border of the orbit is above the middle or anterior part of M^1 in both genera. The skull between the orbits is flat or somewhat concave, much wider than in *A. megalodus*, wider than in most specimens of *T. fossiger*, comparable with *Peraceras* and *A. malacorhinus*; behind the orbits the postorbital crests come together rapidly, to make

a definite sagittal crest towards the occiput. The occipital crest is high, narrow, not broadened out as in *Teleoceras* and the whole occiput has a suggestive resemblance to *Coelodonta* and *Ceratotherium*.

The postglenoid process is exceptionally long and broad curved forward and spatulate distally. The posttympanic-paroecipital process is also unusually long and heavy, closely approximate to the proximal end of the postglenoid but not united, well separated above and below this point, but less widely below than in *Teleoceras* or *Peraceras*.

The occiput is narrow in contrast to *Teleoceras*, but not as narrow as in *malacorhinus* (paratype). It is considerably broadened at the base, by the expansion of the paroecipitals, but not so much as in *Peraceras*.

The frontal region is wide, the narial notch extending backward on each side of a spacious narial opening about as far as the line of the anterior border of the orbits. The space between the orbit and nares is reduced to a narrow slanting pillar, on the anterior face of which lies the infraorbital foramen. The nasals appear to be short and moderately wide at the base, but are not preserved complete.

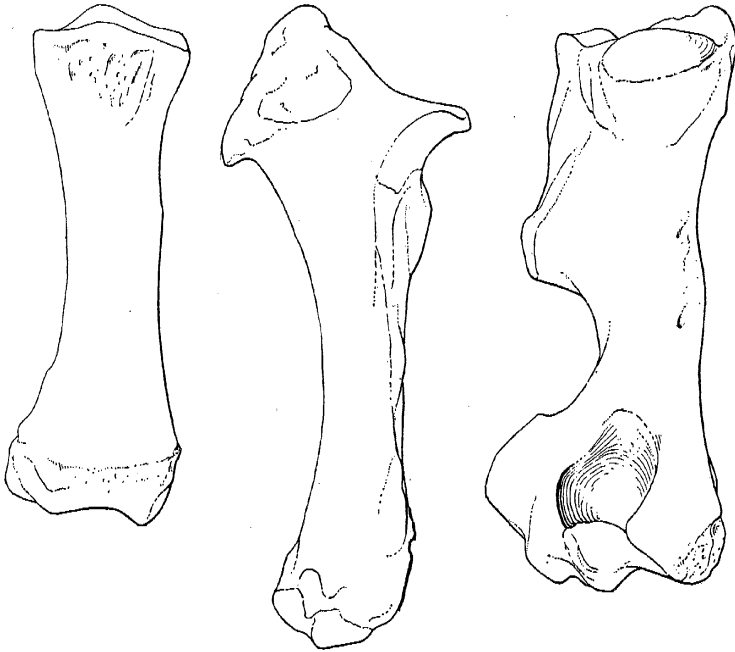
The palate is limited posteriorly by the rather compressed and wedge-shaped opening of the posterior nares, much as in *Teleoceras*, not as broad as in any of the modern genera. Anteriorly the incisive foramina are exceptionally large and extend back to the posterior margin of P², indicating extreme reduction or absence of the palatal branch of the premaxilla, conformant to the great reduction of the rest of this bone. The pterygoid processes are unusually heavy and flaring. The basicranial foramina show no significant peculiarities.

FORE-LIMB BONES AND FOOT BONES—

The scapula is only partly preserved; the proximal half has the proportions of this bone in modern rhinoceroses, widely different from the short triangular scapula of *Teleoceras*.

The *humerus* is only slightly longer than that of *Teleoceras*, somewhat more bulky, the chief differences being, (1) that the tuberosities, especially the greater tuberosity, do not project so high above the head, are more massive and blunt-ended; (2) the bicipital groove is wider but not so sharply divided as in *Teleoceras*; (3) the deltoid crest carries considerably farther down on the shaft; (4) the supinator crest is not so high up on the shaft, more confined to the distal end of the bone.

The *radius* and *ulna* are much longer than in *Teleoceras*, the length of the radius about 50 per cent greater, the shaft a more flattened oval, the distal facets with less convexity and concavity, the facet for the cuneiform considerably broader than in *Teleoceras*. The olecranon is wider, but not so thick, and its border is continued down as a sharp continuous crest along the postero-external border of the shaft, which is uniformly more trigonal in outline. The cuneiform facet of the ulna is more convex, coming down to a rather prominent malleolar process on the outer margin of the facet.



Figs. 5-6-7. *Aphelops nativus* Matthew, from Locality 20, Coffee Ranch, Hemphill County, Texas. Humerus U.C. No. 31510; radius U.C. No. 31511; ulna U.C. No. 31512. $\times \frac{1}{2}$.

These characters of the fore-limb are much as in the modern rhinoceroses, especially the Sumatran species; they also are much the same as in *Chilotherium*.

The fore foot is decidedly longer than in *Teleoceras*, the vertical diameters of nearly all the component bones greater. The scaphoid is higher in proximo-distal diameter, less convex from side to side on the dorsal surface; the proximal external corner of the bone is less extended, the radial facet almost wholly concave while in *Teleoceras* it has a considerable convex portion that fits into the concave lunar facet

of the radius. The lunar is much wider than in *Teleoceras*; the cuneiform is higher but of less width, and has the ulnar facet saddle shaped but decidedly less concave and convex. The magnum does not show any notable differences from that of *Teleoceras*; the trapezoid has a greater height (proximo-distal diameter) but is otherwise similar. The unciform is also somewhat higher and narrower than in *Teleoceras*; its lunar facet faces more entad.

Metacarpals.—These have nearly the proportions of *R. indicus* or of *Chilotherium*, somewhat shorter than in *ceratorhinus* topotype figured by Matthew in 1928, or in the modern African rhinoceroses, decidedly shorter than the topotype metacarpals attributed to *A. malacorhinus* (unfigured material in the American Museum).

PELVIS, HIND LIMB AND FOOT BONES—

No. 30266 has the left side of the pelvis practically complete with the sacrum. Various other footbones from the Coffee Ranch Quarry give the characters of all elements of the pes and show something of the range of variation in most of them.

The *pelvis* has the broadly expanded ilium of the later rhinoceroses, much as in *Teleoceras* so far as comparisons can be made with the photographs and drawings of the skeleton of that animal and the imperfect pelvis figured by Cope.

The *femur* is larger in size than that of *Teleoceras*, comparing with the femur figured by Peterson¹² as of *A. ceratorhinus*. The head is higher, broader and flatter than in Peterson's figure; the crest representing the inner trochanter is broken but may have been as prominent as in the *ceratorhinus* femur. The patellar trochlea is uncrushed, and its inner crest is much higher and wider than the outer crest, as in *Teleoceras* and modern rhinoceroses; in *ceratorhinus* the two crests appear to be of more equal height, but Peterson suggests that this may be due to crushing, and that the same explanation may account for the abnormally low head of the *ceratorhinus* femur.

The *tibia* and *fibula* are much longer than in *Teleoceras*; the astragalar trochlea of the tibia has the internal malleolus somewhat more developed, the grooves of the trochlea are a little wider antero-posteriorly, and are straighter grooves, less cotylar in character. The process at the back of the trochlea is much less massive posteriorly but projects downward as much as in *Teleoceras*. The *fibula* has a more slender shaft than in *Teleoceras*, its distal end is of the same diameter

¹² Peterson, O. A., Mem. Carnegie Mus., vol. 11, pl. 10, figs. 1 and 5, 1928.



Fig. 8. *Aphetops muticus* Matthew, composite hind limb and foot from Locality 20, Coffee Ranch, Hemphill County, Texas. Pelvis U.C. No. 31505; femur U.C. No. 31506; patella U.C. No. 31507; tibia U.C. No. 31508; hind foot U.C. No. 31509. $\times \frac{1}{5}$.

antero-posteriorly, but the transverse diameter is only half as great; and the astragalar facet faces wholly entad instead of distad-entad as in *Teleoceras*.

The *astragalus* is characteristically different; the trochlea is much wider antero-posteriorly than in *Teleoceras*, and the fibular facet is vertical whereas in *Teleoceras* it faces sub-proximad. The astragalo-calcaneal facet is convex and concave, in *Teleoceras* it is smaller and much flattened out. The *calcaneum* has a much shorter tuber calcis, and larger, more curved astragalar facet. The *cuboid* is much less shortened; the proximal-distal diameter nearly equals the transverse diameter, whereas in *Teleoceras* it is hardly more than half as great;



Fig. 9. *Aphelops mutilus* Matthew, composite hind foot, U.C. No. 31509, front view, from Locality 20, Coffee Ranch, Hemphill County, Texas. $\times \frac{1}{6}$.

the calcaneal facet is strongly convex transversely, extending over the external side of the cuboid. The navicular is likewise of much less width, and its astragalar facet is a warped surface instead of the simple concave of *Teleoceras*. The facet for the ectocuneiform is single, while in *Teleoceras* it is partly or wholly separated into two, a dorsal and a plantar facet. The facet for the entocuneiform is unreduced. The ectocuneiform is somewhat differently placed on the metatarsal heads; in *Teleoceras* mt. II lies to a considerable extent under the ectocuneiform, but in *Aphelops* it had its normal position wholly under the mesocuneiform. The entocuneiform also maintains a more primitive position and is less reduced in size; it articulates laterally with the second metatarsal as well as with the navicular mesocuneiform while in *Teleoceras* it is reduced and projects entad wholly free from the metatarsal. In Peterson's illustration the navicular facet of *A. ceratorhinus* is represented as round and concave but in all our specimens of *Aphelops mutilus* it is flat or somewhat convex.

The *metatarsals* are about a third longer than in *Teleoceras fossiger*, the width being about the same. Mt. II, conformant with the characters of the cuneiforms, has its ectocuneiform facet almost wholly lateral (ectad) and of smaller size than in *Teleoceras*. Peterson states that the distal keel of the metapodials is distinctly more developed in *A. ceratorhinus* than in *Teleoceras fossiger*; in our species the reduction of the keels has been carried about as far as in *T. fossiger*.

The *phalanges* are not so short as in that species, but the median ungual phalanx is very broad, apparently broader and shorter than in *A. ceratorhinus*.

EXPLANATION OF MEASUREMENTS ON TABLE 1

- Total length of skull—from the anterior edge of premaxilla to posterior edge of condyles.
- Skull, length, P¹ to condyles—from anterior edge of P¹ to the posterior end of the condyle of the same side.
- Narial notch to occipital crest—from the posterior extension of the narial notch in front of the orbit to the median position of the occipital crest.
- Breadth across zygomata—greatest breadth.
- Height, condyles to occipital crest—from a median position of a line connecting the lowest points of the condyles to the median point of the occipital crest.
- Breadth across palate, opposite M²—from a position of the bony surface on the external side and between the roots of M².
- Width between orbits—between the anterior points of the orbits.
- Width of occiput—greatest distance between outer edges of the mastoids.
- Upper cheek teeth P¹-M³—from anterior edge of P¹ to the posterior edge of M³.
- Upper cheek teeth P²-M³—from anterior edge of P² to the posterior edge of M³.
- Upper premolars P¹-P⁴—from anterior edge of P¹ to posterior median edge of P⁴.
- Upper premolars P²-P⁴—from anterior edge of P² to the posterior edge of P⁴.
- Lower jaw, length, incisor, condyle—from anterior upper edge of alveolus of the incisor to the posterior end of the condyle.
- Width across tusks—at edge of alveoli.
- Width behind tusks—at the narrowest point in front of P₂.
- Lower cheek teeth P₂-M₃—from anterior edge of P₂ to the posterior edge of M₃.
- Lower premolars P₂-P₄—from anterior edge of P₂ to posterior median edge of P₄.
- Length of symphysis—from the anterior and posterior position along the line of sutural fusion of the mandibles.
- Depth of jaw beneath M₁—from the highest bony projection between the external roots of M₁ to the lower part of the mandible directly below.
- Height, angle to condyle—from the lowest point of the angle to the highest point on the condyle.

COMPARATIVE MEASUREMENTS															
	Aphelops mutilus														
	Locality 20					Higgins A					Snake Creek				
	Skull and jaws No. 30252	Palate No. 30253	Lower jaw No. 30254	Lower jaw No. 30255	Lower jaw No. 30256	Skull No. 30300	Skull No. 30301	Skull No. 30302	Skull (Type) AMNH No. 17584	A. malacorhinus-type	A. ceratorhinus-type	A. megalodus-genotype Peraceras sycericolus Genotype Teleoceras fossiger Genotype Teleoceras fossiger from Hinsworth, Neb.			
Total length of skull	660					570	580	580	621			477	600	690	
Skull, length, p ¹ -condyles	627					546	542	532	643			445	564	600	
Narial notch-occipital crest	390					395	392	368	413	382		352	344	380	
Breadth across zygomata	385					340	328	340	336			300	428	347	406
Height, cond. to occ. crest	258					213	226	192	240			181	250	230	183
Breadth across palate approx.	234					220	204	203	210	214		168	252	229	175
Width between orbits	277	255				202	209	238	206	252		174	269	124	
Width of occiput	260					201	207	198	220			188	269	255	210
Upper cheek teeth-p ¹ -m ²	343	350				311	278	292	334		267	241			268
Upper cheek teeth-p ² -m ²										306			296	285	
Upper premolars-p ¹ -p ²	174	179				159	128		170		135	115			112
Upper premolars-p ² -p ²										147			142	97	
L'r. jaw, l'gh, incisor-condyle	600		560	561	580							560	447		530
Width across tusks	130				97								89		104
Width behind tusks	125		82	84	111								88		95
Lower cheek teeth-p ₂ -m ₃	318		290	293	295							270	218		253
Lower premolars-p ₂ -p ₂	144		100	135	131							120	98		85
Length of symphysis	196		194	167	173							115	123		128
Depth of jaw beneath m ₁	125		109	100	105							113	86		84
Height, angle to condyle	296		288	273	276							260	215		200
1. Approximate						5 Upper premolars, p ² -p ²									
2. Skull, length p ² to condyle						6. Anterior edge of maxilla to condyles									
3. Skull, length p ² to condyle															
4. Upper cheek teeth, p ² -m ²															
ALL MEASUREMENTS IN MILLIMETERS															

TABLE 1

COMPARISON OF APHELOPS MUTILUS WITH OTHER SPECIES

The nearest comparisons are clearly with *A. malacorhinus* Cope, of which it might well be regarded as a subspecies or progressive mutation. Cope's species was based on the fine skull American Museum No. 8381. He associated with this skull a number of limb and foot bones from the same general locality, but there is no evidence that any of them belonged to the same individual. It is probable but not certain that they represent the species. The teeth of *malacorhinus* are smaller than in *mutilus* and distinctly shorter crowned and in none of them does the crochet join the crista. The skull is narrower and the occiput more elevated, the crest more elongate, the nasals appear to be much less reduced. The limb bones and such foot bones as are preserved are slightly longer, more slender and somewhat stilted, the tibia and fibula united distally (individual or age character?). The astragalus figured with these bones by Cope belongs to *Teleoceras*. In absence of a series of topotype skulls and skeletal parts of *A. malacorhinus* it is not provable that the above characters constitute a valid species distinction. Most of them are variable in the *mutilus* skulls and skeletal bones. But most of the fauna of the Republican River beds appears to be specifically distinct from that of the Hemphill beds, and it seems probable that an adequate series of topotypes of *malacorhinus* would show it also to be distinct.

Aphelops ceratorhinus Douglas, of which *A. montanus* is probably the female,¹³ is of smaller size and more slender proportions, the teeth more brachydont, the nasals unreduced and bearing in the type a rudimentary (?) horn-base on the tip; the occiput is not elevated as in *malacorhinus* and *mutilus* but is more as in *megalodus*, according to Douglass' figure.

Aphelops megalodus Cope is decidedly smaller with much more primitive characters throughout. The teeth are subbrachydont, the accessory crests little developed. The skull is elongate, the nasals long pointed, the narial notch narrow though long, the limbs and feet more slenderly proportioned.

¹³ Douglass suggests this but dismisses it as improbable without giving any reasons. The small size of the tusks in *montanus* coupled with absence of horns, and large tusks and rudimentary horns in *ceratorhinus*, along with various other differences are the usual sex differences.

Aphelops jemezianus Cope, though little known, appears to be more or less intermediate between *megalodus* and *ceratorhinus*.

Aphelops meridianus Leidy is a small primitive species of about the size of *megalodus*.

COMPARISON WITH CHILOTHERIUM AND OTHER OLD WORLD RHINOCEROTIDAE

Among the Old World Rhinocerotidae the group of species assembled by Ringström under *Chilotherium* make the nearest approach to the American *Aphelops*, and especially to the species here described. Ringström places his genus in the 'Teleocerinae' (=Teleoceratinae) and makes frequent comparisons with *Teleoceras*, from which as he shows, it is a clearly distinct genus. But its real relations appear to be with the *Aphelops*, of which it might represent a more progressive stage than the American series, and with *Aphelops* Ringström makes no comparisons, nor any mention of the genus (save as an erratum for *Teleoceras*). Ringström's setting up of *Chilotherium* and inclusion in it of a considerable number of European and Asiatic species characteristic of the *Hipparion* fauna of Palaeartica, which have hitherto been wrongly referred to *Aceratherium*, *Teleoceras*, etc., is a long step forward toward clearing up the real affinities of the Old World Tertiary rhinoceroses, and the correction of certain erroneous and misleading concepts of their relationship to American genera embodied in Osborn's revision of 1904. His reference of the genus to the Teleoceratinae however seems to have little to support it except a rather slight shortening of the limbs and the broadening of the supra-occipital crest. Whether or not the brachypodine rhinoceroses are really a natural group is very questionable; and to give the group sub-family rank as Osborn has done, is out of all proportion to the really important divergent groups of the Rhinocerotidae. But in any event *Chilotherium* has limbs and feet only slightly shorter than those of the Indian rhinoceros, about the same as in the later species of *Aphelops*, much less shortened than in *Brachypotherium* or *Teleoceras*.

The following tabulation seems to summarize the principal distinctions between the three genera:

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The following tabulation seems to summarize the principal distinctions between the three genera:

Teleoceras fossiger*	Aphelops mutilus*	Chilotherium*
1. Narial notch short, above P ³	Narial notch above M ¹	Narial notch above P ⁴
2. Nasals not retracted, horn-bearing in male	Nasals much retracted, hornless	Nasals retracted, hornless
3. Frontal region slightly or moderately concave	Frontal region strongly concave	Frontal region moderately concave
4. Postorbital crests united	Postorbital crests separate or imperfectly united	Postorbital crests separate
5. Supraoccipital crest broad	Supraoccipital crest narrow	Supraoccipital crest broad
6. Skull of moderate length	Skull rather long	Skull rather long
7. Upper incisors large	Upper incisors vestigial or ? absent	Upper incisors absent ? or vestigial
8. Premolars reduced	Premolars unreduced	Premolars unreduced
9. Molars very high crowned	Molars moderately high crowned and of more uniform size	Molars moderately high crowned, uniform in size
10. M ¹ relatively large		
11. Medifossette on M's and PMS.	Medifossette on PMS.	Medifossette on PMS.
12. Lower incisor strongly curved	Lower incisor less curved	Lower incisor less curved
13. Lower limb segments much shortened	Lower limb segments long	Lower limb segments normal
14. Feet greatly shortened	Feet slightly shortened	Feet slightly shortened
15. Astragalus much shortened	Astragalus normal	Astragalus normal

* The numerous skulls of *T. fossiger* and the several of *A. mutilus* display a considerable range of variation, quite as wide as is seen among the five species described by Ringström from the Chinese Pliocene.

It should be sufficiently obvious from the preceding table that *Chilotherium* is rather nearly related to the Pliocene species of *Aphelops*. The relations correspond rather nearly to those seen between the American and Old World species of *Hipparion*. This might suggest that *Chilotherium*, like *Hipparion*, is an immigrant into the Old World from America. This however, is not supported by the evidence; ancestral types for *Hipparion* are found in the New World Miocene, but not in the Old World; but the *Chilotherium-Aphelops* group might be derived from known Middle Miocene rhinoceroses either in North America or Eurasia.

Until the true affinities of the Old World Tertiary Pleistocene and modern Rhinocerotinae have been more clearly and correctly defined, it is useless to discuss the zoögeographic relations of the American genera. Authorities differ rather widely at present as to the real interrelationship of the modern and Pleistocene genera, and the Tertiary species are in utter confusion, in spite of the able and thorough studies of Abel, Wüst, Wurm, Hilzheimer, Breuning and other authorities. Wüst has brought strong evidence pointing to somewhat isolated position for the Indian rhinoceros group (*R. indicus, sondaicus*); and has argued less convincingly for association of the tichorhine group (*Cœlodonta*), with the Sumatran rhinoceros rather than with the "White" rhinoceros of Africa. This latter view has not found general acceptance, although apparently endorsed by Ringström, and appears to me quite against the evidence of the teeth, and supported by inconclusive skull characters.

TELEOCERAS FOSSIGER (COPE): GENERIC CHARACTERS AND DESCRIPTION OF HEMPHILL MATERIAL

To this species may be referred a number of fragmentary specimens from various localities in Hemphill County. It does not occur in the Coffee Ranch fauna so far as recorded. Some evidence suggests that *Teleoceras* is limited to the lower and middle part of the Hemphill beds, below the level of Locality 20; but not sufficient to make this a probable conclusion. At Higgins Quarry B it occurs in association with *Aphelops*.

The short legs and small compact feet of *Teleoceras*, supporting the massive body, suggests adaptation to comparatively smooth and uniform grassy plains. *Aphelops* has much the proportions of the modern rhinoceroses and may, like them, have been adapted to open

brushy country of more irregular surface. Both genera are wide ranging, from the Rocky Mountains to Florida. *Teleoceras* is doubtfully and *Aphelops* more certainly recorded from the Basin region (Idaho, Nevada, California). The distribution and associations lend no clear support to this suggested difference in habitat. It conforms, however, to the relatively hypsodont character of the cheek teeth.

No. 30308, the conjoined nasal bones bearing the small horn prominence are from Higgins B. No. 30326, and an upper molar and atlas, are from a locality three miles west of Canadian, Texas (Locality 3 of the Reed and Longnecker survey).

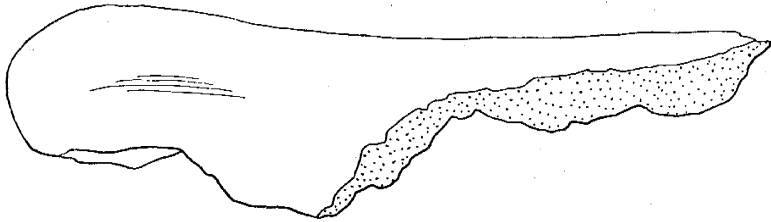


Fig. 10. *Teleoceras*, conjoined nasal bones bearing small horn prominences, U.C. No. 30308 from Higgins B, Lipscomb County, Texas. $\times \frac{1}{2}$.

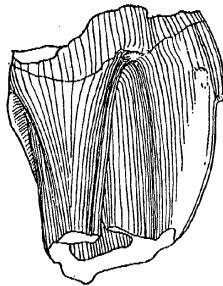


Fig. 11. *Teleoceras*, third upper molar, U.C. No. 30326, from Locality 3, of Reed and Longnecker Survey, 3 mi. west of Canadian, Hemphill County, Texas. $\times \frac{1}{2}$.

A skull and jaws of this genus from near Ainsworth, Nebraska, U.C. Mus. Pal. No. 31034, is here figured as representing *T. fossiger*, although narrower and smaller than most skulls of this species. It shows the characteristic reduced premolars, hypsodont molars, M^2 especially large and high crowned, the more anterior position of the narial notch, the unreduced nasals, with a small thickening at the distal ends usually interpreted as the base of a small horn but perhaps only a little callused knob, certainly not of the character or proportions of

the nasal horn of the modern rhinoceros. The moderate forward pitch of the occiput and of the coronoid process of the mandible, the lack of any symphyseal angulation of the lower border of the jaw are other generic characters in the skull. The upper tusks have been lost, but the alveoli is perfect and uncrushed.

GENERAL DISCUSSION OF PRINCIPLES OF DISPERSAL OF PHYLA

EXPLANATION OF DIAGRAM, EVOLUTION OF RHINOCEROSES

In the accompanying diagram the principal types of the Rhinocerotidae are arranged in accordance with their structural specialization as shown in three outstanding features:

1. Progressive hypsodontism of the cheek teeth.
2. Specialization and subsequent loss of incisor tusks.
3. Development of nasal and frontal horns.

The phyletic relations indicated are in accord with the structural specialization, and in several instances, differ rather widely from the geological age succession of the known types. This is quite to be expected. The rhinoceroses are a group of Holarctic origin and dispersal and all of their living types are to a varying degree "living fossils"¹⁴ surviving in outlying regions or more primitive environment, almost unchanged from earlier stages in the development of the race which originated in the more progressive central regions, but have there progressed to higher stages of specialization and then become extinct. Some of these earlier stages, or near approximations thereto are represented by known fossil types. Others have not yet been discovered.

These relations indicated or suggested in many discussions of phylogenies, and explained more fully by Matthew in "Climate and Evolution," are generally admitted in theory, but not yet applied in practice by many paleontologists. Still less are they generally understood and applied by zoologists in discussions of taxonomy, phylogeny and distribution. This view point as to dispersal is far from new,

¹⁴ As W. K. Gregory has called such primitive survivors among Primates and various other groups.

indeed, and is hardly open to serious question by anyone adequately acquainted with the facts of past and present distribution.¹⁵

Failure to apply this view in practice, even by those who accept it in theory, is largely responsible for the elaborate and complicated phylogenies formulated for various groups. In all its essential features the living Sumatran rhinoceros is a structural ancestor of the two living African rhinoceroses, and these in turn are structurally ancestral respectively to the extinct Etruscan and Tichorhine species of Palaeartica. They do not belong to separate phyla or 'sub-families,' but represent a single phylum, dividing into two branches. The phylum probably originated in central Asia in the middle Ter-

¹⁵ Dr. Maynard Metcalf in a recent article has undertaken to disprove what he supposes to be Matthew's views as set forth in "Climate and Evolution" on the ground that "like the Age and Area hypothesis of Willis, this is too geometrical and too little biological." He attributes to Matthew the idea that "animals dispersing in radiating stream (should) all leave behind them their ability themselves to become centers, springs, of further evolution on a large scale. But," he adds, "and this is more important, the facts do not seem to agree with Matthews' [sic] theory."

I can hardly believe that Professor Metcalf can have read the essay which he criticizes. Most of its pages are devoted to a brief summary of the facts of past and present distribution especially of the mammalia, which the theory as presented by Matthew was formulated to explain. Considerable emphasis was laid there on the secondary centers of dispersal illustrated in the evolution and distribution of certain groups; the general dominance of the northern groups was explained in terms partly of the geographic relations of the continental platforms partly as due to the pressure of changing environment acting during the Tertiary period most strongly and effectively in the northern regions on account of the greater area and comparative unity of the northern lands. I should have thought that the views presented in that essay were about as unlike as could be to the statistical or "geometrical" argument for the age and area hypothesis.

Metcalf however ignores all the data summarized by Matthew, presumably not regarding such data as facts and in the next paragraph sets forth what he apparently does regard as "facts" in the distribution of the Anura, as contradicting Matthew's view. "The genus *Bufo* arose probably in late Cretaceous times in northwestern South America or more probably in southeastern Asia. . . . the genus *Hyla* arose apparently in tropical South America in mid-Tertiary times," etc. These and all of Metcalf's "facts" are what I should call hypotheses of origin and dispersal, based upon modern distribution and taxonomy, competing with other hypotheses advocated by specialists in the Anura, and almost wholly unsupported by any significant fossil evidence. Metcalf's idea of what constitutes fact seems to be very different from mine.

It would be too far afield from the present subject to discuss Metcalf's argument here. It will suffice to say that such able recent authorities on Anura as Noble and Dunn do not agree with his taxonomic views (borrowed apparently from earlier writers) and find no difficulty in interpreting the evolution and dispersal of the Anura on lines concordant with the evidence (far more direct and conclusive) of past and present distribution of the higher vertebrates. Nor would it be at all difficult to formulate an interpretation of the evidence in Metcalf's own field of Anuran parasites, which would equally conform to this evidence, although such interpretations evidently have not occurred to him or to some other students of parasites, who seem chiefly concerned to find in them renewed support for the ancient theories of catastrophic geology, still beloved of zoogeographers though sadly discredited by the progress of modern geology and paleontology.

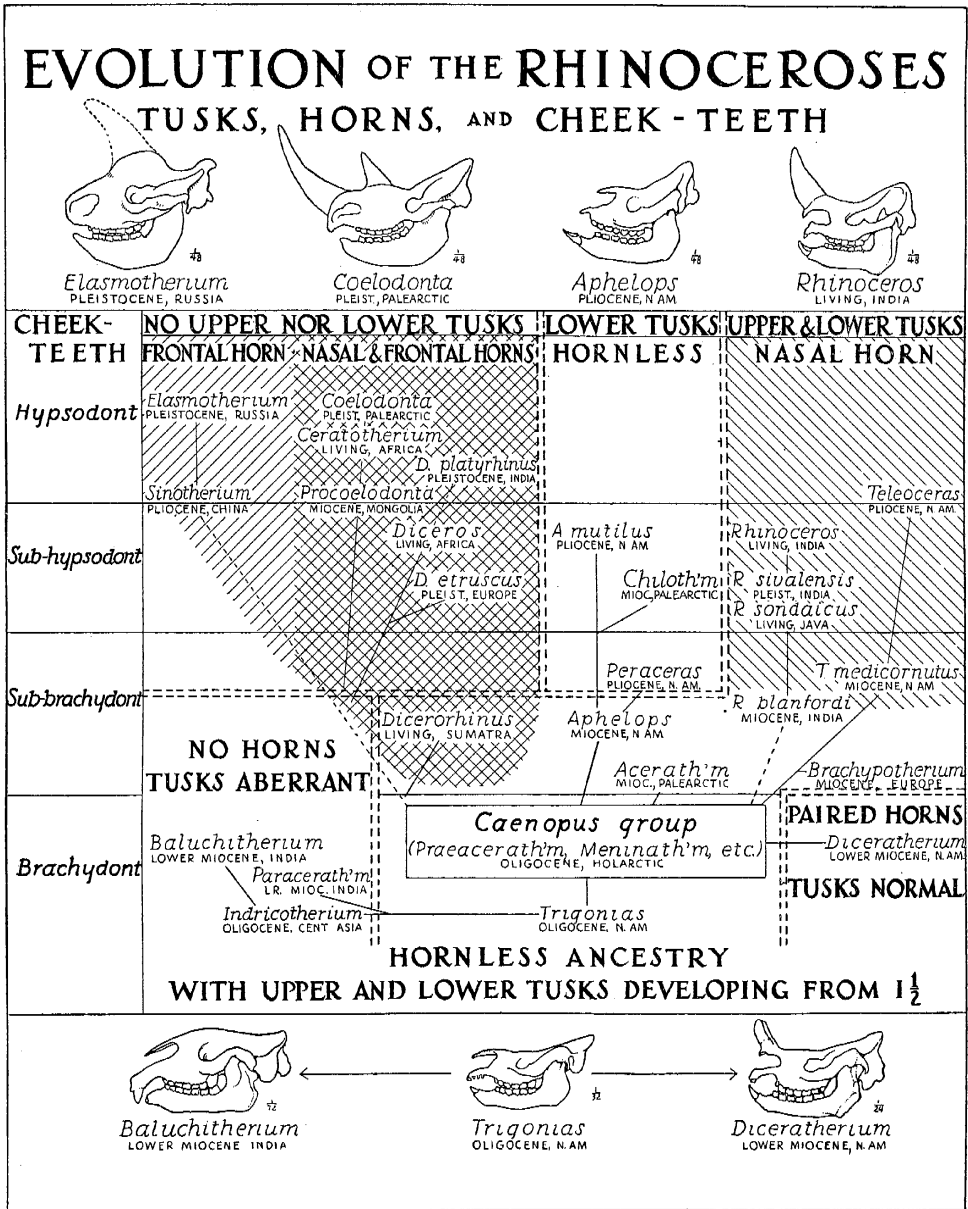


Fig. 12. Chart showing evolution of the rhinoceroses. (After Matthew, 1931.)

tiary. Earlier than the Miocene it appears to be wholly merged with other rhinocerotid phyla. The earliest stage, following the warm forest environment into southeastern Asia, survives today little changed in *Dicerorhinus*. In central Asia it became adapted to a more arid environment, the cheek teeth higher crowned, the tusks degenerating and the horns becoming more powerful. One group became more strongly hypsodont, others more conservative.¹⁶ The latter group invaded Europe and both groups invaded Africa in the later Tertiary where they survive today in the "White" and Black Rhinoceros. The further development in both groups in Asia involved strengthening of the horn base by a bony nasal partition and some extension of the occipital crest, while there was also in both groups a tendency to further hypsodonty of the cheek teeth, probably associated with wider prevalence of grassland and steppe conditions. This stage, found in the later Pliocene and Pleistocene of Europe and Asia, did not reach Africa, the lowlying semi-desert region between constituting a barrier for steppe animals. They are represented by the *tichorhine* and *platyrhine* rhinoceroses and by *hemitocchus* and *etruscus*, *leptorhinus* of the European Pliocene being more nearly equivalent to the African black rhinoceros in stage of specialization.

In any and all fossil phylogenies it must be kept in mind that the known species are rarely if ever, the direct ancestors or descendants of other known species. They are approximations of various degrees of closeness. Nor is the geographic occurrence sufficiently known to document the species range. It must needs be a matter of inference from various lines of evidence. There are moreover comparatively few fossil species known from a sufficient series of specimens to determine the range of individual variation.

If due weight be given to these limitations of the fossil record, and to the geographic dispersal considerations previously discussed, a great part of the elaborate detailed phylogenies advocated by Osborn and others and the complex taxonomy based upon it, appear to be quite illusory, resting upon insufficient critical study of the evidence. The innumerable parallel lines of "polyphyletic" evolution are not really warranted by the evidence. They result from failure to realize how imperfect the evidence really is, from the manufacture of numerous species and genera out of what are probably individual variants, from arbitrary assignment of earlier and later age to different specimens

¹⁶ But as Hilzheimer observes, both the modern African rhinoceroses are hypsodont, though with different pattern.

and species not known to be other than contemporary, from the application to phyletic relations of ancient and long disproven concepts of irreversible trends in evolution, whether it be under the name of rectigradations, orthogenesis or what not; often most unjustly applying the name of Dollo's Law to concepts that Dollo has done more than anyone else to disprove.

The truth is that a general survey of the fossil evidence shows quite as much divergence as parallelism in the evolution of any group, major or minor, in its scope. In each species or larger group there is a tendency for individual variations to be specially marked in certain characters. These are the 'variables' of the species; most related species are apt to show the same variables, and they are apt to persist as variables through several successive stages in the evolution of the race. A few, but only a few of them, may be seized upon by selection and accumulated into progressive or divergent branches of the phylum. The rest remain as individual variables or may be bred out. In each group also there is a tendency to throw off repeated side branches in certain definite directions of adaptation, occupying certain 'niches' whose existence is conditioned by the practical fields of opportunity that must always be present and available, in a given environment. Frequently these successive side branches have been mistaken for a continuous separate phylum parallel with the main one. More adequate knowledge has again and again shown this interpretation to be wrong; but the lesson is seldom taken to heart in dealing with new material.

It would be a very easy matter to split up the large series of skulls, jaws, and teeth that I have referred to *Aphelops mutilus*, into a dozen or more 'species' distinguished by different combinations of structural variations. Examination of the large series of *Aphelops* from the Snake Creek beds would show the same characteristic variations very often in the same combinations; in the Middle Miocene the same variables and often the same combinations would again distinguish a dozen 'species.' In the Middle Oligocene *Caenopus* and in the Lower Oligocene *Trigoniis* the variables also correspond at least in part, and many could be regarded as foreshadowing each one a corresponding 'species' in the later beds. Thus one would construct a dozen "independent parallel phyla" already distinct in the Lower Oligocene and lasting through to the Pliocene with very little divergence. It would moreover be asserted that this was based upon abun-

dant evidence, upon many complete skulls and skeletons 'intensively studied' by the writer.

What it really signifies is a succession of rather variable species, probably approximately although not directly in line of descent. The parallelism is quite illusory. They represent a single phylum, not several.

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