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Charles D. and Mary Vaux Walcott
Research Fund

A STUDY OF THE EARLY TERTIARY CONDYLARTHRAN MAMMAL MENISCOTHERIUM

(With 11 Plates)

By
C. LEWIS GAZIN
Curator, Division of Vertebrate Paleontology
U. S. National Museum
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(Publication 4605)

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Charles D. and Mary Vaux Walcott Research Fund

A STUDY OF THE EARLY TERTIARY CONDYLARTHRAN MAMMAL MENISCOTHERIUM[1]

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INTRODUCTION

The genus *Meniscotherium,* although first described nearly ninety years ago, has heretofore received but little systematic or detailed study. Exception, however, must be made of E. D. Cope's rather thorough treatment of the very limited material available to him by 1884. There are, nevertheless, rather numerous references to *Meniscotherium* in the literature of vertebrate paleontology, and these serve not only to illustrate the wide interest that was early aroused, but also to direct attention to the strikingly diverse opinions held as to its relationships.

Meniscotherium is a condylarthran mammal characterized by primitive flat-nailed unguiculate or subungulate feet with essentially a serial arrangement of the carpals and tarsals, but associated with precociously selenodont teeth. Nearly all the known material is early Eocene or Wasatchian in age, although one, or possible two, Paleocene occurrences have been recorded. Its geographic distribution in Wasatchian time is the San Juan Basin of northwestern New Mexico, the Green River Basin and adjacent areas of southwestern Wyoming, and the valley of the Colorado River in western Colorado.

Investigation of the morphology and relationships of this highly interesting form was inspired by the abundant, unusually well-preserved remains encountered by Smithsonian Institution field parties

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[1] Study of early Tertiary mammals is currently aided by a grant from the National Science Foundation.

while collecting in the Knight and New Fork members of the Wasatch formation in southwestern Wyoming during various field seasons since 1948.

ACKNOWLEDGMENTS

Although the present study is based principally on the *Meniscotherium* remains in the U. S. National Museum, the work has been advanced immeasurably through the courtesies extended by various universities and other museums in permitting access to related comparative materials and in lending certain types and representative specimens for further study in Washington.

Drs. Glenn L. Jepsen and Donald Baird aided particularly in allowing me to study *Phenacodus* skeletal material in the Princeton collections and in furnishing me with a cast of the dentition belonging to a well-preserved specimen of *Meniscotherium* found near Moneta in the Wind River Basin. Drs. Edwin H. Colbert, Bobb Schaeffer, and Malcolm C. McKenna have been of much assistance in the study of related condylarth materials in the American Museum, particularly in lending me foot material of *Phenacodus, Tetraclaenodon,* and *Hyopsodus.* Dr. Joseph T. Gregory, while at Yale University, arranged for me to borrow the type of *Meniscotherium robustum* from Wyoming, and Drs. Elwyn L. Simons and John H. Ostrom made available for this study the *"Hyracops socialis"* foot material and a newly prepared skull of *Phenacodus.* I am indebted to Dr. Tilly Edinger for turning over to me for study endocranial casts of *Meniscotherium, Phenacodus,* and *Periptychus,* and to Dr. Clayton E. Ray for arranging the loan of these materials from the American Museum and the Museum of Comparative Zoology collections. Drs. Rainer Zangerl and William D. Turnbull forwarded to me for study the Chicago Natural History Museum specimens of *Meniscotherium* from western Colorado and graciously permitted me to review the associated mammalian collections for environmental indications. Dr. Craig C. Black lent me for inclusion in this study the Carnegie Museum specimens of *Meniscotherium* from the Colorado area, collected by Earl Douglass.

Dr. George G. Simpson early expressed an interest in making a study of *Meniscotherium* (see Gazin, 1952, p. 61) as a result of his extensive collection for the American Museum of materials representing the San Juan Basin population. Since moving to Cambridge, however, he has indicated with regret the improbability of his carrying out this study in the near future. His deferring to my interest in this undertaking is much appreciated.

The incomparable pencil drawings reproduced in the accompanying plates (except pl. 11), as well as the text figures, were prepared by Lawrence B. Isham, staff illustrator for the Department of Paleobiology in the U. S. National Museum.

HISTORY OF INVESTIGATION

Discovery and description.—Meniscotherium was first described by Cope in 1874. The specimen on which the type species, *M. chamense,* was based is a right maxillary fragment exhibiting the molars and outer wall of the last premolar, found that summer in the San Juan Basin of New Mexico in the region between Canyon Largo and Gallina River. No new material was reported until 1881 (b) when Cope described a left maxilla with three molars and three premolars and an associated lower jaw fragment with two teeth as representing a new and somewhat larger species, *M. terraerubrae.* Description of this material was included with that of Torrejonian Paleocene forms from the "Lowest Eocene beds of New Mexico." Cope stated (p. 495) that the new *Meniscotherium* specimens found by D. Baldwin were from "the red Eocene beds in northwestern New Mexico, from the true Wasatch horizon, or higher than that which produced other species here described." Nevertheless, there must have been some doubt in his mind as to the horizon represented because elsewhere on the same page, in discussing the fauna of the beds he thought were quite possibly the Puerco formation, he stated that he had now added the genera *Hyracotherium* and *Meniscotherium.*

A third and smallest species of *Meniscotherium, M. tapiacitis,* was described by Cope late in 1882(f). At this time there was apparently no confusion with the Paleocene. *M. tapiacitis* is stated to have been collected "by D. Baldwin from beds of probably lowest Wasatch age in New Mexico."

Marsh's description of *Hyracops socialis* in 1892 was based on skull and foot material collected by David Baldwin in 1878. While Marsh's report on meniscotheriid remains from the Wasatchian of New Mexico was much later than Cope's, Baldwin's collecting for Marsh evidently preceded his employment by Cope. The specimens according to Thorpe (1934) came from the head of Gabilan Canyon, a branch of Canyon Largo in the San Juan Basin. The distinction which Marsh made between *Hyracops* and *Meniscotherium* was based essentially on the molariform appearance of the last premolar and possession of an extra sacral vertebra, features that Thorpe has since shown to be invalid in that the premolar described belonged to the deciduous series and the number of vertebrae in the sacrum is consistent with *Meniscotherium.*

Later reports of discovery and description of new materials include an announcement by Granger in 1910 of the finding of *Meniscotherium* in the Lost Cabin beds of the Wind River Basin. He regarded this as the first record outside of the Wasatchian of New Mexico, although in 1915 he noted materials collected from the Wind River Basin as early as 1896. He was evidently not aware of the listing of *Meniscotherium chamense* by Clarence King in 1878 in the fauna for his Vermilion Creek group in Wyoming. The faunal lists in King's work, according to Hay (Bibliography of 1902), were probably furnished by Marsh, and it follows that the material referred to may well have been the Knight skull collected for Marsh in 1875 and that much later became the type of *Meniscotherium robustum* Thorpe. In 1915 Granger reviewed the characters and distribution of the genus *Meniscotherium,* revising the species to include Cope's *M. terraerubrae* as a subspecies of *M. chamense,* and adding the new species *Meniscotherium*(?) *priscum* from the Clark Fork Paleocene of northwestern Wyoming. Regarding it as a second species of Paleocene age, Russell (1929) described *Meniscotherium semicingulatum* from a locality in Alberta, Canada. The age is questioned but thought to be Clarkforkian because of the association of *Ptilodus* with forms of Wasatchian aspect.

It was not until 1934 that the material of *Meniscotherium* referred to above as having come from southwestern Wyoming in 1875 was described. Though rather poorly preserved, the specimen includes most of the skull and lower jaws. It was collected for Marsh by William Cleburne in a railroad cut near Aspen in Uinta County. Thorpe made this the type of the new species *Meniscotherium robustum,* a form that I (1952) found to be characteristic of the La Barge fauna from the Knight beds in the Green River Basin. In this 1934 paper Thorpe also gave the evidence for suppressing Marsh's name *"Hyracops,"* which in any case had long been regarded as a synonym of *Meniscotherium.*

The known distribution of *Meniscotherium* both geographically and geologically was summarized by Van Houten in 1945, and certain suggestions as to its ecology were presented by Simpson in 1948 as a part of his discussion of the occurrence of *Meniscotherium* in the San José beds of New Mexico. In a study of the Knight faunas of southwestern Wyoming in 1952 I summarized briefly the history of *Meniscotherium* discoveries and called attention to the abundant, well-preserved material encountered at certain localities. Peculiarities of distribution attributed to ecology within the southwestern Wyoming area were cited in 1959 and 1962.

Relationships.—In reviewing the hypotheses and conclusions as to *Meniscotherium* relationships it may be noted that in Cope's original description of *Meniscotherium chamense* (1874) he did not make an ordinal assignment but regarded the new form as presenting "a curious combination in structure of its molars of the character of *Palaeosyops, Hyopotamus,* and *Hipposyus.*" He probably did not intend to imply, in citing the latter, any suggestion of primate relationships because at that time he regarded *Hipposyus* (=*Notharctus*) as a primitive horse with *Orohippus* as a synonym. In repeating his description of *Meniscotherium* in 1877, however, Cope listed it in first place among the Perissodactyla, immediately preceding *"Orotherium"* (=*Orohippus*) in which he had included certain species of *Hyracotherium.*

In a further development of a systematic arrangement of perissodactyls in 1881(a) the genera were divided among 10 families, and *Meniscotherium* was listed in the Chalicotheriidae along with certain Eocene titanotheres, Old World *Propalaeotherium* and *Rhagatherium,* as well as the chalicotheres proper. The families as outlined were distinguished essentially by patterns of crescents and cross-crests in upper and lower molars, the extent to which the premolars resemble the molars, and the number of toes. The feet of *Meniscotherium,* however, were not known at that time, so that conclusions as to relationships were based entirely on the dentition, presumably the upper molars only, as displayed in the type of *M. chamense.*

Evidently the newer material cited later in 1881(b) included certain limb elements, possibly associated with tooth material, because in the spring of 1882(a) Cope stated that the astragalus and humerus had the characters of those of *Phenacodus.* As a result he concluded that *Meniscotherium,* for which he proposed the new family rank Meniscotheriidae, belonged with the Phenacodontidae (including the periptychids) in the recently (1881c) erected suborder, Condylarthra, under the Perissodactyla. Meniscotheriidae was distinguished by a lophodont dentition, "with external and internal crescents and deep valleys." Further concern about the foot structure of *Phenacodus* led Cope a couple of months later (1882c) to remove the Condylarthra from the Perissodactyla, and place them along with the Proboscidea in the new order or suborder Taxeopoda, having equal rank with Hyracoidea, Amblypoda, Perissodactyla, and

Artiodactyla under the Ungulata. The basis of this classification was presented in greater detail in his "Classification of the Ungulate Mammalia," published the same year (1882e). It is also this year (1882d) that Cope reported receiving foot material of *Periptychus* which led him to remove the periptychids from the Phenacodontidae as a third family of the Condylarthra.

Cope's ideas on condylarth classification were essentially crystallized by the time of his "Tertiary Vertebrata" (1884b) with little change since 1882, except that he had withdrawn the Proboscidea from the Taxeopoda, but included the Hyracoidea, suggesting a closer relationship of the latter to the Condylarthra. His treatment of *Meniscotherium* in this volume covers in detail the osteology of the skeleton, so far as it was then known, and is the most thorough to date. The more generalized part of this description appeared in a review of the Condylarthra in the American Naturalist for 1884(a) and as a separate brochure.

Later statements by Cope concerning *Meniscotherium* were essentially in defense of his interpretation of its relationships. In 1886 he criticized Schlosser (1886) for including *Meniscotherium* in the Perissodactyla instead of the Condylarthra, in placing more emphasis on teeth than on feet. In the following year he disputed Pavlow's (1887) assumption that *Meniscotherium* belongs to the Propalaeotheriidae and is perhaps a synonym of *Propalaeotherium,* reiterating his belief in the importance of foot structure in interpretations of relationship among ungulates.

Cope's briefly held interpretation (1881a) that *Meniscotherium* belonged with the chalicotheres was evidently favored by Schlosser (1886), as he regarded *Meniscotherium* as a perissodactyl with primitive feet and with teeth strikingly like *Chalicotherium.* This relationship is unquestioned in 1902, as evident from the statement, "Die Chalicotheriiden endlich stammen zwar aus Nordamerika—*Meniscotherium*—. . ." Although Zittel in 1893 followed more closely Cope's arrangement with the Meniscotheriidae, Phenacodontidae, etc., in the suborder Condylarthra, but under the Ungulata rather than Cope's Taxeopoda, Schlosser in a revision of Zittel's texts in 1911 and 1923 still regarded *Meniscotherium* as the ancestor or near the ancestry of the chalicotheres.

No doubt Schlosser was early confirmed in his conclusions regarding chalicothere affinity by Osborn (1891), who felt that the teeth of *Meniscotherium* pointed strongly toward a relationship with the chalicotheres, but awaited information on the structure of the feet.

He was evidently not satisfied with the fragmentary evidence of foot structure available to Cope. Moreover, upon description of the feet of the meniscotheriid *"Hyracops socialis"* by Marsh (1892), Osborn (1892a), in spite of the many discrepancies, concluded that the structures displayed supported a chalicothere relationship, appealing to the time interval separating the known materials of the two groups. It seems evident, however, that he nevertheless retained the Meniscotheriidae in the Condylarthra at that time because in 1895 (with Charles Earle) he suggested that this family as well as the Periptychidae should probably be removed from the order, although no different allocation was made. By 1907 Osborn's conviction concerning chalicothere relationship seems to have weakened because, while in one place (p. 87) he states that, "It is thus suggested that *Meniscotherium* may be related to *Chalicotherium*"; on another page (184) appears, "However recent observations tend to show that these resemblances [in teeth] are not indicative of genetic relationship but that the chalicotheres have more probably been derived from lower Eocene titanotheres."

Weber (1904) and Abel (1914) in textbook treatment followed Schlosser and the earlier conclusions of Osborn in believing that a close genetic relationship existed between *Meniscotherium* and the chalicotheres. Weber's classification included Meniscotheriidae in the Condylarthra with full ordinal status for the latter, but Abel (1914) substituted Protungulata for the ordinal name, including it under the superorder Ungulata. This arrangement, of course, prevailed in Abel's revision of Weber's text in 1928.

It appears that neither Matthew nor Gregory followed Osborn in his interpretation of the relationships of *Meniscotherium*. Matthew in 1897 pointed out the various possibilities that had been suggested, and Gregory (1910) noted that, "The manus of *Meniscotherium* has no suggestion of the Chalicothere type, . . ." and (1920) that *Meniscotherium* was obviously "not ancestral to the titanotheres, and probably not to the chalicotheres." Matthew made no particular investigation of meniscotheres but in 1899 was concerned that the foot material of *Meniscotherium*, probably that in the Cope collection, did not agree with illustrations by Marsh for *"Hyracops."* However, Granger in his taxonomic revision of the species of *Meniscotherium* in 1915 pointed out errors in reconstruction of the *"Hyracops"* carpus, concluding that there was no reason for distinguishing *"Hyracops"* from *Meniscotherium*.

Ameghino (1893) was particularly critical of the concept that

Meniscotherium was ancestral to the chalicotheres. In Ameghino's arrangement the Homalodontotheriidae occupied this position with respect to the chalicotheres of the boreal hemisphere, and the meniscotheres were described as allied with the Proterotheriidae with which they must have had a common but as yet undiscovered ancestry. This was later than Cope's (1891) observation that the dentition of the Macraucheniidae could have been derived from that of the Meniscotheriidae, as well as that the dentition of the Proterotheriidae could easily be derived from that of the Periptychidae. In 1901 Ameghino went so far as to include within the family Meniscotheriidae various genera of litopterns now divided between the Proterotheriidae and Macraucheniidae. In the meantime, Wortman (1896) attributed the appearance of the Proterotheriidae to a southward migration of the meniscotheres and later (1904) enlarged upon this hypothesis to postulate that not only were the Litopterna direct derivatives of *Meniscotherium* but that all South American ungulates were but modified descendents of North American condylarths.

Cope's suggestion of a condylarthran relationship to the hyracoids, which seems first mentioned in 1882(b) and later reflected in his taxonomic arrangement (1884b), was early championed by Wortman (1886). While Cope was concerned with certain resemblances in the structure of feet, Wortman, in reviewing teeth of *Meniscotherium,* saw a marked indication there of hyracoid affinity and was disposed to regard this genus as the direct ancestor of the Hyracoidea.

Marsh (1892) noted the *Hyrax*-like appearance of the carpals and tarsals which he indicated in his name *Hyracops* but evidently did not regard the relationship as close, as he proposed for the meniscotheres the new ordinal name Mesodactyla and about which he stated as follows: "The teeth are somewhat similar to those of Ungulates, but the rest of the skeleton, especially the limbs and feet, are of a generalized type quite distinct from any hoofed animals known, recent or extinct. Some parts of the structure seem to indicate an affinity with *Hyrax,* but the limbs and feet show characters resembling those of Primates, especially the extinct forms, and likewise seen in Insectivores, and even in some of the Rodents."

A little later that year (1892) Scott, although not certain that *Meniscotherium* was a direct ancestor of the modern hyracoids, was convinced from Marsh's (1892) portrayal of the feet of *"Hyracops"* and from his own study of meniscotheriid premolars that the family should be removed from the Condylarthra and included in the Hyracoidea. In 1913 Scott regarded this arrangment as improbable, but in the second edition of his textbook (1937) this latter opinion was modified by the statement that the hyracoids were probably derived from Old World condylarths. Schlosser in his study of the Fayum hyracoids (1911) pointed out that although there was a resemblance in foot structure between *Meniscotherium* and the hyracoids, the tooth structure resemblance is with the recent hyracoids and only one Fayum form (*Saghatherium*). Greater divergence was noted with respect to the bunodont hyracoids of the Fayum. Much more recently Simpson (1937) has referred to meniscotheres as "hyracoidlike" and (1945) in commenting on the hyracoids has observed that ". . . no one has ever fully examined and logically interpreted numerous resemblances, probably but not surely superficial, to various other groups, notably to the meniscotheres and notoungulates."

The European Paleocene genera *Pleuraspidotherium* and *Orthaspidotherium* had a varied history of interpreted relationship, as outlined by Teilhard de Chardin (1922), but in their later treatment, following Zittel (1893), came to be regarded by Weber (1904) and Schlosser (in Zittel and Schlosser, 1923), for example, as having condylarth affinities. It may be noted, however, that following his description of these genera in 1878, Lemoine, in 1892 (see Teilhard de Chardin, 1921-1922, p. 37), thought that *Orthaspidotherium* belonged in a position ancestral to the artiodactyls, an idea that was adopted by Schlosser in 1911 (in Zittel and Schlosser). Teilhard de Chardin in 1920 (and 1922) convinced of a closer relationship to the meniscotheres, included both *Pleuraspidotherium* and *Orthaspidotherium* in the Meniscotheriidae. This assignment was adopted by Simpson (1937) but with subfamily separation of Pleuraspidotheriinae and Meniscotheriinae. In 1929, however, Simpson noted the distinctive features of *Orthaspidotherium* but regarded Schlosser's (Lemoine's 1892) suggestion of an artiodactyl relationship as highly improbable. Most recently D. E. Russell (1964) has described more fully the *Pleuraspidotherium* materials from Cernay and, with detailed consideration of relationships, has followed Teilhard de Chardin and Simpson in including *Orthaspidotherium* as well as *Pleuraspidotherium* in the Meniscotheriidae.

GEOGRAPHIC AND GEOLOGIC OCCURRENCE

The known distribution of *Meniscotherium* is included geographically within the states of Wyoming, Colorado, and New Mexico in this country and in Alberta, Canada. Geologically it ranges from

Clarkforkian or latest Paleocene through or nearly through Wasatchian or early Eocene time. As noted by Van Houten (1945) only two Paleocene occurrences are known: a single specimen, the type of *Meniscotherium priscum* Granger (now lost), came from the Clark Fork beds in the Clark Fork Basin; and two lower premolars, one of which (Dp_4) was made the type of *Meniscotherium semicingulatum* Russell, came from beds of about this age near Cochrane in Alberta, Canada. The small species of *Meniscotherium* represented in the early Wasatchian at the Bitter Creek and Red Desert localities in southwestern Wyoming, earlier (Gazin, 1962) compared with *M. priscum,* I now find cannot logically be distinguished from *M. tapiacitis.*

Although Granger (1915) has listed *M. tapiacitis* as belonging in the Largo fauna of New Mexico, the single specimen of this very small form may have come from much lower beds, recalling Cope's statement that it was collected "from beds of probably lowest Wasatch age. . . ." The locality is given by Granger as "Alto la Zerta," but I have been unable to find this on any map. Possibly his conclusion that Cope's statement was in error was based on the distribution of *M. chamense.*

With the possible exception of *M. tapiacitis, Meniscotherium,* as noted by Granger (1915), Van Houten (1945) and Simpson (1948), is essentially missing from the Almagre facies, but is abundantly represented by *M. chamense* in the Largo facies of the San José sequence in New Mexico. Again in the Wind River Basin, as *M. chamense,* it is known, though sparsely, only in the latest, or in this case, the Lost Cabin fauna. I agree, however, with Van Houten and Simpson that because of the vagaries in distribution this does not warrant a correlation in time between Largo and Lost Cabin as Granger (1915) supposed.

There is no record of *Meniscotherium* in any of the early Eocene or Wasatchian horizons of the Big Horn Basin, following its occurrence in the latest Paleocene Clark Fork beds of the area. On the other hand it is apparently found at all levels in the Wasatchian beds of the southwestern part of the State, except in the southern part of the Fossil Basin and the eastern part of the Washakie Basin. Small *M. tapiacitis* is found in the lower levels of the Knight on both sides of the Rock Springs uplift and has been reported well up in the section, possibly as late as Lysitean, on the east side of the uplift, in the western part of the Washakie Basin near Bitter Creek. *M.* cf. *robustum* is recorded from an intermediate horizon of the Knight at Tipton Butte, and an undetermined species is reported (Henry W. Roehler, personal communication) from a semifluviatile facies of the Tipton tongue on nearby Table Mountain. Thorpe's species is especially characteristic of the La Barge fauna, but a smaller form which may well be *M. chamense* is abundant in the New Fork in the northern part of the Green River Basin, both faunas being included in Lostcabinian time. Farther east, however, although in the same general basin of deposition for the Wasatch formation, no material of *Meniscotherium* has been reported for the Four Mile, Dad, and typical Cathedral Bluffs faunas. In the Fossil Basin sparse remains have been found on Fossil Butte and in the Gray Bull equivalent west of Elk Mountain, but not in type Knight near Evanston, nor in the Gray Bull equivalent (type Almy) in Red Canyon.

The undescribed collections from the valley of the Colorado River, within the structural basin of Tertiary sediments often referred to as the Piceance Creek Basin in western Colorado, are reported by Van Houten (1945) to include *Meniscotherium* abundantly in the lower fossiliferous level of about mid-Wasatchian age and sparingly in the late Wasatchian upper level. Examination of the materials in the Chicago Natural History Museum, however, has revealed that the information furnished Van Houten for the presence of *Meniscotherium* in the late Wasatchian level was based on a jaw fragment with a single premolar belonging to *Lambdotherium* rather than *Meniscotherium.* In the list of materials in the Carnegie Museum from the Piceance Creek Basin the species of *Meniscotherium* given is *M. tapiacitis.* Two species, however, are represented in both the Carnegie Museum and the Chicago Natural History Museum collections. In the better documented, more recently collected Chicago materials it is clear that the two species, which may well be *M. chamense* and *M. tapiacitis,* do not occur together but in rather widely separated areas. *M. chamense* occurs to the northwest of the Colorado River in the Roan Cliffs area, whereas all the *M. tapiacitus* specimens were found to the southeast of the river in the general area of Mam Creek. Nevertheless, there is no evidence that the horizons represented are significantly different and may well be mid-Wasatchian.

The rather sporadic distribution of *Meniscotherium* outlined here is summarized in the accompanying chart, and explanation of these apparent nomalies is attempted in the following section concerning environment.

	Alberta, Canada	Big Horn Basin, Wyo.	Wind River Basin, Wyo.	Washakie Basin, Wyo.		Green River Basin, Wyo.	Fossil Basin, Wyo.		Piceance Creek Basin, Colo.	San Juan Basin, N.M.
				East side	West side		North part	South part		
Lost Cabin or equivalent		absent	*M. chamense* sparse	absent (Cathedral Bluff)	absent (Cathedral Bluff)	*M. chamense* abundant (New Fork)			absent (Upper fossil level)	
				absent (Dad)	*M. sp.* (Table Mt.)	*M. robustum* abundant (La Barge)				
Lysite or equivalent		absent	absent		*M. cf. robustum* (Tipton Butte & Sand Butte)		*M. cf. robustum* sparse (Fossil Butte)	absent (Knight Sta.)	*M. chamense* abundant (Roan Cliffs Area) *M. tapiacitis* abundant (S.E. of Colorado R.)	*M. chamense* abundant (Largo facies)
Gray Bull or equivalent		absent	absent (Indian Meadow)		*M. tapiacitis* (near Bitter Creek)		*M. cf. robustum* sparse (W. of Elk Mt.)	absent (Red Canyon, Almy)		*M. tapiacitis* very sparse (Largo auct. Granger) or *M. chamense* very sparse (Almagre)
Sand Coulee level		absent		absent (Four Mile)	*M. tapiacitis* (Bitter Creek)	*M. tapiacitis* (S.W. of Rock Springs)	*M. tapiacitis* (N.W. of Fossil Butte)			*M. tapiacitis* (Lowermost auct. Cope)
Clarkforkian	*M. semicingulatum* sparse (Cochrane)	*M. priscum* sparse				absent (Buckman Hollow)				

Chart I. – Distribution of species of *Meniscotherium* by horizon in various basins, or areas within basins of deposition.

ENVIRONMENT

There would appear to be but little doubt that the peculiar distribution of *Meniscotherium* during Wasatchian time is largely the result of environmental factors. Where a local population is well represented in a collection, the absence or abundance of remains of an average-size animal such as *Meniscotherium* would not likely be due to collecting chances or methods. In seeking explanation or some understanding of the factors guiding distribution in such cases, three lines of investigation would seem to offer promise of reward. These would involve information to be obtained from the physical characteristics of the containing sediments, from the associated fauna and flora, and from interpretation of the morphological characters of the animal itself. With respect to the first two of these, we are here favored by an animal that although comparatively abundant in some instances is seemingly rather more selective as to habitat than a number of its contemporaries. It is such discrepancies or anomalies of distribution that present opportunities for comparison of characteristics of the two environments with regard to sediments and the associated biota.

Directing attention first to the sediments, Simpson (1948) has commented on this aspect of the problem relative to the distribution of *Meniscotherium* in the San Juan Basin. The abundance of remains in the red beds of the Largo facies and near absence from the relatively more drab-colored Almagre suggested, as an extension of Van Houten's interpretation, adaptation to a more savannalike environment rather than swampy or more aquatic conditions. While the correlation seems evident here in the "different bulk facies," I find it difficult to extend this demonstration, so far as coloration alone is concerned, to conditions in the Green River Basin. I suspect that the larger species of *Meniscotherium* on other evidence may have favored a more savannalike environment, but probably this is not invariably reflected in coloration. In the upper Knight beds between La Barge and Big Piney, Wyo., where *Meniscotherium robustum* is so abundant, it has been quarried repeatedly in both the massive gray and red beds of the variegated sequence. It should be noted, however, that both kinds of beds appear to be fluviatile and there is rather little difference between them, other than coloration. Moreover, *Meniscotherium* cf. *chamense* is abundant in beds of similar composition in the New Fork sequence, but none of these in the fossiliferous area are red, but neither do they appear paludal. On the other hand similar, but deep red, sandy clays in the Dad area, both above and below the Tipton tongue, as well as the red beds of the Big Horn Basin are barren of *Meniscotherium.*

A more nearly paludal facies is represented near the base of the Wasatch at Bitter Creek, where colorless or drab sandy shales alternate with coal or peaty layers. *Meniscotherium,* though sparse, is represented here by small *M. tapiacitis,* which may have been less adapted to a savanna environment or was possibly less discriminating in this respect than the larger, later species. It seems possible, moreover, that *M. tapiacitis* may be represented nearly 700 feet above the base of the Wasatch not far from Bitter Creek. Roehler (unpublished charts) has designated the beds at this higher level as in general semifluviatile, although at the fossil site they are indicated as shaly.

The reported occurrence of *Meniscotherium* in the Tipton tongue on Table Mountain might appear disconcerting and contrary to the supposition that the later *Meniscotherium* preferred a savanna environment, but I find that the rock involved is a massive sandstone in a more general facies described by Roehler as semifluviatile, which he has shown as interfingering with typical lacustral sediments of the Tipton tongue.

While supposing a savannalike environment for later *M. robustum* and *M. chamense,* close proximity of a large body of water, the earlier stages of Bradley's Gosiute Lake in southwestern Wyoming, in no way inhibited their range as represented in fluviatile facies interfingering with lacustral. Nevertheless, coincident with the widespread extension of the Green River lacustral facies, the Tipton or Fontenelle tongue—Gosiute Lake encroaching on the marginal lowlands—*Meniscotherium robustum* evidently became extinct. Following retreat of this tongue the form was replaced, as represented in the overlying fluviatile sequence, by a somewhat smaller, possibly more widely ranging species believed to be the Largo *M. chamense.*

The disappearance of *M. chamense* at or near the close of Wasatchian time would seem unrelated to features of the complex of Green River lakes in Wyoming, Utah, and Colorado, because of its known more widespread distribution, such as in the Wind River Basin. The advent, however, of the more extensively distributed Laney member would suggest climatic change of a regional nature coincident with the extinction. Moreover, Bridgerian time in this region is characterized by voluminous ash falls, so clearly demonstrated in the fluviatile sequences interfingering with the Laney, which may have been detrimental to *Meniscotherium* either directly or by altering the environment.

The regional environment revealed from detailed study of Green River sediments by Bradley (1929) and of the Green River plants by Brown (1929, 1934) was previously summarized (Gazin, 1953, 1958) as it pertained to studies of tillodonts and primates. While much of this may bear more directly on the middle Eocene, it does of course include later Wasatchian time during which *Meniscotherium* flourished in the Green River Basin. Bradley in studies of the physical characters of the lake in comparison with other large lakes concluded that the climate, interpreted particularly for the Gosiute Lake region, was characterized by cool, moist winters and relatively long, warm summers. The temperature probably fluctuated widely from a mean annual temperature of the order of 65° F. The rainfall is described as varying with the seasons and fluctuating widely from a mean annual figure somewhere between 30 and 43 inches. He also pointed out that the relief, as it pertains to the height of the rim of the Gosiute drainage basin relative to the floor, was probably greater than now, although the floor of the basin was likely less than 1,000 feet above sea level.

From the paleobotanical evidence for the regional environment Brown has described "a broad, low-lying warm inland region, with shallow ponds, lakes, and marshes, fed by slow streams, which meandered through muddy and sandy swamps as they flowed out of the distant cooler foothills and surrounding mountains." In this connection Bradley (1929), in discussing topography of the ancient Green River basin, observed, "most of the streams within the Gosiute hydrographic basin were apparently rather short and flowed directly into the lake, but those in the eastern part were longer and may have had considerable volume." It is possible that these statements are not truly at variance, since both are of such general application. Moreover, Brown has noted for the entire area of Green River deposits, "that local conditions of climate, influenced in part by mountains that flanked the basin in the north, east and west, might vary considerably in such a basin." Nevertheless, it is in the part of the Gosiute Lake basin where the streams were evidently shorter that *Meniscotherium* most recently flourished. As discussed above, it does not seem to have been present in the eastern part of the basin during later Wasatchian time.

In attempting to understand the differences between Wasatchian faunal assemblages including or not including *Meniscotherium*, there is, unfortunately, no adequate paleobotanical evidence that might be correlated, so that information on possible local differences in the floristic environment or food supply for the herbivores is not at hand. A comparison of the mammalian faunas, however, reveals other and apparently related discrepancies that are surely significant. Certain of the differences, nevertheless, while provoking speculation, cannot be fully credited because of the sparsity of remains upon which presence was established.

Perhaps the most striking feature revealed in the faunal comparisons made is the seeming incompatibility of *Meniscotherium* and *Phenacodus*. This is most noticeable in the difference between the faunas of the Big Horn Basin and those of the Green River basin. Exception to this relates to the smaller form or forms of *Meniscotherium* which, as well as being found in more paludal sediments, is associated, though very sparsely, with *Phenacodus* in both the Clark Fork and Bitter Creek localities. It may be further noted, however, that in the more abundant materials of the Four Mile fauna, which is close in time to Bitter Creek, some diversity of phenacodonts is represented, but no *Meniscotherium*. Unfortunately, the relative stratigraphic position for much of the Cope collection from the San Juan Basin is not known. Nevertheless, it would seem from Granger's and Simpson's collecting that *Phenacodus* is essentially characteristic only of the Almagre, although one of the specimens mentioned (Granger, 1915) came from the Largo or *Meniscotherium* facies. In the Wind River Basin *Phenacodus* but not *Meniscotherium* occurs in the Lysite, whereas in the Lost Cabin beds both are recorded although *Meniscotherium* is very scarce. Moreover, there is no reported information on the relative stratigraphic position of these, so that no certain conclusions can be drawn. In the Piceance Creek Basin, of the approximately 25 Chicago Natural History Museum specimens certainly identified as *Phenacodus,* only 1 was from the Roan Cliffs area yielding *M. chamense.* Except for three from localities not pinpointed, however, the remainder were from the area southeast of the Colorado River, often in association with *M. tapiacitis.* Finally, *Phenacodus* but no *Meniscotherium* is reported (Peter Robinson, MS.) for the Wasatchian of the Huerfano Basin in Colorado.

Among other elements that seem foreign to the *Meniscotherium* environment are *Homogalax* and *Ectocion,* although the evidence here may not be so convincing, inasmuch as these two are rather sparsely represented outside the Big Horn Basin. For example, *Ectocion* is found in the Clarkforkian beds at Buckman Hollow, Four Mile Creek, and Lost Cabin, and *Homogalax* at Bitter Creek, Four Mile Creek, and Dad. Several specimens of *Homogalax* or a closely related form in the rather scant collections from the Wasatchian beds near Dad, Wyo., are noteworthy because no isectolophid is represented in the contemporary La Barge fauna. *Homogalax* and *Meniscotherium,* small *M. tapiacitis,* have been reported together only at Bitter Creek.

Discrepancies in the distribution of the smaller artiodactyls *Diacodexis* and *Hexacodus* may also merit discussion. *Diacodexis,* while widely distributed, is abundant only in the Big Horn Basin. *Hexacodus,* on the other hand, with the exception of a single Gray Bull specimen, has so far been found only in southwestern Wyoming. Distribution of these may in a general way be related to the environment of *Meniscotherium,* but it must be noted that relatively scant remains of *Diacodexis* have been found in nearly all *Meniscotherium* occurrences. *Diacodexis,* however, is outnumbered by *Hexacodus* better than 5 to 1 in the La Barge fauna.

Of the remaining subungulate and ungulate forms of the Wasatchian, *Hyopsodus* is nearly universal in occurrence. It is possibly of more than casual interest, however, that with the exception of three specimens of *H. walcottianus* reported from the Lost Cabin beds and one from the New Fork, the larger species of *Hyopsodus,* including *H. browni, H. powellianus,* and possibly *H. walcottianus,* seem to avoid *Meniscotherium* or vice versa. Equally widespread *Hyracotherium,* however, would appear in no way influenced by the range of *Meniscotherium* or the factors controlling its distribution. The same may be said of *Heptodon* and *Lambdotherium,* although these are known only from later portions of Wasatchian time, and *Heptodon* seems to have a more restricted geographic range, but unrelated to the distribution of *Meniscotherium.*

Coryphodon has a distribution which in some ways appears at variance with that of *Meniscotherium,* but having collected the two in close proximity at various localities in the Knight, I suspect that abundance of the former is more closely correlated with time. It seems everywhere well represented in Gray Bull levels of the Willwood, Wasatch, and San José formations and particularly abundant in the lowest levels, to judge by its occurrences in the Washakie and Fossil Basins. It is missing or rare in Lysite levels, except possibly for the Fossil Basin, but then again it is not rare in the later Wasatchian of the Wind River and Green River Basins, in the latter being more closely associated with large *Meniscotherium.*

The scarcity of the herbivores *Esthonyx* and *Ectoganus* or *Sty-*

linodon in the basins of southwestern Wyoming and rather better representation in the Big Horn and San Juan Basins may well be related to environmental differences, but these forms are comparatively rare in middle and later Wasatchian levels in any case, so that no significant correlation with *Meniscotherium* one way or the other is evident. It may, however, be of interest to note that of the few San Juan Basin *Esthonyx* specimens for which adequate locality data are known, about a third are from the Largo or *M. chamense* beds, and that Roan Cliffs or *M. chamense* area specimens represent a roughly similar ratio of the Piceance Creek Basin materials. The species of *Esthonyx* are comparable in size to those of *Meniscotherium,* and lower molars show a rather similar selenodonty. The progressive development of the anterior portion of the dentition in both *Esthonyx* and *Ectoganus,* however, suggests food-getting habits rather different from those of *Meniscotherium.*

Among the unguiculate forms, such as the insectivores, primates, rodents, and carnivores, essentially not in competition with *Meniscotherium* as far as food supply is concerned, I have been unable to detect any important discrepancies in distribution that might be correlated. Most such orders include a diversity of genera for Wasatchian time, but only a few of these can be regarded as truly abundant in any instance. Primates, however, because of their special connotation as to environment draw attention. The La Barge fauna, as well as that represented at Bitter Creek, includes a rather striking diversity of primates and certain of these are comparatively well represented. From this we may assume that locally trees were plentiful in the savannalike environment postulated for *M. chamense* and *M. robustum,* as well as in the more paludal environment that we find for *M. tapiacitis.*

The morphological features of *Meniscotherium* which relate most directly to the environment are, of course, the characteristics of the dentition and feet, or adaptation to food and terrain. The anterior part of the dentition is relatively unspecialized, but the cheek teeth, upper and lower, are surprisingly precocious both in degree of selenodonty and in tendency toward molarization of the premolars. Teeth of this kind are better adapted to a more grazing habit, permitting harsher vegetation, than are the more bunodont teeth in other groups, such as contemporary *Hyracotherium.* A rather similar type of tooth structure is seen in the living hyracoids of Africa. Although these latter show a different incisor specialization, molarization of the premolars has proceeded to the anterior extremity of the series.

The hyrax *Procavia* is reported (Coe, 1962) to be selective in its feeding habits with a preference for grasses, mosses, and certain higher plants with succulent leaves. There is no paleobotanical evidence for grasses during the early Eocene, but the grasslike sedges and certain of the possibly harsher elements of the flora may have been more suitable for *Meniscotherium* than for *Phenacodus* or *Hyracotherium.* No doubt mosses and a variety of succulent leaves were available for selection. *Phenacodus,* on the other hand, quite possibly had a more omnivorous habit.

The feet of *Meniscotherium* are moderately robust but show the structural weakness of a serially arranged condylarthran tarsus, somewhat less evident in the carpus. The feet are pentadactyl, but with the lateral digits in the pes, particularly the hallux, reduced. The ungual phalanges are elongate and distally flattened dorsoventrally or spatulate, much more so than in *Tetraclaenodon* but not so broadly as in *Phenacodus.* The structure of the foot is rather similar to that of the hyrax in the serial arrangement of the tarsus, somewhat less so in the carpus, and the feet have about the same relative size although they are a little more robust. They differ most noticeably in the articular arrangement between the tarsus and the tibia and fibula and in less reduction of the lateral digits and ungual phalanges. The lateral digits of the pes are lost in the hyrax, and the pollex (only) is vestigial in the manus. The distal phalanges, moreover, while broadly articulating with the second phalanges, are scarcely more than nubbins of bone in the hyrax.

Although the hyrax has a plantigrade foot with pads developed from the nails to the carpus and tarsus, I suspect that *Meniscotherium* was digitigrade or at least semidigitigrade, to judge by the rather different appearance of the inferior margin of the calcaneum. That in the hyrax is more distinctly flattened. The elongate distal phalanx in *Meniscotherium,* with the dorsoventrally somewhat flattened naillike hoof interpreted, and the character of the articulation between the various phalanges suggest that all these, at least of the three median digits, rested on the ground. From these considerations it would appear that the weight was borne essentially on the ends of the metapodials, quite unlike the hyrax. Any possible interpretation of habit by analogy of foot structure is further complicated by the fact that remarkably different habits are shown by different groups of procaviids. While *Procavia* and *Heterohyrax* are ground- and rock-dwelling forms, *Dendrohyrax* lives in trees. There seems to be little or no actual difference in foot structure among these—a versatility attributed to the characteristics of the foot pads.

I see no difficulty in attributing a ground habit in a savannalike environment to *Meniscotherium,* as suggested for the two larger species; nevertheless, the foot structure seems rather primitive so that a variety of conditions might be included. The readily divergent, although somewhat reduced, pollex and hallux; the flexibility of the foot articulations with tendency toward supination of the feet, particularly noted for the manus; and the indication of strong abductors and adductors suggest that adaptability may have extended to climbing. As a herbivore the comparatively weaker foot structure implied in the near serial arrangement, in comparison with contemporary perissodactyls, suggests less potential toward a cursorial habit, Kowalevsky's inadaptive type, possibly contributing to extinction.

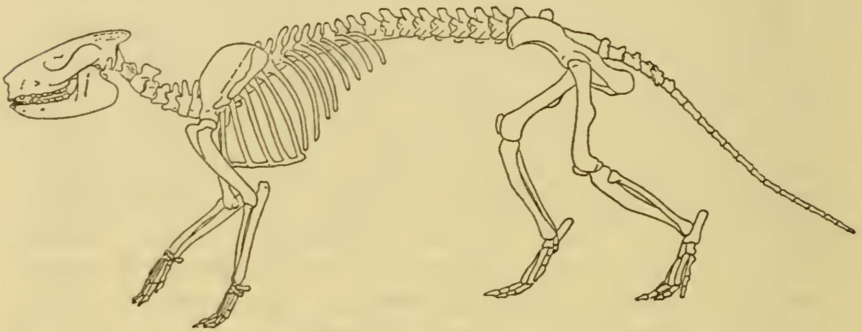


FIG. 1.—*Meniscotherium chamense* Cope. Drawing based on composite skeleton in the American Museum of Natural History. Largo beds of San José formation, San Juan Basin, N. Mex.

Cope (1884b) pointed out that *Meniscotherium* had a relatively larger brain than *Phenacodus* and that the oblique articular surfaces of the cervical vertebrae indicated the elevation at which the head was held. In his "restoration" of *Meniscotherium* he concluded that the body had the robust proportions of a raccoon, with the fore and hind legs rather short and of equal length (see fig. 1).

CLASSIFICATION

Condylarthra Cope, 1881
  Meniscotheriidae Cope, 1882
    Meniscotherium Cope, 1874
      Synonym.—Hyracops Marsh, 1892
      Type species.—Meniscotherium chamense Cope

Meniscotherium chamense Cope, 1874

Synonyms.—*Meniscotherium terraerubrae* Cope, 1881; *Hyracops socialis* Marsh, 1892

Type.—Right maxilla, U.S.N.M. 1093, with M^1-M^3 and part of P^4.

Horizon and locality.—San José formation, San Juan Basin, N. Mex.

Range.—Largo facies, San Juan Basin, N. Mex.; mid-Wasatchian, Piceance Creek Basin, Colo.; Lost Cabin, Wind River Basin, Wyo.; and New Fork, Green River Basin, Wyo. Middle and late Wasatchian early Eocene.

Meniscotherium tapiacitis Cope, 1882

Type.—Portions of both rami of mandible, A.M. 4425, with P_3-M_3 represented.

Horizon and locality.—San José formation, San Juan Basin, N. Mex.

Range.—San Juan Basin, N. Mex.; mid-Wasatchian, Piceance Creek Basin, Colo.; early to mid-Wasatchian, Green River Basin, Wyo.

Meniscotherium priscum Granger, 1915

Type.—Portion of left ramus of mandible, A.M. 16145, with Dp_4 and M_1.

Horizon and locality.—Clarkforkian late Paleocene, Clark Fork Basin, Wyo.

Range.—Not known outside occurrence of type.

Meniscotherium semicingulatum Russell, 1929

Type.—Right Dp^4, Univ. Alberta, Dept. Geol. 120.

Horizon and locality.—Late Paleocene (?), Cochrane, Alberta, Canada.

Range.—Not known outside occurrence of type.

Meniscotherium robustum Thorpe, 1934

Type.—Skull and lower jaw, Y.P.M. 10101.

Horizon and locality.—Knight beds near Aspen, Wyo.

Range.—Middle to late Wasatchian Knight beds beneath Fontenelle or Tipton tongue of Green River formation in southwestern Wyoming.

Among the foregoing I suspect that only three species are valid. These I regard as *M. chamense, M. tapiacitis,* and *M. robustum.* Although there would appear to be certain characters other than size of the skull and postcranial skeleton that may be significant in distinguishing between the two larger forms *M. robustum* and *M. chamense,* size seems to be the only generally definable feature in their separation and is consistently applicable in the Wyoming area. The much smaller *M. tapiacitis* type has been characterized by the weakness of the metastylids of the lower molars, but I find this is somewhat variable in other materials, so that its better development in the correspondingly small *M. priscum* type is probably unimportant. The latter is tentatively retained only because of its earlier geologic age. *M. semicingulatum* also may not be definable, since its description is evidently based essentially on a deciduous lower premolar. Its size would not distinguish it from *M. chamense,* but its geographic separation, as well as its possible age difference, may justify tentative recognition.

While the moderately conservative range in size of *M. robustum* in Knight beds beneath the Fontenelle tongue of the Green River in southwestern Wyoming is clearly separable from that of the smaller, typical *M. chamense* size from above the Fontenelle tongue, the somewhat earlier situation in the San Juan Basin is not so clearly resolved. The range in size there is much greater and is said to be continuous so that no logical separation could be made between *M. chamense* proper and *M. terraerubrae.* Granger (1915) illustrated this by regarding *M. terraerubrae* as a subspecies of *M. chamense,* but this is not strictly tenable unless some ecologic barrier or stratigraphic difference can be shown. With the range in size evident I suspect that there is more than one species represented, not clearly definable in the material represented, or there is a strong potentiality for such a split.

There is no evidence of a developmental sequence from *M. tapiacitis* through *M. chamense* to *M. robustum* as might be suggested by size, because in about mid-Wasatchian time approximately contemporary occurrences are known, although the species are not actually found associated. This is further emphasized by the survival of *M. chamense* into later Wasatchian time than *M. robustum.*

THE SKELETON OF MENISCOTHERIUM, WITH NOTES ON PHENACODUS, HYOPSODUS, AND OTHER CONDYLARTHS

SKULL

In overall appearance the skull of *Meniscotherium* is relatively broad across the frontals, and the robust rostrum is approximately equal in length to the more slender cranial portion. The posterior extremity of the tooth row and the orbital constriction across the frontals come very near a mid cross section of the skull. In longitudinal profile the dorsal surface is only gently convex to nearly straight. The basilar axes, palatal and basicranial, appear nearly parallel but intersect at a relatively low angle in the least distorted specimens. Notable are the prominence of the postorbital processes of the frontals, the extent to which the squamosal portion of the zygomae flare upward and inward, the backward deflection of the lambdoidal crest and the marked length of the paroccipital processes. Moreover, the cheek teeth are strikingly selenodont, and accompanying this the glenoid surface for articulation of the lower jaw is biconcave and anteroposteriorly elongate.

Dorsal view.—In dorsal view (see pls. 1 and 2) the rostrum does not taper forward nearly so abruptly as shown by Cope (1884b, pl. 25f, fig. 13a). The nasals are broad and elongate, extending from about even or slightly forward of the greatest anterior extremity of the premaxillae to a posterior limit well into the frontal segment, nearly halfway in some specimens. They are wide anteriorly, at the anterior extremity of the naso-premaxillary suture, and somewhat constricted about midway in their length, near the premaxillo-maxillary suture, but reach the greatest width where the frontals join the maxillae. Posterior to this they taper gradually, and about a third of the way across the frontals they are abruptly rounded off with a strong reentrant of the frontals along the midline of the skull. The nasals are very much like those in *Phenacodus* except that in the latter there is greater penetration into the frontal area and the greatest width is carried posterior to the fronto-maxillary suture well into the frontal area. In marked contrast the nasals in *Hyopsodus* terminate rather abruptly posterior to the fronto-maxillary suture.

The frontals are broad and flat between the orbits and reach forward to contact with the maxillae, although a short distance laterally the frontals and maxillae are widely separated by the lachrymals. Posteriorly the frontals generally show a shallow depression between the postorbital processes which is posteriorly defined by the strong temporal ridges. The latter converge abruptly medial and posterior to the postorbital processes.

The frontals in *Phenacodus* are much more convex transversely, and a longitudinal convexity is better emphasized somewhat farther forward over the posterior region of the nasals. The postorbital processes are not nearly so well defined in *Phenacodus,* and the temporal crests converge posteriorly much more gradually than in *Meniscotherium.* The frontals in *Hyopsodus* are gently convex transversely, and there are no postorbital processes. The comparatively weak temporal crests diverge forward with little or no flexure to become the orbital rims.

From the union of the temporal crests at about the postorbital constriction in *Meniscotherium* the well-developed sagittal crest extends nearly straight over the elongate-appearing cranial portion to divide again into the two posteriorward flaring halves of the lambdoidal crest. The most conspicuous feature of the elongate temporal fossae is the nearly a dozen or more prominent vascular foramina in the posterior portion of the areas, for the most part near the parieto-squamosal suture but lacking any symmetry with respect to the median plane of the skull. The area of each fossa is divided about equally between the parietal and squamosal, although the lambdoidal crests are for the most part formed of a fringe of the exoccipitals. There is no evidence of an interparietal. In *Phenacodus* the cranial portion appears relatively shorter than in *Meniscotherium*. This is effected in part by the more gradual convergence of the temporal crests resulting in a somewhat more posterior position of the postorbital constriction. It may be further noted that the lambdoidal crests do not project out over the occiput so markedly and are relatively broader in *Phenacodus*. *Hyopsodus* on the other hand exhibits a rather elongate cranial portion, and the occipital crest turns sharply upward, producing a more distinct dorsal concavity in the posterior portion of each of the temporal fossae. An irregular cluster of vascular foramina is noted near the parieto-squamosal suture in the lateral portion of these depressions.

Lateral view.—In lateral view (see pls. 1-3) the premaxilla of *Meniscotherium* is seen as a narrow bar or plate extending from the incisors upward and backward along the anterior margin of the maxilla and wedging out posteriorly between the maxilla and nasal. Only a short length of nasal extends free anterior to the premaxilla. In uncrushed skulls the maxilla is moderately deep and exhibits a large infraorbital foramen approximately above the contact between the third and fourth premolars, well above the tooth row and well forward of the orbital margin. The lachrymal bone extends forward a short distance anterior to the orbital rim and upward almost but not quite to the nasals. In its juncture with the jugal below it excludes the maxilla from the orbital rim. The lachrymal foramen has a position essentially on the orbital rim to just within the orbital fossa, where it may be partially concealed by the lachrymal tubercle on the rim. The anterior margin of the orbit is above approximately the anterior margin of the second molar, not so far forward as in *Ectocion* or the later hyracotheres, and the lower margin is not deflected outward on the jugal so noticeably as in those forms. The jugal is moderately deep and forms a strong, dorsoventrally deep attachment to the maxilla, but the crest of the zygoma does not carry so far forward on the face. Posteriorly the zygomatic process of the squamosal is strikingly deep above the glenoid surface, and the upper portion of the flare is turned decidedly inward toward the crest of the ascending ramus of the mandible and the sagittal crest of the skull. Posterior to the postglenoid process the crest of the zygoma extends onto the cranium defining the lower margin of the temporal fossa, and terminates in the lambdoidal crest just above the mastoid portion.

The *Phenacodus* skull in lateral view shows a relatively greater depth of the snout and a more distinctly convex longitudinal profile. The premaxilla is more slender, and the portion carrying the incisors projects forward, more shelflike than in *Meniscotherium.* The anterior portion of the zygoma joins the rostrum much as in *Meniscotherium,* but the orbit is slightly more posterior with its anterior margin approximately above the middle of the second molar and the larger infraorbital foramen opens anteriorly a little farther back, more nearly above the first molar. The lachrymal foramen is similarly placed just within the orbital rim partially concealed by the somewhat larger lachrymal tubercle. As well as being more subdued, the postorbital processes are more posteriorly placed with respect to the tooth row, and as previously noted the postorbital constriction is distinctly farther back. It is particularly noticeable that the zygomatic process of the squamosal in *Phenacodus* is relatively shorter and much more slender than in *Meniscotherium,* lacking the dorsal flare above and anterior to the region of the glenoid surface. In small *Hyopsodus* the orbit is located with respect to the dentition about as in *Meniscotherium,* but the infraorbital foramen is a little farther forward and perhaps relatively closer to the tooth row. Moreover, the jugal seems relatively deep for so small a form.

Within the orbital fossa of *Meniscotherium* the orbital plate of the maxilla presents a relatively large, broadly concave superior surface exhibiting the large posterior opening of the infraorbital canal at its anterior extremity. The sphenopalatine foramen opens near its posterior margin but faces laterally in the adjacent ascending plate of the palatine, very near the notch in the posterior margin of the horizontal plate of the palatine. Immediately below but actually confluent with the larger aperture of the sphenopalatine foramen is the more dorsally facing posterior opening of the posterior palatine foramen. Farther back in the fossa the optic foramen, if correctly identified, is located slightly higher and well in advance of the sphenoidal fissure, apparently near the anterior margin of the orbitosphenoid. Posterolateral to the sphenoidal fissure and lower but not far removed is the anterior opening of the alisphenoid canal which, as determined from damaged specimens, is confluent in its anterior portion with the foramen rotundum.

The orbital plate of the maxilla in *Phenacodus* is more elongate and relatively narrower than in *Meniscotherium.* The posterior palatine foramen is nearly confluent with the sphenopalatine foramen somewhat as in *Meniscotherium,* and both are above and a little forward of the notch in the posterior margin of the palatine between the maxillary tuberosity and the ascending plate of the palatines. In *Phenacodus,* however, these foramina are posterior to M^3,whereas in *Meniscotherium* they are anterior to the posterior margin of the tooth series.

The optic foramen is relatively closer to the sphenoidal fissure in *Phenacodus,* the actual distance being approximately the same as or somewhat less than in much smaller skulls of *Meniscotherium* and *Ectocion.* Also, the anterior opening of the alisphenoid canal seems more closely appressed and immediately lateral to and somewhat lower than the sphenoidal fissure in *Phenacodus.* In the material observed I have been unable to determine whether there is a foramen rotundum confluent with the anterior opening or whether the second branch of the trigeminal nerve passed through the sphenoidal fissure with the first as Simpson (1933) has suggested. I suspect that these nerves emerged separately as seems demonstrated in *Meniscotherium,* although they possibly left the cranial cavity together through a posterior confluence of the foramen rotundum and sphenoidal fissure. The Cope endocast of *Phenacodus* is ambiguous in this respect, as the two sides are not alike in this area.

In *Hyopsodus* the orbital plate of the maxilla appears relatively short and wide with the long diameter nearly transverse, and the sphenopalatine foramen is about even with or slightly posterior to the hind margin of the last molar. The optic foramen is well in advance of and a little higher than the sphenoidal fissure. As observed in *Phenacodus,* it is just ahead of the anterior extremity or angle of the crest which forms the inferior border of the temporal fossa—the forward extension on the cranium of the anterior root or crest of the zygomatic process of the squamosal. In *Meniscotherium* this crest is not so well defined and does not coincide with the ledge or bulge immediately above the sphenoidal fissure which it forms in *Phenacodus* and *Hyopsodus.* The alisphenoid canal, if correctly interpreted for *Hyopsodus,* is decidedly elongate and the anterior opening, presumed confluent with the foramen rotundum, is somewhat less distinctly lateral to the sphenoidal fissure. It appears as a marked elongation or extension posteroventrally of the opening of the sphenoidal fissure.

Occipital view.—In an occipital view the most striking feature of *Meniscotherium* is the overhang of the occipital crest which consists of two fanlike projections of the supraoccipital supported in the more mature specimens by two low and broadly rounded ridges diverging upward from the broadly convex posterior surface of the occiput above the foramen magnum. Such development of the lambdoidal crest tends to expand posteriorward the area of origin for the temporal muscle and presents a strong rim of attachment for the trapezius, splenius capitis, etc., which function in raising the head. The lateral margins of these two fanlike projections extend downward and forward, becoming nearly parallel, to a point near the upper extremities of the mastoid portions. Below this a lateral flare of the lambdoidal crest on each side is developed on the squamosal. The mastoid portion of the periotic is exposed in a depressed area on either side in the lower half of the occiput, near the lateral margin. It is most broadly exposed in the upper portion and nearly pinches out below between the very elongate paroccipital process and the weakly developed mastoid process of the squamosal. Possibly the sterno-mastoid muscle was attached to the crest of the squamosal which extends as a prominent protecting rim to the lateral margin of the mastoid.

The occipital view of the *Phenacodus* skull is rather similar, although the two flaring projections of the supraoccipital are relatively broader and less overhanging, and the widely diverging ridges on the occipital surface, serving as buttresses to the lambdoidal flares, are more strongly rounded and extend upward and outward from about the foramen magnum. Between these buttresses the occipital surface is triangular and gently concave, lateral to them the surface on each side, including the exposed portion of the mastoid, faces more laterally than in *Meniscotherium*. Moreover, the mastoid portion does not become so nearly pinched out ventrally.

In *Hyopsodus* the flaring of the occipital crest is directed more dorsally and the buttresslike ridges seem comparatively weak and widely separated and may not be well defined. The mastoid portions of the occipital surface, as in *Phenacodus*, face more laterally, and in marked contrast to *Meniscotherium* increase in breadth of exposure ventrally.

Palatal view.—In a ventral view the palate of *Meniscotherium* (see pls. 1 and 2) is seen to be moderately broad and elongate with the lingual margins of the cheek teeth aligned nearly parallel on the two sides, although the palate may be slightly constricted between first premolars. Anteriorly it is about evenly rounded within the margin of canines and incisors. The anterior palatine foramina seem comparatively small but in no specimen are they clearly defined, and the extent of premaxillary exposure in the palatal view would appear to be limited to the rim of bone supporting the incisors anterior to the canines. In the posterior portion of the palate the palatines extend forward to a position about even with the anterior portion or margin of the first molar. The posterior palatine foramina may show one or two openings on each side, on or near the suture between the maxillae and palatines, inward from about the posterior portion of M^1. Posteriorly this suture comes near or reaches the alveolar margin of the last two molars. The posterior narial aperture is a little more than half the width of the palate between the third molars and extends forward to a position about even with or slightly in advance of the anterior margin of the third molars. The forward margin of the aperture is gently rounded to nearly rectangular in outline and exhibits a slightly everted liplike rim in a forward continuation of the inferior margin of the ascending plates of the palatines bounding the narial aperture. Lateral to this lip or crest and medial to the prominent maxillary tuberosity, the posterior margin of the palatines may show a pronounced though broadly rounded notch.

The palate in *Phenacodus* is lower with respect to the basicranium than in *Meniscotherium,* in keeping with the relatively deeper rostrum of *Phenacodus.* It is also noted that the notch between the ascending plate of the palatines and the maxillary tuberosity is more constricted in *Phenacodus* and extends forward more deeply grooved on the ventral surface of the palate.

The palate in *Hyopsodus* is rather like that in *Meniscotherium* and *Phenacodus* with the palatines extending forward to about even with the anterior margin of the first molars. Also, the anterior margin of the posterior narial aperture shows the inflected liplike rim or crest seen in both *Meniscotherium* and *Phenacodus,* but this margin does not extend so far forward in the palate as in *Meniscotherium.* Its anterior margin seems about even with the posterior portion or margin of the last molar. Moreover, the maxillary tuberosity is much nearer the lateral margin of the narial aperture so that there is only a very small notch between them in contrast with the deep and broadly open saddle in *Meniscotherium.*

Basicranium.—The basicranium in *Meniscotherium* (see pl. 3) appears relatively elongate. This is noticeable in the length of the mesopterygoid fossa and in the posterior position of the occipital condyles with respect to the glenoid surfaces for the mandible. The lateral walls of the mesopterygoid fossa extend posteriorly to disappear at a point just median to the foramen ovale. The anterior portion of each wall is composed rather largely of the vertical or ascending plate of the palatines, and a well-developed and widely open pterygoid fossa extends anteriorly well into and dividing the lower margin of these plates posteriorly. The pterygoid plate of the alisphenoid, the principal element composing the outer wall of the pterygoid fossa, is thicker and more sturdy than the pterygoid proper forming the medial wall, and its ventrolaterally directed lower margin exhibits a hamularlike process, possibly better developed than the hamular process of the pterygoid, although this is uncertain because in no specimen at hand does the lower margin of the pterygoid appear to be complete or undamaged. Immediately posterior to the pterygoid fossa, just above the point where the pterygoid and pterygoid plate of the alisphenoid join, is the posterior opening of the alisphenoid canal, lower and rather well in advance of the foramen ovale. The alisphenoid canal is essentially within the lateral wall of the mesopterygoid fossa opening at a distinctly ventral position on its posterior margin. From its posterior extremity the course of the canal, distinctly upward and forward to its junction with the foramen rotundum, has been observed in damaged specimens. Posterior to this junction a fair-size opening on the dorsomedial wall of the canal, about midway in its length, has been observed in one specimen, but the course of this foramen has not been determined. In all probability it enters the body of the basisphenoid.

The foramen ovale, well removed from the alisphenoid canal in *Meniscotherium,* is lateral to and may be slightly in advance of the anterior margin of the foramen lacerum medium. Extending posteriorward into the otic fossa from the medial margin of the foramen ovale is a very feeble crest which would seem to define the path of the eustachian tube. From the posterior margin of the foramen ovale, however, there is a very prominent and anteroposteriorly elongate process or crest, the styloid process of Cope, medial to and well separated from the postglenoid process, which apparently consists of laminae of both the alisphenoid and squamosal. Its position is near or about that of the angular spine of the alisphenoid in man which supports a portion of musculature of the soft palate and of the tympanum. Nevertheless, I suspect that here it is homologous to the prominence in this position in certain other mammals, such as the oreodonts, where it forms a pedicle for support of the anterior portion of the bulla. No tympanic bulla has been discovered during preparation of any of the *Meniscotherium* cranial portions. It may not, however, have been fully ossified or possibly was loosely attached and invariably lost.

The glenoid surface for articulation with the lower jaw is broadly concave transversely as well as fore and aft, with its longest diameter extending anteroexternally. While this would appear to be nearly a ball-and-socket arrangement, considerable forward motion of the jaw is permitted. There is a prominent but relatively narrow postglenoid process, and posteromedial to it is a comparatively large postglenoid foramen. It is interesting to note that in one specimen (see pl. 1) the opening of the postglenoid foramen on the left is through the squamosal but on the right its aperture is bounded medially by a portion of the periotic. Posterior to the postglenoid process the squamosal is broadly concave for the audital tube. This space is bounded posteriorly by a rather weak mastoid process which is nearly pinched out between the descending plate of the squamosal and the very elongate paroccipital process. The striking development of the paroccipital process is indicative of the significance of the digastric muscle which would extend forward to the inner part of the anterior portion of the lower margin of the jaw, possibly also development of an occipito-mandibularis to the posterior margin of the jaw as described by Sisson for the horse, which shows comparable development of this process.

The hypoglossal or condylar foramen is large and circular in outline and lies about in the middle of a depression between the paroccipital process and the occipital condyle on each side. The foramen lacerum posterius is a more elongate, slitlike and medially constricted aperture lying at the anteromedial root of the paroccipital process and bounded forward by the petrosal. I suspect that the constriction of this slit tends to define the jugular (more lateral) portion as partially distinct from the somewhat wider part for nerves IX, X, and XI.

Although much of the *Phenacodus* skull material is rather poorly preserved or not completely prepared in the basicranial area, there would appear to be a number of differences from *Meniscotherium* worthy of comment. There is less evidence for a so well developed pterygoid fossa in *Phenacodus,* suggesting less significance for the internal pterygoid muscle. Its development in *Meniscotherium* would probably correlate with the relatively deeper and more extended angle of the lower jaw. The foramen ovale occurs just lateral to the posterior extremity of the pterygoid flange but is relatively farther forward, much closer to the alisphenoid canal and farther removed from the auditory chamber than in *Meniscotherium.* Moreover, the foramen ovale is not followed by a so well defined crest. The basisphenoid and basioccipital are relatively broad and the ventral surface appears somewhat more convex longitudinally. This may in part be effected by the more prominent development of the area of muscle attachment that would suggest better development of the rectus capitis anterior major that functions in depressing the snout. The glenoid surface for articulation of the lower jaw is not nearly so concave and with less evidence of the fore and aft motion of the jaw interpreted for *Meniscotherium.* The space between the postglenoid process and the mastoid process, which would be occupied by the audital tube, seems relatively shorter anteroposteriorly. The mastoid exposure, however, between the weak mastoid process of the squamosal and paroccipital process is much broader than in *Meniscotherium.* The paroccipital process of *Phenacodus,* as noted, is much less developed. The hypoglossal or condylar foramen is farther forward in *Phenacodus,* as is also the auditory chamber with the petrosal.

The relatively elongate basicranium of *Hyopsodus* resembles that of *Meniscotherium* in a general way, although there are noticeable differences in detail. In the skull material available it would appear that the pterygoid fossa was significantly developed, and as in *Meniscotherium* there is evidence that the lateral wall or descending pterygoid plate of the alisphenoid was stronger and better developed than the pterygoid proper which defined the medial wall of the fossa. The posterior margin of the pterygoid plate of the alisphenoid ascends steeply to a point near or immediately in front of a somewhat elongate aperture which may well be the confluence of the foramen ovale and the posterior opening of an alisphenoid canal, if the latter is present. This is decidedly different from that found in *Meniscotherium* where the foramen ovale and alisphenoid canal are widely separated. As in *Meniscotherium* there is a strong crest posterolateral to the foramen ovale made up of plates from the alisphenoid and squamosal, but more distinctly lateral in *Hyopsodus* and with less participation of the alisphenoid. This leaves a much wider separation between the crest and the foramen lacerum medium. A broad groove in the alisphenoid for the eustachian foramen is relatively closer to the foramen lacerum medium and better separated from the crest or pedicle, attributed to a possible bulla, than in *Meniscotherium.* There seems rather less of the mastoid exposed posterointernal to this crest and lateral to the tegmen tympani, suggested as a position of attachment for the annulus in *Meniscotherium.* External to this crest and decidedly closer is the glenoid surface for the lower jaw articulation. This articular surface though slightly concave transversely is not nearly so much so as in *Meniscotherium,* and its long axis is not nearly so oblique. There is a well-developed postglenoid process posteromedial to the center of the glenoid surface, and immediately posterointernal to the process is a large postglenoid foramen with its aperture entirely surrounded by the squamosal. The broad arch of the squamosal over the external auditory meatus extends posteriorly down the anterior surface of the moderately developed mastoid process, and the relatively greater ventral exposure of the mastoid bone than in *Meniscotherium* causes the position of the audital tube to be relatively farther forward from the condyles and more widely separated from the paroccipital process. The paroccipital process is not complete in any specimen at hand, but its root suggests that it was fairly long and slender, although probably not so elongate as in *Meniscotherium.* The condylar or hypoglossal foramen is located decidedly medial and somewhat posterior to the paroccipital process, close to and partially concealed by the posteroventral margin of the condyle.

Periotic.—Ventrally the petrosal of *Meniscotherium* presents an almondlike oval to nearly triangular shape with its broad surface facing anterolaterally and ventrally, and its long axis extending anteromedially. Posterior to the promontorium the transversely elongate fenestra rotunda faces downward and outward as well as slightly backward, and anterodorsal to it the smaller fenestra ovalis faces almost directly outward. On the ventrolateral surface of the petrosal there can be distinguished a sinuous trace or broad groove from the medial margin of the fenestra rotunda, adjacent to the foramen lacerum posterius forward around the medial portion of the promontorium, then anteromedially to the apex of the petrosal. There would appear to be a branch extending over the anterior portion of the promontorium to the fenestra ovalis. One is tempted to interpret this as the position of the internal carotid and its stapedial branch; however, I am inclined to consider the course of the internal carotid as more medial with respect to the petrosal, as there is a broad groove in the basioccipital that faces ventrally in its hinder part, medially adjacent to the posteromedial angle of the petrosal, where the latter solidly abuts the basioccipital. Forward, this groove turns outward along the lateral margin of the basioccipital and adjacent to the ventromedial margin of the petrosal to near the anterior extent of the basioccipital and the apex of the petrosal where the groove opens broadly into the foramen lacerum medium, and where the internal carotid would enter the cranial cavity. This groove is probably not the inferior petrosal sinus for a vein, as posteriorly it does not seem to join or even approach, as far as visible, the jugular or foramen lacerum posterius. I suspect the above-mentioned grooves on the ventrolateral surface of the petrosal may be for branches of a tympanic nerve plexus.

In the absence(?) of an ossified bulla it may be further observed and interpreted that the facial nerve emerged from the periotic at an aperture in the roof of the tympanic chamber anterodorsal to the fenestra ovalis, extending downward, then flexing backward lateral to the fenestra ovalis into the sulcus facialis which also housed the stapedial muscle dorsoexternal to the fenestra rotunda. At this point the facial nerve was again directed downward and slightly backward at the anterointernal root of the small mastoid process. Medial to this point of departure there is a small pedicle, evidently the tympanohyal, on a posteriorly directed crest or ridge at its union with the posterior rim of the fenestra rotunda. This ridge separates the above fossa for the facial nerve from the foramen lacerum posterius and joins the petrous and mastoid portions of the periotic ventrally.

Anterior to the aperture in the petrosal where the facial nerve emerges there is a deep, anteroposteriorly elongate fossa the roof of which covers the facial canal ventrally and which continues anteriorly after a short hiatus, presumably for a branch of the stapedial artery, with the broad groove in the alisphenoid for the eustachian tube. This fossa would also house the tensor tympani muscle. Lateral to this fossa and partially ventral to it there is a broad exposure of the mastoid near, and occasionally adjacent to, the postglenoid foramen. This exposure of the mastoid, anterodorsal to the position of the audital tube must have been about where the anterior leg of the tympanic annulus made contact. It is immediately behind the posterior margin of the crest or pedicle formed of the squamosal and alisphenoid suspected of supporting a bulla.

The lateral wall of the mastoid, when the squamosal covering is removed posterodorsal to the above exposure adjacent to the audital tube, shows a deeply intrenched, nearly circular, and occasionally branching path for the venous sinus terminating in the postglenoid foramen. It is interesting to note that the lower arc of this sinus, directly above the position of the external auditory meatus, appears to be less curved in small *M. chamense* than in *M. robustum,* as observed in two individuals of each.

The dorsomedial surface of the periotic shows a relatively large internal auditory meatus, directly opposite the promontorium on the ventrolateral surface. Above the horizontal superior rim of this opening is a large, obtuse conical depression for the flocculus of the cerebellum. At the apex of this conical surface in its posteroventral portion there would appear to be a foramen of variable size. Possibly this is the aqueductus vestibuli, but this may be located in a more customary position directly posterior on the rim or crest of the floccular fossa, where there also seems evidence for a foramen. On the broad posteroventral margin of the petrosal, posteroventral to the internal auditory meatus is a very large aperture which inward is reduced to a rather small foramen that may well be the aqueductus cochleae. The hiatus Fallopii for the superficial petrosal nerve is evidently at the anterior apex of the petrosal.

The petrosal seems relatively small in *Phenacodus,* the actual size in large *P. primaevus* being only a little greater than in *M. robustum.* It is clearly a little thicker and broader through its midsection, but its length to the anterior apex is relatively less. The general plan of the ventrolateral surface is rather alike in the two, with the position of the fenestrae and the details of the facial canal and sulcus being not greatly different. The aperture of the facial canal, however, is situated a little deeper anterodorsal to the fenestra ovalis; also the hiatus Fallopii, rather large in one of the two specimens examined, is located more medial to the apex, rather than at the apex as observed in *M. chamense* skulls. In the posterior portion the fenestra rotunda is more widely separated from the foramen lacerum posterius, and the facial sulcus swings around more posterior to this fenestra as it turns more gradually downward in *Phenacodus.*

The inner or dorsal surface of the petrosal in *Phenacodus* shows no striking differences, with the internal auditory meatus large and similarly placed. The aqueductus cochleae shows the same wide aperture to a small foramen but is possibly a little more dorsal along the posterior margin. The aqueductus vestibuli seems decidedly slit-like at the posterior margin of the dorsomedial surface, entering the posterior part of the crest which defines the lower margin of the floccular fossa. In the material at hand I was unable to determine the presence or absence of a foramen in the depth of the floccular fossa noted in *Meniscotherium.*

The petrosal in *Hyopsodus* appears long and slender in ventral view, as a slender cone with its apex directed forward and medially.

The promontorium is not separately defined. The relatively large fenestra rotunda faces backward, outward, and downward. Its posterior rim is joined by a crest from the medial portion of the ventrally exposed mastoid which also forms an anterior root of the paroccipital process. This crest at the posterior rim of the fenestra rotunda may also have supported a tympanohyal. Posteromedial to the fenestra rotunda and anteromedial to the paroccipital process is a comparatively large foramen lacerum posterius. The relations here are closely similar to those in *Meniscotherium.* Anterodorsal to the fenestra rotunda is the smaller outward-facing fenestra ovalis. As in *Meniscotherium* the facial nerve would emerge from an aperture anterodorsal to the fenestra ovalis, descend to a position opposite the fenestra ovalis, turn backward then downward to appear anterolateral to the root of the paroccipital process, were the otic area covered by a bulla.

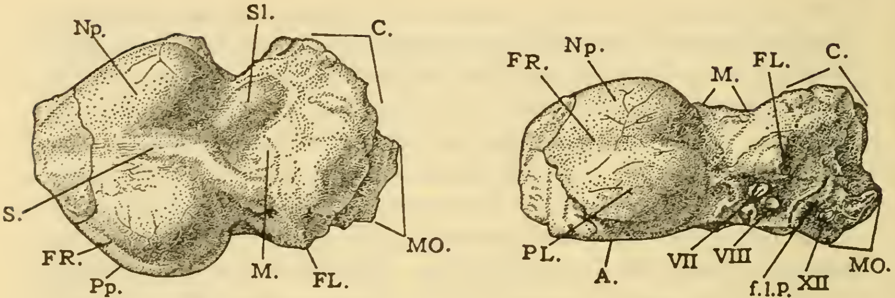
The medial margin of the petrosal in *Hyopsodus* shows a broad longitudinal groove partially formed by the lateral margin of the basioccipital. The posterior extremity is determined by the point at which the petrosal more solidly abuts the basioccipital, closer to the foramen lacerum posterius than in *Meniscotherium.* This groove clearly opens into the cranial cavity medial to the anterior extremity of the petrosal and no doubt carried the internal carotid as interpreted for *Meniscotherium.*

The dorsomedial surface of the petrosal could not be seen in any of the *Hyopsodus* material at hand without damage to the specimen.

ENDOCRANIAL CAST

An endocast of *Meniscotherium* was briefly mentioned by Edinger (1956, p. 17) as being much smaller than that of *Phenacodus* but of the same type. In addition to the specimen that she examined (fig. 2, A.M. 48082), there are at hand two casts in the collections of the U. S. National Museum. One of these (fig. 3, U.S.N.M. 23113) is a natural but somewhat eroded cast which includes the rostral as well as the cranial portion. The other (fig. 4, U.S.N.M. 19509) was prepared in rubber from assembled cranial fragments, but includes essentially only the dorsal surface, as its ventral surface is incomplete posterior to the olfactory bulbs. Cranial fragments of various other specimens present detail in restricted areas.

The endocast of *Meniscotherium,* though actually smaller than in *Phenacodus,* is relatively larger, as observed by Cope (1884b, p. 494). It appears elongate and slender, noticeably in the area of the



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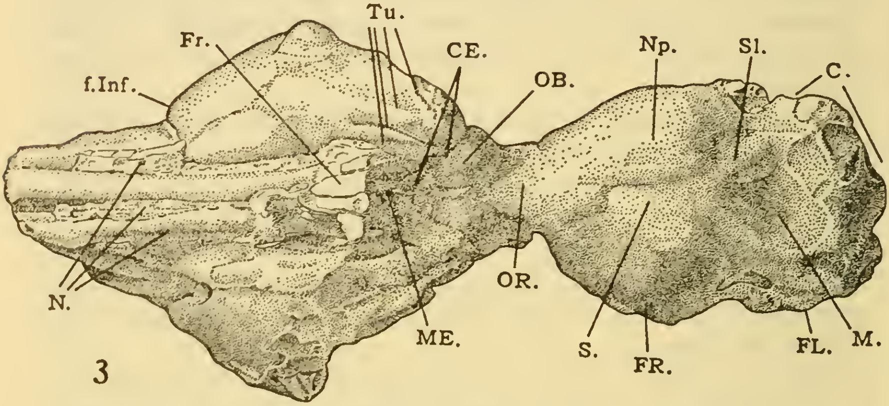

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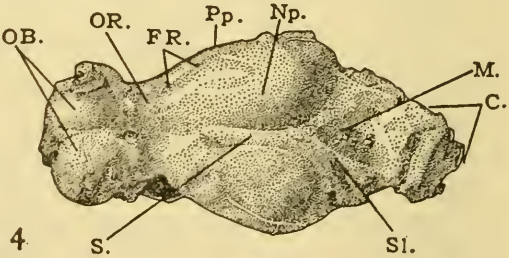

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Fig. 2.—*Meniscotherium chamense* Cope. Natural endocranial cast (A.M. 48082) ; a, dorsal view; b, lateral view of left side. Natural size.

Fig. 3.—*Meniscotherium robustum* Thorpe. Natural endocast of skull (U.S.N.M. 23113), dorsal view. Natural size.

Fig. 4.—*Meniscotherium robustum* Thorpe. Endocast of cranial roof (U.S.N.M. 19509), dorsal view. Natural size.

For explanations see opposite page.

olfactory bulbs and their roots or peduncles, and particularly more slender across the pyriform lobes. It may, however, have been a little less elongate in the cerebral portion than in *Hyracotherium,* as the latter was figured by Edinger (1948, fig. 2). It seems, however, to have reached a rather similar stage of development.

The olfactory bulbs as seen in the rubber mold are distinctly less divergent than in the *Phenacodus* cast and dorsoventrally less compressed. There is a longitudinal fissure separating the lobes on the dorsal surface, but which seems much less deeply impressed than on the ventral surface. Moreover, on the ventral surface this fissure is much less wide open and does not extend posteriorly dividing the olfactory peduncles as it does in *Phenacodus.* In *Meniscotherium* the ventral surface of the olfactory roots shows a gentle concavity, which changes to a gentle convexity posteriorward, and a slight longitudinal ridge on the mold—the trace of the suture between the orbitosphenoids—extends posteriorward from near the fissure between the olfactory bulbs to the optic chiasma. In the *Phenacodus* cast the deep fissure extends almost to the chiasma.

The neopallium in *Meniscotherium* is moderately elongate and

Explanation of figures 2-4

A., Ridge representing groove, possibly the cavernous sinus, and may have contained nerves III, IV, V_{1-2} and VI.
C., Cerebellum.
CE., Cribiform plate.
FL., Flocculus.
f.Inf., Position of infraorbital foramen.
f.l.p., Filling of foramen lacerum posterius.
FR., Rhinal fissure.
Fr., Remnant of frontal bone.
M., General position or covering of midbrain.
ME., Mesethmoid.
MO., Medulla oblongata.
N., Remnants of inferior crests of nasals.
Np., Neopallium.
OB., Olfactory bulb.
OR., Olfactory root.
PL., Pyriform lobe.
Pp., Paleopallium.
S., Sagittal or longitudinal sinus.
Sl., Lateral sinus.
Tu., Impressions of turbinals.
VII., Position of facial nerve in internal auditory meatus.
VIII., Position of auditory nerve in internal auditory meatus.
XII., Filling of hypoglossal or condylar foramen.

tapers forward to anterior poles nearly at the narrows of the olfactory peduncles but well separated from the olfactory bulbs. The cerebral hemispheres would seem comparatively smooth or lissencephalic, suggesting that there were no gyri or sulci, although such, if weakly developed, might have been obscured by the dura mater. There is, however, a slight depression on the dorsolateral surface in the forward portion on either side of the rubber mold, in a position of a sulcus suprasylvius, although it is not a true sulcus or furrow. The fissure rhinalis is clearly defined in all specimens, and it is seen that the neopallium is a little less than half the depth of the endocranial cast as seen in lateral view. The cerebral hemispheres are rather widely separated along the midline, and the impression of the longitudinal or sagittal sinus made on the endocranium is clearly shown. Posteriorly this sinus divides, and the two branches or lateral sinuses diverge obliquely across the space above the midbrain. In their position relative to the midbrain one is tempted to speculate on the possibility of these branches representing instead the corpora quadrigemina, but their direct continuity with the sagittal sinus makes this seem highly improbable. It is interesting to note that at the confluence of the lateral sinuses with the sagittal sinus the right branch invariably leaves the union at a somewhat lower level than the left. The marked size of these structures on the casts, moreover, suggests the importance of these veins in *Meniscotherium.* In *Phenacodus* the cast does not include the form of the sagittal and lateral venous sinuses above.

The cerebellar portion is very poorly preserved in all the casts, but there is evidence that it did not rise as high as in *Phenacodus.* The lateral surface in both natural casts, nevertheless, shows the impression of the petrosal. The small pedicle representing the internal auditory meatus is distinct, and in one cast (A.M. 48082) its apex shows the division into positions of the facial (above) and auditory (below) nerves. Above this, representation of the flocculus of the cerebellum shows the askew conical form, discussed above under description of the petrosal, with its somewhat extended apex directed posteroventrally.

Unfortunately, none of the endocasts of *Meniscotherium* shows much detail on the ventral surface. Both of the natural casts, however, show a generally rounded pyriform lobe, extending outward a little beyond the neopallium, but much less inflated laterally than in *Phenacodus,* possibly indicating a better developed sense of smell in the latter. Immediately medial to the pyriform lobe is seen a very prominent, elongate and broadly rounded ridge (A. on fig. 3b) on both of the natural casts, corresponding in a general way to the space above the broadly expanded bulge at the posterior root of the pterygoid wing of the alisphenoid. It is not complete anteriorly in either specimen but no doubt terminated anteromedially at the sphenoidal fissure in the endocranium. The margins of this crest are obscure so that details of division or possible branching are not evident, and stalks for the various orifices are not preserved, but in its posterior direction it turns definitely upward and outward behind the pyriform lobe and adjacent to the apex of the petrosal. Because of its gross size, I suspect that its total representation may be rather complex, and in addition to the nerves III, IV, V_{1-2}, and VI forward, it possibly represents a cavernous sinus connecting with the ophthalmic vein forward through the sphenoidal fissure and with a petrosal sinus or sinuses posteriorward behind the pyriform lobe. Posteriorly, as far as can be ascertained, its position also conforms with the point of entrance for the internal carotid posteromedially and with the position of the foramen ovale ventrolaterally where the third branch of the trigeminal would emerge.

On one of the casts a small portion of the surface representing the medulla oblongata is preserved around the lower and left side, and on the lower surface, very close to the lateral margin of the dorsoventrally compressed lateral portion, the position of the hypoglossal or condylar foramen is clearly defined. A short distance anterodorsal to this, at the posteroventral margin of the surface formed by the petrosal is a short slightly curved ridge which denotes the cranial opening of the foramen lacerum posterius.

MANDIBLE

The most noticeable features of the lower jaw of *Meniscotherium* are the increase in depth of the inferior ramus posteriorward and the extraordinary fanlike posterior extension of the angle (see pl. 3). The two jaws are strongly united by an elongate symphysis which below its posterior margin leaves a broad surface or pit for the digastric muscle. The importance of this muscle has been attested by the previously mentioned prominence of the paroccipital process. Close to the symphysis on the anteroventral surface of the mandible are a pair of foramina rather close to the roots of the 1st incisors. The anterior of the two mental foramina is located below the first premolar or the space between P_1 and P_2. The second mental foramen is rather generally situated low beneath P_4. The inferior dental foramen is high on the medial surface, a little below and a short distance posterior to M_3.

The extensive breadth and depth of the angle of the lower jaw indicates a large area of attachment for the masseter muscle externally and the internal pterygoid muscle medially. These, of course, correlate with the depth and strength of the zygoma and the prominence of the pterygoid fossa, and are important in the lateral movement of the jaw for grinding as well as in raising it. The masseteric fossa, however, is not deeply excavated, and its forward boundary is very weakly defined. Dorsally a weak ridge extending upward and backward from the anterior margin toward the sigmoid notch would seem to distinguish between the areas of the masseter and temporal muscles.

The anterior margin of the ascending ramus rises abruptly and high to the dorsoventrally elongate and slightly backward curving coronoid process. The coronoid process is not wide anteroposteriorly, and the sharp sigmoid notch is followed immediately by the generally convex and decidedly oblique condyle. The condyle has very little neck and is situated well forward with respect to the posterior margin of the angle.

The lower jaws of other Eocene condylarths do not generally taper forward so markedly through their length as in *Meniscotherium,* although in some specimens of *Hyopsodus* the increase in depth posteriorly was rather noticeable. The depth of jaw in *Phenacodus* and *Ectocion* is relatively less and seems more nearly uniform beneath the cheek teeth. In all these the jaws are strongly united at the symphysis although the symphysis may not extend so far posteriorly with respect to the cheek teeth as in *Meniscotherium.* Moreover, although *Phenacodus* shows a rather prominently expanded angle, it seems relatively less so than in *Meniscotherium.* Also, the masseteric fossa is more noticeably excavated in all and better defined anteriorly than in *Meniscotherium.* In a relatively well preserved mandible of *Hyopsodus* it was observed in addition to the well-excavated masseteric fossa that the coronoid process seems relatively broader anteroposteriorly and not so high, also that the condyle has its long axis distinctly transverse and is a little less convex across this diameter.

The mental foramina in *Phenacodus* appear generally to be two in number and placed about beneath P_1 and P_4. This would appear to be the case also for *Ectocion* in the limited material at hand. In *Hyopsodus,* however, there are frequently, if not generally, three and sometimes four foramina spread out between a position beneath P_1 to P_4 or M_1.

DENTITION

Upper dentition.—Although the cheek teeth of *Meniscotherium* (see pl. 5) are surprisingly precocious in having very early reached a high degree of selenodonty for a condylarth, and the molarization procedure having already extended forward to include the fourth premolar by the beginning of the Eocene, the more anterior teeth are decidedly unspecialized and little differentiated.

The incisors are basically simple, single-cusped teeth, but subspatulate in that high medial and lateral crests are developed. They approximate the form of very simple premolars with the shorter anterior (anteromedial) crest deflected medially at its anterior extremity and the longer posterior (posterolateral) crest straight and with a steeper slope, especially I^3, which may exhibit an incipient lateral cuspule. These teeth may be about the same size or increase slightly to I^3.

The canine is only slightly larger and follows the incisors with essentially no diastema. Its crown is a little higher and the anterior and posterior crests are more subdued and steeper. It evidently functioned more as an extension of the incisor series.

The only diastemata in the rather closely continuous tooth sequence are the short intervals that separate P^1 from the canine and P^2. P^1 is a very simple tooth about the size of the third incisor but with the anterior crest more steeply sloping, as in the somewhat larger canine. P^1, however, has two roots, although these may not be completely divided.

P^2 is appreciably larger than P^1 and relatively much broader across the posterior root. This tooth is highly variable and in some specimens its crown structure is as simple as that of P^1 but with a stronger posterior crest, whereas in others of the same species there may be developed a posterointernal rugosity to a clearly defined deuterocone with accessory cuspules.

P^3 is about intermediate in size between P^2 and P^4 and invariably exhibits a well-developed, conical deuterocone (protocone). This tooth seems highly variable with regard to the development of a tritocone (metacone), and when the latter is fairly well defined, although invariably less prominent than the primary cusp, there may be a very weak, posteriorly placed mesostyle. A small cuspule in the position of a tetartocone (hypocone) is invariably present on the cingulum posterolateral to the deuterocone. A similar cuspule symmetrically placed anterolateral to the deuterocone seems invariable and arises from the anterior cingulum when the latter is developed.

In the anterior part of the small median valley a protoconule, isolated from the anterior cingulum and often from the deuterocone, is attached to the lingual wall of the primary cusp. The metaconule, in the posterior part of this valley, as a crest may join the deuterocone and the tritocone portion of the outer wall but is usually separate from the posterior cingulum or tetartocone in this tooth.

P^4 is distinctly more molariform than P^3. The deuterocone is very large and conical, and the tritocone, while usually somewhat more abbreviated than the primary cusp (paracone), is well defined. The mesostyle may be fully developed but this is not invariable, as in some specimens it is no more than a gentle swelling or flexure of the outer wall and somewhat nearer the posterior margin than in the molars. The ribs, moreover, are a little better defined than in the molars. P^4 is most noticeably different from the molars in the much less lingual position of the tetartocone, which appears more as a cusp on the posterior cingulum, but is strongly joined to the metaconule, and the latter generally shows little or no direct union with either the deuterocone or tritocone. The protoconule forms a short crest parallel to the anterior crest of the primary cusp which it joins posteriorly. This accessory cuspule may also be joined, but somewhat more weakly, by a crest from the deuterocone. The cuspule on the anterior cingulum anterolateral to the deuterocone persists as in the molars, as well as in P^3. Slight plications extending into the central basin from adjacent cusps and walls were noted in certain of the fourth premolars, but this condition was less frequently encountered here than in the molars.

The first two true molars may be discussed together as they are much alike except for the greater size of M^2. The outer walls of these teeth show exceedingly well developed parastyles and mesostyles, and with but feeble or no representation of ribs in the concavities corresponding to the outer walls of the paracone and metacone. The protocone is conical but somewhat more elongate toward the protoconule than is the deuterocone of P^3 and P^4. The hypocone is completely lingual in position and forms with the metaconule an elongate ridge extending anteroexternally well into the central pit or valley of the tooth. Also the posterior cingulum rises lingually and prominently to the crest of the hypocone giving this cusp a crescentic or V-shaped appearance. The anterior cingulum usually extends around the base of the protocone, terminating in the valley between the protocone and hypocone. It carries a prominent cuspule anteroexternal to the protocone as observed in P^3 and P^4. The protoconule is crescentic, paralleling the paracone, and its posterior limb joins the inner wall of the paracone toward the center of the tooth. There is, moreover, rather generally a highly variable complex of plications extending from paracone, metacone, protoconule and metaconule into the median pit or valley of these two teeth.

M^3 differs from the preceding molars in the narrower talon portion, with the much less lingual position of the hypocone and the shorter crest that this cusp forms with the metaconule. The lingual portion of M^3 is surprisingly like that of P^4. The development of the external crests and styles, however, immediately distinguishes these teeth.

Lower dentition.—The lower incisors also appear comparatively simple, although I have been unable to observe any in a completely unworn state. They are much more procumbent than in the premaxilla and exhibit longer and nearly straight roots. They are comparatively small with an anteroposteriorly compressed crown, and I_2, often the largest of the three, shows a more triangular wearing surface. The root portion of the second incisor may also have broader forward and somewhat more compressed (transversely) posterodorsal portion. I_3 is larger than I_1 but may not always equal I_2 in size and is rarely larger. Its wearing surface is oval in outline.

The canine has a stronger root than the incisors and is closely appressed to the third. Its crown, while tapering somewhat upward, shows a high but relatively short anterior crest which wears much as the third incisor. Its weak or subdued posterior crest is steeply sloping and may exhibit an incipient cuspule or small buttress at its base.

P_1, single rooted, has a crown much like that of the canine, although smaller and transversely more slender. P_2 may be single rooted or double rooted, and in the latter instance the roots may not be completely divided. It is a little larger than P_1, and its crown though likewise simple is relatively lower and anteroposteriorly more elongate with a longer anterior crest and usually a somewhat better defined buttress at the base of the posterior crest. Very short diastemata may separate this tooth in the series although occasionally P_1 is the isolated tooth, or still shorter diastemata may tend to isolate both.

P_3 is double rooted and much larger than the preceding premolars. The anterior crest, while somewhat variable in length and height, always shows a marked medial flexure anteriorly, some specimens exhibiting a distinct paraconid. The posterior crest is well defined, and its lower extremity forms a high median crest on a usually broad and well-developed talonid.

P_4 is quite molariform and differs from the anterior molars essentially in the relatively longer and somewhat narrower trigonid portion with its more widely open crescent. This anterior crescent may also show somewhat better evidence of a distinct paraconid than in the molars. Also, the posterointernal extremity of the posterior crescent may be more medial and often shows an extra cusp.

The first two molars, as in the upper series, are much alike with M_2 noticeably larger. They are highly selenodont with the posterior or talonid crescent a little more elongate anteroposteriorly than the anterior or trigonid crescent, and the outer walls of the crescents are more hypsodont than the inner walls. The anterior crest of the trigonid is somewhat recurved posteriorward at its lingual extremity but is not raised to form a definable paraconid. The metaconid and entoconid (or hypoconulid?), however, are well defined and relatively high in unworn teeth. The anterior crest or crista obliqua of the hypocone joins the anterior crescent at the metaconid a little below its apex, and on the posterior slope of this cusp there is almost invariably a well-developed and somewhat lingually flexed metastylid crest which may show a distinct cuspule. This tends to constrict the talonid basin lingually and there may also be a small extra cuspule at the mouth of the valley or basin.

M_3 differs from the anterior molars only in that the talonid portion is a little more elongate and slightly narrower. Moreover, there is a buttresslike extension or crest on the posterior wall of the entoconid (or hypoconulid?). The greater length and narrower talonid portion is a development just the reverse of that observed in P_4.

Deciduous upper premolars.—Dp^3 is a rather distinctive tooth in the upper series, and while it seems to show somewhat the same detail as P^3, it is very much askew with the talonid portion deflected decidedly posterolingually rather than having the nearly symmetrical appearance of the permanent tooth. Moreover the small cuspules anteroexternal and posteroexternal to the deuterocone are very weak or missing, whereas the outer wall shows a rather prominent development of a style at the anterior extremity and the tritocone is better defined than in P^3.

Dp^4 is almost indistinguishable from M^1 except for its smaller size and greater wear, when found associated with it. It does, however, show a relatively more forward position for the parastyle, and occasionally the tooth is a little more askew than M^1. It is, of course, readily distinguished from P^4 by the development and lingual position of the tetartocone (hypocone).

Deciduous lower premolars.—Dp_3 is much like P_3 but appears to be a little more complex. The anterior crest seems more crescentic and its anterolingual extremity is sometimes bifurcate or plicated lingual to the paraconid. Also, in addition to the median posterior crest which is much as in the permanent tooth, rather prominent crests extend down the posterolingual and posterolateral slopes of the protoconid nearly to the talonid.

Dp_4 is almost indistinguishable from P_4 but is a trifle more elongate in both the trigonid and talonid portions. Also, the anterointernal extremity of the trigonid crescent is generally not recurved but there is often a sharply angular flexure or style essentially comparable to and paralleling the metastylid crest. In some Dp_4's the anterior extremity of this crest appears essentially bifurcate, almost as in Dp_3. The deciduous fourth premolar is also distinctly lower crowned than the permanent premolar.

VERTEBRAE

Although ribs are rather poorly preserved in the available skeletal portions of *Meniscotherium* and show very little of interest, which also may be said of the sternal material, significant segments of the vertebral column are included in at least three individuals, two representing *M. chamense* and one of *M. robustum.*

Cervical vertebrae.—The atlas vertebra is decidedly short anteroposteriorly, perhaps more so than in *Phenacodus,* and the transverse processes are not widely expanded, although they appear to be a little more extended than in the larger form. They rise anteriorly, and just ahead of and above the anterior extremity on each side the large foramen for the first spinal nerve is completely enclosed, opening into the neural canal just posterior to the upper extremity of the facet for articulation with the occipital condyle. A decidedly large vertebrarterial canal opens forward on the inferior surface of the transverse process and has its posterior aperture on the deeper posterior margin of the transverse process, just lateral to the widest part of the facet for the axis. These foramina appear to be very much like those in the *Phenacodus* atlas illustrated by Cope (1884b, pl. 57h) although relatively larger.

The axis is much the longest vertebra in the neck and broadest across the ventral surface of the centrum. The spinous process is moderately high and relatively elongate anteroposteriorly but evidently is not extended posteriorly so much as in *Phenacodus*. The transverse processes are slender and curve sharply backward and are pierced anteroposteriorly, close to the centrum, by a large vertebrarterial canal on each side. The anterior aperture of the canal is immediately posterior to, and somewhat recessed behind, the outward flaring lateral margin of the atlantal facet or surface. The odontoid process is stout and nearly cylindrical.

The succeeding cervical vertebrae decrease in length posteriorly with the centra somewhat flattened dorsoventrally and with surprisingly large and relatively broad neural canals. The breadth of the neural arch dorsally is evident in the transversely wide spacing of the zygapophyses. The transverse processes extend prominently outward and downward from essentially the anterior half or two-thirds of the centrum, the sixth cervical showing the characteristic posterior extension or expansion of the inferior lamella. The vertebrarterial canal, as in the atlas and axis, is a conspicuously large foramen in all except the seventh which, lacking the inferior lamella, may show a broad groove on the lower surface of the transverse process close to the centrum. The spinous processes are low on the third to about the sixth cervical, but the seventh shows some elongation and a slight backward tilt. The inferior surfaces of the centra are comparatively broad and flat without hypapophyses (see figs. 5 and 6), although the axis to the fifth cervical shows a low keel which posteriorly on each broadens into a triangular flat hypapophysial table, as noted by Cope (1884b) for both *Meniscotherium* and *Phenacodus*. Also, as

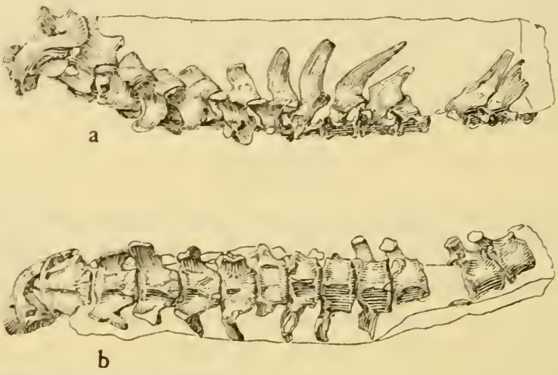

Fig. 5.—*Meniscotherium chamense* Cope. Cervical and anterior dorsal vertebrae (U.S.N.M. 22672) ; a, lateral view; b, ventral view. ½× natural size. New Fork member, Wasatch formation, Green River Basin, Wyo.

noted by Cope, the centra are slightly opisthocoelus and the articular surfaces distinctly oblique.

Dorsal vertebrae.—The number of dorsal vertebrae in *Meniscotherium* is not known, although it was probably close to that of *Phenacodus* which was given by Cope as 14 or 15. In one of the articulated series at hand (see fig. 5) only the first seven are preserved in place and in another the last six. These show a decrease in size from the cervicals, but there is a surprising increase in size near the posterior limit of the sequence and into the lumbars. The anterior dorsals are only slightly shorter than the cervicals but noticeably narrower across the zygapophyses and the centra are dorsoventrally flattened. The neural spines, after the first, are rather slender and backward directed in the anterior part of the series, but posteriorly they become shorter, more erect, and anteroposteriorly wider, with the last one or two tilting forward. The transverse processes carrying the articular surface for the tubercle of the rib are markedly elongate, at least in the first seven, and rudimentary metapophyses extending upward from the transverse processes above the tubercle facet, although mostly damaged, are evident. Posteriorly the facet for the tubercle of the rib is supported by more of a pedicle extending anteroventrally from the transverse process, and the metapophysis becomes better defined and separate from both. In the fourth from the last dorsal the three structures are joined in a common base, and the

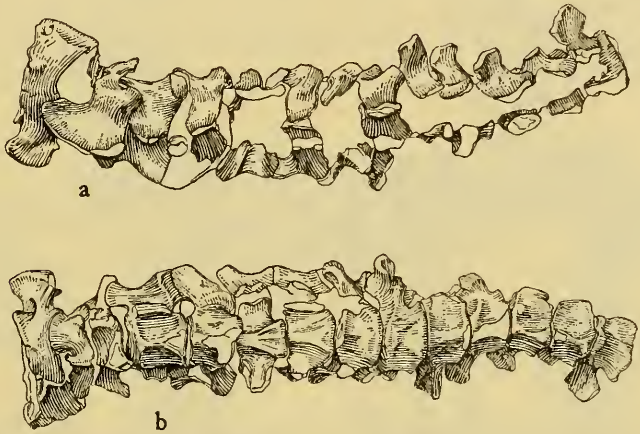

Fig. 6.—*Meniscotherium robustum* Thorpe. Cervical and anterior dorsal vertebrae (U.S.N.M. 18283); a, dorsal view; b, ventral view. ½× natural size. Knight member, Wasatch formation, Green River Basin, Wyo.

anterodorsally and laterally directed metapophysis is much larger than the feeble posteroventrally and outwardly directed transverse process. In the succeeding dorsals the rib has but a single articulation, with the margin of the centrum, and the higher metapophysis has moved up closer to the anterior zygapophysis and is completely separate from the still shorter transverse process. In the last couple of dorsals, in addition to the increasing size and relatively greater depth of the centrum for this portion of the series, the metapophyses are broadly expanded and the transverse processes are much reduced. There are no anapophyses in the sequence, and in no instance was the intervertebral foramen found to be completely closed by the pedicle of the arch.

Lumbar vertebrae.—A lumbar series for both *M. chamense* and *M. robustum* is included in the collections (see figs. 7 and 8). The number is nine in the *M. chamense* skeleton, and the nine articulated presacrals preserved in the *M. robustum* skeleton all seem to be lumbars. Cope considered that *Phenacodus* had six or seven lumbars, but there seem to be only four or five in the *Phenacodus primaevus* skeleton that I examined. These vertebrae in *Meniscotherium* are seen to be extraordinarily large in comparison with the greater part of the dorsal series. The forward sloping spines and transverse processes increase in length posteriorly, at least as far as the sixth, and these appear relatively broader anteroposteriorly in the larger of the two species. The processes of the more posterior lumbars are poorly preserved in both specimens. The metapophyses, beginning with their separation from the transverse processes near the end of the dorsal series, increase in height and strength to about the fifth or sixth lumbar, and posteriorly become subdued with little or no projection beyond the margin of the anterior zygapophyses. Laterally the zygapophyses in the lumbar series turn decidedly upward, beyond which the metapophyses continue upward as well as outward and

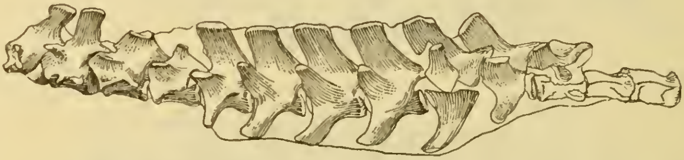

FIG. 7.—*Meniscotherium chamense* Cope. Lumbar and four posterior dorsal vertebrae (U.S.N.M. 22918), lateral view of left side. ½× natural size. New Fork member, Wasatch formation, Green River Basin, Wyo.

forward. The ventral surface of the centrum is broad and only moderately keeled.

Sacrum.—The sacrum includes four well-coalesced vertebrae which

FIG. 8.—*Meniscotherium robustum* Thorpe. Lumbar and sacral vertebrae, and pelvic girdle (U.S.N.M. 18283, ilium restored from U.S.N.M. 19555); a, dorsal view; b, ventral view. ⅖× natural size. Knight member, Wasatch formation, Green River Basin, Wyo.

ventrally appear to have about the same length each as the lumbars. Cope considered that the number of sacral vertebrae was three, but his specimen may have been incomplete. Certainly Marsh's sacrum of *"Hyracops socialis"* with four sacrals does not differ from the normal in *Meniscotherium*. For *Phenacodus* Cope listed the number as three or five. His illustration (1884b, pl. 57h) shows four.

Anteriorly the fused transverse processes, preserving nevertheless the intervertebral foramen, show a strong and deep attachment to the ilium. The anterior spines are not preserved, but the posterior two, although incomplete, were evidently low and backward directed.

Caudal vertebrae.—There are 14 caudal vertebrae (see fig. 9) belonging to one specimen, but most of these were not found articulated, so that any sequential arrangement of these would likely be very incomplete. The first caudal is in articulation with the sacrum described above. Although a little shorter, it is nearly as large as the last sacral and has heavy, laterally directed transverse processes. Posteriorly the caudals become a little shorter as well as smaller in diameter than the first, with more slender, shorter, and backward directed transverse processes. After about the eighth of those at hand their length increases again and the processes and pedicles are reduced to vestiges. Only the first four or five or those represented show evidence of a neural spine, and the anterior caudals lack a distinct ventral keel, but posteriorly the latter is better defined.

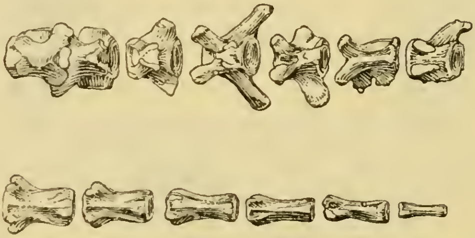

FIG. 9.—*Meniscotherium robustum* Thorpe. Caudal vertebrae, not an articulated series (U.S.N.M. 18283), dorsal view. ½× natural size. Knight member, Wasatch formation, Green River Basin, Wyo.

SCAPULA

The scapula of *Meniscotherium* is relatively elongate and, although in the one well-preserved example at hand (see pl. 6) the margins are not everywhere complete, the suprascapular border would appear to be rounded somewhat as in *Phenacodus,* but the coracoid or anterior border may not expand forward so abruptly near the proximal extremity. The prescapular fossa is distinctly convex and, as in *Phenacodus,* is much wider than the postscapular fossa. The latter is highly concave anteroposteriorly and the glenoid or posterior border is turned sharply outward. The concave glenoid surface is nearly oval but somewhat compressed or acuminate at the proximally directed anterior extremity. The coracoid process here exhibits a strong medially deflected flange or hook which is separated from the glenoid surface by a distinct groove or notch, much as described by Cope for *Phenacodus.*

The most striking feature of the *Meniscotherium* scapula is the very high but posteriorly deflected spine with its prominent anteroproximally directed acromion and strongly recurved but posteriorly directed metacromion. The spine apparently maintains nearly its maximum height from the acromion to about its midpoint and distally from there it tapers to the suprascapular border. The spine was evidently broken off the various scapulae of *Phenacodus* available to Cope, but an equivalent development of the acromion and metacromion was observed on the *Phenacodus* skeleton exhibited at Princeton University.

There is apparently no evidence for a clavicle in either *Meniscotherium* or *Phenacodus.*

HUMERUS

The limb bones of *Meniscotherium* appear to be relatively a little smaller, in proportion to the size of the skull for example, and somewhat less robust than in *Phenacodus.* The humerus (see pls. 6 and 7) is slender and gently curved, more noticeably in the smaller *M. chamense,* but shows, nevertheless, a prominent and elongate deltoid ridge extending from two-thirds to nearly the entire length of the shaft, giving the proximal portion of the shaft a somewhat flattened (anteromedial-posterolaterally) appearance (see Cope, 1884b, pl. 25g, fig. 12). The development of this crest together with the height of the spine and development of the acromion on the scapula testify to the importance and leverage afforded the deltoid muscle in abducting the forelimb. The proximal portion of the humerus is characterized also by a prominently projecting crestlike greater tuberosity, whereas the lesser tuberosity shows very little proximal projection, although its medial prominence exhibits a noticeable dorsomedial facet or scar for the subscapularis muscle. The tuberosities are separated by a broad bicipital groove but are closely joined to the head, leaving little or no anatomical neck. Cope (1884b, p. 502) noted that there were no bicipital ridges, but these may be weakly developed on some specimens. He also described a teres major ridge as distinct and extending on the proximal two-fifths of the length. This I find, however, is variable and usually weak or absent but noted it observably developed on two specimens of *M. robustum.* There is a generally shallow but well-defined fossa or depression, which may be pitted or nearly flat, on the posterior surface or margin of the greater tuberosity at the proximal extremity of the deltoid ridge, evidently the fossa for the teres minor that Cope mentioned as being flat.

The distal extremity of the humerus is broad with a very well developed inner condyle exhibiting an entepicondylar foramen which is relatively larger in the smaller species *M. chamense.* The inner condyle shows a relatively rough or rugose medial and distal margin for the various flexor and certain other muscles to the manus. The external condyle, however, is not nearly so projecting but is roughly pitted for the extensors. The trochlea has an outstanding medial margin anteriorly and distally and a posteriorly raised lateral margin which arises from the nearly median convexity of the trochlea as it extends around toward the posterolateral side, as noted by Cope. With a posterior root continuous with this posterior lateral crest of the trochlea and with an anterior root originating on the external condyle, a flaring supinator ridge extends prominently upward and somewhat backward for about the distal third of the shaft. Above the trochlea, as noted in several specimens, the bone seems incomplete, leaving usually a broadly open supratrochlear foramen.

The humerus of *Phenacodus* was illustrated by Cope (1884b, pl. 57g, fig. 2) and briefly described. It is surprisingly like that of *Meniscotherium* in a number of details, although it differs noticeably in its generally straighter and relatively somewhat stronger appearance. The proximal tuberosities seem a little more robust and anteriorly more projecting. The bicipital groove is relatively broader and, as Cope noticed, there is a low ridge medially placed in the bicipital groove, which is not seen in *Meniscotherium.* The deltoid and supinator ridges have about the same relative extent as in *Meniscotherium,* but the former crest seems somewhat less sinuous. The distal extremity appears to be less expanded transversely, but the trochlea has relatively greater anteroposterior diameter than in *Meniscotherium.* The details of the marginal crests of the trochlea, however, are somewhat alike in the two forms.

In *Hyopsodus paulus* the proximal extremity of the humerus exhibits much less developed tuberosities. The greater tuberosity is more rounded, less crestlike, and does not extend proximally above the head, but shows a rounded, well-defined fossa for the teres minor. The lesser tuberosity is scarcely more than a scar for the subscapularis on the medial side of the head. The distal portion of the humerus is known for *Hyopsodus paulus,* as well as *Hyopsodus walcottianus* (see Matthew, 1915, fig. 10). In both of these the trochlea shows the high anterior crest on the medial margin and the high outer crest extending posteriorly from the median convexity on the anterior surface, quite as in *Meniscotherium,* and possibly more emphasized in *H. walcottianus.* The entepicondylar foramen is present and a broadly open supratrochlear foramen. The greater part of the shaft of the humerus is not preserved in *Hyopsodus* material at hand.

RADIUS

The elements of the forearm in *Meniscotherium* are distinctly smaller, relative to the humerus and hind limbs than in *Phenacodus.* This would appear in part to be in keeping with the disparity in size of vertebrae relative to these quarters. The radius (see pl. 7) is decidedly slender proximally but shows a noticeable transverse expansion of the proximal extremity or head for articulation with the humerus. The articular surface is nearly rectangular in appearance with a broad median depression for the anterior convexity of the trochlea, and the internal portion or margin of the surface turns distally in conformity with the forward-extending medial margin of the trochlea. The head of the radius articulates with the ulna at the distal margin of the sigmoid notch, anterolateral to the coronoid process.

The proximal portion of the shaft of the radius may show a rather pronounced groove on its posteromedial surface curving somewhat more medially distally, most noticeable in *M. robustum.* This may well define a portion (fifth) of the origin of the flexor profundus digitorum. Distally the shaft of the radius increases in diameter and curves inward, passing from an anterolateral position proximally to a more medial position distally with respect to the ulna. The posterolateral margin of the distal half of the radius is generally somewhat rugose for attachment of the interosseous membrane. The anterior surface shows a prominent crest arising on the distal half of the shaft and extending distomedially to terminate near the styloid process, and a somewhat more subdued crest terminating anterior to the lateral portion of the distal extremity.

The distal extremity is enlarged and shows two nearly circular, slightly concave facets side by side, the lateral or lunal somewhat the larger, anteroposteriorly. The medial facet for the scaphoid, however, extends a short distance medially over the anteroposterior crest of the styloid process.

The radius in *Phenacodus* resembles that of *Meniscotherium* in the character of the proximal articular surface for the humerus but appears relatively a little deeper anteroposteriorly. However, the shaft is relatively much more sturdy, so that the head does not seem to be so expanded. Distally the shaft is more rounded with less prominent crests than in *Meniscotherium,* and as noted by Cope, the distal portion close to the extremity is enlarged and converges toward the facets for the carpus.

ULNA

The *Meniscotherium* ulna (see pl. 7) is decidedly flattened in an anterolateral-posteromedial direction, and a nearly uniform width is maintained from just distal to the sigmoid notch nearly to the distal extremity. The sigmoid notch is markedly convex transversely and, in keeping with the form of the trochlea of the humerus, shows flaring proximolateral and distomedial margins. The olecranon process is anteroposteriorly deep and elongate and shows a rather broad posterior margin, widening proximally and curving somewhat forward to a rugged medially deflected crest for insertions of the triceps group or extensors of the forearm. On the anteromedial surface of the shaft, just distal to the coronoid process there is a deeply impressed and proximodistally somewhat elongate pocket or fossa, presumably for the tendon of the brachialis and clavobrachialis muscles. On the posteroexternal surface of the shaft a prominent median crest arises a short way distal to the sigmoid notch and extends distally toward the posteroexternal margin where it abruptly widens or divides, as noted in *M. chamense.* In the more robust form, however, the broadening of this crest commences more proximally with the anterior margin continuing medially on the shaft. This crest evidently bounds posteriorly the area of attachment or origin for the extensor brevis policis. Anterior to the crest the shaft of the ulna is noticeably concave anteroposteriorly. Distally the anteromedial margin of the shaft widens or divides with included space slightly rugose for the interosseous membrane. The distal extremity is broad and usually somewhat flattened, much as the shaft in general. The distal articular surface for the cuneiform is variable but approximately cylindrical with the long axis parallel to the plane of flattening and distinctly oblique to the long axis of the shaft, extending distally toward the styloid or posterolateral margin.

In attempting to articulate the bones of the fore limb I note that a comparatively prone position for the manus requires that the posterior margin of the ulna be turned decidedly outward and although articulation with the humerus permits appreciable rotation, a relatively normal relationship requires appreciable abduction of the arm.

In *Phenacodus,* as noted above, the ulna is relatively larger and the shaft appears less flattened than in *Meniscotherium.* The proximal portion of the sigmoid notch is very much like that in *Meniscotherium* with a similar transverse convexity and lateral flare, but the distal portion of the surface is much more expanded lateral to the coronoid process so that the head of the radius has a more nearly transverse articulation with the ulna, and a slightly more anterior or ungulate-like position with respect to its humeral articulation. Moreover, this expansion of the sigmoid notch lateral to the coronoid process is accompanied by a proximally more nearly triangular shaft. The robust olecranon in *Phenacodus,* though similar, has a straighter posterior margin or it curves somewhat backward rather than forward as in *Meniscotherium.*

The distal portion of the *Phenacodus* ulna is rather enlarged from the moderately flattened shaft, and the long axis of the distal articular surface for the cuneiform appears more transverse with respect to the flattening of the shaft, seemingly less oblique to the axis of articulation at the sigmoid notch than in *Meniscotherium.*

MANUS

As noted with regard to the forearm, the forefoot of *Meniscotherium* (see pl. 7) is relatively much smaller than that of *Phenacodus;* also, the carpals are proximodistally more compressed than in the latter. The carpals, however, show somewhat the same serial arrangement observed in *Phenacodus* but with slightly more overlapping. I was unable to verify the presence of a central in the carpus of *Meniscotherium,* although Marsh (1892, fig. 1) shows this element in the *"Hyracops socialis"* foot that he figured. Slightly more preparation on the specimen (Y.P.M. 10276) that evidently guided Marsh reveals that the prominence in the position of a central is firmly joined to the distolateral angle of the scaphoid and may well be an integral part of that bone. Although this process is variable, it is more prominently developed in the Marsh specimen than in others at hand and possibly began ossification from a separate center before joining the scaphoid.

Scaphoid.—The scaphoid is relatively shortened proximodistally but noticeably elongate in a dorsoventral direction and exhibits a knoblike ventromedial extremity. Displayed across the shorter dorsal portion of the proximal surface, the prominent articular convexity or radial facet extends distad on the dorsal surface nearly to the distal facet for the trapezoid. The distal surface is lunate in outline and the dorsal or anterior portion shows an obliquely oriented concavity for articulation with the trapezoid. Ventromedial to this there is a more flattened to somewhat convex surface for the trapezium. The distolateral angle of the dorsal surface is developed as a small process which may be relatively prominent as discussed above. Ventral from this point a rounded dorsoventral ridge articulates narrowly with the magnum. This ridge divides the concave trapezoidal area medial to it from the small, flattened, dorsally situated, and laterally facing lunar facet immediately proximal to it.

The *Phenacodus* scaphoid as well as being much deeper is distinctly less attenuated ventral to the radial and trapezoidal facets. Moreover, the convexity for articulation with the radius does not extend relatively so far down the dorsal surface as in *Meniscotherium.* The facet for the trapezoid is comparatively flat, and that for the lunar may be small and dorsodistally placed on the lateral surface. There does not appear to be any contact with the lunar unless these may touch at a point ventral to the lunar facet, but evidently not near the dorsal surface of the wrist as in *Meniscotherium.*

Lunar.—The lunar in *Meniscotherium* is an arcuate, proximodistally compressed tonguelike structure. It laps dorsoventrally over the proximal hump of the magnum, and its proximal convexity is essentially concentric with its distal concavity. The essentially convex facet for the lateral or lunar facet of the radius covers the entire proximal surface and dorsally approaches the distal surface. Ventral to the median transverse crest this surface is slightly concave before reaching the ventral margin. The concave distal surface is divided for articulation medially and somewhat more dorsally with the magnum and laterally and more ventrally with the unciform. The dorsal portion of the arcuate medial surface of the lunar is faceted for articulation with the scaphoid. The ventral portion of the proximodistally somewhat deeper or less arcuate lateral surface shows a comparatively large facet for the unciform.

The deep, more nodulelike *Phenacodus* lunar has a strongly convex proximal articular surface for the radius, but this does not appear so well faceted farther ventrally nor does it extend relatively so far distally on the dorsal surface. The distal surface for the magnum is more flattened dorsally but exhibits a deep circular concavity on the ventral half for the proximal prominence of the magnum. The more lateral and dorsoventrally concave facet for the unciform faces slightly more laterally and is decidedly narrow and ventrally more restricted than in *Meniscotherium.* Medially the lunar is slightly concave and shows a variably developed facet or facets for the scaphoid. Lateral faceting for the cuneiform is likewise variable and may be restricted to a dorsoventrally elongate zone along the distal portion. The ventral extremity of the *Phenacodus* lunar presents a somewhat more rounded knob; a less-flattened protuberance than in *Meniscotherium.*

Cuneiform.—The relatively compressed cuneiform is elongate much as the scaphoid, but its long axis is more nearly transverse with its lateral extremity deflected ventrally. The proximal surface shows a dorsoventrally concave and transversely elongate surface for articulation with the ulna. The relatively acute, transversely elongate ridge that bounds the concavity ventrally divides the ulnar surface from a narrow but transversely somewhat elongate proximoventral facet for the pisiform. The facet for the unciform covers the entire transverse portion of the distal surface and is slightly concave dorsoventrally. Transversely a very gentle saddle divides a larger medial portion from a somewhat smaller lateral area. The roughened dorsal surface is distoproximally very shallow laterally but becomes a little deeper medially. The ventral two-thirds of the medial surface is faceted for articulation with the lunar. The ventrally directed lateral extremity is an irregularly flattened prominence that apparently does not support any of the pisiform articulation.

The *Phenacodus* cuneiform is dorsoventrally as well as proximodistally deeper relatively, and the ventrally directed lateral extremity is longer and more massive. The ventrolaterally tapering extension or extremity carries most of the large triangular facet for the pisiform on its steeply sloping proximal surface. The concave proximal articular surface for the ulna is approximately as in *Meniscotherium* but relatively deeper dorsoventrally. Also the more uniformly concave distal facet for the unciform is dorsoventrally deeper relative to its length transversely. The acutely angled medial surface shows a crescentic facet for the lunar adjacent to the arcuate distal margin.

Pisiform.—The *Meniscotherium* pisiform is moderately elongate, about equaling the greater diameter of the cuneiform. Its articular surfaces are transversely broad but proximodistally shallow, although both increase somewhat in depth laterally. The surface for the ulna is longitudinally concave near the lateral extremity and makes a sharp angle with the more flattened facet for the cuneiform. The shaft of the pisiform is broad proximally but transversely constricted along it's distomedial margin. The posterior extremity of the pisiform exhibits an enlarged knob.

In *Phenacodus* the articular extremity of the large pisiform is relatively not so broad transversely, the articular facets are proximodistally deeper, and there is much less of an angle between them than in *Meniscotherium*. The facet for the cuneiform is decidedly triangular, articulating well down on the ventrolateral projection of the cuneiform. The shaft of the pisiform is relatively much deeper proximodistally than in *Meniscotherium* and appears comparatively narrow. The shaft is elongate and terminates posteriorly in a similarly enlarged tuberosity or knob.

Trapezium.—The trapezium is broad and proximodistally deep in *Meniscotherium*, and its medial facing surface is comparatively flat. The proximal portion narrows somewhat toward its articulation with the scaphoid, but more distally the dorsal margin is dorsally expanded or flaring, although the ventral margin is nearly straight. The distal extremity exhibits an oval-shaped, slightly concave facet for the first metacarpal. The lateral facing surface has a distinct prominence proximally which supports a narrow but transversely elongate facet on its dorsolateral surface for articulation with the trapezoid, and just below or distal to this a somewhat arcuate surface extends dorsodistally out on the dorsal flare of the trapezium for contact with the base of the second metacarpal.

The *Phenacodus* trapezium appears more nearly rectangular and relatively thicker transversely along the ventral margin. The proximal articular surface for the scaphoid is convex, and that distally for the first metacarpal is concave and somewhat larger. The lateral surface shows pairs of facets proximally and distally for the trapezoid and second metacarpal respectively.

Trapezoid.—The trapezoid in *Meniscotherium* is noticeably compressed proximodistally and nearly wedge-shaped with the deepest part at the dorsomedial angle of the bone. The dorsal surface exhibits a prominence distally near the medial margin. The proximal surface for the scaphoid is dorsoventrally convex in the dorsal part but changes to concave in the ventral portion. The distal facet for the second metacarpal is transversely convex but slightly concave dorsoventrally. It articulates medially by a narrow but dorsoventrally elongate facet with the trapezium but slightly, if at all, with the magnum along its rather thinner lateral margin. It is excluded from contact with the lunar by articulation between the scaphoid and magnum.

The *Phenacodus* trapezoid is not nearly so compressed and presents a quadrilateral rather than nearly triangular dorsal surface. The distal surface for the second metacarpal is similar to that in *Meniscotherium,* but the proximal surface for the scaphoid is more nearly flat. The medial surface exhibits facets for the trapezium, and the lateral surface, unlike *Meniscotherium,* shows a broad crescentic facet for the magnum. There may have been also limited contact with the lunar proximodorsally on the lateral surface, although Cope thought not.

Magnum.—The *Meniscotherium* magnum is an irregularly shaped bone relatively narrow transversely and with a proximodistally restricted dorsal exposure. It has a nearly triangular shape in lateral or medial view with the deeper median portion surmounted by a knoblike proximal convexity which with the proximodorsal slope of this triangle articulates with the lunar. Adjacent and parallel to this lunar facet but on the medial surface, the magnum shows a facet for the scaphoid (no central). Along the ventral margin of the medial surface there is an arcuate, slightly concave and elongate surface for the base of the second metacarpal. This surface makes a nearly right angle with the dorsoventrally concave distal surface for the third metacarpal. The entire proximodistal extent of a little more than the dorsal half of the lateral surface articulates with unciform. The ventral part of the magnum is slightly enlarged and extended somewhat beyond the trapezoid and unciform, presumably supporting attachment of a part of the flexor brevis pollicis and possibly certain adductor muscles.

The dorsal surface of the *Phenacodus* magnum is much deeper proximodistally so that the bone does not appear so nearly triangular in lateral or medial view. Also, the surface for the lunar, immediately dorsal to the proximal hump or knob, is more concave. Articulations for the second and third metacarpal and for the unciform are similar to those in *Meniscotherium,* but there may be no articulation with the scaphoid, or it is restricted to a small area on the medial side of the proximal apex. On the other hand, articulation with the trapezoid is rather extensive in the dorsal part of the medial concavity of the magnum, where there seems to be little or no contact in *Meniscotherium.*

Unciform.—The dorsal face of the *Meniscotherium* unciform appears of nearly uniform depth because of the distally extending lip on the lateral half. In ventral view, however, the bone is decidedly triangular with the sloping proximal surface for the cuneiform reaching in a thin lateral margin the facet for the fifth metacarpal. A dorsoventrally convex and transversely narrow facet for the lunar is deflected more medially from the proximomedial margin of the broad surface for the cuneiform. The distal surface is dorsoventrally concave, and a low saddle separates the larger medial surface for the fourth metacarpal from the smaller surface for the base of the fifth metacarpal. The proximal two-thirds of the nearly flat dorsal portion of the deep medial surface articulates with the magnum. The distal margin of this surface articulates with the broad base of the third metacarpal.

The *Phenacodus* unciform is relatively much deeper proximodistally, and although there is some lateral convergence of the dorsoventrally more convex surface for the cuneiform with the concave surface for the fifth metacarpal, the lateral margins of these surfaces appear well separated. It should be noted, moreover, that proximomedially the unciform articulated with the magnum, somewhat as in *Meniscotherium,* but with relatively narrower contact, although Cope saw no facet for this on the unciform. Presumably that for the magnum blended too smoothly with the surface for the cuneiform in the specimen he examined. The facet is particularly evident on the magnum. As in *Meniscotherium* much of the dorsal portion of the medial surface articulates with the lunar and the dorsodistal part of this surface with the third metacarpal.

Metacarpal I.—The first metacarpal is somewhat reduced in *Meniscotherium;* about half the length of the third and with a relatively more slender and dorsally bowed shaft. The proximal extremity is noticeably enlarged with a convex articular surface for the trapezium which is elongated corresponding to the broad dimension of the trapezium's distal surface. I see no evidence for articulation with the second metacarpal. The distal extremity is enlarged but to a somewhat less extent with a transversely narrow and medially tapering articular surface for the first phalanx. The subdued keel appears displaced toward the lateral side.

The *Phenacodus* first metacarpal is evidently somewhat variable in length in comparison with the other metacarpals but appears relatively more robust through the shaft than in *Meniscotherium* and is distinctly less bowed or arched. Proximally it evidently also articulated only with the trapezium.

Metacarpal II.—The second metacarpal of *Meniscotherium* is next to the third metacarpal in length and only slightly shorter. The greater part of the nearly triangular proximal surface articulates with the trapezoid. This facet is slightly convex dorsoventrally but distinctly concave transversely. Its lateral margin is a low ridge which divides the trapezoidal surface from a narrow somewhat distally deflected facet for the magnum. Distal to this on the lateral surface of the proximal extremity is a deep concavity with a somewhat distally facing dorsoventrally concave facet for the proximal extremity of the third metacarpal as the base of the second metacarpal overrides it. The medial side of the proximal extremity of the second metacarpal shows an arcuate facet along the proximodorsal margin for the trapezium. The shaft of the metacarpal is essentially straight and dorsoventrally somewhat flattened, but its width narrows only slightly from the base, then expands to the distal extremity which is a little wider transversely than the proximal portion.

The distal extremity shows an evenly rounded articular surface for the proximal phalanx, with a distinct keel only on the ventral half. The transverse axis of this convexity is slightly oblique to the long axis of the shaft.

The proximal extremity of the more robust *Phenacodus* second metacarpal is rather similar to that of *Meniscotherium,* although the trapezoidal facet is perhaps somewhat flatter and more nearly rectangular, and that for the trapezium of relatively smaller area. The shaft of the metacarpal, moreover, is not so slender and appears much less compressed dorsoventrally. The length of this bone in *Phenacodus primaevus* is at least two and one-half times that in *Meniscotherium chamense,* whereas the length of the humerus is a little less than twice that of the latter.

Metacarpal III.—Proximally the base of the third metacarpal in *Meniscotherium* has the form of a truncated triangle or trapezial outline, somewhat more so than that of the second metacarpal. The surface for the magnum is decidedly convex dorsoventrally but nearly straight transversely, sloping distally toward the medial margin and grading almost imperceptibly into a relatively broad marginal surface for the distally facing facet on the lateral side of the second metacarpal. The dorsal two-thirds of the lateral margin of the base of the third metacarpal exhibits a crescentic, nearly lateral facing facet for the unciform, and distal to this, much as in the second metacarpal, there is a lateral concavity with a dorsoventrally concave, essentially distal facing facet accommodating a portion of the proximal surface of the fourth metacarpal, overriding it much as the second overrides the third. The shaft of the third metacarpal is much like that of the second but is a little longer and shows, moreover, a noticeable scarlike prominence on the medial side of the dorsal surface about a quarter of the length distally from the base, evidently for insertion of the extensor carpi radialis brevis. The distal articular surface for the proximal phalanx is similar to that of the second metacarpal but more nearly symmetrical, and the transverse axis is perpendicular to the long axis of the shaft.

The proximal extremity of the *Phenacodus* third metacarpal is much like that of *Meniscotherium* except that the surface for the second metacarpal is much more restricted and turns sharply distal with respect to that for the magnum. The lateral surface of the proximal extremity differs from that in *Meniscotherium* in that the facet for the fourth metacarpal is deflected somewhat more laterally. The shaft of the bone is relatively not so slender and is distinctly less compressed dorsoventrally.

Metacarpal IV.—The fourth metacarpal is appreciably shorter than the second, but because of the successively overlapping proximal extremities the distal extremities in the articulated foot are about even. The proximal surface of the *Meniscotherium* fourth metacarpal is more nearly triangular than on the second metacarpal. This surface is decidedly convex dorsoventrally but only slightly so transversely. Much of the triangular surface to the lateral margin articulates with the unciform and projects distally onto the lateral margin of the dorsal surface to a noticeable extent, corresponding to the extension of the dorsal lip of the unciform in its lateral part. Distal to the lateral margin of the proximal surface there is a concavity, not so deep as in the second and third metacarpals, and the facet for the fifth metacarpal is strongly arcuate, has a marked dorsal extension, but faces more laterally than in the second and third. The medial margin of the proximal surface is slightly offset distally in its dorsal portion for the overriding margin of the third metacarpal. The ventral portion of this surface, however, appears to be nearly separate, and is more oblique and may project proximally somewhat from the unciform facet. The shaft of the fourth metacarpal is relatively straight and dorsoventrally flattened as in the others. Its distal extremity shows a slight asymmetry in which the lateral half of the articular surface has less diameter and its transverse axis is slightly oblique to the long axis of the shaft, the asymmetry being in reverse of that characterizing the second metacarpal.

In *Phenacodus* the proximal surface is relatively broader dorsally, and the lateral margin of surface for the unciform does not extend so noticeably distal on the dorsal surface. Moreover, the facet for the third metacarpal appears more sharply deflected from the unciform surface, and that for the fifth metacarpal faces more laterally than in *Meniscotherium.*

Metacarpal V.—The fifth metacarpal is approximately three-quarters the length of the fourth with a more slender and compressed shaft but with moderately large extremities. The dorsal surface of the bone is nearly straight so that the ventral surface appears distinctly concave longitudinally. This element in *Meniscotherium* is a little longer and distinctly more robust than the first metacarpal and is not so noticeably bowed. The proximal extremity is broad but not deep dorsoventrally. The surface for the unciform is strongly convex dorsoventrally, and transversely it is of nearly uniform width and straight or only slightly convex. Sharply deflected distally from the inner or medial margin of the unciform facet is an elongate, crescentic surface extending medially and distally for articulation with the fourth metacarpal. The distal extremity is a little smaller than that of the fourth but the form is nearly identical. Its asymmetry is not so striking as in the first metacarpal.

In the *Phenacodus* skeleton that Cope described, the fifth metacarpal is about the same length as the first but very much sturdier. In another articulated fore foot (A.M. No. 2961) the fifth metacarpal is much longer as well as heavier than the first. In either case the fifth is shorter relative to the fourth than in *Meniscotherium.* While short in comparison with *Meniscotherium,* the *Phenacodus* fifth metacarpal has a relatively much greater diameter. In an instance where the ratio of lengths is about two to one, diameters of the shaft are between three and four to one. The proximal extremity of the fifth metacarpal is deeper dorsoventrally in comparison with its width than in *Meniscotherium* and the facet for the fourth metacarpal is relatively smaller and does not extend distomedially so noticeably. Both exhibit a strong process or tuberosity on the lateral surface of the proximal extremity for the extensor carpi ulnaris.

Phalanges.—The proximal phalanges of the *Meniscotherium* manus are approximately half the length of the corresponding metacarpals. They are slender and of nearly uniform width, tapering only slightly toward the distal extremity, that of the third digit being broadest. The proximal extremity of each is the deeper, corresponding to the distal extremity of the metacarpal, but through the shaft and distally they are rather flattened. The second phalanges in II to V are about two-thirds the length of the first in each, also slightly tapering and more flattened distally. The distal phalanges are about the length of the penultimate in each, with a slender shaft but distally spatulate. The dorsal surface is convex, and the ventral or palmar surface is flat. They have a surprisingly human appearance, and in all probability possessed a primatelike nail rather than hoofs or claws, as suggested by Marsh (1892, p. 448).

The *Phenacodus* phalanges are relatively shorter and much broader, and the broadly spatulate form of the distal or ungule phalanges in digits II to IV extends to the proximal extremity. The latter have been described as subungulate in character and are quite unlike those in *Meniscotherium.*

PELVIC GIRDLE

The innominate bone of *Meniscotherium* is moderately elongate with a strongly curved ilium flaring outward craniad to the auricular or sacral surface (see fig. 8). The ilium is essentially triangular in cross section from the acetabulum through most of its length, with the lateral (acetabular) border converging with, and then paralleling, the medial ventral (pubic) border toward the anterior superior spine at the ventrolateral extremity of the supra-iliac border. The external iliac or gluteal surface is strongly concave transversely in its mid portion, opposite the sacral surface, and the uniformly curved crest of the ilium commences caudad about opposite the posterior margin of the rugosity for the sacrum and swings forward and outward to the somewhat recurved anterior superior spine. This anterolateral extremity of the long crest of the ilium is distinctly rugged, possibly implying importance to the sartorius and tensor muscles, but surely significant for the superficial gluteus muscle which would be inserted on the third trochanter of the femur. The acetabular border has a curvature similar to that of the crest of the ilium and terminates caudad in a prominent and rugged anterior inferior spine extending forward from the margin of the acetabulum for the rectus femoris, a part of the extensor group for the shank.

The margin of the acetabulum is well separated by a broad dorsal surface from the ischial border and by a broad ventral surface from the pubic border. The cotyloid notch is deeply impressed and directed posteriorly along the shaft of the ischium. The ischium is elongate, straight, and comparatively slender, with a transversely concave medial surface. The ischial spine is small but fairly acute; however, the ischial tuberosity is prominently developed, accommodating the biceps femoris and other flexors of the leg. The shaft of the pubis is somewhat flattened and slender. Unfortunately, the ramus of this bone and that of the ischium are poorly represented and badly preserved in the material at hand; nevertheless enough remains to indicate a large, oval-shaped obturator foramen.

The *Meniscotherium* innominate bone is surprisingly like that of *Phenacodus,* although the latter is relatively more elongate, and the crest of the ilium would appear to be more flaring and recurved. The ischial spine in *Phenacodus* is more rugged, but the ischial tuberosity may not be relatively so well developed. The anterior inferior spine of human anatomy seems prominent on the acetabular border of the ilium, but it may be noted that the "deeply impressed subtriangular fossa" described by Cope (1884b, p. 455) as located just above the position of the anterior inferior spine and near the edge of the acetabulum is much less significant in *Meniscotherium.*

The *Hyopsodus* innominate bone is elongate and slender. The ilium shows the similarly arcuate and flaring dorsal margin, but the gluteal surface may be a little less concave. The anterior extremity is missing in the specimen at hand. The base or posterior portion of the ilium is a little less trihedral in cross section with the pubic border on the ilium much more subdued than in *Meniscotherium.* There is little or no evidence for an ilio-pectineal eminence on the dorsal margin, although this is weak or subdued in *Meniscotherium.* The anterior inferior spine on the acetabular border, however, which supports the origin of the rectus femoris, is surprising well developed. The ischium is slender but possibly a little less elongate than in *Meniscotherium.* The ischial tuberosity is prominent and the ischial spine perhaps more so than in *Meniscotherium.* Much of the pubic bone is missing, as is the ramus of the ischium. The cotyloid notch in the acetabulum for the ligmentum teres is constricted but directed along the ischium much as in *Meniscotherium.*

FEMUR

The femur of *Meniscotherium* is comparatively robust, as noted by cope in his very brief description, and its shaft is straight, although proximally the anteromedial margin is decidedly curved as it approaches the head (see pl. 8). The head may be somewhat oval to nearly circular in proximal view and its neck moderately slender and anteromedially directed. The fossa for the ligmentum teres is noticeably posterior in position and essentially marginal, in keeping with the posteriorly directed cotyloid notch of the acetabulum. The greater trochanter is robust and extends proximally a little more than the head, from which it is separated by a well-defined notch. The posterior crest of the greater trochanter partially covers posteriorly a deep and elongate digital fossa into which are inserted the obturator muscles. Distally this comparatively thick or well-rounded crest appears to divide, and a more feeble, sometimes poorly defined crest or intertrochanteric line crosses the shaft distomedially to join the distal extremity of the medially outstanding, nearly triangular lesser trochanter for the iliopsoas on the posteromedial margin of the shaft. The apex of the lesser trochanter has a position about a quarter of the length of the bone distal to the proximal extremity. The better defined lateral portion of the posterior crest from the greater trochanter extends distally to join the prominent and flattened third trochanter, which is almost halfway down the shaft. The development of this process emphasizes, as in the horse, the importance of the superficial gluteus muscle in abducting the limb and flexing the hip joint. The outline of the third trochanter varies somewhat from a proximodistally elongate flare to a shorter but more laterally projecting prominence.

On the enlarged distal extremity the patellar trochlea is narrow, elongate, and prominently raised. The condyles are large and separated by a broadly open intercondyloid notch, and the lateral and medial surfaces of the extremity are strongly divergent posteriorly. The condylar tuberosities or epicondyles are noticeable, and the outer, more subdued, is at the extremity of the prominent lateral supracondyloid crest which extends distally from the third trochanter. A similar medial supracondyloid crest disappears a short distance proximally on the shaft.

Much that Cope said (1884b, pp. 455-456) about the *Phenacodus* femur applies to that of *Meniscotherium,* particularly with regard to the proximal extremity and much of the shaft, but I note that the greater tuberosity in *Phenacodus,* although anteroposteriorly deeper, is a little less extended proximally, and the shaft is relatively more robust. Distally the fossae at the posterior base of the condyles are much less significant in *Meniscotherium,* and the transversely oriented posterior portion of the inner articular surface is as wide as or wider, rather than narrower, than the more oblique or transversely more convex outer articular surface in *Meniscotherium.* The patellar trochlea in *Phenacodus* seems broad, and the patella itself is comparatively wide and not so elongate and distally tapering as in *Meniscotherium* (see pl. 8).

The straight or but slightly curved *Hyopsodus* femur is slender, elongate, and somewhat flattened anteroposteriorly. The proximal extremity is transversely narrow, as the head and slender neck do not extend medially so noticeably as in *Meniscotherium.* The head, moreover, is nearly spherical and the fossa for the ligmentum teres is centrally located, well removed from the margin of the articular surface. The greater tuberosity is comparatively small and does not project proximally as far as the head. The digital fossa is proximodistally much shorter than in *Meniscotherium,* and the lesser tuberosity is nearer the proximal extremity. The lateral margin of the shaft from the greater tuberosity to the lateral condyle is compressed, and just beyond to the midpoint of the shaft is laterally expanded into a well-defined, proximodistally elongate third trochanter, with a rugged crest for the superficial gluteus muscle. The distal extremity of the *Hyopsodus* femur at hand is poorly preserved, but I note that the patellar trochlea is relatively broader than in *Meniscotherium.*

TIBIA

The *Meniscotherium* tibia is a little shorter than the humerus. It is relatively slender and noticeably bowed anteriorly (see pl. 9). It exhibits an elongate cnemial crest that is laterally deflected and extends straight nearly half the length of the shaft. The crest is distally somewhat roughened, evidently for the tendon of the semitendinous muscle which would have its origin at the prominent ischial tuberosity. From this point the crest rapidly subsides as a well-rounded ridge or margin crossing obliquely to the medial side and then directed more or less subdued toward the inner malleolus. Proximally the shaft shows a broad, gently convex anteromedial surface and narrower, concave lateral and posterior surfaces which are separated by a sharp posteromedial crest that would support the interosseous membrane. This crest curves strongly outward proximally to where it reaches the facet for the head of the fibula and distally swings somewhat forward and subdued to a more medial position at the place of contact for the distal extremity of the fibula. The posteromedial margin of the shaft is also acute proximally, beneath the medial tuberosity or condyle of the tibia but loses this character distally, near the midpoint of the shaft. Distally, the shaft is slender and essentially rounded.

The proximal extremity of the tibia is broad and laterally overhanging. The two surfaces for the femur appear roughly equal. The medial surface is somewhat concave transversely but distally offset and broad posteriorly. Along the posterolateral margin of this there is a noticeable facet, offset or obliquely turned from the foregoing and adjacent to the popliteal notch, for attachment of the posterior crucial ligament. The outer surface for the femur rides smoothly up the median spine which forms the medial apex of the surface and accords with the transversely more oblique appearance of the outer articular condyle of the femur. The distal surface of the laterally overhanging outer condyle shows a small, convex, oval and almost distally facing facet for the fibula. On the anterior portion of the proximal extremity there is a distinct transverse notch or step which tends to define the proximal extremity of the cnemial crest and is evidently the position for attachment of the patellar ligament.

The distal extremity of the tibia is somewhat enlarged and exhibits a pronounced distal extension medially of the internal malleolus which articulates with the inner side of the astragalus. The distal articular surface shows a shallow, anteroposteriorly elongate concavity adjacent to the inner malleolus for the inner crest of the astragalus. The transversely more elongate outer surface for the medial side of the outer crest of the astragalus is decidedly oblique to the longitudinal axis of the shaft. This oblique facet terminates proximolaterally adjacent to the fibular contact.

Cope (1884b, pp. 503-504) has called attention to several differences between the tibia of *Meniscotherium* and that of *Phenacodus*. In the character of the cnemial crest, he noted that it is relatively shorter and more obliquely truncated proximally, and its distal extension does not cross to the internal malleolus in *Phenacodus*. With regard to "the early disappearance of the external posterior angle and its reappearance on the distal two-fifths of the length of the shaft" in *Meniscotherium*, I suspect that his specimen was unusual or defectively preserved, as seems evident in his illustration (1884b, pl. 25g, figs. 16, a, b, and c). His fifth point evidently refers to the disappearance on the middle of the shaft of the posterior inner angle, rather than the posterior external angle, because as actually stated this was part of his fourth point. He further noted that the posterior face of the shaft distally is roughened for muscular insertion in

Meniscotherium, and that the internal malleolus is obliquely truncate and acuminate as in many creodonts. In *Phenacodus* the internal malleolus is much more blunt. It may be further noted that the tibia in *Phenacodus* is essentially straight, not bowed as in *Meniscotherium,* and the shaft is much more robust.

A distal portion of a tibia is known for *Hyopsodus paulus,* as well as for *H. walcottianus.* Both show the anteroposteriorly concave surface for the astragalus which lacks any clearly defined median flexure, denoting a very shallow trochlear groove in the latter. This surface, moreover, is not so oblique transversely as in *Meniscotherium.* The internal malleolus is abruptly truncated distally and the rounded anteromedial margin becomes more anterior in position proximally on the shaft, in the direction of the cnemial crest. A lateral crest for the interosseous membrane is somewhat better defined in the *H. paulus* specimen, but at its distal extremity, at the margin of the astragalar facet, the internal malleolus is roughly acuminate and I find no evidence of a facet for the fibula.

FIBULA

The *Meniscotherium* fibula is a decidedly slender bone with moderately enlarged extremities (see pl. 9). The shaft is slightly thicker distally and this portion shows a better defined anteromedial crest for the interosseous membrane. The proximal extremity exhibits a proximally facing, anteroposteriorly elongate oval concavity for articulation with the external tuberosity of the tibia. The anteroposteriorly expanded proximal extremity affords attachment for muscles believed to be the peroneous longus and the soleus, and more medially the tibialis posterior, that aid in flexing and extending the foot. The distal extremity exhibits an oblique, distomedially facing surface which articulates with the outer side of the astragalus and with the calcaneum. On the lateral surface of the extremity is a short but prominent longitudinal crest or process bounding anteriorly a smooth, broad groove, evidently for the tendons of the peroneus muscles.

The *Phenacodus* fibula has a similar appearing proximal extremity, but the shaft is sturdier and the distal extremity more enlarged. It also appears that the fibula in *Phenacodus* makes a more expansive contact with the tibia, both proximally and distally. Moreover, the lateral crest or process on the distal extremity is much less developed than in *Meniscotherium.*

The distal portion of a fibula belonging to *Hyopsodus paulus* shows a somewhat enlarged external malleolus with an oblique facet for the astragalus. The lateral margin of the distal surface is turned outward, evidently for some articulation with the calcaneum, but this marginal facet is anteroposteriorly convex rather than concave as in *Meniscotherium*. The lateral tubercle of the malleolus that bounds the groove for the peroneus longus anteriorly is somewhat more posterior in position, and the peroneal groove though narrower is well defined. The posterior margin of the preserved portion of the fibula is rather more sharply ridged than in *Meniscotherium*. Medially, the external malleolus is slightly roughened proximal to the astragalar facet, and there is no evidence of a facet for the tibia.

PES

The hindfoot of *Meniscotherium* (see pl. 10) appears to be as much as 25 percent larger than the forefoot, as determined by the length of the metatarsals relative to that of the metacarpals. The tarsus, however, does not appear to be so proximodistally compressed as the carpus, so that in dorsal aspect the tarsus more nearly resembles that of *Phenacodus*. Most noticeable differences from the *Phenacodus* foot lie in the appearance of the tibial surface of the astragalus and the shorter, more wedge-shaped cuboid in *Meniscotherium*. Moreover, the distal extremities of the metatarsals are relatively not so broad as in *Phenacodus primaevus*. The *Meniscotherium* hindfoot bears a resemblance also to the *Tetraclaenodon* hindfoot, but in the latter the elements are relatively more elongate and slender.

Astragalus.—The astragalus is a distinctive bone in *Meniscotherium*, somewhat compressed dorsoventrally on the medial side but not on the lateral side. The inner crest of the trochlea or tibial surface is subdued and rounded, whereas the lateral crest is high and acute. The neck is sturdy but elongate and directed medially as well as distally. The transversely broad head has a strongly biconvex navicular surface that tapers somewhat medially. The ventral surface of the astragalus, or that facing the calcaneum, exhibits two obliquely elongate and nearly parallel facets. The lateral or ectal facet is uniformly concave in its long direction and extends out on a prominent distolateral process. This process also deflects laterally the distoventral margin of the large, otherwise nearly vertical facet for the fibula. The medial or sustentacular facet is longitudinally convex and broader distally where it extends onto the neck. Posteriorly (proximally) this facet narrows and near its extremity is sharply flexed ventrally where it articulates with the acute posterodorsal margin of the sustentaculum. Lateral to this flexure and at the posterior extremity of the deep groove for the interosseous ligament, separating the ectal and sustentacular facets for most of their length, is the ventral opening of the astragalar foramen. Dorsally this foramen opens near the posterior margin of the tibial surface. Between these apertures the posterior margin of the astragalus shows a smooth, very broad, shallow, and somewhat oblique groove interpreted as conducting the flexor longus hallucis. The medial surface of the astragalus, as noted by Cope (1884b, p. 505) "is oblique, and has a central fossa and a prominent shelf-like angle below it." There is apparently no articulation with the cuboid.

The *Phenacodus* astragalus is noticeably different in exhibiting a much better developed inner crest on the astragalus with a deeper trochlear groove which extends to the posterior margin. The medial or inner surface is essentially vertical, not nearly so oblique as in *Meniscotherium.* The neck of the astragalus is shorter, and with the head is relatively wider transversely than in *Meniscotherium.*

The *Hyopsodus* astragalus appears anteroposteriorly short, but the most noticeable feature in comparison with *Meniscotherium* is the much less raised outer crest of the tibial surface. The low, broadly rounded inner crest and the ventral shelflike inner projection are much alike in the two forms, but between the subdued inner and outer crests there is left only a very weakly developed trochlear groove. This also leaves the tibial surface transversely much less oblique than in *Meniscotherium.* The neck is somewhat oblique, nearly as in *Meniscotherium,* but appears relatively shorter. Matthew (1915) has described an astragalar facet on the cuboid; such an articulation, however, is not evident on the head of the astragalus at hand. The facet for the fibula is at a 90-degree angle from the tibial facet, less acute than in *Meniscotherium.* The lateral prominence of the anteroventral portion of the fibular surface, which supports anterior extension of the ectal facet beneath, is less projecting than in *Meniscotherium.* The oblique ectal and sustentacular facets on the ventral surface of the *Hyopsodus* astragalus are much like those in *Meniscotherium* but a little less elongate. The groove between them for the interosseous ligament is deeply impressed as in *Meniscotherium,* but the astragalar foramen in ventral view is more posteriorly placed. The groove on the posterior margin of the astragalus for the flexor longus hallucis is similarly broad and well defined, but dorsoventrally perhaps a little more elongate.

In the hindfoot of *Tetraclaenodon* the astragalus has an elongate neck and a relatively large head that is highly convex transversely.

The trochlea for the tibia is shallow but the inner crest, particularly posteriorward, is not nearly so subdued. The inner and outer walls of the astragalus are both somewhat oblique, lacking the striking difference noted in *Meniscotherium.* On the ventral surface the ectal facet is a short, oval concavity whose long axis is nearly transverse, more oblique to the sustentacular facet than in *Meniscotherium.* Moreover, it is interesting to note that the groove for the flexor longus hallucis on the posterior margin is surprisingly prominent, better defined than in *Meniscotherium,* and the astragalar foramen is not centrally located in the groove of the trochlea, but close to the inner crest.

Calcaneum.—The calcaneum of *Meniscotherium* is elongate with the posterior (proximal) projection comprising a little more than half the length. The bone is dorsoventrally deep and transversely somewhat compressed in the posterior half. It terminates posteriorly in an enlarged, slightly bilobate extremity for the Achilles tendon, extending posteriorly a little more on the medial than on the lateral side. A little forward of the middle of the calcaneum the astragalar condyle, as noted by Cope, is placed diagonally across the superior or dorsal ridge, with its convex articular facet facing anteromedially and slightly dorsally. Anterolaterally the condyle thickens and the rounded dorsal margin articulates with the distal margin of the external malleolus. A prominent ridge on the calcaneum extends anterolaterally to the well-developed peroneal tubercle near the anterior (distal) extremity, which bounds dorsally the broad groove for the peroneus longus. The sustentaculum is a prominent knob medial to the astragalar condyle, with a dorsally facing, transversely elongate oval facet for the astragalus. This facet turns sharply ventral on the posterior margin of the sustentaculum, as has been noted for the sustentacular facet of the astragalus. The posteroventral surface of the sustentaculum is smooth and broadly grooved for continuation of the extensor longus hallucis. The anterior or distal extremity articulates with the cuboid in a dorsoventrally concave and transversely highly oblique facet that extends posteromedially almost to the anterior margin of the sustentaculum. The dorsal margin of this oblique concavity extends dorsomedially from near the peroneal tubercle toward the neck of the astragalus and is less oblique or nearly at right angles to the long direction of the shaft. The more ventral margin extends ventromedially to the inferior margin of the calcaneum.

The *Phenacodus* calcaneum is similar but with stronger, more massive construction. The sustentaculum is deep and thick, not so elongate and slender. The lateral crest from the astragalar condyle to the peroneal tubercle is rugged and outstanding, but with less definition of the tubercle itself. The surface for the cuboid extends ventromedially somewhat oblique, but is much less concave, evidently lacking the flexibility of the *Meniscotherium* articulation.

The *Hyopsodus* calcaneum is relatively shorter than that of *Meniscotherium,* and the posterior portion between the astragalar condyle and the enlarged tuberosity for the Achilles tendon is a little more compressed transversely. The astragalar condyle is similar but a little less dorsally projecting. The sustentaculum is dorsoventrally more compressed, but anteroposteriorly broader and perhaps a little less extended medially. The shortened anterior portion of the calcaneum, correlated with the relatively short neck of the astragalus, exhibits a somewhat less oblique and less concave facet for the cuboid, although in its transverse direction it is nearly aligned with the anterior margin of the sustentaculum. The dorsal margin of this surface is transversely shorter and more curved, with a long lateral margin extending down to a more ventrally placed peroneal tubercle. The peroneal groove consequently is decidedly more ventral in position.

The slender *Tetraclaenodon* calcaneum has a long anterior or distal portion, in keeping with the elongate neck of the astragalus, as well as a lengthy posterior portion. The sustentaculum is slender and outstanding, about as in *Meniscotherium.* The articular facet for the cuboid, although oblique and concave, is rather less so than in *Meniscotherium,* and it does not approach so near the sustentaculum posteromedially.

Navicular.—The *Meniscotherium* navicular is proximodistally short and has a deeply concave proximal surface occupied entirely by the head of the astragalus. The rim of the concavity is broadly curved dorsally and medially, but the lateral margin is more nearly straight and rises to a low prominence ventrolaterally. The medial margin, however, rises to a higher, more acute process ventrally, and between these there is a sharp notch in the ventral border for passage of the tendon of the posterior tibialis. The lateral side of the distal surface shows a flat facet for the external cuneiform which is dorsoventrally elongate and noticeably tapering ventrally. Medial to this the facet for the middle cuneiform is dorsoventrally shorter and distinctly convex. The more ventromedial surface of this convexity articulates with the internal cuneiform, and rises to the prominence at the ventromedial angle of the proximal surface. The lateral surface of the navicular shows a dorsoventrally elongate and slightly convex facet along its more proximal portion for articulation with the cuboid. On the ventral surface of the navicular, lateral to the notch, is a small knob or process that may have supported a part of the insertion for the tibialis posterior. It is located just above the posterior extremity of the facet for the external cuneiform but in *Meniscotherium* evidently does not make contact with that bone.

A few differences were noted with respect to the *Phenacodus* navicular, although the two are rather similar. On the proximal rim the ventrolateral prominence is more significant than that of the ventromedial angle, and projects laterally as well as proximally in *Phenacodus*. The more obliquely facing facet for the cuboid is proximodistally deeper and rides well up on the proximoventral prominence. Also, the ventral tubercle is larger, more median in position, and its distal surface carries a small facet, not seen in *Meniscotherium*, for articulation with the ventral extension of the external cuneiform. The facet for the middle cuneiform appears relatively longer and less convex.

In the *Tetraclaenodon* navicular the ventral tubercle and the ventrolateral prominence of the proximal rim together form a strongly developed, oblique, and ventrolaterally projecting process. This results also in a dorsoventrally concave surface articulating with the cuboid.

Cuboid.—The *Meniscotherium* cuboid viewed dorsally in an articulated foot appears relatively short proximodistally, with the exposed area in the form of a parallelogram or nearly rectangular, inasmuch as the articular surface for the calcaneum extends distally well down the dorsal surface. Disarticulated, the calcaneal facet is seen to be dorsoventrally very convex and highly oblique in a nearly transverse plane. Moreover, the dorsal and ventral surfaces are convergent in a proximolateral direction. Distally the ventral surface shows a pronounced ventromedial flare, ventrally covering the deeply impressed peroneal groove. The distal surface anterior to the elongate peroneal groove is nearly oval in shape and essentially concave both dorsoventrally and transversely. The surface is principally for articulation with the fourth metatarsal, although the lateral extremity of the transversely elongate oval flattens out or is somewhat deflected proximally for articulation with the fifth metatarsal. Also, the ventral margin of the oval facet is rounded into the peroneal groove for the recurved surface of the fourth metatarsal. The proximal portion of the broad medial surface of the cuboid has a dorsoventrally elongate facet for the navicular. On the distal portion of this surface the facet for the external cuneiform is variable and may be dorsoventrally long and possibly bilobate or separated into two parts. Occasionally the surfaces for the navicular and external cuneiform are in contact or partially merged.

The *Phenacodus* cuboid is much more elongate, and the proximal surface though convex and oblique is much less so than in *Meniscotherium.* The broad distal articular surface also provides a relatively larger area for the fifth metatarsal. The ventral surface is broadly expanded and ventrodistally flaring, extending well down over the peroneal groove but does not appear so triangular in outline as in *Meniscotherium.* On the medial surface the large facet for the navicular is proximoventrally located and about as deep as it is long.

In *Tetraclaenodon* the cuboid is decidedly slender and elongate in dorsal view, and the proximal extremity is more like that of *Phenacodus.* The ventral surface although expanded over the peroneal groove is relatively much narrower transversely, and the medial surface is narrower dorsoventrally. Also, the facet for the navicular is noticeably convex dorsoventrally. It is straight or slightly concave in *Meniscotherium.*

Internal cuneiform.—The internal cuneiform is flattened with its medial facing surface relatively broad and long. Proximally this surface in *Meniscotherium* narrows and its proximodorsal margin is deeply concave for articulation with the navicular. Marginal to this concavity the lateral surface exhibits an arcuate facet, convex in its more dorsal portion but concave proximally, that articulates with the medial side of the middle cuneiform. The distal extremity, which extends well beyond the middle cuneiform, has a dorsoventrally elongate concavity for articulation with the first metatarsal. There does not appear to be any definable facet for the second metatarsal in the material at hand.

The *Phenacodus* internal cuneiform is similar appearing, but the ventral margin is thicker, and the dorsoventrally elongate facet for the navicular is less concave and faces more nearly proximal. In consequence the relatively flattened facet for the middle cuneiform has a more dorsoventral orientation. Except for its thicker ventral margin the *Tetraclaenodon* internal cuneiform more nearly resembles that of *Meniscotherium,* notably in the deeply concave, proximodorsally placed navicular facet. The distal extremity is similar in all three forms.

Middle cuneiform.—The dorsoventrally elongate middle cuneiform is the smallest element of the *Meniscotherium* tarsus. Its limited dorsal surface has convex proximal and distal margins that lap slightly onto the dorsal surfaces of the navicular and second metatarsal respectively. Both the proximal and distal surfaces of the element are dorsoventrally concave, that for the navicular more decidedly so. The surface for the second metatarsal is, moreover, transversely convex and tapers ventrally. The medial and dorsoventrally compressed lateral surfaces of the middle cuneiform articulate in an uneven, arcuate facet with the internal cuneiform and in a narrow dorsoventrally elongate facet with the external cuneiform respectively. Behind the upturned ventral margin of the navicular surface a small but distinctly rugose prominence, and possibly the adjacent tip of the internal cuneiform, may well have received a part of the tibialis posterior, which extending through the ventral notch of the navicular would have been inserted as well on the ventral tubercle of that bone, as mentioned in a foregoing section. This muscle, of course, functions with the peroneus longus in extending the tarsus, and against it in turning the foot inward.

The *Phenacodus* middle cuneiform is much like that in *Meniscotherium,* but the proximal and distal facets, though similar, are a little more flattened, notably that for the navicular. This is true also for the *Tetraclaenodon* middle cuneiform, and the dorsal surface is more nearly square. The medial facet for the *Phenacodus* internal cuneiform is also relatively flat and essentially straight, rather than arcuate. It may be further noted that the ventral tubercle, evidently for the tibialis posterior, though large in *Phenacodus,* is relatively not so rugged as in *Meniscotherium.* This portion of the *Tetraenodon* middle cuneiform is missing in the specimen examined.

External cuneiform.—The external cuneiform is significantly larger than the middle cuneiform in *Meniscotherium,* with its surface for the third metatarsal more distal than the corresponding surface on the middle cuneiform. The dorsal surface on some specimens appears to be nearly twice as long proximodistally as that of the middle cuneiform. The proximal surface for the navicular is dorsoventrally elongate and ventrally tapering. That on the distal surface for the third metatarsal is also dorsoventrally elongate but somewhat projecting ventrally, and distinctly concave. It is also transversely broad anteriorly and markedly constricted about midway. The medial surface shows a narrow, dorsoventrally elongate facet, adjacent to the proximal surface, for articulation with the middle cuneiform. Distal to this on the medial surface there are two well-separated, oval facets adjacent to the distal surface, for articulation with the second metatarsal. The lateral surface of the external cuneiform on its more proximal portion shows the dorsoventrally elongate, but variable and often bilobed, surface for the cuboid. On the proximal portion of the transversely narrow ventral surface there is an elongate process that extends somewhat medially as well as ventrally and exhibits a distally deflected, hooklike extremity. The concave portion bounded proximally by this hooklike process, and in part distally by the ventral extension of the distal surface, is the continuation medially of the peroneal groove, so well defined on the cuboid. The ventral process of the external cuneiform extends beyond that on the middle cuneiform, and while it may have included an insertion of the tibialis posterior, it no doubt supported part of the ligamentous cover of the peroneus groove and probably tendon for certain of the interosseous muscles.

The *Phenacodus* external cuneiform differs only in minor respects from that of *Meniscotherium.* The distal articular facet for the third metatarsal is less concave dorsoventrally. That laterally for the cuboid is generally large and oval shaped, not extending onto the ventral process. The ventral process appears to be relatively a little shorter but deeper and more massive.

The external cuneiform of *Tetraclaenodon* is proximodistally elongate and relatively more slender, dorsoventrally as well as transversely, than in *Meniscotherium.* The facet for the cuboid is rather like that in *Phenacodus.* The ventral process is missing on the specimen examined.

Metatarsal I.—The first metatarsal, the smallest of the five in *Meniscotherium* is about half the length of the second, and its slender dorsally bowed shaft is more compressed transversely than dorsoventrally. The extremities are somewhat enlarged, the proximal extremity being the larger, with a simple, dorsoventrally convex proximal surface for the internal cuneiform. This surface, moreover, is broad and slightly convex transversely as well, permitting abduction as well as flexure and extension. Ventrolaterally the base is roughened and may be enlarged, evidently for the terminal or most medial insertion of the peroneus longus. The distal articular surface is dorsoventrally convex and shows a weak median keel. It is, moreover, relatively narrower and more oblique than in the second metatarsal.

The *Phenacodus* first metatarsal has about the same relative length as in *Meniscotherium* but is comparatively straight and not nearly so slender. The *Tetraclaenodon* first metatarsal, however, is relatively longer, being nearly two-thirds the length of the second, and only a little more slender. The shaft is somewhat bowed as in *Meniscotherium.* The base or proximal extremity, it is further noted, exhibits a short ventrolateral spur, unlike *Meniscotherium,* and the articular surface for the internal cuneiform is only slightly convex.

Metatarsal II.—The second metatarsal of *Meniscotherium* is intermediate in length between the third and fourth, but its distal extremity is about even with that of the fourth in the articulated foot, because of the more proximal position of the base of the second metatarsal. The proximal surface for the middle cuneiform is nearly triangular in outline, dorsoventrally elongate and slightly convex. Transversely the facet is distinctly concave. The medial surface of the base is somewhat roughened and a short distance distally exhibits a low knob. Apparently, however, there is no faceting for either the internal cuneiform or the first metatarsal. The lateral surface of the base, however, shows a slightly concave facet proximodorsally and a smaller flattened facet proximoventrally for the external cuneiform. More distally, the lateral surface conforms to the medial surface of the third metatarsal base, but I find no evidence of articular contact. The shaft maintains a width at least as great as the base, becoming little wider distally, and is relatively compressed dorsoventrally. It is essentially straight but may be slightly bowed dorsally in some individuals. The convexity of the transversely wider distal extremity is slightly oblique and shows a pronounced median keel only on the ventral surface.

Except for its more flattened proximal extremity for articulation with the middle cuneiform and relatively wider distal extremity, the second metatarsal in *Phenacodus* appears very much like that in *Meniscotherium.* That in *Tetraclaenodon* is more elongate and relatively slender. The proximal surface of the base, like that in *Phenacodus,* is flattened although the outline is similar to that in *Meniscotherium.* The distal extremity is broad in comparison with the width of the base, but these are small relative to the length of the shaft.

Metatarsal III.—The *Meniscotherium* third metatarsal averages about 5 or 6 percent longer than the second. The shaft is broad and flat, increasing somewhat in width distally. The proximal extremity shows the asymmetric T-shaped base so frequently encountered in the mammalian third metatarsals. This surface for the external cuneiform is gently convex dorsoventrally, slightly oblique transversely, and markedly constricted ventral to the broad and dorsally convex superior margin. The constriction is greatest on the lateral side, and ventral to this the ventrolateral margin of the surface for the middle cuneiform may be slightly deflected proximally. Adjacent to this there is a small flattened facet on the lateral surface for the ventral portion of the fourth metatarsal base. Dorsal to this facet on the lateral side of the third metatarsal there is a deeply concave, ventrolaterally facing surface for articulation with a medial knob or prominence close to the proximal extremity of the fourth metatarsal. The medial surface of the base of the third metatarsal shows a distinct knob, proximodorsally, that fits into a depression distal to the dorsal facet for the external cuneiform on the base of the second metatarsal. The convexity of the relatively broad distal extremity has an axis at right angles to that of the shaft and exhibits a prominent keel ventrally.

The similar appearing *Phenacodus* third metatarsal, as the second, has a generally flatter proximal surface for the external cuneiform and a relatively broader distal extremity. It should be noted, however, that the proportions of the metatarsals as outlined here apply more particularly to comparison with *Phenacodus primaevus* material, as the *Phenacodus copei* metatarsals are relatively elongate and slender, somewhat more as described for *Tetraclaenodon.*

Metatarsal IV.—The *Meniscotherium* fourth metatarsal is a trifle shorter than the second, and somewhat more so than the third, as noted above. The shaft is dorsoventrally compressed but more slender than that of the third and has a slight lateral curvature so that the distal extremities tend to diverge. The proximal surface for the cuboid is dorsoventrally and transversely convex over its broader dorsal portion, but the narrower, ventromedially directed part is noticeably deflected proximally, so that the ventral margin of the base extends into the deeply impressed peroneal groove of the cuboid. Adjacent to the recurved ventral portion of the cuboid surface, on the medial side of the fourth metatarsal, is a facet for the third metatarsal. A prominent knob on the medial side of the base, just distal to the dorsomedial margin of the cuboid facet, is convexly faceted for the concavity on the lateral side of the third metatarsal base. The lateral side of the fourth metatarsal base is also deeply concave and exhibits a distolaterally and somewhat ventrally facing concave facet for the fifth metatarsal. The convexity on the distal extremity of the fourth metatarsal is narrower laterally and its axis is slightly oblique, more distal on the medial side.

Differences from the *Phenacodus* and *Tetraclaenodon* fourth metatarsal are essentially those noted with regard to the second and third metatarsals, but it may be noted that the ventral portion of the cuboid facet is not nearly so recurved, so that in these forms the base of the fourth metatarsal does not extend so noticeably into the peroneal groove.

Metatarsal V.—The fifth metatarsal of *Meniscotherium* is a little longer than the first and about two-thirds the length of the fourth. The shaft is compressed in a dorsolateral-ventromedial direction, and the broadly expanded proximal extremity is gently deflected ventromedially. The base is essentially trilobed with a dorsomedial lobe or prominence that articulates with the lateral concavity in the base of the fourth metatarsal. The margin from this lobe to the more proximoventral lobe lies adjacent to the lateral margin of the cuboid surface of the fourth metatarsal. With the posterior margin of this latter surface, the proximoventral lobe of the fifth metatarsal extends into the peroneal groove and, I suspect, receives a portion of the insertion of the peroneus longus. The third or ventrolateral lobe probably includes insertion of the peroneus brevis, an extensor from a more dorsal direction.

The *Phenacodus* fifth metatarsal is also about two-thirds the length of the fourth, but is straighter and much more robust. Its proximal extremity lacks the trilobed appearance, and the articulation with the cuboid is not so oblique to the shaft. The base of the fifth metatarsal in *Tetraclaenodon* is transversely flattened, somewhat as in *Meniscotherium,* and exhibits a prominent ventral knob, evidently for the peroneus longus, which is less proximally directed than in *Meniscotherium,* but the ventrolateral process, noted in the latter, is missing.

Phalanges.—The proximal phalanges in the second to the fourth digits are a little less than half the length of the metatarsals. They are broad but taper somewhat distally and are flattened, particularly the shaft, and the distal extremity is much more compressed dorsoventrally than the proximal. The second phalanges are nearly two-thirds the length of the first in each digit and are also distally tapering and flattened. The phalanges of the third digit are broader than those of the second and fourth. The distal phalanges are elongate but a little shorter than the first, with a somewhat spatulate anterior half and a narrow posterior neck. The spatulate portion is dorsally convex and ventrally flat, and there is a small dorsal depression near the anterior margin which itself is not notched or fissured.

The *Phenacodus primaevus* phalanges are relatively shorter and broader, and the distal phalanges are more broadly spatulate with little or no posterior neck. The *Tetraclaenodon* phalanges are long and slender, not flattened, and the distal phalanx in each digit is transversely compressed and very little spatulate, clearly for a more clawlike structure. Matthew (1915) described the *Hyopsodus* phalanges as short, with the unguals clawlike, fissured, and not compressed.

SUMMARY OF RELATIONSHIPS

Although the highly selenodont teeth of *Meniscotherium* early gave rise to considerable speculation as to its relationships, particularly to such perissodactyls as the chalicotheres and propalaeotheres, to the hyracoids and to the notoungulates, there is no doubt of its condylarthran affinities. While it differs importantly in many characters, evidently of more adaptive significance, from the typical condylarth *Phenacodus,* its rather numerous resemblances, presumably of conservative or basic significance, demonstrate a closer affinity to *Phenacodus* than to any other mammal whose skeleton is adequately known. This relationship, nevertheless, is best expressed by their being retained in separate families of the order. Similarities were also noted in comparisons with the limited skeletal materials of *Hyopsodus* available, but while rather striking in certain instances, the degree of relationship is perhaps a little less close than with *Phenacodus.*

Meniscotherium would appear to be rather less like *Tetraclaenodon,* although the latter is generally regarded as being in an ancestral position with regard to *Phenacodus,* and it was largely on the basis of this relationship that Matthew (1897) concluded that the more serially arranged foot structure characterizing *Phenacodus* was not primitive but secondary. The somewhat less fully acquired serial arrangement in *Mensicotherium* than in *Phenacodus* must then have been a parallel development, if not truly primitive, as I would not postulate *Tetraclaenodon* in an ancestral position to *Meniscotherium.*

Structural resemblances to the predaceous arctocyonids, with which the condylarths no doubt converged in much earlier time, show certain rather generalized similarities, but the interlocking elements in both the carpus and tarsus and the more significant differences in the astragalus and calcaneum suggest that the relationship to *Menisco-*

therium, clearly the most distinctly herbivorous of the condylarths, is rather remote. Nevertheless, this relationship is evidently less remote than that to the periptychids on the basis of teeth as well as feet, although the latter are now usually included within the Condylarthra. The periptychid foot structure as represented by *Ectoconus* is not condylarthran but of the taligrade type, as observed by Matthew, more closely allied to that of the pantodonts. A foot structure of this type was also observed for the tillodonts, whose teeth incidentally are basically more *Pantolambda*-like than arctocyonid. A slight resemblance between lower molars of *Meniscotherium* and *Esthonyx* deserves comment, although the two patterns are truly different and any thought of relationship is discredited by the upper molar structure as well as feet.

A relationship to the perissodactyls was early predicated on tooth structure as outlined in a foregoing section, but this was abandoned as more became known of the foot structure in *Meniscotherium.* The tooth structure somewhat less closely resembles that of the chalicotheres than perhaps certain of the Old World palaeotheres, although discrepancies in detail may be observed such as the somewhat more crescentic character of the protoconule in the upper molars and the very different third lower molar in *Meniscotherium.* Resemblances in molar structure are no doubt due to parallelism in development of the selenodont or crescentic tooth pattern, inasmuch as the interlocking arrangement of the elements of the carpus in the early perissodactyls readily excludes *Meniscotherium* from a close relationship.

The artiodactyls are even more remote, and although a roughly similar selenodonty has occurred in certain forms, as far as I can determine, the structures are not all homologous. Generally the position of the hypocone has been taken by the metaconule in early development of the selenodont pattern in upper molars of artiodactyls (or by the protocone in the cainotheres), but these would both appear to be definable in *Meniscotherium.* The artiodactyl foot structure, of course, is quite unlike that in *Meniscotherium.*

A resemblance which may be more than casual involves the late Paleocene and early Eocene litopterns of South America. The relative age of the São José de Itaborai, as well as the Casamayor assemblage, however, would seem to preclude the possibility of *Meniscotherium* having given rise to these earlier proterotheriids, as would be implied in Wortman's postulation. Ameghino was, no doubt, closer to the truth in suggesting a common but as yet undiscovered ancestry. Perhaps the closest resemblance is seen in a comparison with the proterotheriid *Anisolambda* which de Paula Couto (1952) has shown includes *Josepholeidya,* and occurs in beds regarded as of late Paleocene age in Brazil. Remarkably selenodont for so early a form, nevertheless I note a somewhat different trend in the development of the accessory cuspules of the upper molars. The protoconule, for example, is less crescentic and more closely connected to the protocone, whereas the metaconule may be somewhat crescentic but shows little or no tendency to form a metaloph with the hypocone. The lower molars are perhaps less easily distinguished from those in *Meniscotherium* and show the metastylid crest as in the latter, but I note that the trigonid is relatively a little shorter anteroposteriorly and the labial wall of the protoconid perhaps more acute.

The litopterns are presumably of condylarthran affinity, as well as the more bunodont didolodonts which are included within the latter order, so that *Meniscotherium* may not be too distantly related to such a form as *Anisolambda;* nevertheless, one was not derived from the other as presently defined, and there is no evidence to show that *Meniscotherium* represents a return to the Northern Hemisphere of a South American condylarth.

The possibility of a close relationship between *Meniscotherium* and the hyracoids provoked considerable speculation during the earlier history of investigation. I am inclined to believe, however, that the relationship is decidedly remote. I suspect that much of the resemblance between them is adaptive in nature. There would appear to be certain similarities in form and proportions but the details often seem incompatible with any close affinity. There is, of course, a great interval of time between the recent hyracoids and *Meniscotherium,* as well as a wide geographic separation, and certain of the more obvious differences in the skull may be attributed to its shortening and the increase in the relative size of the brain.

The shortening of the skull has resulted in the orbits being farther forward with respect to the molar teeth, greatly affecting the orbital plate of the maxilla, and with the convergence anteriorly of the orbital margin of the frontals the possibility of binocular vision is much better in the hyracoids than in the meniscotheres. Moreover, the orbit is almost closed posteriorly by processes from the jugal and parietal. The postorbital processes of the frontals only are well developed in *Meniscotherium.* The parietals are not involved. Another feature of interest in skull shortening is the more vertically elongate and backward-facing pterygoid fossae, nearly as in man.

The glenoid surface for articulation with the lower jaw also has a nearly human appearance in its sigmoid flexure, quite unlike *Meniscotherium*. It should be particularly noted that the jugal participates in the glenoid articular surface and extends backward above this, almost completely obscuring the zygomatic process of the squamosal in lateral view. There would appear to be no tendency toward reduction of the zygomatic process of the squamosal in *Meniscotherium*. Anteriorly, however, the jugal is not so extended and does not reach the lachrymal, as it does in *Meniscotherium*, so that the maxillary forms a part of the orbital rim.

With the more expanded brain case there is much less development of the temporal or sagittal and lambdoidal crests, and the mastoid has a distinct lateral as well as occipital exposure. This bone, however, is even more nearly excluded from the basicranial surface than in *Meniscotherium* and is exposed only on the anterolateral margin of the root of the paroccipital process, posterior to the external auditory meatus. The hyracoid skull also retains a clearly defined interparietal in fully mature specimens. This has never been found in *Meniscotherium* or observed in any of the other condylarths for which skull material is known.

The cheek teeth of the modern hyracoids are specialized somewhat similarly to those in *Meniscotherium*, but the upper are more lophodont and a little less crescentic. Moreover, the premolars have become so completely molariform that few clues are left as to the stages through which the pattern may have developed. Also, incisor specialization has become highly distinctive. A more interesting comparison may be made with the early Oligocene forms of Africa, such as *Megalohyrax* and *Saghatherium*. While molarization of the premolars is well advanced, as in the later forms, the upper molars are rather more crescentic, particularly in the outer walls. A most noticeable difference from *Meniscotherium* is the weak or obscure character of the accessory cuspules in the upper series, particularly the protoconule which is so well developed and crescentic in *Meniscotherium*. In this respect the early hyracoids more nearly resemble the Cernaysian *Pleuraspidotherium*, at least as far as the molars are concerned.

The number of presacral vertebrae in hyracoids is the greatest for any of the living land mammals, and while *Meniscotherium* has one more lumbar vertebra than *Procavia*, I suspect that the number of dorsals was much less, as inferred from *Phenacodus*. The scapula has a very different appearing spine, proximally subdued and entirely lacking the acromion and metacromion, so well developed in *Meniscotherium*. In the pelvic girdle the ilium is relatively very long and straight, quite unlike that in *Phenacodus* or *Meniscotherium*.

In the forelimb of *Procavia* the proximal extremity of the humerus is similar to that in *Meniscotherium*, but the distal trochlea shows a more simple, grooved pulley construction and there is no entepicondylar foramen. The distal articular surface of the ulna for the cuneiform is highly concave rather than convex as in *Meniscotherium*, and that of the radius for the scaphoid and lunar is distally extended on the scaphoid side, binding the carpus medially, much as the peculiar extension of the medial side of the tibia effectively binds the astragalus medially. Individually the elements of the carpus bear almost no resemblance in detail to those of the Eocene condylarth, although there is some approximation to the serial alignment. The recent hyracoid carpus, moreover, retains a separate central, and the first digit is reduced to a vestige.

Differences in the hind limb are noted in the very proximal position of the third trochanter and the very broad patellar trochlea on the femur and the tendency toward coossification of the tibia and fibula, as well as of the radius and ulna in the fore limb. The tarsus is noticeably different in the peculiar offset of the neck and head of the astragalus, and the articulation between the astragalus and calcaneum is principally through the enlarged ectal facet, there being no sustentaculum on the calcaneum. Moreover, the articulation between the calcaneum and cuboid is nearly flat, as is that between the astragalus and navicular.

Pleuraspidotherium from the Paleocene at Cernay, France, would appear to be condylarthran and possibly related to *Meniscotherium*. Moreover, there seems to be logic in including them in the same family, although some of the differences are rather striking, so that I cannot believe that *Meniscotherium* was derived from this form. Possibly P^3-M^3 in *Meniscotherium* could have evolved from teeth of the form seen in *Pleuraspidotherium*, but the long diastema ahead of these teeth in the latter, the reduction in size and single-rooted character of the anterior upper premolars, as well as the frequent reduction in number of the lower series (see D. E. Russell, 1964), would surely preclude it as an ancestor.

The problem of relationship may be further complicated by a question of homology, relating to certain upper molar cusps. Simpson (1929) in discussing *Pleuraspidotherium* and *Othaspidotherium* in relation to *Meniscotherium* refers to the posterointernal cusp as a "pseudhypocone" or displaced metaconule. This would imply a cusp origin similar to that of the early selenodont artiodactyls, and the upper molars do show a surprising resemblance to some of the selenodont forms of the later American Eocene. Support of the metaconule origin for the posterointernal cusp might be inferred from the development, although weak, of the cingulum around the "pseudhypocone" in *Pseudaspidotherium.* The hypocone from an origin on the cingulum would less likely show this, unless a secondary cingulum were developed. The evidence from *Meniscotherium* would appear to contradict such an origin for the posterointernal cusp, as this cusp seems to have originated from the cingulum, from the evidence of the premolars, for what it is worth, as well as from the cingulum itself. P^3 and P^4 of *Meniscotherium* suggest between them something of the transition in the relations of the generally well defined accessory cuspules to the deuterocone and tetartocone. Moreover, the posterointernal cusp of the molars, as well as the tetartocone of the premolars, seems to be an integral part of the cingulum. The latter shows no tendency to divide as in *Pleuraspidotherium.* The posterior upper premolars are rather *Phenacodus*-like, as observed by D. E. Russell (1964), so that the relations there of the metaconule and tetartocone are missing. I am much inclined to consider that the *Meniscotherium* upper molars, though decidedly selenodont, have a cusp pattern essentially homologous with that in the *Tetraclaenodon–Phenacodus* line, with the posterointernal cusp as the hypocone. If it can be demonstrated that the cusp in this position is not homologous in *Pleuraspidotherium* (and *Orthaspidotherium*) the meniscotheriid relationship certainly becomes much weakened.

Russell (1964) has given a detailed description of the skull of *Pleuraspidotherium,* and Pearson (1927), as well as Russell, has presented the characters of the basicranium. In a comparison of the basicranium of *Pleuraspidotherium* with that of *Meniscotherium,* however, a number of features are noteworthy. The pterygoid fossa is well developed, and although the walls are broken down they are not so flaring, and it would appear that the fossa is not carried so low with respect to the basisphenoid or the roof of the narial passage as in *Meniscotherium.* Posterior to this fossa there is no evidence for an alisphenoid canal in the position that it is found in *Meniscotherium.* The foramen ovale is prominently displayed in about the same position relative to the foramen lacerum medium, but less widely removed from the glenoid surface. The glenoid surface, though not complete in the specimen examined, does not appear to be so elongate anteroposteriorly or so concave transversely. The postglenoid process may be more rugged and posteriorly better envelops the postglenoid foramen. The crest posterior to the foramen ovale, though damaged, seems prominently developed but possibly not so compressed transversely as in *Meniscotherium.* Posterior to the position of the external auditory meatus the mastoid process, which carries a lamina of the squamosal on its anterior face, is much more elongate in an anteromedial-posterolateral direction. Also, the extent of the mastoid exposed ventrally between the mastoid and paroccipital processes is much greater than in *Meniscotherium* in the skull that I examined. This, however, is evidently not constant, as Russell, in pointing out the variability of the paroccipital process, has indicated that it is sometimes indistinct and then closely applied to the mastoid process. According to Pearson (1927) the greater part of the paroccipital process is formed of the mastoid. It is apparently never developed as in *Meniscotherium.*

The petrous portion of the periotic in *Pleuraspidotherium* is very differently shaped than in *Meniscotherium,* as it is broad posteriorly and very rapidly tapering anteriorly. The slenderness of the anterior portion is suggestive of *Hyopsodus,* although in the latter it is not as broad posteriorly and more smoothly conical. The sulcus facialis would seem rather similar in the two forms, and the aperture for the facial nerve appears similarly situated, although the positions of the fenestrae ovalis and rotunda cannot be precisely determined because of damage to the specimen examined. Posteriorly the facial sulcus is directed downward toward the position of a stylomastoid foramen opposite the posterior extremity of the exposed petrosal, but this is farther back with respect to the medial root or extremity of the mastoid process than in *Meniscotherium.* Lateral to the facial sulcus there is much more of an epitympanic recess in *Pleuraspidotherium.* In *Meniscotherium* the mastoid portion lateral to the sulcus is essentially flush with the medial margin of the squamosal above the external auditory meatus, although separated from it by a groove.

Medial to the petrosal the lateral portion of the basioccipital is deep and broadly grooved, which forward leads to the foramen lacerum medium. Presumably this was occupied by the internal carotid, as suspected for a rather similar appearing structure in *Meniscotherium.*

The limb and foot material attributed to *Pleuraspidotherium* seem rather condylarthran, certainly not artiodactyl in form, but, as cautioned by Pearson (1927), these were not found in direct association with teeth so that their allocation is speculative and based on relative abundance. These elements were figured and briefly described by Teilhard de Chardin (1921-1922), and certain of them were compared by Simpson (1929) to *Meniscotherium.* The distal part of the humerus figured by Teilhard de Chardin resembles that of *Meniscotherium* although the crests of the trochlea are less pronounced and there is evidently no entepicondylar foramen as Simpson noted. The proximal position of the lesser and third trochanter and the shortness of the digital fossa of the femur are rather unlike *Meniscotherium,* and I note in this a greater similarity to the recent hyracoids. The distal extremity of the femur is also rather dissimilar in the relatively smaller condyles. The shorter and wider patellar groove noted by Simpson is also suggestive of the hyracoids. The long, slender, and nearly straight ilium with the little-developed anterior inferior spine adjacent to the acetabulum is decidedly unlike *Meniscotherium.* I note that the calcaneum has a rather prominent peroneal tubercle and a large and rather elongate astragalar condyle, but the anterior portion of the bone is relatively short, although the astragalus has an elongate neck as in *Meniscotherium.* The sustentacular facet extends far forward on the neck of the astragalus, and the ectal facet is oval concave and nearly transverse, somewhat more as in *Tetraclaenodon* in this latter respect. Simpson regarded the presence of an astragalar foramen in *Pleuraspidotherium* as distinctive. We now know, however, that this foramen is present in the astragalus of *Meniscotherium* as well.

Orthaspidotherium offers many more problems in its comparison with *Meniscotherium,* and the character of the lower teeth is rather inconsistent with any rather close relationship to *Pleuraspidotherium.* Their artiodactyl-like structure is rather striking. A close relationship to *Pleuraspidotherium* has been postulated on the close resemblance of the upper teeth. An interpretation of homologies of cusps of the upper teeth suggested by Simpson would not be inconsistent with a supposition of artiodactyl affinities for *Orthaspidotherium.* Nevertheless, foot bones attributed to *Orthaspidotherium* by Teilhard de Chardin, if correctly assigned, would scarcely be compatible with an artiodactyl relationship.

It has been suggested to me that possibly *Protoselene* is ancestral to *Meniscotherium.* In a comparison of these two it would seem that the teeth of *Protoselene* possess a distinct potentiality for such a development. Nevertheless, the change required is rather striking in degree for an interval such as between Torrejonian or early Tiffanian and Clarkforkian Paleocene. The fourth premolars above and below show no approach toward the molariform condition observed in *Meniscotherium.* The outer wall of the upper molars shows some tendency toward the stylar condition in the latter, but the accessory cuspules are situated on the crests or horns of the protocone. In *Meniscotherium* these cuspules are distinctly separated from the protocone, with the protoconule independently crescentic and the metaconule aligned in a crest with the hypocone. Moreover, the distinct cingulum around the protocone of *Meniscotherium* is missing in *Protoselene.* The lower molars would seem to possess an equivalent potentiality, but the trigonid is comparatively short and the paraconid arm or crest has become rather abbreviated in the earlier form. Possibly *Protoselene* is better situated in time and in the character of the accessory cuspules of the upper molars for a possibly closer affinity to the litopterns than are any of the other North American Paleocene condylarths.

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EXPLANATION OF PLATES

Plate 1. *Meniscotherium* skull from the early Eocene of Wyoming

Meniscotherium chamense Cope

Skull (U.S.N.M. 22672), dorsal, lateral, and ventral views. Natural size. New Fork member, Wasatch formation, Green River Basin. Wyo.

Plate 2. *Meniscotherium* skull from the early Eocene of Wyoming

Meniscotherium robustum Thorpe

Skull (U.S.N.M. 18260), dorsal, lateral, and ventral views. ¾× natural size. La Barge, Knight member, Wasatch formation, Green River Basin, Wyo.

Plate 3. *Meniscotherium* skull from the early Eocene of Wyoming

Figs. 1, 2. *Meniscotherium chamense* Cope. 1, Skull and mandible (U.S.N.M. 22918), lateral view. Natural size. 2, Basicranium (U.S.N.M. 22672), ventral view. 2× natural size. New Fork member, Wasatch formation, Green River Basin. Wyo. Explanation of abbreviations follows:

a.c., alisphenoid canal.
e.a.m., position of external auditory meatus.
f.l.m., foramen lacerum medium.
f.l.p.,foramen lacerum posterius.
f.o., foramen ovale.
fen. o., fenestra ovalis.
fen. r., fenestra rotundum.
gl., glenoid surface.
h.f., hypoglossal foramen.
p.gl.f., postglenoid foramen.
p. gl.p., postglenoid process.
p.p., paroccipital process.
VII., aperture in facial canal for facial nerve.

Plate 4. *Meniscotherium* type specimens

Fig. 1. *Meniscotherium robustum* Thorpe. Skull and mandible (Y.P.M. 10101), type specimen, lateral view. ⅔× natural size. Left upper cheek teeth (Y.P.M. 10101), type specimen, occlusal view. Natural size. Aspen, Knight member, Wasatch formation, Green River Basin, Wyo.

Fig. 2. *Meniscotherium terraerubrae* Cope. Maxilla and jaw portion (A.M. 4410), type specimen, occlusal view of upper teeth, lateral and occlusal view of lower jaw fragment. Natural size. San José formation, San Juan Basin, N. Mex.

Fig. 3. *Meniscotherium tapiacitis* Cope. Lower jaw portions (A.M. 4425), type specimen, lateral and occlusal views. Natural size. San José formation, San Juan Basin, N. Mex.

Fig. 4. *Meniscotherium chamense* Cope. Right maxilla (U.S.N.M. 1093), type specimen, occlusal view. Natural size. San José formation, San Juan Basin. N. Mex.

Plate 5. *Meniscotherium* dentitions from the early Eocene of Wyoming

Figs. 1, 2. *Meniscotherium robustum* Thorpe. 1, Left upper dentition, I^1, C, P^2–M^3 (U.S.N.M. 18314), occlusal view. 2, Right ramus of mandible, P_3–M_3 (U.S.N.M. 18314), occlusal and lateral views. 1½× natural size. La Barge, Green River Basin, Wyo.

Figs. 3, 4. *Meniscotherium chamense* Cope. 3, Left upper dentition I^3—M^3 (U.S. N.M. 22435), occlusal view. 4, Left ramus of mandible, I_2–M_3 (U.S.N.M. 22435), occlusal and lateral views. 1½× natural size. New Fork, Green River Basin, Wyo.

Figs. 5, 6. *Meniscotherium tapiacitis* Cope. 5, Right maxilla, P^3, M^1–M^2 (U.S.N.M. 22431), occlusal view. 6, Right ramus of mandible, M_1–M_2 (U.S.N.M. 22432), occlusal and lateral views. 1½× natural size. Bitter Creek, Washakie Basin, Wyo.

Plate 6. *Meniscotherium* humerus and scapula
from the early Eocene of Wyoming

Figs. 1, 2. *Meniscotherium robustum* Thorpe. 1, Right humerus (U.S.N.M. 19555, restored from U.S.N.M. 19519 and 19556), lateral, posterior, distal, proximal, and medial views. 2, Left scapula (U.S.N.M. 18314), proximal and lateral views. Natural size. La Barge, Knight member, Wasatch formation, Green River Basin, Wyo.

Plate 7. *Meniscotherium* fore limb and foot material from the early Eocene

Figs. 1–10. *Meniscotherium chamense* Cope. 1, Right humerus (U.S.N.M. 22672), anterior and medial views. 2, Left radius (U.S.N.M. 22435), anterior and lateral views. 3, Left ulna (U.S.N.M. 22435), anterior and lateral views. 4–7, Articulated right carpus (U.S.N.M. 22672, pisiform introduced from U.S.N.M. 22918, and trapezoid from Y.P.M. 10276); 4, proximal view; 5, distal view; 6, lateral view; and 7, medial view. 8, Left metacarpals I–V (I, U.S.N.M. 18314; II–IV, U.S.N.M. 22672; V (reversed), U.S.N.M. 22918), proximal view of bases. 9, Articulated, partially composite, right manus, excluding phalanges (U.S.N.M. 22672, except pisiform introduced from U.S.N.M. 22918, trapezoid from Y.P.M. 10276, and metacarpals I (reversed), U.S.N.M. 18314, and V, U.S.N.M. 22918 (II–IV of 22672 reversed)), dorsal view. 10, Phalanges of digit II or IV (U.S.N.M. 22918), dorsal view. All natural size.

Fig. 11. *Meniscotherium robustum* Thorpe. Distal phalanx of manus (U.S.N.M. 18282), dorsal view.

Plate 8. *Meniscotherium* femur and patella from the early Eocene of Wyoming

Figs. 1, 2. *Meniscotherium robustum* Thorpe. 1, Right femur (U.S.N.M. 18283), posterior, distal, medial, proximal, and anterior views. 2, Patella (U.S.N.M. 18283), anterior view. Natural size. La Barge, Knight member, Wasatch formation, Green River Basin, Wyo.

Plate 9. *Meniscotherium* tibiae and fibula from the early Eocene of Wyoming

Fig. 1. *Meniscotherium robustum* Thorpe. Right tibia and fibula U.S.N.M. 18283), proximal, lateral, anterior, and distal views. Natural size. La Barge, Knight member, Wasatch formation, Green River Basin, Wyo.

Fig. 2. *Meniscotherium,* cf. *chamense* Cope. Right tibia (U.S.N.M. 22675, restored from U.S.N.M.: 22672), anterior and lateral views. Natural size. New Fork member, Wasatch formation, Green River Basin, Wyo.

Plate 10. *Meniscotherium* pedes from the early Eocene

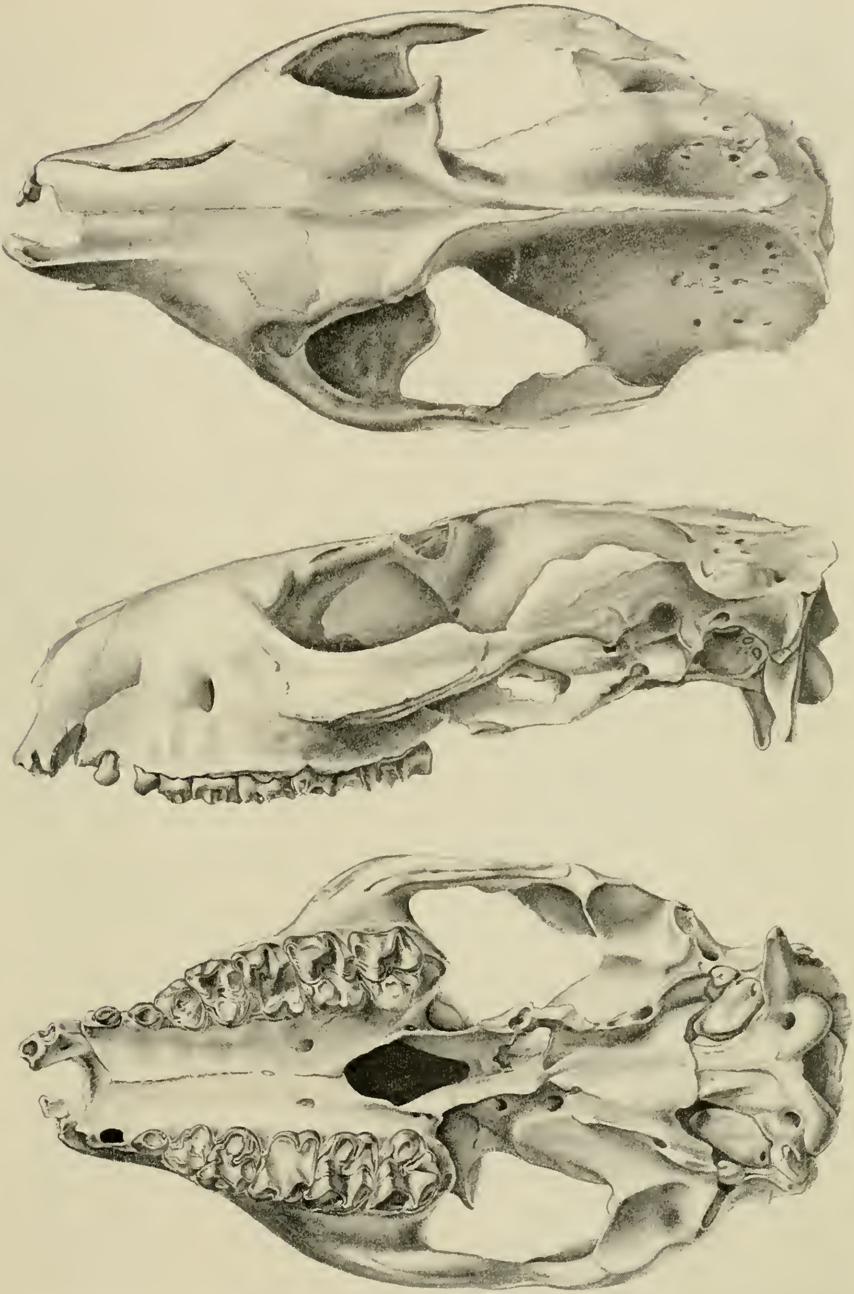
Figs. 1–4. *Meniscotherium chamense* Cope. 1, Left navicular (U.S.N.M. 22918) and left cuboid (Y.P.M. 20950), proximal and distal views, and lateral view of navicular. 1½× natural size. Navicular from New Fork member, Wasatch formation, Green River Basin, Wyo. Cuboid from San José formation, San Juan Basin, N. Mex. 2, Left pes (U.S.N.M. 22435, with cuboid restored from Y.P.M. 20950), medial and dorsal views. Natural size. New Fork member, Wasatch formation, Green River Basin, Wyo. (except cuboid from San Juan Basin). 3, Metatarsals I–V (I, V, U.S.N.M. 22918; II, Y.P.M. 20949; III, Y.P.M. 20948; IV, Y.P.M. 10559), proximal view of bases 1½× natural size. Metatarsals I and V from New Form member, Wasatch formation, Green River Basin, Wyo. Metatarsals II–IV from San José formation, San Juan Basin, N. Mex. 4, Left calcaneum and right astragalus (U.S.N.M. 22918), dorsal and ventral views respectively. 1½× natural size. New Fork member, Wasatch formation, Green River Basin, Wyo.

Figs. 5–8. *Meniscotherium robustum* Thorpe. 5, Left external cuneiform U.S.N.M. 18283), proximal, medial, and distal views. 1½× natural size. 6, Left pes (U.S.N.M. 18282, lacking 1st and 5th digits and distal phalanges), dorsal view. Natural size. 7, Second phalanx, 3d(?) digit (U.S.N.M. 18283, dorsal and lateral views. 1½× natural size. 8, Distal phalanx, 3d(?) digit (U.S.N.M. 18283), dorsal, lateral and ventral views. 1½× natural size. La Barge, Knight member, Wasatch formation, Green River Basin, Wyo.

Plate 11. Restoration of *Meniscotherium*

Restoration of *Meniscotherium* by the artist Walter Ferguson based on a composite skeleton from the San Juan Basin of New Mexico. Photograph by courtesy of the American Museum of Natural History.

PLATES



Meniscotherium skull from the early Eocene of Wyoming
(See explanation of plates at end of text.)

Meniscotherium skull from the early Eocene of Wyoming
(See explanation of plates at end of text.)

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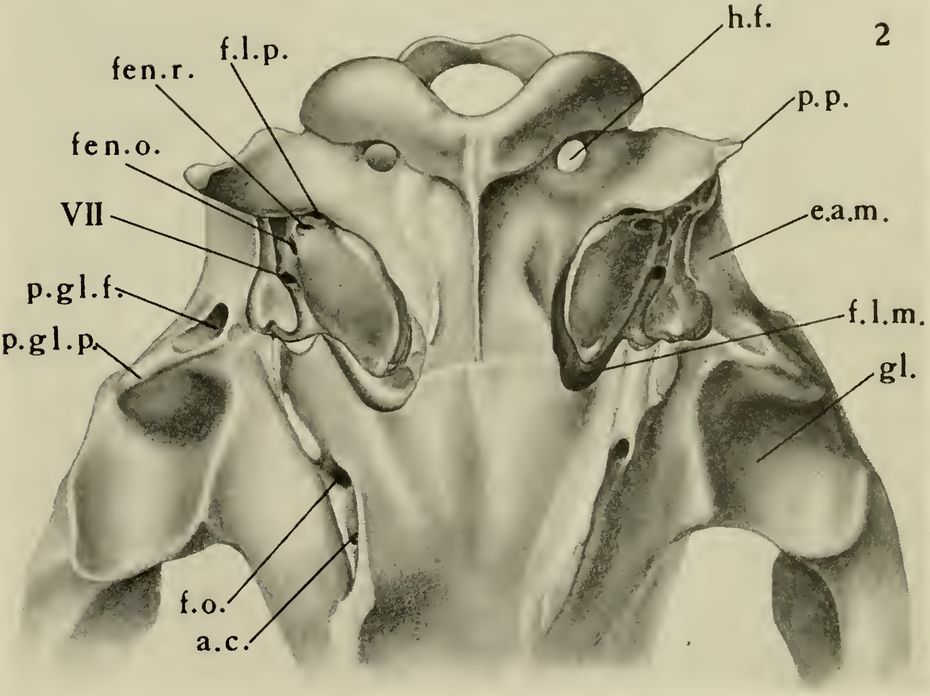

Meniscotherium skull from the early Eocene of Wyoming
(See explanation of plates at end of text.)

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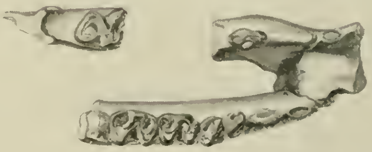

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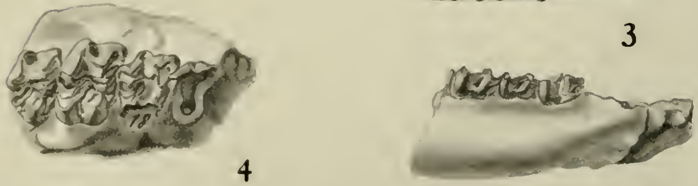

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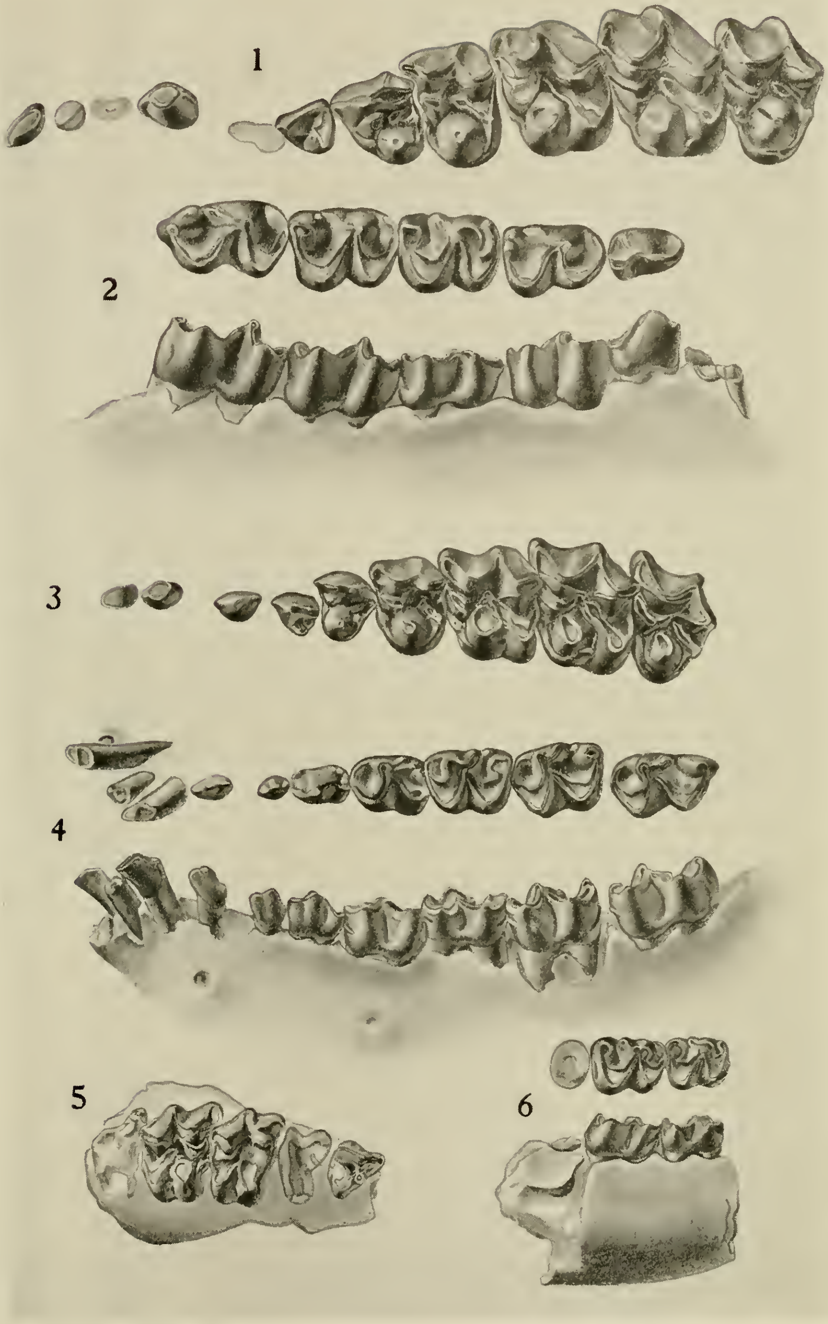
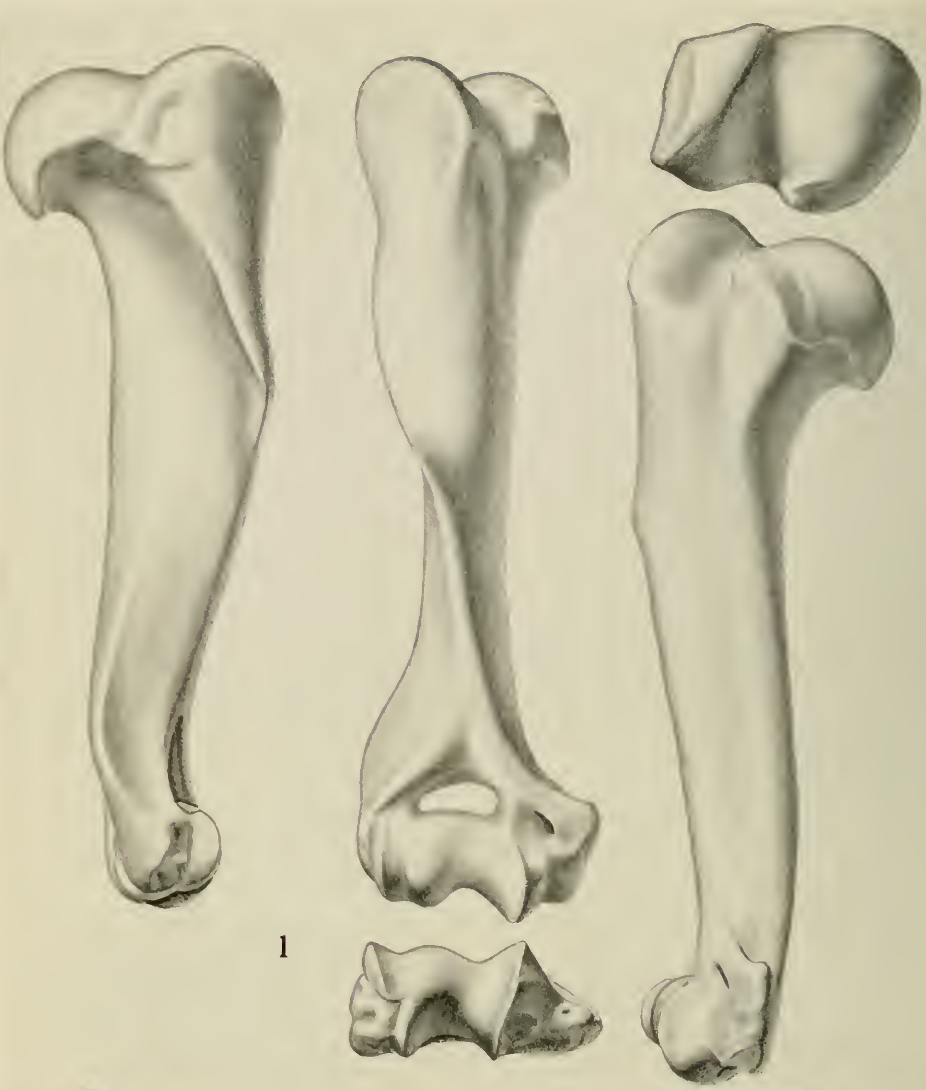
Meniscotherium type specimens
(See explanation of plates at end of text.)



Meniscotherium from the early Eocene of Wyoming
(See explanation of plates at end of text.)



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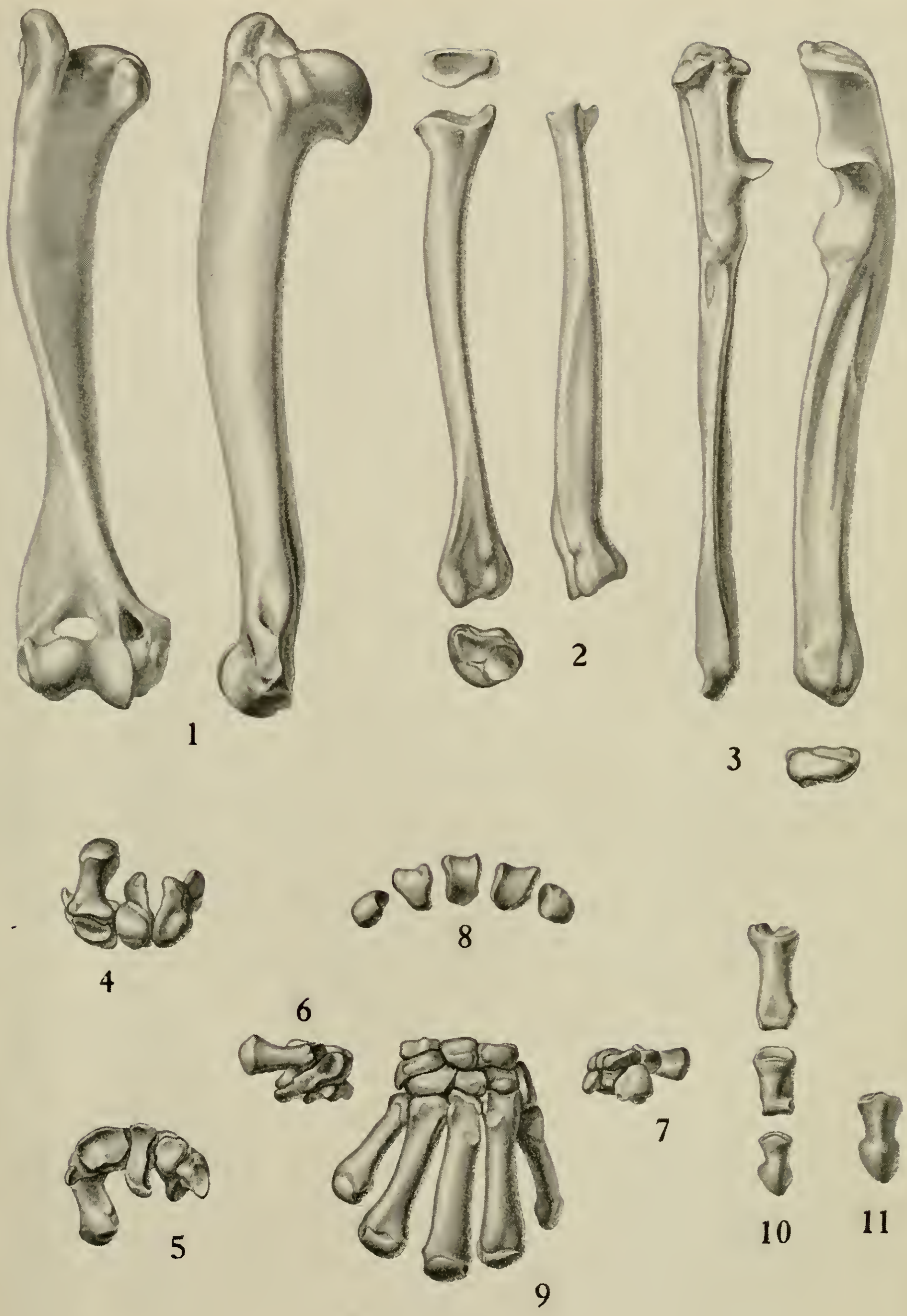
Meniscotherium humerus and scapula from the early Eocene of Wyoming
(See explanation of plates at end of text.)



Meniscotherium fore limb and foot material from the early Eocene
(See explanation of plates at end of text.)

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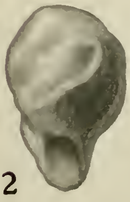

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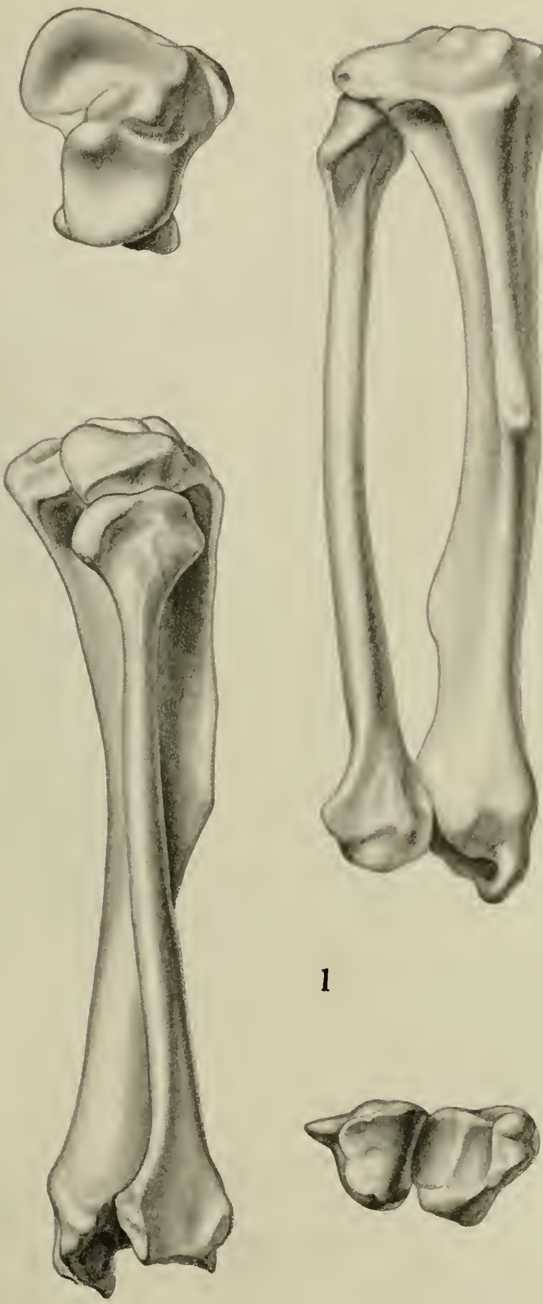
Meniscotherium femur and patella from the early Eocene of Wyoming
(See explanation of plates at end of text.)



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Meniscotherium tibiae and fibula from the early Eocene of Wyoming
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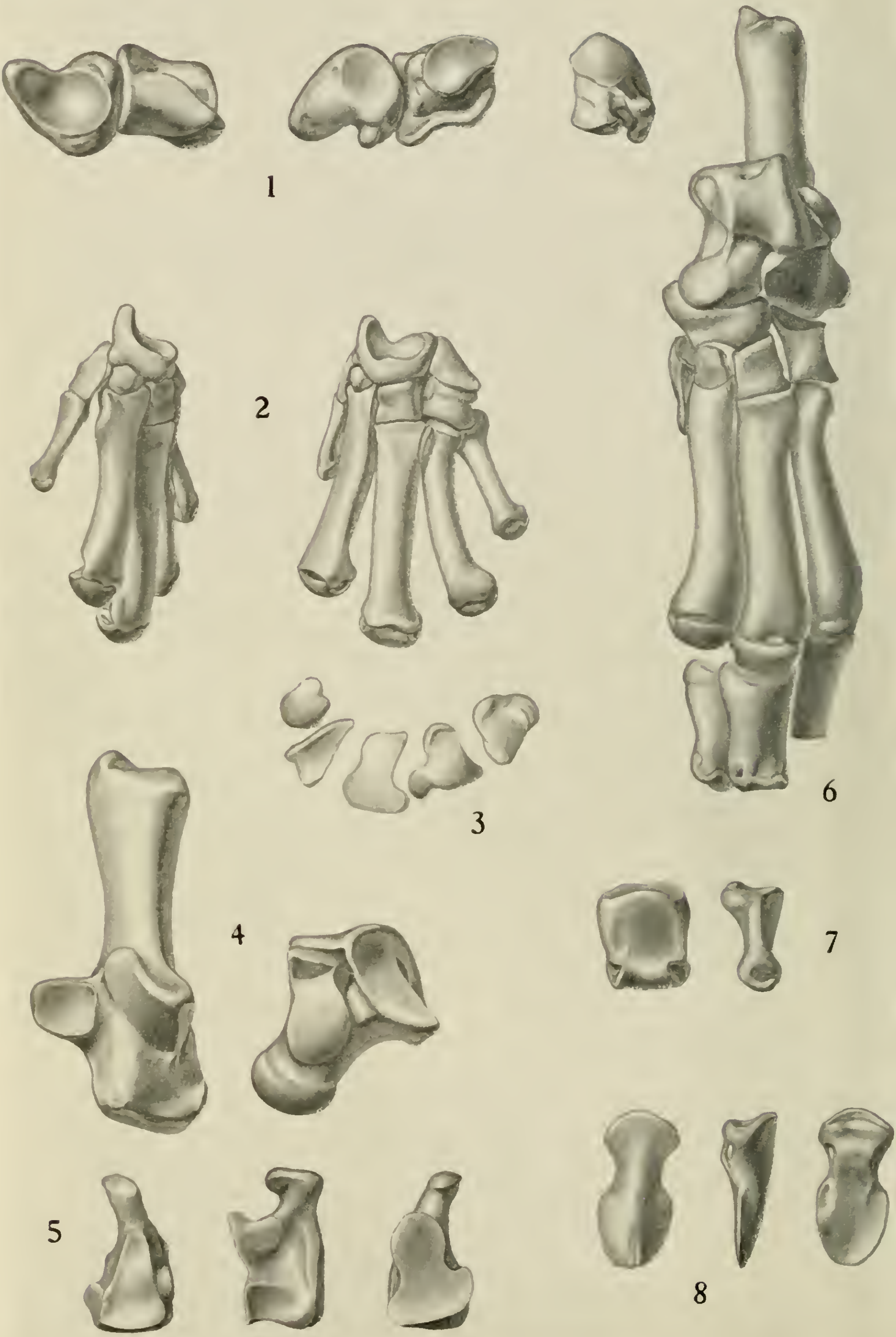

Meniscotherium pedes from the early Eocene
(See explanation of plates at end of text.)

Restoration of Meniscotherium
(See explanation of plates at end of text.)