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Beginning with Volume 47 (2006), the *Bulletin of the Peabody Museum of Natural History* was converted to a journal format.

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The original monograph series incorporated the *Bulletin of the Bingham Oceanographic Collection*, which ceased independent publication with Volume 19, Article 2 (1967). The *Postilla* series, which ceased publication with Number 232 (2004), was merged into the journal. These archives are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at <https://elischolar.library.yale.edu/>.



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P.O. Box 208118 | New Haven CT 06520-8118 USA | peabody.yale.edu

PEABODY MUSEUM OF NATURAL HISTORY
YALE UNIVERSITY
BULLETIN 17

Origin and Early Evolution
of North American Tapiroidea

BY
LEONARD RADINSKY

*Department of Vertebrate Paleontology
American Museum of Natural History*

NEW HAVEN, CONNECTICUT
1963

Printed in the United States of America

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New Haven, Connecticut, 1963

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ORIGIN AND EARLY EVOLUTION OF NORTH AMERICAN TAPIROIDEA

BY LEONARD RADINSKY

ABSTRACT

North American Eocene tapiroids evolved along two main lines, represented by the families Isectolophidae and Helaletidae. Taxonomic revision of these two families here reduces twenty-five previously accepted species to thirteen, for which statistical data on tooth measurements are summarized. Four out of ten previously accepted genera are relegated to synonymy, *Parisectolophus* and *Schizolophodon* with *Isectolophus*, and *Desmatotherium* and *Chasmotheroides* with *Helaletes*. *Desmatotherium kayi* and *D. woodi* are assigned to *Colodon*.

Isectolophids, including *Homogalax* and *Isectolophus*, show little specialization with time besides increase in size. The main helaletid line, consisting of *Heptodon*, *Helaletes*, and *Colodon*, exhibits size increase, premolar molarization and specialization of molars for transverse shearing. In addition, the appearance of a greatly enlarged nasal incision in *Helaletes* and subsequent shortening of nasals in *Colodon* indicate the development of a proboscis; this feature supports dental evidence suggesting a helaletid derivation for the Tapiridae. *Dilophodon* is a dwarf offshoot from *Helaletes* in which premolar molarization was retarded. A new species, *Colodon? hancocki*, represents a transitional form between *Helaletes* and *Protapirus*, the earliest tapirid.

Review of the literature on European and Asiatic tapiroids suggests an early Tertiary deployment of the superfamily along at least five other major lines: *Lophiodon-Lophiaspis-Atalonodon* and *Chasmotherium* in Europe; *Indolophus*, *Teleolophus-Deperetella-Christidentinus-Diplolophodon* and *Schlosseria-Lophialetes-Lunania* in Asia.

INTRODUCTION

The oldest known perissodactyls appear in the fossil record at the beginning of the Eocene, about fifty million years ago, represented by two closely related genera, *Hyracotherium* and *Homogalax*. The former was the earliest member of the suborder Hippomorpha, which includes horses, titanotheres, and chalicotheres; the latter was ancestral to the later ceratomorphs, including rhinoceroses and tapirs. Shortly after this initial perissodactyl divergence the ceratomorph line separated into two families, both tapiroid: the Isectolophidae, comprising at that time the primitive *Homogalax* stock, and the Helaletidae, a more advanced offshoot. From these two families rhinocerotoids and all later tapiroids arose. Elucidation of early tapiroid evolution would thus seem crucial for understanding of basic perissodactyl radiations.

Despite the obvious importance of such an investigation, no comprehensive review has previously been made of either the Isectolophidae or the Helaletidae. No Eocene tapiroid genus or species has been revised in the light of modern taxonomic concepts, with recognition of intraspecific variation, although adequate material for such a study has long been available in several museum collections. This state of affairs provided the impetus for the present investigation.

The purpose of this study was to review the taxonomy of isectolophid and helaletid tapiroids to provide a firmer basis for further evolutionary studies. An attempt has been made to revise all North American species of these families in conformity with modern species concepts and to adjust higher taxonomic categories where necessary. Elucidation of phylogenetic relationships has been emphasized, with attention given also to the origin of perissodactyls, the hippomorph-ceratomorph divergence, tapiroid-rhinocerotoid separation, and the origin of the Tapiridae.

HISTORY OF INVESTIGATION

Isectolophid or helaletid tapiroids are found in most North American Eocene and Oligocene mammal-bearing deposits but usually comprise only a small element of the total perissodactyl fauna. Despite this comparative rarity, the history of scientific study of these early tapiroids reflects to a surprising degree the development of vertebrate paleontology in America.

The first description of a North American Tertiary tapiroid appeared in 1868, when Leidy proposed the new species *Lophiodon occidentalis* for an isolated last lower molar collected by Hayden in South Dakota Oligocene beds. Subsequent early workers also referred newly discovered North American tapiroids to the European genus *Lophiodon*, which at the time was the only known early Tertiary tapiroid genus.

The following two decades witnessed the discovery of many richly fossiliferous Eocene collecting localities in the West, and the subsequent description of several new genera and species of tapiroids. In 1871, Marsh gave the name *Lophiodon nanus* to a small species of tapiroid from the Bridger Basin of Wyoming. The following year he proposed a new genus, *Helaletes*, to which he referred

L. nanus and a new species, *H. boops*, also from middle Eocene Bridger deposits.

Cope was the first to describe early Eocene tapiroids when, in 1880, he named *Lophiodon calciculus* and *L. ventorum* from the Wind River Basin, Wyoming. Two years later he referred them to the European equoid genus *Pachynolophus*, along with a third new species from the Bighorn Basin, *P. posticus*. Shortly thereafter, Cope (1882c) erected the genus *Heptodon* to include *calciculus*, *ventorum*, and *posticus*.

In 1881 Cope proposed the well-known but invalid early Eocene tapiroid genus *Systemodon* (= *Homogalax*). The first illustrations of both *Systemodon* and *Heptodon* appear in Cope's important work of 1884.

Material collected in the Bridger Basin by the Princeton Scientific Expedition of 1877 provided for Osborn, Scott and Speir (1878) the types for two new tapiroid species, *Helaletes latidens* and *Hyrachyus intermedius*. The former was soon thereafter referred to *Isectolophus*; the latter, in the present revision, is assigned to *Helaletes*.

In 1878 a Princeton expedition collected two tapiroid specimens in either the Bridger or Washakie Basin, which were described by Scott (1883) as new genera, *Desmatotherium guyotii* and *Dilophodon minusculus*.

Four years later Scott and Osborn (1887) named another new tapiroid genus and species, *Isectolophus annectens*, based on material found in late Eocene deposits in the Uinta Basin, Utah, by the Princeton expedition of 1886. In 1889, Osborn (*in* Scott and Osborn, 1889) published a fuller description of *Isectolophus annectens* and referred to that genus the middle Eocene *Helaletes latidens*.

During the 1890's research on North American tapiroids proceeded along two lines: elaboration and consolidation of knowledge of previously known early Eocene forms, and description of new Oligocene species of late helaletids and early tapirids, or true tapirs.

In 1892 Osborn (*in* Osborn and Wortman, 1892) summarized knowledge of *Homogalax* and *Heptodon* which had been extensively supplemented by new material collected during the previous year in the Bighorn and Wind River Basins by Wortman for the American Museum of Natural History. In the same publication Osborn used for the first time the family name Helaletidae to include *Heptodon* and *Helaletes*. Four years later, Wortman (1896) published a fuller description of *Homogalax* and *Heptodon* and proposed two new species, *Systemodon* (= *Homogalax*) *protapirinus* and *S. primaevus*.

In one of his last contributions to tapiroid research, Marsh (1890) described a new genus and species of Oligocene helaletid, *Colodon luxatus*. Three years later, in the first paper concerned solely with North American tapiroids, Wortman and Earle (1893) synonymized *Colodon luxatus* Marsh with *Lophiodon occidentalis* Leidy, but retained the former genus and added it to the family Helaletidae. In the same paper they described the first North American species of *Protapirus* and speculated on the origin of that genus.

In a description of new Oligocene perissodactyls published two years later, Osborn and Wortman (1895) named two species of *Colodon*, *C. dakotensis* and *C. procuspidatus*—both from White River beds in South Dakota.

The following year in an excellent review of recent and fossil tapirs, Hatcher (1896) made detailed comparisons between *Protapirus* and *Colodon*, relegated to synonymy some of the recently-named species of the latter genus, and discussed Eocene and Oligocene tapiroid phylogeny. In recognizing the importance of intraspecific variation to taxonomy, Hatcher was unusually advanced for his time.

In the present century papers on North American Tertiary tapiroids have appeared at infrequent intervals, and, with a few notable exceptions, have been primarily concerned with describing newly discovered species. In the first of these, Douglass (1901) named a new species of Oligocene helaletid from Montana, *Colodon cingulatus*.

In the most comprehensive review of tapiroids which has appeared to date, Peterson in 1919 described in great detail all that was known at the time of middle and late Eocene isectolophids and middle Eocene helaletids. He erected the family Isectolophidae, placed *Isectolophus latidens* in a new genus, *Parisectolophus*, split off from *I. annectens* a new species, *I. scotti*, and named a new genus and species, *Schizolophodon cuspidens*. (In the present revision *Parisectolophus* is considered synonymous with *Isectolophus*, and *I. scotti* and *Schizolophodon cuspidens* are synonymized with *I. annectens*.) Peterson also figured for the first time the type of *Helaletes boops*, noting the greatly enlarged nasal incision in that genus.

Three years later Troxell (1922a) briefly reviewed the genus *Homogalax* and, on the basis of previously undescribed material in the Marsh Collection at Yale, named two new species, *H. bridgerensis* and *H. uintensis*. The former is here considered synonymous with *Isectolophus latidens* and the latter with *I. annectens*. In the same year, Troxell (1922b) also published a short review of *Helaletes*, in which the type of *H. nanus* was figured for the first time.

In 1931 a new genus and species, *Heteraletes leotanus*, was named by Peterson, based on a diminutive immature jaw from the Uinta Basin, Utah. In the same year, Seton (1931) published a preliminary notice of an almost complete skeleton of *Heptodon* which he named *H. brownorum*.

The most complete taxonomic and morphologic review of *Colodon* available to date appeared in 1941 in a monograph on Oligocene faunas of South Dakota by Scott (*in* Scott and Jepsen).

In a paper on Lysitean faunas from the Wind River Basin, Kelley and Wood (1954) noted that features used to separate species of *Heptodon* might merely be expressions of intraspecific variation.

In 1955, in a discussion of the late Eocene Sage Creek fauna from Montana, Hough proposed a new species, *Desmatotherium kayi*, and placed *Heteraletes* Peterson into synonymy with *Dilophodon*. The following year, Gazin (1956) gave the name *Desmatotherium woodi* to a tapiroid species in the late Eocene Badwater fauna of the Wind River Basin, Wyoming. In the same paper he summarized knowledge of tapiroid lineages in the most comprehensive phylogenetic chart ever published for the group. Gazin's paper is also notable for its original suggestion that *Dilophodon* was ancestral to *Protapirus*.

DEFINITIONS

The concept of a species denotes a population or group of populations within which gene exchange is possible but which is reproductively isolated from other such groups.* This situation usually results in fairly continuous intraspecific phenotypic variation, with morphological discontinuities between species. Since the species described in this review are extinct, they are of necessity based on morphological criteria; if morphology varies continuously within a sample from a

* Limitations inherent in dealing with fossils have led some paleontologists (e.g. Weller, 1961) to reject a genetic definition of species in favor of one which emphasizes morphology. While I realize that most species are recognized by morphological criteria, I nevertheless feel that the concept of a species should be based on its most fundamental character, which is genetic isolation.

given horizon and locality the included specimens are considered to have been part of the same interbreeding population and hence assigned to one species. With adequate samples and well preserved material it should be possible to closely approximate the once-living species represented by fossil specimens.

If samples were available from all tapiroid populations that ever existed, morphological gradation would be essentially continuous throughout and species boundaries would have to be delimited arbitrarily. In practice, however, breaks in the stratigraphic section or gaps in the fossil record are so frequent and extensive that the problem of chronological demarcation of species rarely arises.

The problem of recognition of sibling species (reproductively isolated populations which are morphologically indistinguishable) in the fossil record seems unimportant since such relationships are rare in mammals and, in any case, of short duration. Present sibling species are only recently genetically isolated and should soon exhibit phenotypic differences. Compared to the immensity of time encompassed by the evolutionary record here considered, the duration of a sibling species is so insignificant that failure to recognize it would hardly affect elucidation of evolutionary history.

The term "subspecies" as used in neontology implies partial genetic isolation of a population within a species. Paleontologists have used this term to distinguish samples which differ significantly in statistical means of a given character but overlap extensively in range of that character. The subspecies concept has not been used in this paper because the fossil record does not provide the morphological and zoogeographical evidence necessary for recognition of "partial genetic isolation." Usually only a few characters are available for definition of fossil subspecies; the one most commonly used is size. The use of other characters might result in different alignment of subspecific boundaries. Among recent populations, where much more morphological detail is available, different combinations of characters frequently allow different demarcation of subspecies (see *inter alia* Hagmeier, 1958).

Furthermore, fossil tapiroid species are known only from a few geographically isolated localities; slight morphological differences between samples from different localities might be due to clinal variation so that were the intervening populations available, morphology would vary continuously.

In short, fossil evidence is not appropriate for recognition of tapiroid subspecies. By implying greater knowledge of extinct populations than is actually available, such usage might be misleading. Morphological differences between samples from different localities should of course be noted, perhaps with geographic names such as "Bighorn Basin *Homogalax protapirinus*," or "Big Piney *Heptodon calciculus*," etc., but should not be designated by more formal names.

METHODOLOGY

A study was first made of osteological material of all living species of the recent genus *Tapirus* with two purposes in mind: first, to observe the kinds of interspecific differences evident in the skeletal system; and second, to estimate the kind and amount of intraspecific variability in species of living tapirs. Such information, it was hoped, might help in evaluation of specific criteria for fossil tapiroids.

All specimens of Eocene and Oligocene tapiroids in virtually every major museum in the United States were then studied and the validity of all previously named species subjected to critical examination. Since enamel is the hardest tissue in the body, teeth are more commonly preserved than any other part of the skele-

ton. As a result, most fossil tapiroids are known primarily from teeth, and practical classification must be based on those remains. Fortunately, Eocene and Oligocene tapiroid cusp patterns contain complex morphological details which change with time and serve well as taxonomic criteria. It is perhaps significant that the four living species of tapirs may be identified from dentitions alone.

Many previous workers seem to have been essentially typologically oriented, basing species on single individuals rather than considering all available specimens in a sample. Most isectolophid and helaletid tapiroid species were defined on the basis of size and details of premolar cusp patterns. Since premolars in these families were undergoing molarization and are highly variable in morphology, the typological approach resulted in the frequent naming of several closely related species from the same horizon and locality, with the type specimens usually representing extremes of continuous variation. In the present study as large a sample as possible was examined to determine range of intraspecific variation, and all available specimens from a given horizon were considered along with types in evaluating validity of species.

Size differences frequently appeared significant for distinguishing species. To allow objective evaluation of this criterion, length-width measurements were made on all teeth examined and the resultant data summarized statistically for all species. Due to lack of accurate stratigraphic data and small size of collections, samples used in calculating statistics usually included specimens from different stratigraphic horizons and therefore cannot be considered representative of contemporaneous populations. (This temporal mixing may account for coefficients of variation which are slightly higher than would be expected for samples drawn from restricted time zones.) This limitation by no means nullifies the value of the statistics since a species consists not of a single contemporaneous population, but rather a series of interbreeding populations, continuous through time. Therefore even a stratigraphically heterogeneous sample may be useful for estimating expected ranges of intraspecific variation. Of course, more temporally restricted samples are desirable for allowing more precise and detailed analysis of evolutionary trends.

To facilitate comparison between samples and to provide graphic representation of predicted size range of a population or species, bivariate equiprobability ellipses were used, after the method discussed by Defrise-Gussenhoven (1955). These are calculated to encompass a given predicted per cent (in this paper 95 per cent and 99 per cent) of the population from which the sample was drawn. They show at a glance the size range of a population based on two linear measurements and allow visual estimate of the probability that a given specimen belonged to the population described (see fig. 1). All calculations were done with the aid of a Monroe desk computer; total time for calculating a bivariate ellipse for a sample of 50 specimens averaged about three hours. The resultant data also include in addition to the ellipse, the mean, standard deviation, coefficient of variation, and standard errors of the preceding for both variates, and the coefficient of correlation and reduced major axis. Equiprobability ellipses were preferred to the population range diagrams used by Colbert and Imbrie (1956) because the former fit the data more closely and more accurately represent the desired information.

Details of isectolophid and helaletid postcranial anatomy at present have little bearing on taxonomic and phylogenetic interpretations and therefore are omitted from this work. A comprehensive study of tapiroid anatomy now being prepared by the writer will deal with all available information on this subject.

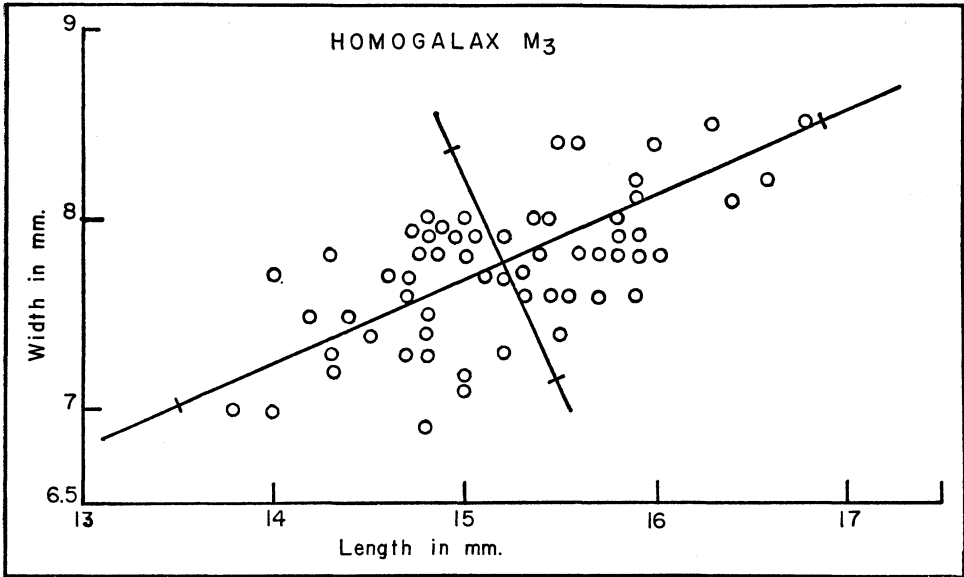


Fig. 1. Scatter diagram of length-width measurements of 60 *Homogalax protapirinus* M_3 's with axes of 95% and 99% equiprobability ellipses superimposed to show accuracy of estimate.

ACKNOWLEDGMENTS

I am indebted to Dr. Joseph T. Gregory for originally suggesting this project. During the course of the investigation discussions with Drs. Elwyn L. Simons and John H. Ostrom were helpful in elucidating phylogenetic problems; these gentlemen also provided encouragement and guidance which aided completion of this paper. Dr. Glenn L. Jepsen and Dr. Malcolm McKenna also offered valuable criticism.

Dr. J. Arnold Shotwell generously allowed me to study and describe recently discovered tapiroid material from the collections of the University of Oregon Museum of Natural History, for which I have proposed a new species.

For generous hospitality and assistance received during museum visits and for permission to examine and borrow specimens I thank Dr. Donald Baird, Dr. Craig C. Black, Dr. Theodore Downs, Dr. Childs Frick, Dr. C. L. Gazin, Dr. Morton Green, Dr. Joseph T. Gregory, Dr. Gideon T. James, Dr. Glenn L. Jepsen, Miss Jeanne Lyons, Dr. Paul O. McGrew, Dr. Malcolm McKenna, Dr. Bryan Patterson, Dr. Horace Richards, Dr. C. Bertrand Schultz, Dr. J. Arnold Shotwell, Dr. Morris Skinner, Dr. William D. Turnbull, Mr. G. E. Untermann, Mr. Dan Witter, and Dr. Horace E. Wood II.

I am grateful to Mrs. Margaret E. Freeman for help in preparing the plates.

My wife, Terry Radinsky, made most of the statistical calculations and provided assistance and encouragement which were invaluable in preparation of the manuscript.

Two years of research were supported by National Science Foundation Cooperative Graduate Fellowships. Field work during the summer of 1961 was aided by grants from the Sigma Xi-RESA Research Fund and the J. T. Doneghy research fund in Vertebrate Paleontology, Yale Peabody Museum.

ABBREVIATIONS

| | |
|--------|---|
| AMNH | American Museum of Natural History |
| ANSP | Academy of Natural Sciences of Philadelphia |
| CIT | California Institute of Technology |
| CM | Carnegie Museum |
| CNHM | Chicago Natural History Museum |
| F:A.M. | Frick American Mammals (American Museum of Natural History) |
| GSC | Geological Survey of Canada |
| LACM | Los Angeles County Museum |
| MCZ | Museum of Comparative Zoology, Harvard College |
| PU | Princeton University Geological Museum |
| SDSM | South Dakota School of Mines and Technology |
| UC | University of California Paleontological Museum |
| UFH | Utah Field House |
| UOMNH | University of Oregon Museum of Natural History |
| USNM | United States National Museum |
| YPM | Yale Peabody Museum |

L = anteroposterior length (maximum)
W = labiolingual width (maximum)
mm = millimeters (all measurements given in millimeters)
N = number of specimens included in sample
OR = observed range
SR = span of standard range
M = mean and its standard error
 σ = standard deviation and its standard error
V = coefficient of variation and its standard error

TAXONOMY

SUPERFAMILY TAPIROIDEA Gill, 1872

INCLUDED FAMILIES: Isectolophidae, Helaletidae, Lophiodontidae, Tapiridae.

DIAGNOSIS: Very small to large perissodactyls with complete cross lophs on upper and lower molars but with ectoloph short and metalophid incomplete or absent. Teeth brachydont.

FAMILY ISECTOLOPHIDAE Peterson, 1919

TYPE: *Isectolophus* Scott and Osborn, 1887.

INCLUDED GENERA: *Homogalax*, *Isectolophus*.

DISTRIBUTION: Early to late Eocene of North America.

DIAGNOSIS: Small to medium-sized cursorial tapiroids with full placental dentition. No major diastemata. P² narrow, with or without a small lingual crista; P³ with one or two lingual cusps, the hypocone appearing as an isolated cuspule in advanced forms. P⁴ with one lingual cusp. M¹⁻³ paracone and metacone subequal and convex. M³ trapezoidal in outline, with metaloph as long as protoloph. P₂₋₄ do not exhibit trend towards molarization: P₂ with single main cusp and anterior and posterior medial ridges; P₃ with metaconid close to protoconid and low medial metalophid with hypoconid barely distinct; P₄ with incipient entoconid or cingular cuspule. M₁₋₃ metalophid well developed. M₃ with large hypoconulid. No enlarged nasal incisions.

DISCUSSION: The subfamily Systemodontinae was erected by Osborn (*in* Osborn and Wortman, 1892, p. 124) to include one genus, *Systemodon* [= *Homogalax*]. This form was considered by Osborn to be ancestral to the true tapirs and consequently was ranked in the family Tapiridae. Peterson (1919, p. 116) gave the subfamily a new name, Homogalaxinae, and proposed another subfamily, Isectolophinae (p. 116) which he regarded as including *Parisectolophus* [= *Isectolophus latidens*] and *Isectolophus* [= *Isectolophus annectens*]. The two subfamilies, distinguished by the presence of two internal cusps on P³ of issectolophines but only one in homogalaxines, were placed in a new family, Isectolophidae (Peterson, 1919, p. 115).

Homogalax has one internal cusp on P³ while *Isectolophus annectens* has two. *I. latidens*, however, shows the transition from one to two lingual P³ cusps. For this reason, and also because it seems evident that *Homogalax* and the Bridgerian and Uintan species of *Isectolophus* form an evolutionary lineage, it would be unrealistic and unnecessary to divide them into subfamilies. The differences between the known early and later species are emphasized sufficiently by taxonomic distinction on the generic level only. It is therefore suggested that for the present the category of subfamily in the family Isectolophidae be suppressed, and that the next lower taxon in the family be that of genus. (This accords with the classification of Simpson, 1945, p. 140.)

Indolophus Pilgrim, 1925, from the late Eocene Pondaung formation of Burma, was referred to the family Isectolophidae by Matthew (1929, p. 515) and Colbert (1938, p. 346) and this allocation was followed by Simpson (1945, p. 140). The type and sole specimen (Geol. Surv. India, C347) consists of P²-M¹ and DP⁴, which exhibit convex metacones characteristic of issectolophids. However, examination of a cast of the type (AMNH cast no. 17617) revealed other features critical for taxonomic assignment, some of which were mentioned and figured by the original describer, Pilgrim (1925, pp. 22-25, pl. 2, figs.

8a-d), which were not dealt with in the later papers. P² shows a higher degree and different manner of molarization than is seen in any North American isectolophid, while P³⁻⁴, in the labiolingual flattening and posterior elongation of the protocone, show closest resemblance to corresponding teeth in middle Eocene helaletids. Also, P²⁻⁴ have higher lophs and, with the associated M¹, display smaller parastyles than in any known isectolophid. For these reasons *Indolophus* is removed from the family Isectolophidae and, pending further information, considered tapiroid *incertae sedis*.

GENUS HOMO GALAX Hay, 1899

non *Systemodon* Cope, 1881, p. 1018.

Systemodon Wortman, 1896, p. 89.

Homogalax Hay, 1899, p. 593.

TYPE: *Homogalax primaevus* (Wortman) 1896 = *H. protapirinus* (Wortman) 1896.

INCLUDED SPECIES: type only.

DISTRIBUTION: Early Eocene of North America.

DIAGNOSIS: Small isectolophids with a more variable and more primitive dental morphology than later members of the family. Premolar series longer relative to molar series than in any later tapiroids. Short diastemata sometimes present in dental series between I₃³ and P₂². P³ with one lingual cusp. M¹⁻³ with proto- and metaconules sometimes distinct. P₁¹ and P₂₋₃²⁻³ major cusps relatively higher and sharper than in later isectolophids. Metastylid present on M₁₋₃¹⁻³.

HISTORY OF TAXONOMY: Cope (1875, p. 20) erected the species *Orohippus tapirinus* for some equoids from early Eocene beds in New Mexico; two years later, (1877, p. 263) he referred this species to *Hyracotherium*. Shortly thereafter, in 1880, Wortman found several tapiroid specimens in the Willwood formation of the Bighorn Basin, Wyoming, which Cope described as conspecific with *Hyracotherium tapirinum*. Since these specimens lacked the long upper diastemata found in some species of *Hyracotherium*, Cope (1881, p. 1081) made *tapirinum* the type of a new genus, *Systemodon*.

A year later, Cope (1882b, p. 184) proposed the species *Systemodon semihians*, based on a Bighorn Basin specimen (first figured in Cope, 1884, pl. 56, fig. 3). Enlarging Cope's description of this species, Osborn (in Osborn and Wortman, 1892, p. 124-6) gave a detailed comparison of *S. tapirinus* and *S. semihians*, following Cope in basing critical observations of the former species not on the New Mexican type, but on Bighorn Basin specimens. Beside the type, no additional New Mexican specimens referable to *Systemodon* had then been found.

Wortman was the first to suggest in print that the type of *S. tapirinus* belonged to *Hyracotherium*, and in 1896 (p. 89) he proposed a new species, *Systemodon protapirinum*, for all Bighorn Basin specimens that had been previously referred to *S. tapirinus*. In the same publication he erected another specific name, *Systemodon primaevus* (p. 89).

Wortman evidently failed to realize that the type of a type species acts as name bearer for the genus, and that transferral of the type of *Systemodon tapirinus* to *Hyracotherium* would thereby invalidate the name *Systemodon*. Hay (1899, p. 593) corrected this oversight and proposed the generic name *Homogalax* for the three species, *semihians*, *protapirinus*, and *primaevus*.

Several years later, Troxell (1922a, p. 288-292) extended the genus *Homogalax* to include middle and late Eocene isectolophids.

Although isectolophid dental morphology is fairly stereotyped there are well-defined differences between the middle and late Eocene forms. Also, one population of *Homogalax* apparently gave rise to another tapiroid line, that of the Helaletidae, through the middle and late early Eocene genus *Heptodon*. For these reasons it seems best to restrict *Homogalax* as a distinct, essentially "horizontal" genus, comprising the stem form from which, so far as is known, all later tapiroids arose.

DENTITION: The following description of *Homogalax* dentition is based on a large series of specimens collected in the lower part of the Willwood formation of the Bighorn Basin, Park, Bighorn, and Washakie counties, Wyoming.

I_{1-3}^{1-2} are small, spatulate, and subequal in size. I^3 is larger than I^1 or I^2 and asymmetrical, with a short convex anterior edge and longer concave posterior edge.

C_1^1 are long, slightly labiolingually compressed fangs. A few specimens have smaller and more slender canines, possibly indicative of sexual dimorphism, although intermediate sizes occur.

Small diastemata, shorter than the length of P^2 , occur variably between P^2 , P^1 , C^2 , and I^2 , the latter accommodating C_1 in occlusion. In the lower jaw a diastema slightly longer or shorter than P_1 usually separates P_2 and P_3 ; short gaps also occur variably between P_2 , C_1 , and I_3 . At present, development of anterior diastemata seems too variable and inconsistent to be of taxonomic value.

P^1 is an anteroposteriorly elongated, double-rooted, single cusp with a short, slightly convex anterior edge and a longer, slightly concave posterior edge. Anteriorly and posteriorly, small cingular ridges comprise parastyle and metastyle.

P^2 varies in outline from a narrow ellipse to a 30-60-90 degree triangle with short base to the rear. A small parastyle, high paracone, somewhat smaller, barely distinct metacone, and a small metastyle comprise the main part of the tooth. Prominent cingula are present on all but the labial side. An interesting feature of P^2 is the variable development, lingual to the paracone, of a small basal crista, which may arise from the lingual cingulum or be completely separate (labially) from that cingulum. An extreme development of this crista is seen in AMNH 4460, where it appears as a low, short protoloph, trending posterolingually; this extension renders the tooth wider than long. AMNH 144 exhibits the other extreme, with no crista at all. Most *Homogalax* P^2 's fall in a gradational series between these two extremes, with internal cristae ranging from non-existent to prominent. No correlation with lingual cusp development in P^{3-4} is evident (*contra* Gazin, 1962, p. 77).

P^3 is more or less triangular in outline, with paracone and metacone sub-equal in size and close together but distinct. Anteriorly, a thin ridge extends down the side of the paracone, ending in a low, sharp, parastyle; a small posterior ridge occasionally terminates in a very small metastyle. At the lingual apex a prominent conical protocone almost equals paracone and metacone in height. A sharp protoloph, decreasing in height labially, extends from the protocone towards the parastyle. No metaloph develops, but in some individuals a small irregular crista occurs at the lingual base of the metacone. Prominent cingula bound the tooth anteriorly and posteriorly, with the posterior cingulum often extended as a wide shelf.

P^4 is roughly triangular and usually more symmetrical than P^3 . A prominent parastyle, high, conical, well-separated paracone and metacone, and low metastyle comprise the ectoloph. At the lingual apex a high, conical protocone merges into a strong protoloph which extends towards the parastyle. Occasionally a low metaloph, slightly convex posteriorly, extends from protocone to anterolingual base of metacone. Some specimens display an irregularly shaped crista at the lingual base of the metacone, usually pointing towards the protocone. Occasionally two cristae may occur here, converging lingually in a V, sometimes merging and continuing as a thin metaloph to the protocone. These features vary too independently and inconsistently to be of taxonomic value. They indicate that the tendency to develop a topographic high between protocone and metacone occurs initially and most strongly at the lingual base of the metacone, extending secondarily to the protocone; this contrasts with the protoloph, which develops most prominently at the protocone and never occurs in an incomplete stage. Prominent cingula bound P^4 anteriorly and posteriorly.

M^1 is quadrate with slightly oblique anterior and posterior sides. The high, conical paracone and slightly flattened and lingually displaced metacone bear thin anterior and posterior ridges and are separated by a deep notch in the ectoloph. A high, sharp, blade-like parastyle arising from the anterior cingulum stands slightly anterolabially and relatively far from the paracone. High, conical protocone and hypocone merge labially with

protoloph and metaloph respectively, with a small notch variably marking the division between cusp and loph. The high, sharp, continuous cross lophs extend obliquely towards anterolingual corners of paracone and metacone; protoconule and metaconule are sometimes barely distinct. The protoloph is slightly longer than the metaloph and extends part-way up the anterolingual side of the paracone, while the metaloph usually ends abruptly at the base of the metacone. Narrow cingula occur on all sides of the tooth, but are least developed labially.

M^2 corresponds to M^1 in cusp configuration but is somewhat larger.

M^3 is similar in structure to the preceding molars but still larger. More oblique anterior and posterior sides, shorter metacone, and extension of the posterolingual and anterolabial corners produce a characteristic trapezoidal outline.

P_1 consists of a high, sharp, labiolingually compressed, single-rooted single cusp, with a shorter, slightly convex anterior edge and longer, somewhat concave posterior edge.

P_2 bears a high, sharp, narrow central cusp (= protoconid and metaconid). The short, slightly convex anterior edge (incipient paralophid) terminates anteriorly in a very small basal cusp (paraconid); the longer, slightly concave posterior edge ends in a broadened incipient talonid, bounded posteriorly by a prominent cingulum. A faint posterolabial groove on the trigonid marks the position of what is a deep fold in P_{3-4} and in P_2 of later isectolophids, situated immediately labial to the junction of metalophid with protolophid.

P_3 has a high sharp trigonid with a very small metaconid budding off the posterolingual slope of the protoconid. From the anterolabial edge of the protoconid a low paralophid extends anteriorly and then slightly lingually. A short low metalophid originates medially between protoconid and metaconid and extends back to the posterolabial corner of the broadened slightly posterolingually basined low talonid. No entoconid occurs.

P_4 is roughly rectangular in outline, with a relatively high trigonid and low talonid. Separate, equal-sized, conical protoconid and metaconid stand close together, with the protoconid slightly more anteriorly situated. The paralophid extends down from the anterolabial slope of the protoconid to the anterolabial corner of the tooth, where it turns lingually and extends across the anterior edge like a sharp cingulum. A metalophid, originating halfway up the protolophid between protoconid and metaconid, extends posterolabially to a small hypoconid from which a short posterior cingulum may extend lingually. A small entoconid is variably present, and may develop from a raised portion of the posterolingual cingulum or appear entirely within the cingulum.

M_1 is rectangular in outline, with protoconid and hypoconid slightly anterior to metaconid and entoconid respectively. All four steeply conical cusps stand out anteriorly from their respective cross lophs. A metastylid occurs immediately posterolingual to the metaconid. Thin, slightly notched transverse ridges comprise protolophid and hypolophid. The much-reduced paralophid extends forward as a low ridge from the protoconid and trends lingually across the anterior edge of the tooth. A low metalophid extends anteriorly and slightly lingually from the hypoconid and usually terminates before reaching the protolophid. The very small hypoconulid occurs medially at the posterior base of the hypolophid.

M_2 is virtually identical to M_1 , but slightly larger.

M_3 resembles M_{1-2} in cusp configuration, except that the hypoconulid extends posteriorly as a prominent heel. A high, sharp ridge, originating near the hypoconid, bounds the hypoconulid labially and posteriorly, enclosing a small basin. The hypoconulid is variable in length and width, and frequently bears small cusps on the posterolabial crest. No consistent patterns in size, shape, or cusp configuration allow use of this feature as a taxonomic criterion.

DECIDUOUS DENTITION: DP^2 is shaped like a 30-60-90 degree triangle with the short base to the rear. Prominent parastyle and separate paracone and metacone comprise the ectoloph. A high sharp cingulum occurs lingually, while posterolingually, the tooth extends out as a basin-like shelf.

DP^3 is subquadrate, with the anterolabial corner extended far forward. Labial cusps include prominent parastyle and well separated paracone and metacone. A low metaloph, with metaconule sometimes distinct, extends to a hypocone, the highest

lingual cusp. Anterolingually a less prominent protocone gives rise to a low protoloph.

DP⁴ is quadrate and fully molariform, differing from M¹ only in being relatively longer and narrower.

DP₃ is elongate with a widened talonid. The narrow trigonid bears a prominent protoconid with a distinct metaconid posterolingual to it, and anteriorly, a relatively high paralophid. The talonid has a well-developed entoconid and hypoconid, and thus is more molariform than P₄. The hypoconid is connected to the metaconid by an oblique metalophid.

DP₄ is essentially molariform, differing from M₁ in being relatively narrower and more elongate, especially in the trigonid.

Homogalax is distinguished from its closely related contemporary, *Hyracotherium*, by the following features: larger size; no long diastemata; P³⁻⁴ protoconule not distinct; M¹⁻³ relatively wider (labiolingually), with protoloph and metaloph relatively higher and sharper, protoconule and metaconule usually not distinct, parastyle higher and more separated from paracone; M³, and to a lesser degree M² and M¹, trapezoidal in outline; M₁₋₃ protolophid and especially hypolophid more complete and metalophid less lingually directed.

Homogalax protapirinus (Wortman), 1896
(Plate 1, figs. 1, 5.)

non *Systemodon tapirinus* (Cope), 1881, p. 1018.

non *Systemodon semihians* Cope, 1882b, p. 184.

Systemodon primaevus Wortman, 1896, p. 89.

Systemodon protapirinum Wortman, 1896, p. 89.

Homogalax primaevus, Hay, 1899, p. 593.

Homogalax protapirinus, Hay, 1899, p. 593.

TYPE: AMNH 4460: maxilla with P¹-M³; mandible with P₂-M₃.

HYPODIGM: Type and AMNH 126, 131, 141, 144, 147, 149, 150, 152, 153, 2930, 4461, 4472, 15371, 15375-15377, 15386, 15389, 15390, 15393-15395, 15399, 15402, 15404, 15407, 15409, 15410, 15413, 15415, 15417-15419, 15491-15493, 15796, 15801, 15803, 15806, 15807, 15809, 15813-15817, 15856, 16769, 16857, 16859. PU 13081-13084, 13090-13092, 13109, 13183, 13219, 13224, 14691, 16142, 16143, 16168, 16181-16186, 16188-16190, 16213.

KNOWN DISTRIBUTION: Early Wasatchian: Sand Coulee and Gray Bull faunas, Willwood formation, Bighorn Basin, Wyoming; Powder River Basin (Sussex), Wyoming; Bitter Creek local fauna, Washakie Basin, Wyoming.

DIAGNOSIS: Small isctolophids. Mean length M₁₋₃ = 36.0 mm. P² with variably developed lingual crista. See Table 1.

DISCUSSION: The type of *Homogalax semihians*, AMNH 4485, consists of a maxilla of an old individual, with the broken roots of C¹ and P¹, P²⁻⁴ with cusps worn beyond recognition, and M¹⁻³ worn down to the roots. C¹ was slender. Alveoli indicate no C¹-P¹ or P¹-P² diastemata. P²⁻⁴ are very small for *Homogalax*, and look more like *Hyracotherium* premolars. M¹⁻³ are large for *Hyracotherium* but lack the trapezoidal outline characteristic of *Homogalax*. The premolars appear unusually small for the molars but it is possible that the sides of M¹⁻³ have been somewhat outwardly displaced by crushing. Cracks in the thin rims of enamel left around the crowns may be indicative of such distortion. AMNH 4485 may belong to *Hyracotherium*; in any event, it cannot with any degree of certainty be assigned to the genus *Homogalax*. Since the type is indeterminate and there are no other specimens assignable to this species, it is suggested that the species *semihians* be suppressed.

Wortman erected the species *protapirinus* and *primaevus* in 1896, distinguishing them by degree of development of the lingual crista on P². The type of *protapirinus*, AMNH 4460, has an extremely large crista; the type of *primaevus*, AMNH 144, has no P² lingual

TABLE 1
Statistical Data on Teeth of *Homogalax protapirinus*

| | N | OR | SR | M | σ | V |
|------------------|----|-----------|-----|--------------|-------------|--------------|
| P ¹ L | 6 | 6.1- 7.2 | 2.6 | 6.67 ± 0.16 | 0.40 ± 0.12 | 6.05 ± 1.75 |
| W | 6 | 3.2- 4.4 | 2.6 | 3.80 ± 0.16 | 0.40 ± 0.12 | 10.66 ± 3.08 |
| P ² L | 25 | 6.2- 8.7 | 4.1 | 7.72 ± 0.13 | 0.63 ± 0.09 | 8.16 ± 1.15 |
| W | 25 | 5.1- 7.6 | 4.0 | 6.06 ± 0.12 | 0.61 ± 0.09 | 10.05 ± 1.42 |
| P ³ L | 42 | 7.0- 9.8 | 3.6 | 8.34 ± 0.09 | 0.56 ± 0.06 | 6.68 ± 0.73 |
| W | 42 | 7.9-10.0 | 3.3 | 8.85 ± 0.08 | 0.51 ± 0.06 | 5.75 ± 0.63 |
| P ⁴ L | 54 | 7.2- 9.6 | 2.8 | 8.75 ± 0.06 | 0.44 ± 0.04 | 5.05 ± 0.49 |
| W | 54 | 9.3-11.9 | 3.9 | 10.52 ± 0.08 | 0.60 ± 0.06 | 5.69 ± 0.55 |
| M ¹ L | 57 | 8.9-11.1 | 3.4 | 9.92 ± 0.07 | 0.53 ± 0.05 | 5.35 ± 0.50 |
| W | 57 | 10.4-13.2 | 3.8 | 11.91 ± 0.08 | 0.59 ± 0.06 | 4.93 ± 0.46 |
| M ² L | 69 | 9.5-12.0 | 3.4 | 10.71 ± 0.06 | 0.52 ± 0.04 | 4.90 ± 0.42 |
| W | 69 | 11.7-14.9 | 3.8 | 12.98 ± 0.07 | 0.58 ± 0.05 | 4.48 ± 0.38 |
| M ³ L | 57 | 9.7-12.2 | 3.8 | 10.74 ± 0.08 | 0.58 ± 0.05 | 5.45 ± 0.51 |
| W | 57 | 12.3-15.4 | 4.7 | 13.72 ± 0.10 | 0.73 ± 0.07 | 5.34 ± 0.50 |
| P ₂ L | 8 | 7.2- 8.4 | 2.3 | 7.80 ± 0.13 | 0.36 ± 0.09 | 4.64 ± 1.16 |
| W | 8 | 4.0- 5.0 | 2.6 | 4.55 ± 0.14 | 0.40 ± 0.10 | 8.79 ± 2.20 |
| P ₃ L | 29 | 8.0- 9.8 | 3.0 | 8.87 ± 0.08 | 0.46 ± 0.06 | 5.14 ± 0.67 |
| W | 29 | 5.0- 6.0 | 2.1 | 5.38 ± 0.06 | 0.32 ± 0.04 | 5.92 ± 0.78 |
| P ₄ L | 38 | 7.6- 9.8 | 3.1 | 8.85 ± 0.08 | 0.48 ± 0.06 | 5.40 ± 0.62 |
| W | 38 | 5.3- 6.8 | 2.2 | 6.01 ± 0.06 | 0.34 ± 0.04 | 5.60 ± 0.64 |
| M ₁ L | 43 | 8.4-10.8 | 3.3 | 9.77 ± 0.08 | 0.51 ± 0.06 | 5.21 ± 0.56 |
| W | 43 | 5.8- 7.2 | 2.3 | 6.49 ± 0.05 | 0.36 ± 0.04 | 5.50 ± 0.59 |
| M ₂ L | 52 | 9.9-11.8 | 3.0 | 11.00 ± 0.06 | 0.46 ± 0.04 | 4.17 ± 0.41 |
| W | 52 | 6.8- 8.2 | 2.3 | 7.36 ± 0.05 | 0.35 ± 0.03 | 4.81 ± 0.48 |
| M ₃ L | 63 | 13.8-16.8 | 4.2 | 15.20 ± 0.08 | 0.65 ± 0.06 | 4.27 ± 0.38 |
| W | 63 | 6.9- 8.5 | 2.5 | 7.76 ± 0.05 | 0.38 ± 0.03 | 4.84 ± 0.43 |

crista. Both specimens are virtually identical in all other features, including size. Other *Homogalax* specimens with P² preserved may be arranged in a completely gradational morphological series between the two extremes (see fig. 2). Since there are no other criteria by which *protapirinus* and *primaevus* may be separated, they are here considered conspecific.

As a consequence of the foregoing, the question of which has priority now arises. Wortman named *protapirinus* and *primaevus* in the same publication (1896, p. 87, 89). *H. protapirinus* has page precedence and, what should be more important, is the more complete specimen. Nevertheless, *H. primaevus* was chosen by Hay (1899, p. 593) as the type species for *Homogalax*. When Troxell (1922a, p. 288-289) reviewed the genus *Homogalax* he considered *H. primaevus* the sole and type species, but, since he did not cite the name *protapirinus*, he never clearly synonymized it with *primaevus*. Exercising the privilege of first reviewer, as stated in the International Code of Zoological Nomenclature, (Art. 8, sec. 2, in Bull. Zool. Nomen., v. 14, p. 71-72), I hereby select *Homogalax protapirinus* as having precedence over *primaevus*. By this synonymy *H. protapirinus* (type AMNH 4460) becomes the type species of *Homogalax*.

Examination of well over a hundred *Homogalax* specimens from the Bighorn Basin

failed to reveal any discontinuous or bimodal variations in morphology. Due to lack of sufficiently accurate stratigraphic data the whole assemblage was given statistical treatment as one group. Although known specimens range vertically throughout over 2,000 feet of strata, tooth dimensions vary little, with coefficients of variation as low as would be expected in one contemporaneous population. (See Table 1.) Since the Bighorn Basin *Homogalax* sample cannot be subdivided on the basis of morphological or other criteria, only one species, *H. protapirinus*, needs to be recognized there.

Collection of large samples of *Homogalax* with accurate stratigraphic data from various levels in the Willwood formation might make it possible to recognize several chronoclines, or gradations in morphology with time. Since *Homogalax* apparently had small ancestors (see discussion of Four Mile tapiroid below), and larger descendants (middle Eocene *Isectolophus latidens*), one might expect to find a tendency towards increase in size with time, with specimens from higher horizons larger than those from lower beds. Kitts (1956, p. 40-41) suggested that such a trend occurred in *Hyracotherium* during Wasatchian time. However, of the four specimens of *Homogalax* known from the early Graybullian Sand Coulee beds, only two (PU 13167, 17354) fall noticeably below mean size; one (PU 17356) lies near the mean, while another (PU 17355) appears large, compared with the hypodigm from Gray Bull beds. About 25 other *Homogalax* specimens assignable to lower, middle or upper Gray Bull beds show no consistent change in size with time.

Species of the middle to late Wasatchian helaletid *Heptodon* probably evolved from a Graybullian population of *Homogalax*. Therefore one might hope to find in some *Homogalax* specimens tendencies toward *Heptodon* dental morphology, such as development of a lingual cusp on P², shortening of the M₁ hypoconulid or lengthening of post-canine dias-

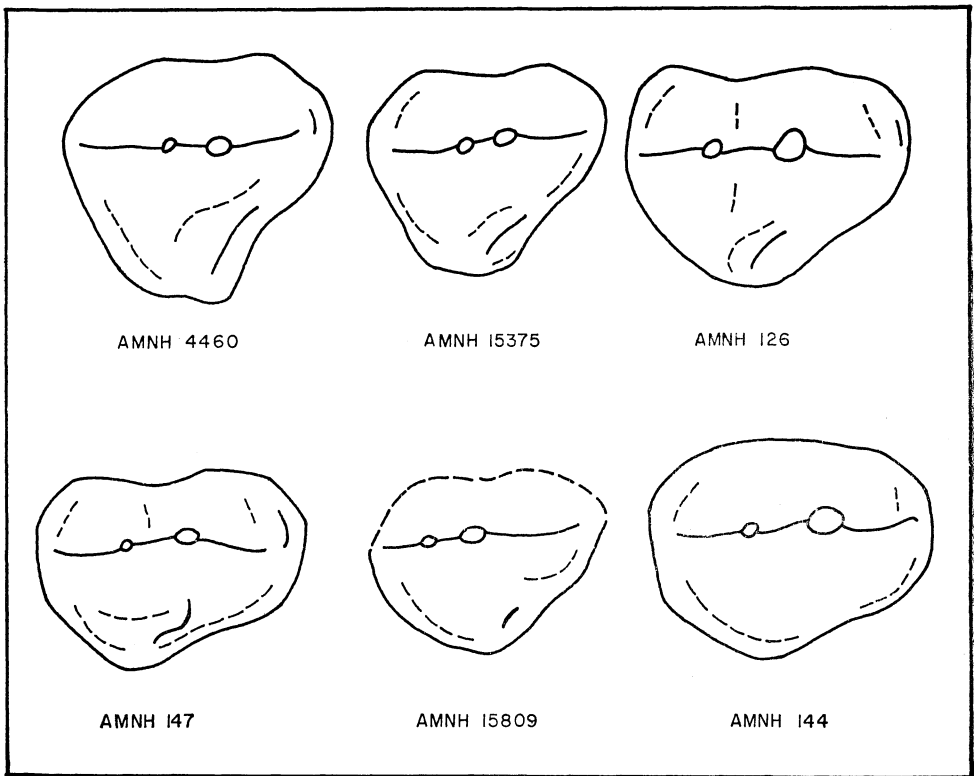


Fig. 2. Diagrammatic drawings of Bighorn Basin *Homogalax* right P²s, showing range of variation in development of lingual crista. All $\times 4$. (AMNH 15809 and 144 reversed.)

temata. AMNH 4460 resembles *Heptodon* in one feature, an unusually large P⁸ internal crista; unfortunately pertinent stratigraphic data is not available for this specimen. YPM 17104, from high in the Gray Bull beds has an abnormally short (for *Homogalax*) M₃ hypoconulid. These few unusual individuals indicate some of the potentialities for change in dental morphology in the *H. protapirinus* gene pool. However, more accurate stratigraphic work and intensive collecting must be done to allow postulation of subgeneric evolutionary trends. The Bighorn Basin Willwood formation, with its thick section of fossiliferous strata, contains the information for working out detailed evolutionary lineages of many other genera in addition to *Homogalax*. For almost three-quarters of a century a great deal of potentially important data inherent in specimens brought back from this classic early Eocene collecting ground have been lost because exact locality and horizon records were not kept; now, before the opportunity disappears, accurate biostratigraphic investigations should be carried out.

Although long known only from the Bighorn Basin, *Homogalax* in recent years has been found in strata outside that area. The H. E. Wood collection at the American Museum of Natural History contains a few isolated *Homogalax* teeth from near the town of Sussex, in the Powder River Basin, Wyoming. AMNH 55520 (M⁸), AMNH 55521 (M₂) and a few molar fragments, from Sec. 14, T48N, R78W, Johnson Co., fall within the size range of *H. protapirinus*. The M⁸ parastyle lies further labial than usual. Another lot, from Sec. 2, T45N, R78W, Johnson Co., includes a relatively wide M₃ (AMNH 55522), medium-sized DP⁸ (AMNH 55523) and one or two fragments. These few teeth serve to establish the presence of *Homogalax* in the Powder River Basin. On the basis of size they cannot be separated from *H. protapirinus*, but more complete specimens are needed before specific allocation can be made with certainty.

Gazin (1962, p. 77) recorded a few specimens of *Homogalax* from the early Graybullian Bitter Creek locality in the Knight formation, Washakie Basin, Wyoming. USNM 22767 (P⁸-M², M₁₋₃), YPM 14061 (P⁴), YPM 15296 (M₁₋₂), and YPM 17606 (M₁) are somewhat narrower than corresponding teeth of *H. protapirinus* but fall well within the predicted 95 per cent size range of that species. Since no differences in cusp configuration were discerned, the Bitter Creek *Homogalax* specimens may tentatively be assigned to *Homogalax protapirinus*.

Homogalax cf. *H. protapirinus*

G. L. Jepsen (in press) reported collection of several *Homogalax* specimens from the Golden Valley formation in North Dakota (SW¼, Sec. 29, T139N, R97W, Stark Co.). PU 17157, 17161, 17164, 17165, 17229, 17230, 17284, 17285, 17358-17362 cannot be distinguished from *H. protapirinus* on the basis of cusp configuration but definitely average smaller than the Bighorn Basin sample, with some specimens falling outside the predicted 99 per cent size limit. The Golden Valley *Homogalax* population may represent a smaller northern race of *H. protapirinus* or perhaps is specifically distinct. Chronological correlation between Bighorn Basin and Golden Valley faunas is not exact enough to indicate whether or not their respective *Homogalax* populations existed synchronously; thus the observed disparity in size may represent time difference. In any event, definite specific allocation of the Golden Valley *Homogalax* population should await collection of further material.

Homogalax sp.

McKenna (1960, p. 119-120) called attention to a new species of isctolophid in the early Graybullian Four Mile fauna, from the Hiawatha member of the Wasatch formation in northwestern Colorado. UC 44066, 46628, 46631-46635, 46638, and 58284, all isolated M⁸'s, resemble *Homogalax* in relatively short, wide, trapezoidal outlines and relatively prominent parastyles. Distinct proto- and metaconules and wide basal cingula, on the other hand, suggest close relationship to *Hyracotherium*. In size, the Four Mile specimens fall intermediate between the contemporaneous *Hyracotherium angustidens* and *Homogalax protapirinus*, averaging about 18 per cent smaller than the latter species.

Assignment to *Homogalax* rather than *Hyracotherium* is based mainly on the trapezoidal M^3 outline, a feature characteristic of isectolophids but divergent from hyracothere evolutionary trends.

Intermediate size and cusp configuration suggest this Four Mile tapiroid as an ideal transition form between *Hyracotherium* and *Homogalax*. Had there been no descendent perissodactyls, the two Four Mile species of an equoid and tapiroid might be considered congeneric; however, reflection of phylogenetic relationships requires the vertical classification which places these closely related species in different suborders.

The infrequent occurrence of teeth referable to this primitive species of *Homogalax* (only ten specimens recovered out of 11,000 in the Four Mile collection) may in part be due to misidentification as *Hyracotherium* (other teeth are not as diagnostic as M^3), or may reflect a real paucity of *Homogalax* in the fauna. Nevertheless, formal naming and diagnosis of the species should await collection of more and better material.

? *Homogalax* sp.

Several small perissodactyl specimens from the Lostcabinian Dad local fauna, Washakie Basin, Carbon County, Wyoming, were referred by Gazin (1962, p. 77-78) to "Isectolophid near *Homogalax primaevus*." In size, these specimens approach *Hyracotherium* and the early Graybullian Four Mile tapiroid discussed above, averaging well below the 99 per cent predicted lower limit for Bighorn Basin *Homogalax protapirinus*. USNM 22787 and 22790, both maxillary fragments with M^{2-3} , display trapezoidal outlines, relatively high parastyles, and barely distinct protoconules and metaconules, features suggestive of *Homogalax*. USNM 22789, a worn M_{1-3} , appears to have had a high hypolophid and anteriorly directed metalophid, as in *Homogalax*. However, in USNM 22788, a maxillary fragment with P^{3-4} considered by Gazin (loc. cit., p. 78), "rather more like *Homogalax* than *Hyracotherium*," distinct protoconules suggest the latter genus rather than the former. Small parastyle, large cingula, and long ectoloph on an isolated M^3 (USNM field no. 14-54) and notched hypolophids in two isolated M_2 's (USNM field no. 15-54) likewise suggest *Hyracotherium*. Finally, a worn M^{2-3} (USNM field no. 15-54) shows trapezoidal outlines reminiscent of *Homogalax*, but extreme wear and fragmentary nature of the specimen preclude positive identification.

In summary, three specimens from the Lostcabinian Dad local fauna, (USNM 22787, 22789, and 22790), display features suggestive of *Homogalax*, heretofore known only from the early Wasatchian Gray Bull faunal zone. However, due to scarcity and incomplete nature of relevant material, definite generic assignment should await collection of further specimens; probably *Homogalax*, but possibly *Hyracotherium*, is represented. If indeed *Homogalax* is represented, the small size and late age of the specimens remove them from the main line of isectolophid evolution.

GENUS ISECTOLOPHUS Scott and Osborn, 1887

Parisectolophus Peterson, 1919, p. 121.

Schizolophodon Peterson, 1919, p. 122.

Homogalax Troxell, 1922a, p. 289, 291 (nec Hay).

TYPE: *Isectolophus annectens* Scott and Osborn, 1887.

INCLUDED SPECIES: *I. annectens*, *I. latidens*.

DISTRIBUTION: Middle to late Eocene, North America.

DIAGNOSIS: Medium-sized to large isectolophids. No diastemata. P^1 relatively small. P^2 with minute lingual crista. P^3 submolariform, with one or two lingual cusps. M^{1-3} relatively longer and narrower than in *Homogalax*, with protoconules and metaconules never distinct. P_1 relatively low; P_{2-3} with relatively low trigonid and high posterior medial ridge (= metalophid). No metastylid on M_{1-3} .

HISTORY OF TAXONOMY: The Bridgerian species *Isectolophus latidens* was originally

referred to *Helaletes* (Osborn, Scott and Speir, 1878, p. 54; Scott and Osborn, 1887, p. 260). In 1887, Scott and Osborn erected the new genus and species *Isectolophus annectens*, based on Uintan specimens. In 1889, Osborn (*in* Scott and Osborn, 1889, p. 519), referred *latidens* to *Isectolophus*, with the provision that more information on the premolars of *I. annectens* might show *latidens* to be generically distinct. Hatcher (1896, p. 177-178) considered the upper molars of *I. latidens* different enough from those of *I. annectens* to warrant generic distinction. However, he refrained from proposing a new name because he did not have access to Marsh's *Helaletes* specimens to make comparisons.

Peterson (1919, p. 121) erected the genus *Parisectolophus* for *latidens*, basing generic separation on the following characters:

"First, the molars of *Isectolophus* are considerably advanced, because of the greater posterior enlargement of the ectoloph, making the para- and metacones equal in size; secondly, the cross-crests of the molars are slightly higher and sharper; the cingulum of the upper molars are much heavier."

Peterson based his diagnosis of *I. latidens* on the sole specimen known to him, the type, PU 10251, an incomplete and rather worn dentition. Recent examination of all available specimens of *I. annectens* and *I. latidens* suggests that the differences Peterson cited as evidence of generic distinction are merely due to individual variation and to the larger size of *I. annectens*. Some specimens of *I. annectens* do not show the slight posterior ectoloph enlargement, regarded by him as taxonomically significant, while some specimens of *I. latidens* do. The development of cingula around the upper molars varies greatly within each species; those of *I. annectens* are not consistently relatively heavier. Cross crests of *I. annectens* molars are not relatively higher than those of unworn molars of *I. latidens*. The main differences between *I. latidens* and *I. annectens* are the larger size of the latter species and its consistent possession of a hypocone on P³. These differences suggest specific separation only; therefore, *I. annectens* and *latidens* are here considered congeneric.

Peterson (1919, p. 122) erected the genus *Schizolophodon* for two Uintan isectolophid specimens (CM 3045, CM 3010), citing the following generic characters:

"Lower molars with incomplete cross-crests, especially on M₃ and the anterior cross-crest of M₂. Hypoconulid of M₃ comparatively small."

The specimen designated as paratype, CM 3010, from Uinta C, consists of a lower jaw with C₁ and P₁₋₃. These teeth can in no way be distinguished from those of *I. annectens*; it is difficult to imagine why Peterson included this specimen in *Schizolophodon*.

The type, CM 3045, consists of a lower jaw with rather worn teeth from Uinta B beds. Lower molar cross-crests, with the exception of the hypolophid on M₃, are no less complete and the M₃ hypoconulid is no smaller than those seen in many specimens of *I. annectens*. The one M₃ hypolophid preserved is split in the middle, so that the entoconid and hypoconid are separated by a sharp notch.

CM 3045 fits within the size range of *I. annectens* and can be distinguished from that species only by the cleft M₃ hypolophid. Some specimens of *I. annectens* (YPM 12902, CM 3113) have a small notch in the posterior crest of the M₃ hypoconulid; in YPM 12902 the notch extends forward onto the hypolophid as a minute groove. Possibly this feature was not too rare an abnormality in *I. annectens* dentitions. Since CM 3045 cannot otherwise be distinguished from *Isectolophus annectens*, it is here considered an aberrant specimen of that species, and the genus *Schizolophodon* is suppressed.

Troxell (1922a, p. 288-292) stressed the similarities in dental morphology between all species of isectolophids by placing specimens of *I. annectens* (his *uintensis*) and *I. latidens* (his *bridgerensis*) in the genus *Homogalax*. This is the opposite extreme from the taxonomic scheme suggested by Peterson, since it emphasizes common characteristics of the lineage rather than divergences. Reasons for maintaining generic separation of *Homogalax* and *Isectolophus* have been given in the discussion under *Homogalax* (p. 10), and also may be seen in the diagnoses of the two genera.

DENTITION: Dentitions of *Isectolophus latidens* and *I. annectens* are extremely similar,

differing mainly in larger size and consistent P³ molarization in the latter species.

I₁₋₃¹⁻³ were not preserved in any *Isectolophus* specimens examined. Incisor alveoli indicate laterally compressed I₁₋₃ roots with I₃ larger than I₁₋₂.

C¹ occurs in large and small sizes, probably due to sexual dimorphism. Small, presumably female, C¹'s preserved in YPM 12563 (*I. latidens*) and CM 2337 (*I. annectens*) are oval, almost circular in cross section, with anterior and posterior edges produced into ridges. The lingual side is more convex than the labial and has shallow vertical troughs immediately lingual to the ridges. The anterior edge is shorter than the posterior. Two fragments of a large C¹ preserved with the upper dentition of CM 3043 (*I. annectens*) represent a tooth about twice as large as that in CM 2337.

No small lower canines were observed, but a small C₁ alveolus is preserved in YPM 12563 (*I. latidens*). Large C₁ roots are preserved in PU 10251 (*I. latidens*), and whole canines are seen in YPM 12561, CM 3010, and CM 11951 (all *I. annectens*). The tooth is steeply conical with anterior, posterolingual, and posterolabial vertical ridges. In old individuals a flat wear surface occurs on the posterior side, immediately lingual to the labial ridge. Worn C¹'s presumably bear a corresponding wear facet on the anterior side, slightly labial to the leading ridge.

No diastemata occur in the upper dental series (C¹-M³ inclusive), and almost none in the lower. An extremely short (2.5 mm) gap between the roots of P₁ and P₂ occurs in PU 10251 but not in YPM 12563 (both *I. latidens*). CM 3113 has a gap of about 3.0 mm between P₁ and C₁, but no diastemata occur between C₁-M₃ inclusive on CM 11752 (both *I. annectens*). Thus diastemata are virtually nonexistent and of no apparent taxonomic value in *Isectolophus*.

Only one specimen, CM 2337 (*I. annectens*) preserves P¹, a low, obtuse two-rooted single cusp, almost circular in outline, with convex labial side and straight anterolingual border. Posterolingually a large wear surface has obliterated morphological detail; the tooth may have been slightly widened posterolingually.

P² is anteroposteriorly elongate, with the posterolingual slope extended lingually. The paracone and slightly smaller metacone are close but separated by a shallow vertical groove on the labial and lingual slopes. A small basal crista occurs lingual to the paracone. Posterior to this crista the metacone lingual slope extends out as a slight shelf. Anteriorly the cingulum suggests an incipient parastyle. Anterolingually, in the region of the crista, there is virtually no cingulum; posteriorly it is more prominent.

P³ is the only tooth in *Isectolophus* which shows significant evolutionary change over the patterns seen in *Homogalax*. A small parastyle and conical, subequal paracone and metacone comprise the ectoloph. In *I. latidens* the tooth varies in outline from triangular to quadrangular; one or two lingual cusps may be present. See specific discussion below for a more detailed description.

In *I. annectens*, P³ is the most variable tooth in the dental series, ranging in outline from triangular to quadrangular. Two internal cusps are always present, but they vary in size and relative proportions (see fig. 3). In YPM 15250 a large isolated hypocone occurs posterolingually, while only a very short, low, protoloph is present anterolingually. UFH 218a displays prominent hypocone and, anterolabial to it, a short protoloph. In UFH 55 the hypocone is much larger than the protoloph, but the latter extends more lingually. In these three individuals P³ is roughly triangular in outline. In CM 2337 and UFH 4, protocone and hypocone are about equal in size, with hypocone situated slightly more lingually. CM 3043 displays a prominent protoloph and small hypocone. In addition, a minute supernumerary cuspule occurs budding from the lingual side of the protocone in both left and right P³'s. In these three specimens P³ is almost quadrangular. Prominent cingula bound P³ anteriorly and posteriorly.

P⁴ is triangular in outline with prominent parastyle and well-separated paracone and metacone. The only lingual cusp, a high conical protocone, merges labially into a well-developed protoloph. Frequently the protoloph displays a slight anterior bulge. (In YPM 15229 P⁴ is aberrant in lacking a protoloph; only a minute crista or cuspule occurs anterolabial to the protocone.) A metaloph, usually lower than the protoloph, extends

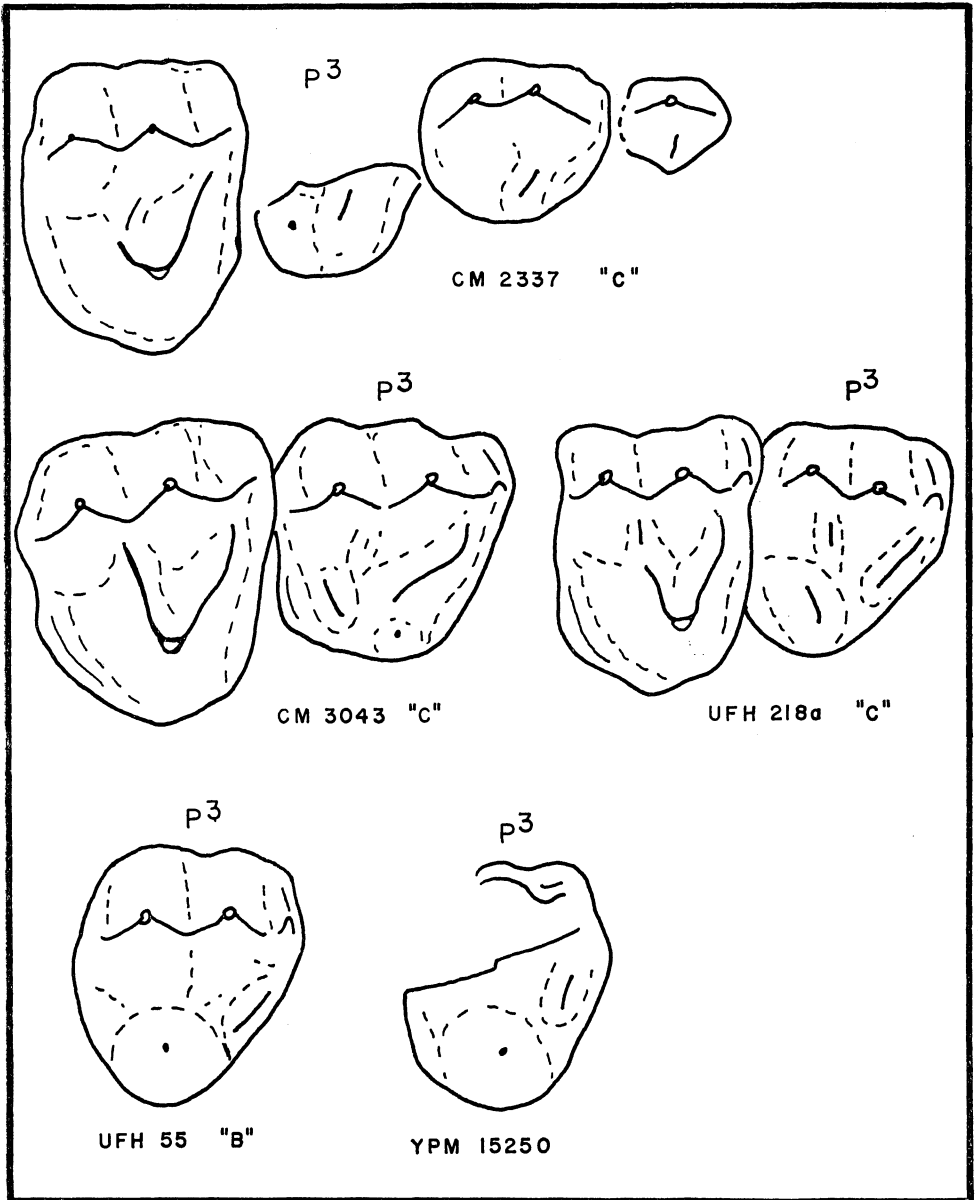


Fig. 3. Diagrammatic drawings of *Isectolophus annectens* premolars showing range of variation in development of P^3 lingual cusps. "B" and "C" refer to Uinta formation horizons. All $\times 3$. (UFH 55 reversed.)

from protocone to anterolingual slope of metacone. The posterior slope of the metaloph extends backwards as a flat, narrow shelf, giving the tooth in some specimens an almost quadrangular outline. Prominent cingula bound P^4 anteriorly and posteriorly.

M^1 is quadrate in outline, with a high parastyle and convex, equal-sized paracone and metacone. Protoloph and metaloph are complete, with protoconule and metaconule never distinct. Prominent anterior and posterior and occasionally lingual cingula are present.

M² is similar to M¹ but larger. The ectoloph often appears slightly more continuous than in M¹.

M³ is similar in cusp configuration but larger and displays a markedly trapezoidal outline, with a relatively longer lingual side than in M¹ or M². The flattened parastyle varies in size and proximity to the paracone and is often divided into two equal lobes by a shallow vertical groove.

P₁ is a low, mediolaterally compressed single cusp with a shorter convex anterior edge and longer, slightly concave posterior edge. Medial ridges extend anteriorly (paralophid) and posteriorly (metalophid) from the main cusp.

P₂ is elongate, with a low central cusp. A prominent paralophid extends anteriorly and a slightly lower metalophid posteriorly. A distinct fold occurs immediately labial to the metalophid-protoconid junction.

P₃ is subrectangular in outline, with a low triangular trigonid and widened talonid. The protoconid bears a smaller metaconid budding off from its posterolingual slope, with the separation marked by a prominent labial fold. A high paralophid runs anteriorly and then slightly lingually at the anterior apex of the tooth. A lower metalophid extends posteriorly and slightly labially from the metaconid, leaving an incipient posterolingual talonid basin. At its posterior end, the metalophid is thickened and raised into an incipient hypoconid.

P₄ is rectangular with well-separated protoconid and metaconid connected by a short protolophid. A relatively low paralophid runs anteriorly from the protoconid and bends lingually around the front of the tooth. A low metalophid extends from the small hypoconid to the protolophid, joining it between protoconid and metaconid, with a deep labial fold. The broad talonid has a posterolingual basin bounded by a high lingual cingulum (= incipient entoconid).

M₁ is rectangular with protolophid and hypolophid parallel and trending slightly anterolabially. There is no metastylid. A low external ridge on the anterolabial and anterior sides of the tooth represents the paralophid. The metalophid is reduced in height, extending from the hypoconid down to the posterolingual base of the protoconid. A low ridge extends anteriorly from the entoconid (= anterior slope of the entoconid?) but does not reach the metaconid. A minute hypoconulid occurs medially at the base of the hypolophid.

M₂ is similar to M₁, but slightly larger.

M₃ is similar to M₁ and M₂, but with protolophid and hypolophid slightly more oblique. The hypoconulid extends back as a large heel, bounded labially and posteriorly by a ridge. There is frequently a narrow notch in the posterolabial corner.

DECIDUOUS DENTITION: DP¹ consists of a single low elongate cusp, with a faint suggestion of a metacone halfway down the posterior slope. A vertical ridge and minute basal crista occur lingually, slightly forward of the mid-line. Posteriorly the lingual side is slightly widened. This tooth resembles P² except that the metacone has hardly differentiated from the main cusp.

DP² looks in outline like a 30-60-90 degree triangle with the short base posterior. A minute parastyle, and conical, well-separated paracone and metacone comprise the ectoloph. A small posterolingual hypocone and a low, anterolingual protoloph recall the P² cusp pattern seen in some specimens of *I. annectens*.

DP³ is subquadrangular, with a long, oblique anterior side. A low parastyle and well-separated paracone and metacone comprise the ectoloph. A low but unbroken metaloph connects the prominent hypocone to the metacone. The protocone is smaller and labially located relative to the hypocone and gives rise to a low protoloph.

DP⁴ is similar to M¹ but smaller and relatively longer.

DP₃ exhibits molariform talonid and very elongate trigonid. The metaconid is as high as the protoconid but more posteriorly located. A long paralophid extends anteriorly from the protoconid and curves lingually around the front of the trigonid.

DP₄ is essentially molariform and differs from M₁ only in possessing a longer and narrower trigonid.

Isectolophus teeth differ from those of *Homogalax* in the following features: larger size; no diastemata; P¹ smaller and rounder; P² metacone relatively larger, lingual crista never large; P³ becomes submolariform; P⁴ metaloph better developed, posterior shelf more pronounced; M¹⁻³ ectoloph more complete and longer posteriorly, no distinct proto- or metaconules. P₁ has tiny anterior and posterior vertical ridges; P₂₋₃ trigonid relatively lower, paralophid and metalophid relatively higher, labial fold more prominent; P₄ with only a cingular entoconid; M₁₋₃ with no metastylid, metalophid less lingually directed and less complete, hypolophid more complete; DP² with hypocone; DP³ metaloph more complete.

Isectolophus latidens (Osborn, Scott and Speir), 1878
(Plate 1, figs. 2-4, 6)

Helaletes latidens Osborn, Scott and Speir, 1878, p. 54.

Isectolophus (Helaletes) latidens, Osborn, in Scott and Osborn, 1889, p. 519.

Parisectolophus latidens, Peterson, 1919, p. 121.

Homogalax bridgerensis Troxell, 1922a, p. 289.

TYPE: PU 10251: maxilla with P³-M³; mandible with I₁-P₁ roots, P₃, M₁₋₃.

TABLE 2
Statistical Data on Teeth of *Isectolophus latidens*

| | N | OR | SR | M | σ | V |
|------------------|---|-----------|-----|--------------|-------------|-------------|
| P ² L | 1 | | | 8.0 | | |
| W | 1 | | | 6.1 | | |
| P ³ L | 3 | 8.2- 9.1 | 2.9 | 8.63 ± 0.26 | 0.45 ± 0.18 | 5.24 ± 2.14 |
| W | 3 | 8.1- 9.7 | 5.2 | 8.87 ± 0.46 | 0.80 ± 0.33 | 9.04 ± 3.69 |
| P ⁴ L | 5 | 8.9- 9.3 | 1.0 | 9.06 ± 0.07 | 0.15 ± 0.05 | 1.67 ± 0.53 |
| W | 5 | 10.3-11.2 | 2.3 | 10.74 ± 0.16 | 0.36 ± 0.11 | 3.40 ± 1.08 |
| M ¹ L | 6 | 10.7-11.4 | 1.6 | 11.17 ± 0.10 | 0.24 ± 0.07 | 2.15 ± 0.62 |
| W | 6 | 12.3-12.8 | 1.2 | 12.57 ± 0.08 | 0.19 ± 0.05 | 1.54 ± 0.45 |
| M ² L | 6 | 11.9-13.6 | 3.8 | 12.77 ± 0.24 | 0.58 ± 0.17 | 4.58 ± 1.32 |
| W | 6 | 13.7-14.9 | 3.2 | 14.22 ± 0.20 | 0.49 ± 0.14 | 3.42 ± 0.99 |
| M ³ L | 5 | 11.4-12.5 | 3.0 | 12.06 ± 0.21 | 0.46 ± 0.15 | 3.83 ± 1.21 |
| W | 5 | 13.8-15.1 | 3.5 | 14.46 ± 0.24 | 0.54 ± 0.17 | 3.74 ± 1.18 |
| P ₂ L | 1 | | | 8.2 | | |
| W | 1 | | | 4.2 | | |
| P ₃ L | 2 | 8.7- 8.8 | | 8.75 | | |
| W | 2 | 5.3- 5.5 | | 5.40 | | |
| P ₄ L | 4 | 8.6- 9.4 | 2.2 | 9.00 ± 0.17 | 0.34 ± 0.12 | 3.74 ± 1.32 |
| W | 4 | 6.0- 6.5 | 1.6 | 6.38 ± 0.12 | 0.25 ± 0.09 | 3.92 ± 1.39 |
| M ₁ L | 5 | 10.5-11.1 | 1.5 | 10.88 ± 0.10 | 0.23 ± 0.07 | 2.10 ± 0.66 |
| W | 5 | 6.4- 7.7 | 3.4 | 7.10 ± 0.23 | 0.52 ± 0.16 | 7.39 ± 2.34 |
| M ₂ L | 7 | 10.8-12.2 | 3.1 | 11.83 ± 0.18 | 0.48 ± 0.13 | 4.07 ± 1.09 |
| W | 7 | 7.5- 8.8 | 2.7 | 8.10 ± 0.15 | 0.41 ± 0.11 | 5.04 ± 1.35 |
| M ₃ L | 7 | 16.4-18.8 | 6.2 | 17.66 ± 0.36 | 0.95 ± 0.25 | 5.36 ± 1.43 |
| W | 7 | 7.9- 9.2 | 2.9 | 8.69 ± 0.17 | 0.45 ± 0.12 | 5.12 ± 1.37 |

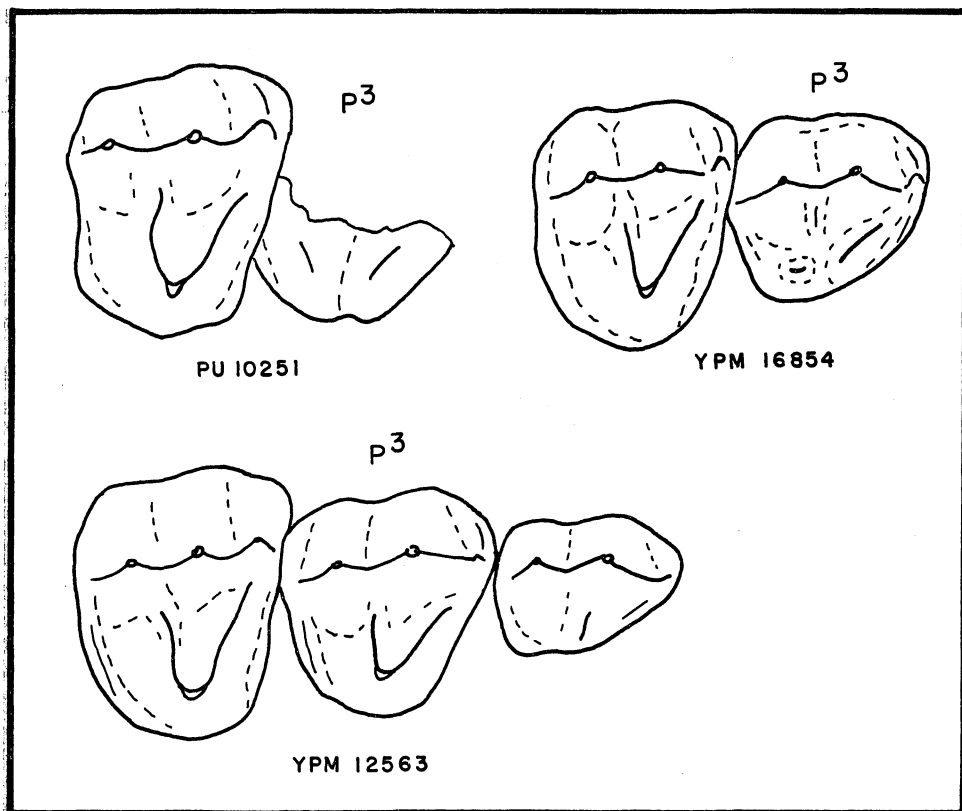


Fig. 4. Diagrammatic drawings of middle Eocene isectolophid premolars showing range of variation in development of P^3 lingual cusps. All $\times 3$. (YPM 16854 reversed.)

HYPODIGM: YPM 12563, 12901, 15297-15300, 16337, 16854; AMNH 11669-11671, 12132, 12221, 12222; USNM 22879-22881.

KNOWN DISTRIBUTION: Middle Eocene: Bridger B-D, Bridger formation, Bridger Basin, Wyoming.

DIAGNOSIS: Medium-sized isectolophids. Mean length $M_{1-3} = 40.4$ mm. P^3 with one or two lingual cusps. See Table 2.

DISCUSSION: For almost fifty years the type of *I. latidens*, PU 10251, was the only known specimen referable to that species. Then Troxell (1922a, p. 289) erected the species *Homogalax bridgerensis* for an almost complete dentition (YPM 12563); in his comparisons he made no mention of *I. latidens*. The only subsequent mention of these species was a personal communication from H. E. Wood, quoted by Van Houten, (1945, p. 457, footnote 68) which stated that *H. bridgerensis* was referable to *I. latidens*. Recent searching in many museum collections has uncovered several heretofore undescribed specimens of middle Eocene isectolophids, ranging from Bridger B through Bridger D (see hypodigm). Except for P^3 all the dentitions are virtually identical.

P^3 is preserved in only 4 specimens (see fig. 4). In YPM 12563 (the type of *H. bridgerensis*), from Bridger B-D, and in AMNH 12221, from Bridger D, P^3 is triangular in outline and looks like a smaller replica of P^4 , with only a protocone lingually. A low protoloph extends from the protocone towards the parastyle but is sharply terminated just before reaching the ectoloph. A lower metaloph extends towards the anterolingual corner of the meta-

cone; in AMNH 12221 it is incomplete. Posterior to the metaloph and lingual to the metacone there is a small basin, bounded posteriorly by a broad cingulum.

In YPM 16854 (Bridger formation, horizon unknown), P³ is shaped approximately like a 90 degree triangle with the hypotenuse forming the anterolingual side. The labial half of the tooth looks like that in the above described specimens; lingually it is not so wide. There is a low ridge (= protoloph) on the anterolingual border, lingual to the paracone. A prominent cingulum bounds a deep posterolingual basin, inside of which is a minute cuspule, an incipient hypocone. The tooth looks like a smaller replica of P³ in some specimens of *I. annectens*, except somewhat less developed lingually.

PU 10251, the type of *I. latidens*, from Bridger C-D, preserves the worn lingual half of P³, showing two well-developed internal cusps. The hypocone is slightly larger than the protocone, but both are equally lingually situated. This fragmentary tooth resembles a smaller replica of some seen in *I. annectens*.

P³ in YPM 12563 is not molariform, and is hardly advanced over the condition in *Homogalax*, while PU 10251 has a molariform P³ in essentially the same condition seen in *I. annectens*. One might question whether two such dissimilar cusp patterns could have been produced from the same gene pool, i.e., should be included in the same species. Several factors which favor this interpretation are as follows: first, all the other teeth exclusive of P³ show virtually no differences in cusp patterns between specimens. This lends weight to the theoretical argument that all were part of one interbreeding population, and to the practical argument that without P³ no specimens could be assigned to one type rather than the other. Second, both primitive and advanced P³'s are found in the same horizon (upper Bridger), and in the same sedimentary basin, and therefore cannot be separated on a stratigraphic or geographic basis. Third, the condition of P³ in YPM 16854 suggests that the transition from non-molariform to molariform was abrupt, with no gradational series of intermediate forms as is the case in the Helaletidae. This might be explained by the molarization field theory expounded by Butler (1939, p. 2), by postulating that a molarization field extended anteriorly only for a certain period of time during ontogeny. If the P³ enamel organ were forming at the right time, it would be influenced by the field and conform to a molariform (i.e., with two internal cusps) pattern. If the enamel organ were formed slightly earlier or later (with P⁴) it would not be influenced by the field and would be shaped as a simple premolar. Control of the time of formation of the enamel organ, directly or indirectly, is probably genetic, and would vary within a population. Thus slight intraspecific genotypic variation might allow very dissimilar cusp patterns to result.

For the above reasons *Homogalax bridgerensis* is here considered synonymous with *Isectolophus latidens*, and all Bridgerian isectolophids are referred to the latter species.

Future collecting of middle Eocene isectolophids with good stratigraphic data may allow differentiation between lower (B) and upper (C-D) Bridgerian forms. The scanty data available at present suggest no increase in size during Bridgerian time, but other characters, such as per cent of individuals from a given horizon with molariform P³'s, might differ significantly with time.

Isectolophus annectens Scott & Osborn, 1887

Isectolophus scotti Peterson, 1919, p. 120.

Schizolophodon cuspidens Peterson, 1919, p. 122.

Homogalax uintensis Troxell, 1922a, p. 291.

TYPE: PU 10400: P⁴, M³, M₃.

HYPODIGM: CM 2337, 2370, 2385, 2924, 3010, 3030, 3043, 3045, 3113, 9676, 11752, 11950, 11951; UFH 4, 55, 58, 72, 113, 114, 218a; AMNH 2043, 2045, 2511; YPM 12560, 12561, 12564, 14337; PU 10399, 10401; MCZ 9315; UC 31851.

KNOWN DISTRIBUTION: Late Eocene: Uinta B-C, Uinta formation, Uinta Basin, Utah.

TABLE 3
Statistical Data on Teeth of *Isectolophus annectens*

| | N | OR | SR | M | σ | V |
|------------------|----|-----------|-----|--------------|-------------|-------------|
| P ¹ L | 1 | | | 5.4 | | |
| W | 1 | | | 4.7 | | |
| P ² L | 3 | 8.7- 8.8 | 0.5 | 8.73 ± 0.04 | 0.07 ± 0.03 | 0.75 ± 0.31 |
| W | 3 | 7.2- 7.6 | 1.4 | 7.43 ± 0.12 | 0.21 ± 0.09 | 2.83 ± 1.16 |
| P ³ L | 6 | 9.2-11.1 | 4.3 | 10.33 ± 0.27 | 0.67 ± 0.19 | 6.53 ± 1.89 |
| W | 6 | 10.4-13.1 | 6.7 | 11.45 ± 0.42 | 1.04 ± 0.30 | 9.06 ± 2.62 |
| P ⁴ L | 11 | 10.0-12.1 | 3.8 | 10.88 ± 0.18 | 0.59 ± 0.13 | 5.42 ± 1.16 |
| W | 11 | 11.8-13.9 | 4.1 | 12.85 ± 0.19 | 0.63 ± 0.13 | 4.92 ± 1.05 |
| M ¹ L | 9 | 11.9-13.3 | 2.9 | 12.71 ± 0.15 | 0.45 ± 0.10 | 3.53 ± 0.79 |
| W | 9 | 12.9-15.6 | 5.1 | 14.41 ± 0.26 | 0.79 ± 0.18 | 5.48 ± 1.23 |
| M ² L | 11 | 14.0-15.6 | 3.0 | 14.79 ± 0.14 | 0.47 ± 0.10 | 3.19 ± 0.68 |
| W | 11 | 15.5-18.0 | 5.0 | 16.80 ± 0.23 | 0.77 ± 0.16 | 4.57 ± 0.97 |
| M ³ L | 14 | 13.9-17.3 | 6.0 | 15.08 ± 0.25 | 0.93 ± 0.18 | 6.17 ± 1.17 |
| W | 14 | 15.6-19.8 | 6.7 | 17.44 ± 0.28 | 1.03 ± 0.19 | 5.88 ± 1.11 |
| P ₁ L | 1 | | | 6.5 | | |
| W | 1 | | | 4.0 | | |
| P ₂ L | 2 | 8.9- 9.2 | | 9.05 | | |
| W | 2 | 5.0- 5.1 | | 5.05 | | |
| P ₃ L | 8 | 9.2-10.6 | 3.4 | 9.89 ± 0.19 | 0.53 ± 0.13 | 5.39 ± 1.35 |
| W | 8 | 5.8- 6.4 | 1.4 | 6.09 ± 0.08 | 0.22 ± 0.06 | 3.56 ± 0.89 |
| P ₄ L | 10 | 10.0-11.4 | 2.9 | 10.81 ± 0.14 | 0.44 ± 0.10 | 4.08 ± 0.91 |
| W | 10 | 6.4- 7.9 | 2.9 | 7.25 ± 0.14 | 0.45 ± 0.10 | 6.14 ± 1.37 |
| M ₁ L | 10 | 11.0-13.0 | 3.9 | 12.10 ± 0.19 | 0.60 ± 0.13 | 4.94 ± 1.11 |
| W | 10 | 7.4- 8.8 | 3.0 | 8.10 ± 0.15 | 0.47 ± 0.11 | 5.85 ± 1.31 |
| M ₂ L | 17 | 12.5-15.3 | 4.8 | 14.01 ± 0.18 | 0.74 ± 0.13 | 5.31 ± 0.91 |
| W | 17 | 8.8-10.2 | 3.4 | 9.45 ± 0.13 | 0.52 ± 0.09 | 5.50 ± 0.94 |
| M ₃ L | 13 | 19.2-22.8 | 6.7 | 20.69 ± 0.28 | 1.03 ± 0.20 | 4.99 ± 0.98 |
| W | 13 | 9.4-11.5 | 4.3 | 10.33 ± 0.19 | 0.67 ± 0.13 | 6.49 ± 1.27 |

DIAGNOSIS: Large isectolophids. Mean length $M_{1-3} = 46.8$ mm. P³ with two lingual cusps. See Table 3.

DISCUSSION: Peterson (1919) stated that two species of *Isectolophus* existed during Uintan time, distinguished by the presence or absence of a lower postcanine diastema. He erected *I. scotti* (1919, p. 120), based on PU 10401, for those specimens without a lower diastema. *I. annectens* was considered to have a long, laterally-constricted diastema because of a single specimen, AMNH 1828, which shows this feature, and which Peterson referred to the type of *I. annectens*.

AMNH 1828 consists of three lower jaw fragments. A left M₃ and a fragment of M₁ belong to *I. annectens*. A right M₂ and M₁ may be isectolophid or possibly rhinocerotoid. The third fragment consists of a laterally constricted symphysis with a long postcanine diastema and roots indicating small canines. This last piece has no contact with either of the other fragments and there is no reason to consider it as belonging to the same

individual as the M_3 . No other specimens of *Isectolophus* have a long lower post-canine diastema and it seems most probable that the symphysis of AMNH 1828 belongs to another genus, possibly the hyracodont *Triplopus*. This probability eliminates the only feature by which *I. scotti* was separated from *I. annectens* and the two species are therefore here considered synonymous.

Schizolophodon cuspidens (Peterson, 1919) is here considered to be synonymous with *Isectolophus annectens* for reasons given in the generic discussion on p. 18.

Homogalax uintensis was erected by Troxell (1922a, p. 291) for an isectolophid specimen (YPM 12561) from the Uinta Basin. Troxell compared it with *Isectolophus latidens* (his *bridgerensis*) but did not mention *I. annectens*. *Homogalax uintensis* can in no way be distinguished from *I. annectens* and therefore the two species should be considered synonymous.

Individuals of *Isectolophus annectens* from the Uinta B faunal zone are slightly smaller than those from the later Uinta C zone, indicating an increase in size with time. This is consistent with the general trend towards larger size seen in the isectolophid lineage *Homogalax-Isectolophus latidens-Isectolophus annectens* (see fig. 5). With statistical analysis of larger samples than are available at present, it may be possible consistently to separate specimens of *I. annectens* coming from Uinta B and Uinta C horizons.

P^3 in *I. annectens* varies greatly in the relative proportions of the two lingual cusps, but at present there is not enough evidence to indicate whether or not there is a consistent difference between earlier and later specimens.

Isectolophus annectens differs from *I. latidens* only in its larger size and consistent molarization of P^3 . The latter species constitutes an ideal ancestor for the former. *Isectolophus annectens* is the youngest known isectolophid; no descendants have yet been found.

FAMILY HELALETIDAE Osborn, in Osborn and Wortman, 1892

TYPE: *Helaletes* Marsh, 1872

INCLUDED GENERA: *Heptodon*, *Helaletes*, *Dilophodon*, *Colodon*.

DISTRIBUTION: Early Eocene to late Oligocene of North America; late Eocene to early Oligocene of Asia.

DIAGNOSIS: Small to medium-sized cursorial tapiroids. Dental formula $I_3^1: C_{1-0}^{1-0}: P_{4-3}^4: M_3^3$. Long post-canine diastemata. P^{1-4} tend to become molariform, with hypocone separating posteriorly from protocone. M^{1-2} metacone flattened, shortened, and lingually displaced, with labial cingulum. M^3 relatively long and narrow, with metacone reduced and metaloph shorter than protoloph. P_1 present only in early Eocene forms; P_{2-4} tend to become molariform but never develop a hypolophid. M_{1-3} metalophid greatly reduced to absent. M_3 hypoconulid short and narrow except in *Dilophodon* where it is lost. Greatly enlarged nasal incisions in middle Eocene and later forms.

DISCUSSION: Osborn (in Osborn and Wortman, 1892, p. 127) proposed the family Helaletidae to include the genera *Heptodon* and *Helaletes*. (In the latter genus he included *Dilophodon* and *Desmatotherium*.) In the same paper Osborn first used the term Helaletinae, but without diagnosis or discussion.

Wortman and Earle (1893, p. 173) divided the family Helaletidae into Helaletinae and Colodontinae. The Helaletinae were described as having a complete lower dentition (actually this is true only of *Heptodon*), with the premolars simple or some of them molariform. The Colodontinae were distinguished by the lack of I_3 (actually it is C_1 which disappears), and a tendency towards monodactylism.

In 1895 Osborn and Wortman (p. 358) included *Heptodon*, *Helaletes* and *Colodon*, with the European genus *Lophiodon* in the family Lophiodontidae. However, Hatcher (1896:161) and later writers returned to the original usage of the family Helaletidae.

Scott (in Scott and Jepsen, 1941, p. 763) placed the family Helaletidae in the superfamily Rhinoceroidea but recognized that it may be more properly referable to the Tapiroidea.

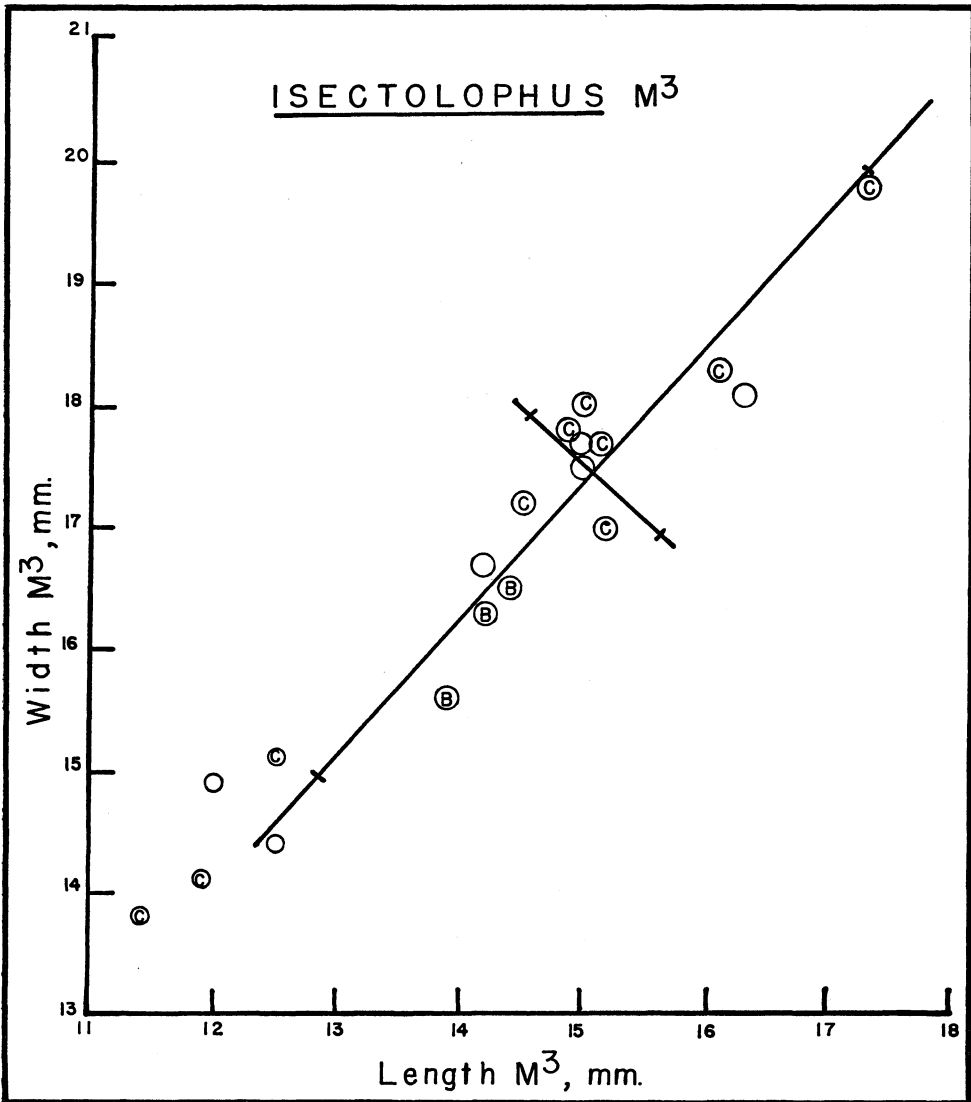


Fig. 5. Scatter diagram of length-width measurements of *Isectolophus* M³s with 95% and 99% equiprobability ellipse axes calculated for *I. annectens*. Small circles = *I. latidens*: C = Bridger C, empty circle = Bridger horizon unknown. Large circles = *I. annectens*: B and C refer to Uinta horizons, empty circle = Uinta horizon unknown.

Present knowledge of dentition indicates closer relationship of *Helaletidae* to *Isectolophidae*, *Lophiodontidae* and *Tapiridae*, than to any rhinocerotoid family (except *Hyrachyidae*, which appears equally close to *Tapiroidea*). Proboscis development in later *Helaletids* definitely indicates close affinity to *Tapiridae*. Therefore, *contra* Scott, the *Helaletidae* are here referred to the superfamily *Tapiroidea*.

Division of the *Helaletidae* into subfamilies *Helaletinae* and *Colodontinae* was followed by Peterson (1919, p. 104) and Simpson (1945, p. 140). Gazin (1956, p. 17) recognized that *Helaletes-Desmatotherium-Colodon* formed a phylogenetic sequence and argued against separation of the lineage into subfamilies. In the present revision the genera *Helaletes*

and *Colodon* are expanded to include early and late species of *Desmatotherium* respectively. This does not alter the phylogeny recognized by Gazin, since the sequence of species is still the same. The present reviewer agrees with Gazin's conclusion and finds supra-generic division of the *Helaletes-Colodon* line arbitrary and unnecessary.

Several species and genera of Asiatic tapiroids have been referred to the family Helaletidae. These forms will not be revised in the present work.

GENUS HEPTODON Cope, 1882c

Lophiodon (in part) Cope, 1880 (*nec* Cuvier)

Pachynolophus (in part) Cope, 1882a (*nec* Cuvier)

TYPE: *Heptodon ventorum* (Cope), 1880 = *H. calciculus* (Cope), 1880.

INCLUDED SPECIES: *Heptodon calciculus*, *H. posticus*.

DISTRIBUTION: Middle to late Wasatchian (early Eocene) of North America.

DIAGNOSIS: Small to medium-sized helaletids. Canines relatively large. P¹ simple; P²⁻⁴ non-molariform, with metaloph less prominent than protoloph and with only one lingual cusp, a steeply conical protocone. M¹⁻² metacones slightly convex to flat; not shortened and not as lingually displaced as in later helaletids. M³ metacone not as reduced as in later helaletids. P₁ usually present. P₂ a high elongate cusp with small median posterior cuspule. P₃₋₄ trigonids relatively high, with long paralophids. Small entoconid variably present on P₄. Nasal incision not enlarged.

HISTORY OF TAXONOMY: In 1880, Cope (p. 747) referred to the genus *Lophiodon* two new tapiroid species, *calciculus* and *ventorum*, based on material from the Wind River Basin, Wyoming. Two years later, he noted (1882a, p. 197) that the presence of P¹ excluded *L. ventorum* from *Lophiodon* and therefore referred that species and *L. calciculus* to the genus *Pachynolophus*. In the same year, Cope (1882b, p. 187) named a third species of tapiroid, *Pachynolophus posticus*, based on a specimen from the Bighorn Basin. Still later in 1882, he proposed (1882c, p. 1029) a new genus, *Heptodon*, with *L. ventorum* as type and including *calciculus* and *posticus*. These three species of *Heptodon* were first figured two years later by Cope (1884, pl. 56, 58, 58b).

Osborn and Wortman (1892, p. 127-131) and Wortman (1896, p. 84-86) gave further detailed descriptions of *Heptodon*. Except for the addition of a fourth species, *H. brownorum*, by Seton (1931, p. 45), specific taxonomy of *Heptodon* has since remained as originally proposed by Cope.

In 1875, Cope (p. 19) erected a new species, *Hyrachyus singularis*, based on a palate with P³-M³, from early Eocene strata in New Mexico. Nine years later he stated (1884, p. 653) that *Hyrachyus singularis* probably belonged to *Heptodon*, and in 1887 (p. 990) listed it as *Heptodon singularis*. Wortman (1896, p. 86), in discussing the species of *Heptodon*, remarked that *H. singularis* might prove to belong to another genus, and Matthew (*in* Osborn, 1909, p. 94) listed *Heptodon singularis* as *incertae sedis*. Wood (1934, p. 185-6), however, stated that examination of the type fully confirmed Matthew's reference of *singularis* to *Heptodon*.

Recent examination of the type and sole specimen of *H. singularis* (USNM 1106) revealed the following features: protoconule distinct on P³; M¹⁻² with distinct proto- and metaconules, metacone not flattened or lingually displaced; M³ relatively short. These characters definitely preclude inclusion of *singularis* in *Heptodon*, and suggest instead the equoid genus *Hyracotherium*.

DENTITION: I¹⁻³ are small, loosely-spaced, subequal and spatulate, with I³ slightly larger than I¹⁻². In AMNH 294 (*H. calciculus*) I¹⁻³ are higher than long; in MCZ 17670 (*H. posticus*) they are relatively smaller and, discounting effects of wear, probably relatively lower and longer.

I₁₋₃, seen in AMNH 294 and MCZ 17670, resemble the upper incisors except for somewhat greater height. Also, I₃ is relatively larger compared to I₁₋₂.

C¹ is separated from I³ by a short gap, which accommodates C₁ in occlusion. C₁ is rooted close behind I₃. C₁¹ are moderately long, slightly labiolingually compressed fangs, relatively smaller than those of *Homogalax*, and relatively large compared with later helaletids. A long diastema separates C₁¹ from P₁¹.

P¹ is a relatively small, low, elongate, two-rooted, single-cusped tooth with medial, anterior and posterior sharp edges and a very slight posterolingual widening.

P², approximately triangular in outline, exhibits a great amount of intraspecific variation. Primitive *Heptodon* P²'s, as seen in AMNH 294 (*H. calciculus*) and AMNH 14971 (*H. posticus*) have only a single labial cusp, and a small, low protoloph, hardly more than a prominent lingual cingulum, which joins the ectoloph at an angle less than 45 degrees. Advanced P²'s, seen in AMNH 14884 (*H. calciculus*) and AMNH 17524 (*H. posticus*) have two labial cusps, with metacone close to and smaller than paracone. The protoloph is a high sharp ridge which joins the ectoloph at an angle greater than 45 degrees, sometimes ranging up to 90 degrees. Posteriorly the protoloph grades into a broad flat slope which extends to the posterior and only cingulum. All gradations are seen between primitive and advanced extremes with no one condition restricted to either species or any particular horizon.

P³ is triangular in outline, with a conical metacone as large as, but still close to, the paracone. The parastyle is distinct but very small. The protoloph is high and sharp, and terminates lingually in a steeply conical protocone. A metaloph, varying from a small crista to a ridge only slightly lower than the protoloph, extends from the metacone to the protocone. Posteriorly the metaloph grades into a broad flat slope, extending to a prominent posterior cingulum. A small anterior cingulum bounds the steep anterior protoloph slope.

P⁴ is similar to P³, with a high conical protocone the only lingual cusp. It differs from the preceding tooth in being larger and relatively wider, having a more prominent parastyle, the conical metacone further apart from the paracone, and the metaloph relatively more prominent and with a narrower, steeper posterior slope.

YPM 17067, from the Lysite faunal zone, Willwood formation, Bighorn Basin, Wyoming, includes a P⁴ which deviates markedly from this simple pattern. The parastyle, paracone, metacone, and protoloph are typical for *Heptodon*. The protocone, however, instead of being steeply conical, extends as a posteriorly sloping ridge to the posterolingual corner of the almost rectangular tooth. A shallow groove on the lingual face of this ridge marks the incipient separation of hypocone from protocone. This development is typical of advanced individuals of the middle Eocene genus *Helaletes*. A still more remarkable feature of YPM 17067, however, is the extreme development of the metaloph, which is about as prominent as the protoloph, and which extends to the hypocone in the posterolingual corner of the tooth. This degree of P⁴ molarization occurs only rarely in *Helaletes* and is not fully realized in the Helaletidae until the late Eocene, in early species of *Colodon*.

YPM 17067 includes M¹⁻³ in association with the P⁴. These exhibit cusp configurations typical of *Heptodon* and cannot be distinguished from other individuals of that genus found in the same beds. In the past some students would have based new species or genera on unique features of a single tooth such as occurs in YPM 17067. For several reasons, in the present case such a course seems unrealistic and unnecessary taxonomic splitting. First, out of several dozen *Heptodon* specimens from the same beds and from synchronous strata elsewhere, no other even approximates such a molariform condition of P⁴. Second, except for P⁴, YPM 17067 is indistinguishable from other sympatric *Heptodon*, strongly suggesting that all were part of one interbreeding population. Third, the evidence from all other helaletids suggests a basic evolutionary trend in the family toward increasing premolar molarization, with early Eocene species characterized by simple premolars, and the type of P⁴ seen in YPM 17067 not appearing until the middle or more probably late Eocene. Recognizing YPM 17067 as a distinct species would be inconsistent with the phylogenetic history suggested by all other known specimens. Therefore, in accord with modern taxonomic practice, which treats a species as a population of variable individuals,

the P^4 of YPM 17067 is considered an aberration, due to an advanced isolated mutation, and the specimen merely an unusual member of the Lysitean *Heptodon* population, exhibiting a morphology that was later to become fixed genetically.

M^2 is rectangular in outline, with prominent parastyle, high, sharp, conical paracone, and lingually displaced, flat to slightly convex metacone. Larger specimens, especially those assigned to *H. posticus*, apparently exhibit the more convex metacones. A cingulum bounds the metacone labially. Paracone and metacone are of equal length and separated by a deep notch in the ectoloph. The metaloph is slightly shorter than the protoloph; both are high and sharp and curve posterolingually. Anterior and posterior cingula are usually present; a lingual cingulum occasionally blocks the median valley, but rarely completely girds the protocone and hypocone.

M^2 is similar to M^1 but larger.

M^3 resembles M^{1-2} anteriorly in the development of parastyle, paracone and protoloph. Posteriorly, however, it is relatively narrower, with a much shorter metaloph and shortened metacone. The squat, relatively long and narrow outline of M^3 in *Heptodon* and later helaletids differs from the trapezoidal, relatively short, wide M^3 of *Homogalax* and later isctolophids. A few specimens of *Heptodon*, such as AMNH 4855, resemble *Homogalax* in having somewhat trapezoidal M^3 's.

P_1 is a small, elongate, sharply pointed, single-rooted cusp, with a short slightly convex anterior edge and a longer, somewhat concave posterior edge. P_1 , or the appropriate alveolus, was noted in four Lysitean and sixteen Lostcabinian specimens, including extremely small and extremely large individuals, both in *H. calciculus* and *H. posticus*. P_1 was definitely determined to be absent in only four specimens, all Wind River Basin Lostcabinian, and all very small (including AMNH 4858, the type of *H. calciculus*). These available data suggest that variable loss of P_1 may have been confined to small members of the *H. calciculus* Wind River Basin Lostcabinian population. Absence of P_1 is a constant character in all later helaletids and therefore some variation towards that condition might be expected in the ancestral *Heptodon* species.

P_2 is a labiolingually compressed blade with a single main cusp (= protoconid). A very small metaconid can sometimes be distinguished halfway down the posterolingual slope. Typically, the anterior edge of P_2 is produced into a thin ridge, the paralophid, which descends and curves lingually at the front of the blade. The talonid is marked by a slight posterior widening, with a low central terminal cuspule. This incipient hypoconid is connected to the protoconid by a short thin medial ridge, the metalophid.

P_3 is elongate, with the metaconid distinct but still lower, very close and posterior to the protoconid. A prominent paralophid extends anteriorly from the protoconid and curves lingually around the pointed front of the tooth. The talonid is broad, but short and low. A weak metalophid extends back from the protoconid, or from between the protoconid and metaconid, to the low posterolabial hypoconid. Posterolingually, the talonid is basined, with no indication of an entoconid.

In P_4 the metaconid is as high as the protoconid, almost as anteriorly located, and connected to it by a short protolophid. The trigonid is shortened by the reduction of the paralophid and is essentially molariform. The talonid bears a low posterolingual hypoconid and posterolabially exhibits all gradations from a basin to a small cingular entoconid. The degree of development of the entoconid apparently varies independently and inconsistently within a given sample and therefore is valueless as a taxonomic criterion.

M_1 is elongate with the protolophid and hypolophid prominent, sharp, very slightly notched cross crests. The protoconid and hypoconid are slightly more anterior than the metaconid and entoconid respectively. The paralophid is much reduced, consisting of a short low ridge extending forward from the protoconid and around the anterior edge of the tooth. A low metalophid descends directly anteriorly from the hypoconid and usually dies out before reaching the protoconid. A low posterior cingulum rises medially into a minute hypoconulid. A faint labial cingulum is sometimes present.

M_2 is similar to M_1 , but larger.

M_3 is similar to M_{1-2} , except for the possession of a short narrow hypoconulid. The size

and shape of this posterior cusp are extremely variable and at present are of no taxonomic value.

DECIDUOUS DENTITION: DP¹ was not preserved in any specimen examined. UC 43103 had a two-rooted alveolus immediately anterior to DP².

DP³⁻⁴ are preserved in YPM 17063 (Lysitean) and AMNH 14873, 14865, UC 43703, and USNM 19780 (all Lostcabinian).

DP² is triangular in outline, with the long base forming the anterolingual side. In AMNH 14873, 14877, and 14865, there is only one labial cusp, a sharp conical paracone; in YPM 17063 and UC 43703 a very small metacone is located immediately posterior to the paracone. A small parastyle is situated at the acute anterolabial angle, and a low sharp protoloph occupies the entire anterolingual side of the tooth, joining the ectoloph at an angle less than 45 degrees. DP² differs from P² in the greater height of the protoloph where it joins the ectoloph, and the generally more acute anterolabial angle.

DP³ is molariform except for the relatively shorter proto- and metalophs, and the more lingual position of the hypocone relative to the protocone. The metacone is less convex than the paracone, slightly lingually displaced, and has a small posterolabial cingulum.

DP⁴ is a smaller replica of M¹, except relatively longer.

DP₁ was not preserved in any specimen examined. A single-rooted alveolus is present immediately anterior to DP₂ in UC 43703.

DP₂₋₄ were examined in AMNH 16861 (Lysite) and AMNH 14865, UC 43703, USNM 19780, and 19787 (all Lostcabinian).

DP₂ resembles P₂ except for a wider talonid.

DP₃ is long, narrow, and molariform except for the close proximity and slightly posterior position of the metaconid relative to the protoconid.

DP₄ is a smaller replica of M₁, except relatively longer and narrower.

Heptodon teeth closely resemble those of *Homogalax*, but may be distinguished from those of the latter genus by the following features: long postcanine diastemata, P² lingual loph more prominent; P³⁻⁴ metaloph more prominent; M¹⁻³ metacone flatter and more lingually displaced, protoloph and metaloph higher, with no trace of proto- or metaconules; M³ relatively longer and narrower, not trapezoidal, metaloph shorter than protoloph; P₂₋₄ somewhat more molariform, with trigonids relatively lower; M₁₋₃ protolophid and hypolophid better developed, metalophid less prominent, no metastylid; M₃ hypoconulid shorter and narrower.

SPECIFIC TAXONOMY: Evaluation of subgeneric taxa of *Heptodon* has been difficult due to insufficient material and inadequate stratigraphic data. The following species have been named:

Heptodon calciculus (Cope) 1880.

TYPE: AMNH 4858. Left and right rami with small P₃-M₃.

Horizon and locality: "*Bathyopsis* beds" = Lost Cabin faunal zone, Wind River formation, Wind River Basin, Wyoming.

Heptodon ventorum (Cope) 1880.

TYPE: AMNH 4850. Left ramus with medium-sized P₁-M₁.

Horizon and locality: "*Bathyopsis* beds" = Lost Cabin faunal zone, Wind River formation, Wind River Basin, Wyoming.

Heptodon posticus (Cope) 1882.

TYPE: AMNH 4687. Left and right rami with large P₃-M₃.

Horizon and locality: ? Lysite faunal zone*, Willwood formation, Bighorn Basin, Wyoming.

* The specimen label gives for horizon only "*Coryphodon* beds," which includes Gray Bull through Lost Cabin zones. Osborn (1929, p. 70) listed the type of *H. posticus* in the Lysite zone, with no explanation.

Heptodon brownorum Seton, 1931.

Type: MCZ 17670. A nearly complete skeleton, with large I_1^1 — M_3^3 .

Horizon and locality: Lost Cabin faunal zone, Wind River formation, Wind River Basin, Wyoming.

DISCUSSION: Cope (1880, p. 747) originally distinguished *Heptodon ventorum* from *H. calciculus* by its larger size, larger M_3 hypoconulid, and possession of an entoconid on P_4 . In his description of *H. posticus*, Cope (1882b, p. 187) noted its large size and gave measurements, but did not make comparisons with *H. ventorum* or *H. calciculus*.

Wortman (1896, p. 86-87) discussed the species of *Heptodon*, distinguishing *ventorum* from *calciculus* and *posticus* by the presence of an entoconid on P_4 , and *calciculus* from *posticus* by its smaller size. In addition, on the basis of referred upper dentitions, *ventorum* was separated from *calciculus* by its having two external cusps on P^2 , rather than one.

Seton (1931, p. 45-48) proposed a new species of *Heptodon*, *H. brownorum*, based on an almost complete skeleton. He distinguished it from *H. ventorum* by its larger size, relatively larger M_3 hypoconulid, M_{1-3} metalophids, and less curved superior molar series axis; from *H. calciculus* by its larger size, relatively larger M_3 hypoconulid, M_{1-3} metalophids, presence of P_1 , and antero-internal cingula on M_{1-3} ; from *H. posticus* by the relatively large M_3 hypoconulid, presence of P_1 , and less curved inferior molar series axis.

Kelley and Wood (1954, p. 362-363) referred several Lysitean Wind River Basin specimens of *Heptodon* to *ventorum* and *posticus*, but remarked that the latter might merely be a large variant of the former species. They noted that characters used in differentiating species of *Heptodon*, such as presence or absence of P_4 entoconid, relative size of M_3 hypoconulid, tooth size, and prominence of lophs and cingula, could be extremely variable within a population, and therefore should be used with caution.

Recent examination of all available *Heptodon* specimens confirmed the conclusions of Kelley and Wood (*loc. cit.*). With one exception, all criteria heretofore used to distinguish species of *Heptodon*, such as degree of separation of P^2 labial cusps, and size of P_4 entoconid, M_3 hypoconulid, M_{1-3} metalophids, and cingula show independent and continuous variation within a sample from a given locality. No significant differences were discerned in curvature of molar series axes in undistorted specimens. Cope (1884, p. 656) noted that presence or absence of P_1 was an inconstant character; in any case, incomplete preservation generally precludes determination of this feature, and the scanty data now available (see p. 85-86) is inadequate for specific diagnosis. At present, the only criterion which allows recognition of more than one species of *Heptodon* is that of size.

Lost Cabin Wind River Basin specimens include three of the four types and comprise the largest single sample of *Heptodon*. Therefore, this collection was used in an attempt to evaluate statistically the significance of size differences between types and to define limits of size variation for the species considered valid.

On the basis of length and width of upper and lower molars, over 90 per cent of Lost Cabin Wind River Basin *Heptodon* specimens may be included in one group, with the types of *H. calciculus* and *H. ventorum* representing small and large extremes respectively, with essentially continuous size gradation between them. Three specimens, including the type of *H. brownorum*, are discontinuously large, and cluster outside the boundary of an ellipse calculated to include 99 per cent of the main group (see fig. 6). The type of *H. posticus*, from the Bighorn Basin, corresponds in size to the *H. brownorum* group. Thus, on the basis of size (at present the only useful specific criterion), two species of *Heptodon* may be recognized: a common small species, including *H. calciculus* and *H. ventorum*; and a rarer large species, including *H. posticus* and *H. brownorum*. Size differences between the two groups are most conspicuous in the upper molars (see fig. 7), and progressively decrease in more anterior teeth.

Specific assignment of *Heptodon* samples from other localities often proved difficult due to insufficient material and intermediate size of specimens, which usually fell between the two Wind River Basin group means (see fig. 8). Differences in means between over-

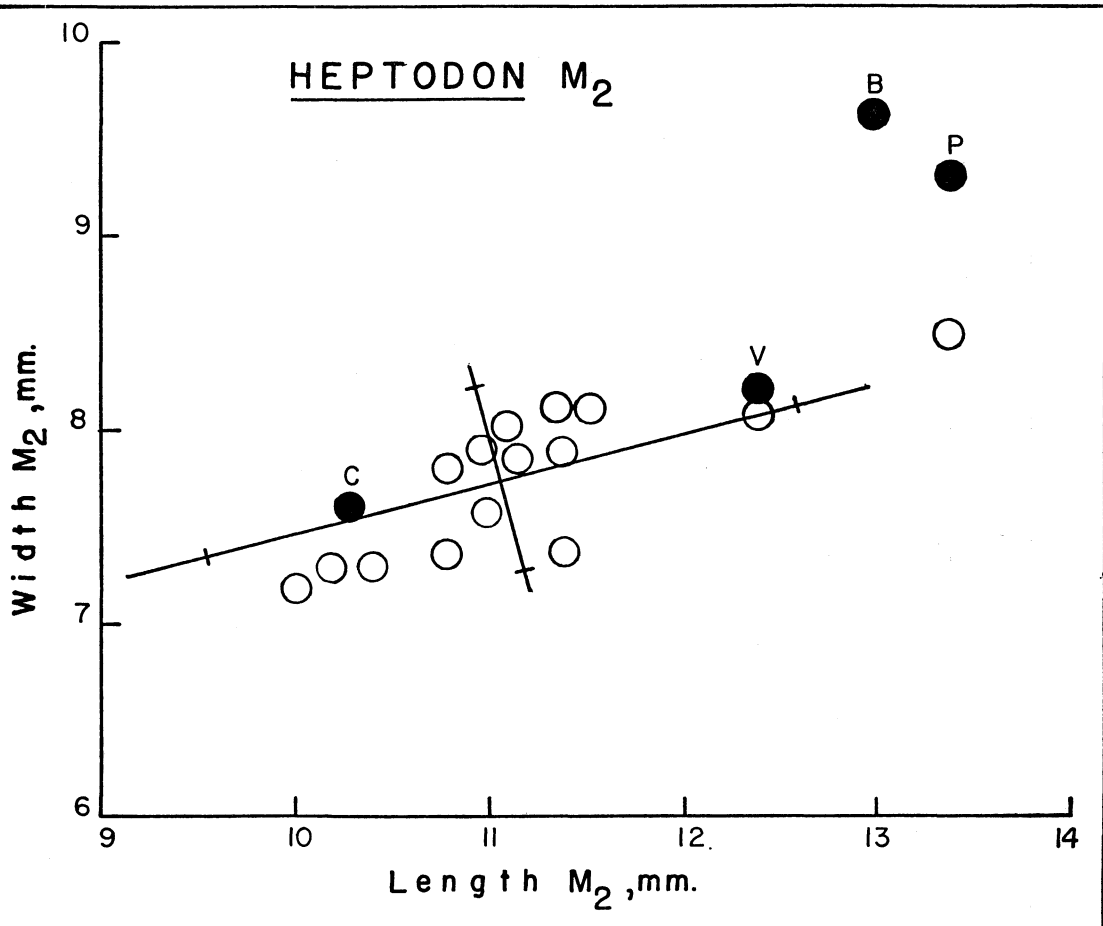


Fig. 6. Scatter diagram of length-width measurements of Lostcabinian Wind River Basin *Heptodon* M₂'s with 95% and 99% equiprobability ellipse axes calculated for the *calciculus-ventorum* group (= *H. calciculus*). Solid circles = named types: C = *H. calciculus*, V = *H. ventorum*, B = *H. brownorum*, P = *H. posticus*.

lapping samples, due to temporal or spatial separation, have been used by other workers (see *inter alia* Kitts, 1956, p. 35, Gazin, 1962, p. 79) to distinguish subspecies. Subspecific names or trinomials have not been applied in the present revision for reasons discussed in the introduction. Even if one preferred to use these somewhat dubious categories, *Heptodon* samples are not large enough to permit adequate statistical comparisons. Collections of *Heptodon* from other than type localities were referred to *H. calciculus* if they fell within the 99 per cent ellipse size limits of that species, or, if most of the specimens were larger, assigned to *H. posticus*. This somewhat arbitrary method of specific assignment seemed the only practical way to treat taxonomically such inadequate samples. No specimens differed enough to warrant recognition of a third species. The suggested specific taxonomy of *Heptodon* is as follows.

Heptodon calciculus (Cope) 1880
Plate 2, figs. 1, 6

Lophiodon calciculus Cope, 1880, p. 747.

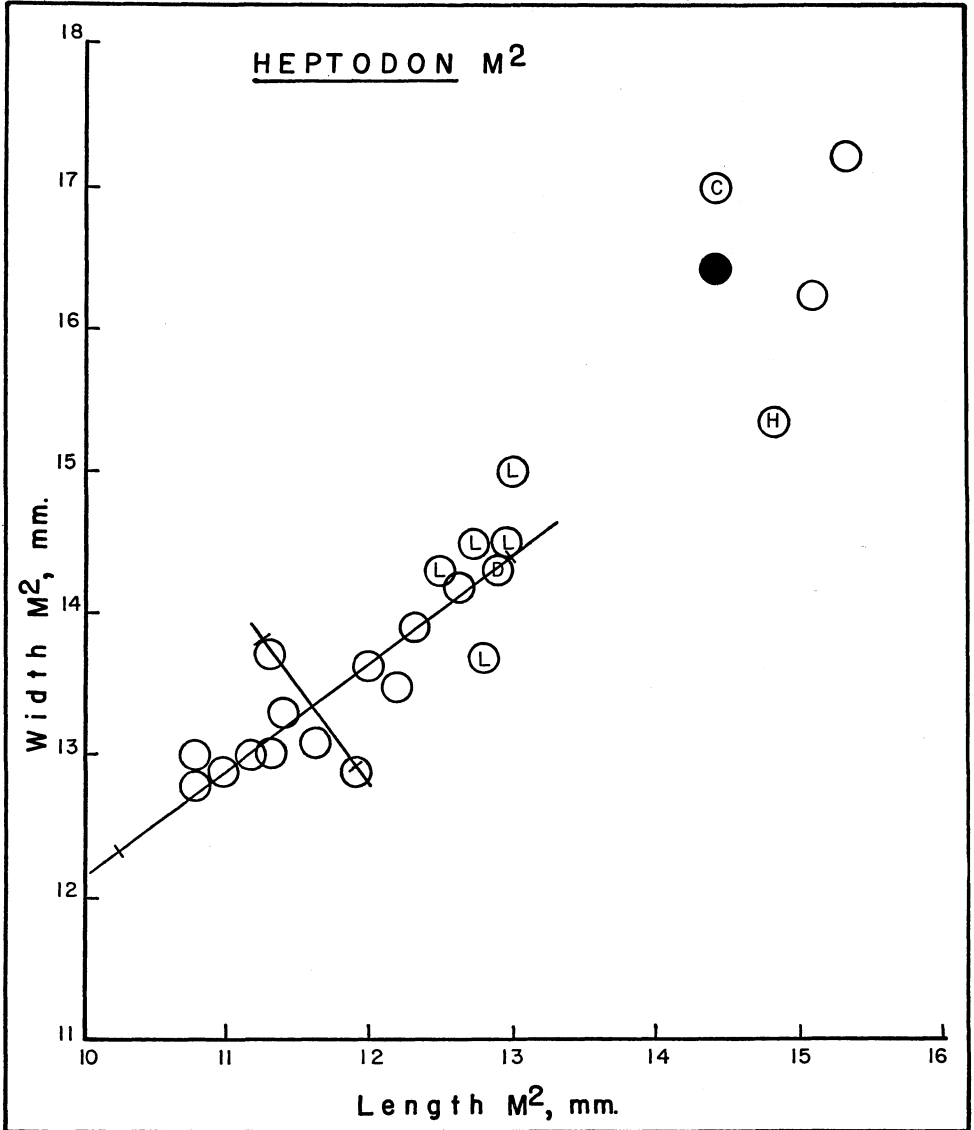


Fig. 7. Scatter diagram of length-width measurements of all known *Heptodon* M²s, showing disjunct size distribution. 95% and 99% equiprobability ellipse axes calculated for the *calciculus-ventorum* group (= *H. calciculus*). Open circles = Lost Cabin; solid circle = type of *H. brownorum*; L = Lysite; D = Dad; C = DeBeque; H = Huerfano.

Lophiodon ventorum Cope, 1880, p. 747.

Pachynolophus calciculus, Cope, 1882a, p. 197.

Pachynolophus ventorum, Cope, 1882a, p. 197.

Heptodon ventorum, Cope, 1882c, p. 1029.

Heptodon calciculus, Cope, 1882c, p. 1029.

TYPE: AMNH 4858: left and right rami with P₃-M₃.

HYPODIGM: Type and AMNH 294, 4852, 4855, 4857-4859, 14855, 14863, 14865, 14867-14870, 14872, 14873, 14875, 14876, 14882, 14884, 14885, 14970, 55524-55526; MCZ 3442, 3452, 3471, 3478; USNM 14655, 18467, 18468; PU 13440; (all Wind River Basin Lost Cabin beds).

KNOWN DISTRIBUTION: Lysite to Lost Cabin faunal zones: Willwood formation, Bighorn Basin; Wind River formation, Wind River Basin; Knight formation, Knight Station, LaBarge-Big Piney, New Fork, Dad-Baggs, Wyoming. DeBeque formation, Colorado.

DIAGNOSIS: Size small: mean length $M_{1-3} = 35.08$ mm. See Table 4.

DISCUSSION: Since characters used to distinguish *Heptodon ventorum* from *H. calciculus*, such as larger size, larger M_3 hypoconulid, and possession of P_4 entoconid, have been found to vary continuously within a sample, and since there are no other distinguishing features, the two species are here considered synonymous. *H. calciculus* and *H. ventorum* were named on the same page of the same work (Cope, 1880, p. 747), the former preceding

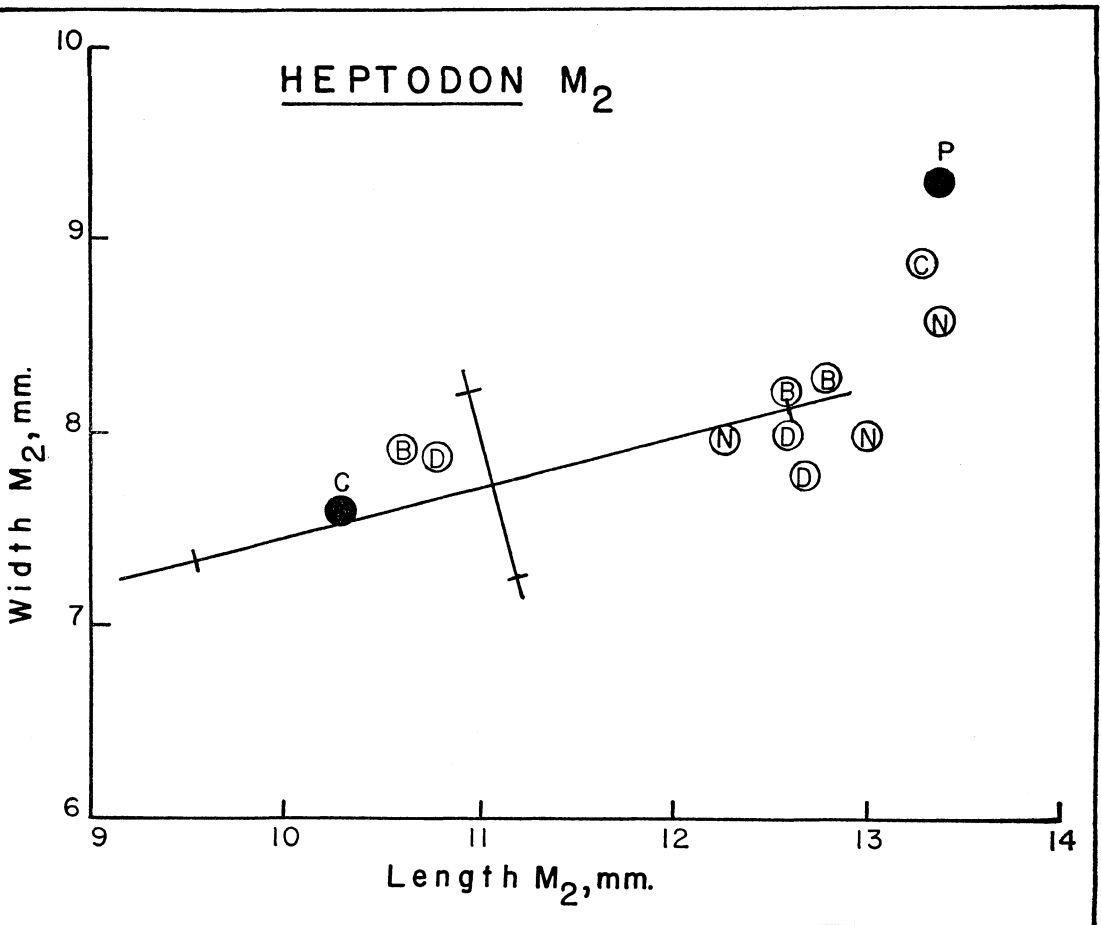


Fig. 8. Scatter diagram of length-width measurements of Lostcabinian *Heptodon* M_2 's found outside the type localities, with 95% and 99% equiprobability ellipse axes calculated for Wind River Basin *H. calciculus*. Solid circles indicate types of *H. calciculus* and *H. posticus*. Letters within circles refer to localities discussed later in text: B = LaBarge, D = Dad, N = New Fork, C = DeBeque.

TABLE 4
 Statistical Data on Teeth of Lostcabinian
Heptodon calciculus from the Wind River Basin

| | N | OR | SR | M | σ | V |
|------------------|----|-----------|-----|--------------|-------------|--------------|
| P ¹ L | 1 | | | 6.6 | | |
| W | 1 | | | 4.7 | | |
| P ² L | 4 | 6.2- 7.0 | 2.2 | 6.52 ± 0.17 | 0.34 ± 0.12 | 5.22 ± 1.84 |
| W | 4 | 6.4- 7.4 | 2.8 | 7.00 ± 0.22 | 0.43 ± 0.15 | 6.17 ± 2.18 |
| P ³ L | 6 | 7.5- 8.2 | 1.5 | 7.80 ± 0.09 | 0.23 ± 0.07 | 2.92 ± 0.84 |
| W | 6 | 9.0-10.2 | 3.1 | 9.47 ± 0.20 | 0.48 ± 0.14 | 5.02 ± 1.45 |
| P ⁴ L | 7 | 8.1- 8.9 | 2.1 | 8.37 ± 0.12 | 0.32 ± 0.09 | 3.77 ± 1.01 |
| W | 7 | 10.7-11.7 | 2.5 | 11.13 ± 0.14 | 0.38 ± 0.10 | 3.38 ± 0.90 |
| M ¹ L | 9 | 9.5-10.8 | 2.8 | 9.99 ± 0.14 | 0.43 ± 0.10 | 4.32 ± 1.02 |
| W | 9 | 11.0-13.1 | 4.2 | 11.87 ± 0.22 | 0.65 ± 0.15 | 5.47 ± 1.29 |
| M ² L | 12 | 10.8-12.6 | 3.7 | 11.51 ± 0.16 | 0.57 ± 0.12 | 4.98 ± 1.02 |
| W | 12 | 12.8-14.2 | 3.0 | 13.28 ± 0.13 | 0.46 ± 0.09 | 3.45 ± 0.70 |
| M ³ L | 9 | 10.9-12.9 | 4.0 | 11.59 ± 0.21 | 0.62 ± 0.15 | 5.38 ± 1.27 |
| W | 9 | 12.6-13.9 | 3.0 | 13.10 ± 0.15 | 0.46 ± 0.11 | 3.54 ± 0.83 |
| P ₂ L | 4 | 5.7- 6.8 | 3.1 | 6.35 ± 0.24 | 0.48 ± 0.17 | 7.55 ± 2.67 |
| W | 4 | 3.7- 5.3 | 4.3 | 4.62 ± 0.34 | 0.67 ± 0.24 | 14.49 ± 5.12 |
| P ₃ L | 11 | 7.0- 8.6 | 3.4 | 7.48 ± 0.16 | 0.53 ± 0.11 | 7.10 ± 1.51 |
| W | 11 | 4.5- 6.0 | 2.9 | 5.25 ± 0.14 | 0.45 ± 0.10 | 8.56 ± 1.83 |
| P ₄ L | 18 | 7.2- 9.2 | 4.2 | 8.21 ± 0.15 | 0.64 ± 0.11 | 7.78 ± 1.30 |
| W | 18 | 5.2- 7.0 | 3.0 | 6.18 ± 0.11 | 0.47 ± 0.08 | 7.58 ± 1.26 |
| M ₁ L | 18 | 8.9-10.7 | 3.8 | 9.61 ± 0.14 | 0.58 ± 0.10 | 6.05 ± 1.01 |
| W | 18 | 6.2- 7.8 | 2.8 | 6.93 ± 0.10 | 0.44 ± 0.07 | 6.41 ± 1.10 |
| M ₂ L | 16 | 10.0-12.4 | 4.5 | 11.08 ± 0.17 | 0.69 ± 0.12 | 6.23 ± 1.10 |
| W | 16 | 7.2- 8.2 | 2.2 | 7.74 ± 0.08 | 0.34 ± 0.06 | 4.35 ± 0.77 |
| M ₃ L | 12 | 13.3-15.7 | 5.1 | 14.39 ± 0.23 | 0.79 ± 0.16 | 5.48 ± 1.12 |
| W | 12 | 7.3- 8.8 | 3.1 | 7.91 ± 0.14 | 0.48 ± 0.10 | 6.07 ± 1.24 |

the latter. Because the type of *H. calciculus* (AMNH 4858) is a more complete specimen, it is chosen as type, and *H. ventorum* is relegated to synonymy. By virtue of this synonymy, *H. calciculus* replaces *ventorum* as type of the genus.

Almost all Wind River and Willwood Lysitean specimens of *Heptodon* fall within the size range of a single species, averaging slightly larger than the *H. calciculus* mean, but included within the predicted 99 per cent size limits of that species (see fig. 9). The samples include: YPM 17051, 17059, 17060, 17062, 17063, 17065, 17067, 17070, 17074, 17076, 17077; AMNH 2821, 4688, 15499, 15653, 15656, 16861 (all Bighorn Basin); AMNH 12832, 14871, 14879; PU 13439, 18008 (all Wind River Basin). AMNH 12840, from Knight station, and PU 16174, from near Fossil, Wyoming, considered Lysitean by Gazin (1952, p. 10), correspond in size to Wind River and Bighorn Basin Lysite material, and are included with the above-listed specimens in *Heptodon calciculus*.

Several specimens of *Heptodon* from the Lost Cabin of the Knight formation in the LaBarge-Big Piney area, Sublette County, Wyoming, were referred by Gazin (1952, p. 69) to *H. ventorum*, on the basis of size. USNM 19780, 19781, 19783-19788, and LACM 2343

(an uncrushed skull) average larger than the *H. calciculus* mean, but most specimens fall within the 99 per cent ellipses calculated for that species. Therefore, the above-listed specimens are referred to *Heptodon calciculus*.

Lost Cabin *Heptodon* specimens from beneath the Tipton tongue on the east side of the Washakie Basin, between Dad and Baggs, Carbon County, Wyoming, include UC 43703 (very small), USNM 22781 (slightly smaller than average), and USNM 22488 (relatively large), all of which fall within the size range of *H. calciculus* and are assigned to that species.

Three *Heptodon* specimens (PU 11616, 16128, and 18007) from the Hiawatha formation, Washakie Basin, Wyoming, range from medium to large within *H. calciculus* size limits, and are referred to that species.

Late Lostcabinian *Heptodon* specimens from the New Fork tongue of the Knight formation, Green River Basin, Wyoming (USNM 22775-22778) average slightly larger than the LaBarge-Big Piney sample and overlap the large end of the *H. calciculus* 99 per cent ellipse. The New Fork specimens might equally well be considered large *H. calciculus* or small *H. posticus*: Gazin (1962, p. 79) regarded the New Fork *Heptodon*

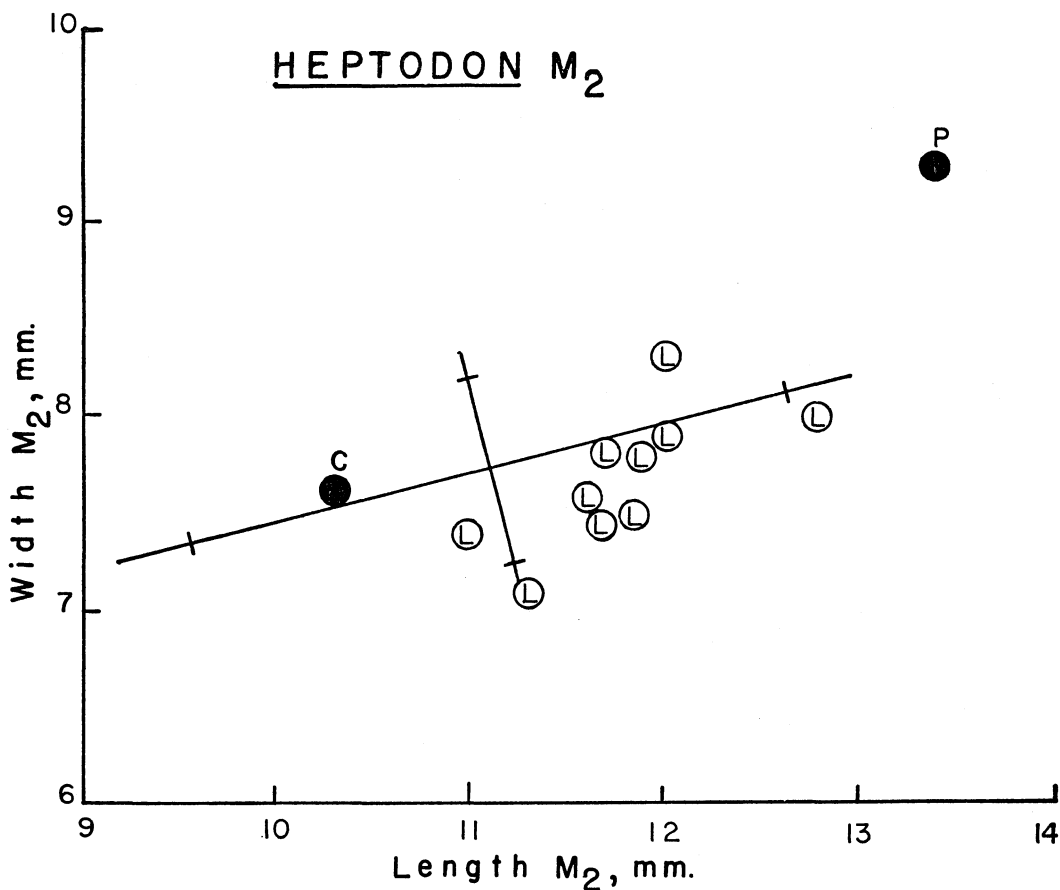


Fig. 9. Scatter diagram of length-width measurements for Lysitean *Heptodon* M₂'s with 95% and 99% equiprobability ellipse axes calculated for *H. calciculus*. Solid circles indicate types of *H. calciculus* and *H. posticus*. L refers to Lysite.

as representative of a "mutation in time" and suggested citing the sample as "*H. ventorum* mut. *posticus*." This usage is not followed in the present revision for the following reasons: the term "mutation" may signify different concepts to geneticist and taxonomist and is not recognized in formal zoological nomenclature; available data is inadequate for formal infraspecific designation of *Heptodon* samples (see discussion, p. 33).

Since the New Fork specimens so closely approximate the LaBarge-Big Piney sample, which in turn lies nearer the *H. calciculus* mean, they are here provisionally referred to *Heptodon calciculus*.

Two isolated upper molars from the Rifle member of the DeBeque formation, Mesa County, Colorado, are much smaller than the other *Heptodon* specimens in the collection. CNHM P15780 and P26625 fall near the *H. calciculus* mean and are therefore tentatively assigned to that species.

Heptodon posticus (Cope) 1882

Pachynolophus posticus Cope, 1882b, p. 187.

Heptodon posticus, Cope, 1882c, p. 1029.

Heptodon brownorum Seton, 1931, p. 45.

TYPE: AMNH 4687: left and right rami with P_s-M₃.

HYPODIGM: Type and YPM 17066, 17075, 17092 (all Bighorn Basin); MCZ 17670; AMNH 14874, 14971 (all Wind River Basin).

KNOWN DISTRIBUTION: Lysite to Lost Cabin faunal zones: Willwood formation, Bighorn Basin; Wind River formation, Wind River Basin; Knight formation, LaBarge-Big Piney, Wyoming. DeBeque formation, Colorado; Huerfano (A), Colorado.

DIAGNOSIS: Size large: mean length M₁₋₃ = 43.23 mm. See Table 5.

DISCUSSION: The type of *Heptodon brownorum*, MCZ 17670, differs in no significant way from comparable parts of the type of *H. posticus*. The latter is somewhat damaged and distorted, precluding determination of presence or absence of P₁ or molar series axis curvature. Size differences between the M₃ hypoconulids fall within the range of continuous variation observed for the genus. These were the only differences given by Seton (1931, p. 47) to distinguish *H. brownorum* from *H. posticus*. Comparison with other large specimens of *Heptodon* indicates that the differences between MCZ 17670 and AMNH 4687 are merely those of individual variation. Despite the possible earlier age of *H. posticus* and despite the fact that MCZ 17670 is the most complete specimen of *Heptodon* known, since the two cannot be separated morphologically there seems to be no alternative but to synonymize *H. brownorum* with *H. posticus*.

In contrast to the abundance of *H. calciculus*, only three specimens referable to *H. posticus* are known from the Wind River Basin Lost Cabin horizon (see hypodigm). Three large isolated upper teeth from the Wind River Lysite (Amherst 11058, 11211, 11212) fall outside of *H. calciculus* 99 per cent ellipses and may represent *H. posticus*.

Heptodon posticus is represented in the Bighorn Basin Willwood Lysite by a single M^s, YPM 17066. The only *Heptodon* specimens definitely known from the Bighorn Basin Lost Cabin zone, YPM 17075 and 17092, are referable to *H. posticus*.

One very large specimen (USNM 19779) from the Knight formation Lost Cabin beds in the LaBarge-Big Piney area, apparently represents *Heptodon posticus*.

A small collection of *Heptodon* from the Rifle member of the DeBeque formation, Mesa and Garfield Counties, Colorado, includes several large specimens (CNHM PM343, P26529, P26785, and P26846) which are best referred to *H. posticus*.

Three specimens from Huerfano (A), Huerfano formation, Colorado, (AMNH 17523, 17524, 17563) apparently represent large *Heptodon posticus*.

The provisional nature of the preceding specific taxonomy should be emphasized. On the basis of the available data it appears to represent the most logical and useful arrangement for formal reference to known specimens of *Heptodon*. However, none of the sam-

TABLE 5

Statistical Data on Teeth of *Heptodon posticus*

| | N | OR | M |
|------------------|---|-----------|-------|
| P ¹ L | 1 | — | 5.9 |
| W | 1 | — | 4.0 |
| P ² L | 2 | 7.3- 8.1 | 7.70 |
| W | 2 | 7.1- 7.4 | 7.25 |
| P ³ L | 2 | 8.5- 9.3 | 8.90 |
| W | 2 | 10.9-11.0 | 10.95 |
| P ⁴ L | 2 | 9.3- 9.4 | 9.35 |
| W | 2 | 12.2-12.3 | 12.25 |
| M ¹ L | 1 | — | 13.8 |
| W | 1 | — | 14.7 |
| M ² L | 3 | 14.4-15.3 | 14.90 |
| W | 3 | 16.2-17.2 | 16.60 |
| M ³ L | 2 | 14.0-15.0 | 14.50 |
| W | 2 | 16.1-16.5 | 16.30 |
| P ₂ L | 1 | — | 6.8 |
| W | 1 | — | 4.4 |
| P ₃ L | 2 | 8.0- 8.6 | 8.30 |
| W | 2 | 5.3- 5.7 | 5.50 |
| P ₄ L | 2 | 9.3- 9.6 | 9.45 |
| W | 2 | 6.6- 7.1 | 6.85 |
| M ₁ L | 3 | 11.5-12.1 | 11.83 |
| W | 3 | 7.8- 8.9 | 8.20 |
| M ₂ L | 3 | 13.0-13.4 | 13.27 |
| W | 3 | 8.5- 9.6 | 9.13 |
| M ₃ L | 3 | 17.3-18.9 | 18.13 |
| W | 3 | 8.1-10.0 | 9.03 |

ples of teeth are large enough to allow conclusive statistical comparisons, and virtually nothing is known of possible specific cranial and postcranial variation in this primitive tapiroid. Much more information must be evaluated before we can elucidate relationships within the complex of evolving populations of Lysitean and Lostcabinian *Heptodon*.

Remains of *Heptodon* have been found at most Lysitean and Lostcabinian localities in Wyoming and Colorado but are conspicuously absent from the contemporaneous Largo fauna in the San Juan Basin, northern New Mexico. Similarly peculiar is the geographic distribution of the condylarth *Meniscotherium*, very abundant in Largo beds, but absent from more northern Lysitean strata. Van Houten (1945, p. 444) suggested environmental interpretations based on lithology, which Simpson (1948, p. 381) applied to the problem of *Meniscotherium* distribution. Kitts (1956, p. 56) further speculated on related ecological implications of hyracothere species distribution. Such paleoecological speculation, based on evaluation of both faunal and lithological information, should be encouraged, for it may provide new insights into evolutionary problems, such as inexplicable gaps in chronologic and geographic ranges of many genera. However, present information on *Heptodon*

appears insufficient to allow much paleoecological speculation. One might suggest, for example, that the apparent shift towards smaller size in the *H. calciculus* Wind River Lost Cabin population was due to the appearance of and competitive interaction with the large hyracothere, *Hyracotherium craspedotum*, or perhaps the titanotheres *Lambdaotherium*. However, for such ideas to be meaningful, much more must be known about relationships between populations of *Heptodon* as well as those of other early perissodactyls.

GENUS HELALETES Marsh, 1872

Lophiodon Marsh, 1871 (nec Cuvier)

Dematotherium Scott, 1883

Chasmotheroides Wood, 1934

TYPE: *Helaletes boops* Marsh, 1872 = *Helaletes nanus* (Marsh), 1871.

INCLUDED SPECIES: *Helaletes nanus*, *H. intermedius*.

DISTRIBUTION: Middle Eocene of North America.

DIAGNOSIS: Small to medium-sized helaletids. Canines small. P¹ simple. P²⁻⁴ submolariform, metaloph less prominent than protoloph, tendency for hypocone to separate off from protocone. M¹⁻² metacone slightly convex to flat, slightly shortened. M³ metaloph relatively shorter and metacone not as reduced as in *Colodon*. P₁ absent. P₂₋₄ trigonids low but parolophids still long; talonids relatively narrower than in *Colodon*. Small entoconid present on P₃₋₄. Greatly enlarged nasal incisions.

HISTORY OF TAXONOMY: Marsh (1871, p. 37) briefly described a new species of tapiroid, *Lophiodon nanus*, comparing it to *Hyrachyus*. The following year, Leidy (1872, p. 20) referred two lower jaws to the latter genus under the name *Hyrachyus nanus*. He stated that his specimens perhaps belonged to Marsh's *Lophiodon nanus*, but it is not clear whether he intended to erect a new species, *Hyrachyus nanus*, or was formally referring his specimens to Marsh's *nanus* and transferring that species to *Hyrachyus*.

Also in 1872, Marsh (p. 218) defined a new genus and species of tapiroid, *Helaletes boops*, and transferred *Lophiodon nanus* to that genus. A year later, Leidy (1873, p. 67-69) published a fuller description, with illustrations, of the specimens he had referred to as *Hyrachyus nanus*. He stated again that he suspected they belonged to *Lophiodon nanus* Marsh, but made no reference to Marsh's new genus *Helaletes*.

Cope (1873, p. 605; 1884, p. 661) referred *boops* and *nanus* to *Hyrachyus*, acknowledging Marsh as the author of *boops*, but crediting Leidy with the original designation of *nanus*. *Helaletes boops* Marsh was listed by Osborn, Scott, and Speir (1878, p. 54) but no mention was made of *nanus*. Osborn (in Scott and Osborn, 1889, p. 505) confirmed Marsh's reference of *Lophiodon nanus* Marsh to *Helaletes*. In later papers, however, Osborn (in Osborn and Wortman, 1892, p. 131), Wortman and Earle (1893, p. 180), and Matthew (1899, p. 45) list *Helaletes nanus* Leidy, making no mention of Marsh's *nanus*. Peterson (1919, p. 112) acknowledged Marsh as the author of *Helaletes nanus*, but listed for the hypotype "*Hyrachyus*" *nanus* Leidy.

If Marsh's *nanus* and Leidy's *nanus* were different species, referring both to *Helaletes* would make Leidy's a homonym and therefore unacceptable. If Leidy's *nanus* were conspecific with Marsh's, as Leidy himself suggested, then *nanus* Leidy would be a junior synonym and invalid. In other words, *Helaletes nanus* (Leidy) does not exist, as Troxell (1922b, p. 556) has pointed out.

Hyrachyus nanus Leidy could only be saved if it were not congeneric with Marsh's *nanus*. Scott (1883, p. 51) referred it to *Dilophodon*. However, recent examination of Leidy's type (ANSP 10313) indicates that it is conspecific with *Helaletes nanus* (Marsh). (The evidence for this will be discussed below.) Therefore, *Hyrachyus nanus* Leidy, if indeed it was ever meant to be a new species, is invalid and must be suppressed.

Osborn, Scott, and Speir (1878, p. 51) described a new species, *Hyrachyus intermedius*, based on one specimen with M¹⁻². They distinguished it on the basis of size (intermediate

between *H. agrarius* and *H. modestus*) and "the position of the postero-external lobe, which is pushed to the posterior aspect of the tooth; this is carried so far in the last molar that the two external lobes stand on nearly the same transverse line."

Wood (1934, p. 187) stated that *Hyrachyus intermedius* was not a hyrachyid and could not be assigned to any known genus. He therefore proposed the genus *Chasmotheroidea* to receive *H. intermedius* and tentatively assigned it to the family Helaletidae.

Examination of the type of *Chasmotheroidea intermedius* revealed a close resemblance to *Helaletes nanus*, suggesting a congeneric relationship. The main morphological difference between comparable parts of *C. intermedius* and *H. nanus* is the larger size of the former species. This distinction should be considered indicative only of specific separation. Therefore, *C. intermedius* is here assigned to the genus *Helaletes*, and *Chasmotheroidea* becomes a synonym of *Helaletes*.

Desmatotherium guyotii was erected by Scott (1883, p. 46) as a new genus and species close to *Hyrachyus*. Scott listed the presence of two internal cusps on P³⁻⁴ of *Desmatotherium* as the main feature by which it differed from *Hyrachyus*. He also noted the better development of the two external cusps on P², the lack of a metastyle on P⁴, the greater similarity of the metacone to the paracone on M¹, and in M¹⁻³ the greater size of the parastyle and its closer proximity to the paracone, as features by which *Desmatotherium* differed from *Hyrachyus*. It should be noted that in these features *D. guyotii* resembles *Helaletes nanus*.

Six years later, Osborn (*in* Scott and Osborn, 1889, p. 505) without explanation synonymized *Desmatotherium* with *Helaletes*. However, again without explanation, Matthew (*in* Osborn, 1909, p. 98) listed *Desmatotherium* as a valid genus, and later writers have followed this usage.

Peterson (1919, p. 127-128) removed *Desmatotherium guyotii* from the Tapiroidea, and ranked it together with *Hyrachyus* in the rhinocerotoid family Hyracodontidae. He emphasized the degree of development of the premolars as indicating affinities to several genera of Oligocene rhinocerotoids. Later writers, however, returned *Desmatotherium* to the tapiroid family Helaletidae because of basic similarities in molar cusp patterns. It would seem at present that resemblance between tapiroid and rhinocerotoid premolar molarization may best be ascribed to parallel acquisition of similar features.

Troxell (1922b, p. 365) noted that *Desmatotherium guyotii* resembled *Helaletes boops* (= *H. nanus*) in the partial separation of the internal cusps on P³⁻⁴, the form of the molars, and the diastema anterior to C¹. (Perhaps this was a misprint for P¹, since in no known specimen of *D. guyotii* is the palate preserved anterior to C¹.) Troxell considered, however, that the features by which *Desmatotherium* differed from *Helaletes* (he listed greater size, relatively larger M³, and disproportion between the large molars and premolars) indicated at least subgeneric distinction.

Osborn (1923, p. 2) distinguished *Desmatotherium guyotii* from *Helaletes* by ". . . double internal cones in the upper premolars; in *Helaletes* these cones are single." This observation is erroneous, for only P³⁻⁴ in *D. guyotii* have two internal cusps. In *Helaletes nanus* the degree of molarization of the premolars is a variable character, but several specimens do show two internal cusps on P³⁻⁴, comparable to the condition in *D. guyotii*.

In a discussion of the late Eocene Sage Creek fauna, Hough (1955, p. 31) referred a new species of tapiroid, *kayi*, to *Desmatotherium*. She distinguished *Desmatotherium* from *Colodon*, an early Oligocene helaletid tapiroid, on the grounds that it has larger canines, smaller cheek teeth, relatively longer (anteroposteriorly) premolars, especially P⁴, and relatively smaller premolars compared to the molars. These features are based mainly on *D. guyotii* but also characterize *Helaletes nanus*.

In describing the late Eocene Badwater fauna, Gazin (1956, p. 17-19) named a new species of tapiroid *Desmatotherium woodi*. He cited the more progressive condition of the premolars as the principle feature distinguishing *Desmatotherium* from *Hyrachyus*, while noting that this feature was also seen in *Helaletes nanus*. In distinguishing *Desmatotherium* from *Helaletes nanus*, Gazin described features of *D. woodi* and *D. kayi*, listing

better separation of lingual cusps on P^{3-4} , shorter and broader lower premolars with larger entoconids. It should be noted that these features are also shared by *Colodon*.

In distinguishing *Desmatotherium* from *Colodon*, Gazin noted features mainly to be seen in *D. guyotii* alone, listing the less progressive premolars, especially P^3 , and the narrower (labiolingually) upper molars and premolars. These features are also characteristic of *Heleletes nanus*.

Examination of most of the known specimens of *Heleletes*, *Desmatotherium*, and *Colodon*, has led the present reviewer to the conclusion that *Desmatotherium guyotii* more closely resembles *Heleletes nanus* than *D. kayi* or *D. woodi*, and that these latter two species more closely approximate *Colodon*. Comparisons with *D. guyotii* are limited to the upper dentition, since no lower teeth of that species are known. The upper molars of *D. guyotii* are essentially enlarged replicas of those of *Heleletes nanus*, but are relatively longer and narrower, and have longer, less reduced metacones than those of *D. kayi*, *D. woodi*, and *Colodon*. The upper premolars of *D. guyotii* are relatively long and narrow (compared to those of late Eocene and Oligocene heleletids), and incompletely molariform, with a small metaloph, as in *Heleletes nanus* (although in *D. guyotii* the metaloph extends to the protocone). In *D. kayi* and *D. woodi*, on the other hand, P^{3-4} (P^3 is not completely known) are essentially molariform, relatively short and wide, with the metaloph extending to the hypocone and equal in size to the protoloph, as in *Colodon*. The lower teeth of *D. kayi* (not known for *D. woodi*) are smaller but otherwise virtually indistinguishable from those of *Colodon*.

For these reasons *Desmatotherium* can no longer be maintained as a distinct genus. The differences between *D. guyotii* and *Heleletes nanus*, mainly size distinctions, are better expressed on a specific level. *D. guyotii* is therefore again referred to the genus *Heleletes*, and since it is the type species of *Desmatotherium*, that genus falls into synonymy with *Heleletes*. The late Eocene species *D. kayi* and *D. woodi* are here referred to *Colodon*.

DENTITION: $I_1^1-3^3$ were not preserved in any specimens of *Heleletes* examined. Alveoli of $I_1^1-3^3$ in premaxillae of USNM 22481 and YPM 11807 are small, round, and loosely spaced. Roots of I_1-3 in ANSP 10316 are anteroposteriorly compressed and closely spaced.

C^1 in YPM 11807 (a very small *H. nanus*) is a comparatively small, low, labiolingually compressed blade, separated from I^8 by a short diastema which accommodated C_1 in occlusion. In USNM 22481 (a large *H. nanus*) C^1 appears to have been relatively larger. C^1 roots in PU 10166 (*H. guyotii* = *H. intermedius*) indicate a still relatively larger fang. Observations were too few, however, to determine whether canine size differences were due to sexual dimorphism or allometric growth, or are of taxonomic significance.

C_1 in AMNH 11645 and ANSP 10316 (large and small *H. nanus*) is small and rooted close behind I_3 .

Long diastemata separate C_1^1 from P_2^1 .

P^1 in *H. nanus* is a small, low, labiolingually compressed, single-cusped, two-rooted blade, with a slight posterolingual widening. P^1 roots in *H. intermedius* indicate a small, elongate tooth, slightly wider posteriorly.

The basic *Heleletes nanus* P^2 cusp pattern resembles an advanced *Heptodon* P^2 , roughly triangular in outline, with two distinct but closely spaced labial cusps, a very small parastyle, and a prominent posterolingually-directed protoloph. Unworn specimens exhibit a very small short metaloph extending from the anterolingual corner of the metacone towards the protoloph, anterior to a short posterior continuation of the protoloph. Five out of ten specimens examined, including the type, YPM 11807, conform to this pattern, varying mainly in size of metaloph. The other five individuals exhibit a shallow lingual groove on the protoloph, a short distance before the posterior end, apparently marking the incipient separation of protocone and hypocone. USNM 22481 displayed the most advanced P^2 , with hypocone distinct from protocone and metaloph longer than protoloph and extending to hypocone.

P^2 in PU 10166 (*Heleletes intermedius*) is triangular in outline, with well-separated

paracone and metacone, virtually no parastyle, a prominent protoloph with no lingual groove, and a broad posterior slope. The absence of a metaloph may be due to wear. The lingual half of P² preserved in YPM 15233 appears somewhat shorter and wider, but does not differ otherwise.

P³ in *Helaletes nanus* is triangular, with well-separated conical paracone and metacone, small parastyle, and prominent protoloph, which curves posteriorly at the lingual apex of the crown. In all but two of the thirteen specimens examined, a groove on the anterolingual face of the protoloph marks incipient separation of hypocone from protocone. Development of the groove varies from non-existent (YPM 11807) to deep (YPM 11080). A low, variably developed metaloph extends from the anterolingual corner of the metacone towards the posterior end of the protoloph, behind the lingual groove. Posteriorly, the metaloph grades into a broad flat shelf bounded by a well-developed posterior cingulum. In specimens such as YPM 11080, where the metaloph reaches the hypocone, it is longer than the protoloph. USNM 22481, with the most molariform P³, shows the metaloph as prominent as the protoloph and the protocone as lingual as the hypocone.

In the two P³'s known for *Helaletes intermedius*, separation of protocone and hypocone is marked, less so in YPM 15233 than PU 10166. Differing from *H. nanus*, a groove occurs on the lingual, not anterolingual, face of the protoloph, so that the hypocone is not more lingual than the protocone. Significantly different from *H. nanus* is the extension of the metaloph to the protocone, completely bypassing the hypocone.

P⁴ is triangular, with conical paracone and metacone, and small parastyle. In *H. nanus* a prominent metaloph joins the protoloph at the lingual apex of the crown; the protocone extends for a short distance posterior to this junction. In only three out of fourteen specimens examined a small groove was discernible on the lingual face of the protocone. P⁴ thus shows less tendency towards molarization than either P² or P³, the short posterior lengthening of the protocone being the main advance over the *Heptodon* condition. Posterior and anterior cingula were observed in all specimens.

In the two specimens of *H. intermedius* in which the premolars are preserved, P⁴ is more molariform than in *H. nanus*. In PU 10166 P⁴ is essentially a slightly larger, relatively wider duplicate of P³, with prominent protoloph, and small metaloph bypassing the hypocone and extending to the protocone. P⁴ in YPM 15233 is slightly less molariform in lacking a lingual groove separating hypocone from protocone. The small metaloph, as is apparently typical for the species, extends to the protocone.

M¹⁻³ essentially duplicate the pattern described for *Heptodon*; the main differences include slightly shorter, flatter (but still slightly convex) and more lingually depressed metacones, and more prominent posterolabial cingula in *Helaletes*.

In the absence of *H. intermedius* lower dentitions, the following descriptions are confined to *H. nanus*.

P₁ was not present in *H. nanus*.

P₂ is an elongate triangle with a prominent paralophid, relatively low protoconid, small metaconid posterolingual and close to the protoconid, prominent metalophid extending to the posterolabial corner, and small posterolingual basin. The slightly wider, more basined, talonid and lower trigonid mark the main advances over *Heptodon*.

P₃ is roughly triangular, with a relatively less prominent paralophid, a metaconid distinct from and not very posterior to protoconid, a low metalophid extending from protoconid to hypoconid, and a broad basined talonid with small entoconid developed from posterolingual cingulum. Except for the entoconid, this condition is essentially that of some of the more molariform individuals in the Wind River Basin Lostcabin *Heptodon calciculus* population.

Further reduction of the paralophid renders the P₄ trigonid essentially molariform, although still slightly longer and narrower. The low talonid is structured as in P₃, except that it is slightly wider and has a more prominent entoconid.

M₁₋₃ have essentially the form seen in *Heptodon*, with paralophid and metalophid perhaps slightly more reduced. M₃ hypoconulid varies greatly in length but appears to average relatively smaller than in *Heptodon*.

DECIDUOUS DENTITION: The following descriptions are based almost entirely on USNM 22893 (*H. nanus*), an uncrushed skull with virtually complete milk dentition.

DI¹⁻³ very small and spatulate. DC¹, separated from DI³ by a short gap, is a small, low, labiolingually compressed blade, with a shorter convex anterior edge and a longer, less convex posterior edge.

DP¹ is an elongate, low, labiolingually compressed blade.

DP² is roughly triangular in outline, with one main labial cusp and a small parastyle and metastyle comprising the ectoloph, and a prominent protoloph which curves posteriorly at the apex of the crown. Heavy wear on the protoloph prevents determination of presence or absence of a lingual groove. Advanced *Heptodon* DP²'s suggest that some *Heleletes* DP²'s would have a small metacone budding off from the paracone.

DP³, as in *Heptodon*, is molariform, except for relatively shorter protoloph and metaloph, and slightly more lingual position of hypocone relative to protocone. The metacone is flattened, lingually depressed, and bounded labially by a low cingulum.

DP⁴ is like M¹, but relatively longer.

DP₂ very nearly duplicates P₂.

DP₃ has a long, narrow trigonid, with a short protolophid, and a broad, molariform talonid.

DP₄ is molariform, but relatively longer and narrower than M₁.

The permanent dentition of *Heleletes* differs from that of *Heptodon* in the following features: premolars more molariform; M¹⁻³ metacones slightly shorter, flatter, and more lingually depressed; P₁ absent; M₁₋₃ with paralophid and metalophid slightly more reduced; M₃ hypoconulid slightly smaller. *Heleletes* also differs in possessing greatly enlarged nasal incisions.

Heleletes can be distinguished from *Hyrachyus*, the contemporary form it most closely resembles, by the following features: small size (*H. nanus* is smaller than any *Hyrachyus*; *Heleletes intermedius* overlaps in size only the smallest species of *Hyrachyus*); P²⁻⁴ usually more molariform; M¹⁻³ metacone with external cingulum, ectoloph less complete, metacone not extended posteriorly, parastyle usually more prominent; P₁ absent (usually present in *Hyrachyus*); P₂₋₄ more molariform; M₁₋₃ metalophid and paralophid reduced; M₃ with short hypoconulid (absent in *Hyrachyus*); greatly enlarged nasal incisions.

Molar patterns of small specimens of *Hyrachyus*, i.e. *affinis*, appear to most closely approximate those of *Heleletes*, with relatively (for *Hyrachyus*) short metacone, incomplete ectoloph, short paralophid and metalophid, and traces of an M¹⁻³ posterolabial cingulum. Should M₃ hypoconulid be lacking in *Heleletes intermedius*, most specimens of lower teeth alone would be practically indistinguishable from those of *Hyrachyus affinis*; this may account for the lack of *H. intermedius* lower dentitions.* The apparent increasing dissimilarity between *Hyrachyus* and *Heleletes* molar patterns with increasing disparity in size suggests allometric growth as a possible explanation of the dental differences between the two genera. The close resemblance of *Hyrachyus* to *Heleletes* in almost

* While this paper was in press reexamination of all hyrachyid specimens at the AMNH by the author led to the discovery of a lower jaw which seems referable to *Heleletes intermedius*. AMNH 12672, consisting of left and right rami with C₁, P₂-M₃, from Bridger D beds, Bridger Basin, Wyoming, was questionably referred by H. E. Wood (1934, p. 236) to *Ephyrachyus*, a genus very close to, if not congeneric with, *Hyrachyus*. The specimen in question resembles *Heleletes nanus* and differs from hyrachyid lower dentitions in the following features: P₁ lost; P₂₋₄ talonids relatively wide, P₃₋₄ with relatively large entoconids; M₁₋₃ metalophids reduced so that posterior cross crests are almost bilaterally symmetrical. In size AMNH 12672 fits well with *Heleletes intermedius* upper dentitions (L P₂₋₄ = 28.3 mm; L M₁₋₃ = 44.4 mm).

AMNH 12672 differs from *Heleletes nanus* lower dentitions in possessing relatively more robust canines, slightly more molariform premolars, and a greatly reduced M₃ hypoconulid. In this latter feature AMNH 12672 resembles *Hyrachyus*. However, the M₃ hypoconulid is equally reduced in some specimens of *Heleletes nanus*, in *Dilophodon*, *Colodon kayi* and the Asiatic "*Desmatotherium mongoliense*" and therefore is not a surprising feature to find in *Heleletes intermedius*.

all osteological features strongly suggests a not too distant common ancestor, for which the Lysitean *Heptodon* is ideally suited.

Helaletes nanus (Marsh), 1871
Plate 2, figs. 2, 3, 7.

Lophiodon nanus Marsh, 1871, p. 37.

Hyrachyus nanus Leidy, 1872, p. 20.

Helaletes boops Marsh, 1872, p. 218.

TYPE: YPM 11080: fragments of both maxillae with right P²-M³ and left P⁸-M².

HYPODIGM: Type and YPM 11807, 12566A, 12566B, 12578, 14350, 15226, 15243-15245, 16355, 16357, 16358, 16363; AMNH 11635, 11636, 11637, 11639, 11640, 11645, 11647, 11672, 12660, 12661, 12663, 13121, 13124, 13125, 15234, 19226, 19227, 19228; USNM 13406, 13407, 13409, 17821, 17823, 17825, 17828, 17830, 17831, 17833, 22481, 22883-22893; ANSP 10313.

KNOWN DISTRIBUTION: Bridgerian: Bridger B-D, Bridger Basin, Wyoming.

DIAGNOSIS: Size small: mean length M¹⁻⁸ = 31.6 mm. P²⁻⁴ vary greatly in degree of molarization; P⁸ metaloph extends toward incipient hypocone; protocone less lingual than hypocone. See Table 6.

DISCUSSION: The type of *Helaletes nanus* (Marsh), YPM 11080, consists of left and right maxillae with badly shattered P²-M³. Marsh based *Helaletes boops* on a partial skeleton and crushed skull and mandible, YPM 11807, with C¹-M³, and P₄-M₃. In comparing *boops* with *nanus* Marsh (1872, p. 218) wrote:

"The teeth agree in size with those of *Lophiodon nanus* Marsh, but the last upper molar has a small tubercle on the outer margin between the cusps, which appears to be wanting in the type specimen of the latter species. There are also other differences of importance. Both species doubtless belong to the same genus."

The small tubercle on the outer margin between the cusps of M³ in the type of *H. boops* represents merely a minor individual variation and is not a suitable criterion by which to distinguish species of *Helaletes*. The "other differences of importance" were not subsequently elaborated by Marsh.

It was not until almost fifty years later that a detailed comparison was made between *Helaletes nanus* (Marsh) and *H. boops*. Peterson (1919, p. 104-113), after an exhaustive description of *H. boops* based on YPM 11807, listed the following features by which *nanus* differed from *boops*:

". . . P⁸ with tetartocone more distinctly separated from the deutocone than in *H. boöps*; styles at the exit of the median valley of the superior molars smaller; cingula on anterior and posterior faces of upper molars smaller, but larger on the ectoloph near the posterior angle. Animals of the same size as *H. boöps*." (p. 113)

However, in the following paragraph this author wrote:

"For the present it is thought most prudent to continue to keep the above type specimen under a separate species as established by Marsh. The writer is, however, under the impression that the features of the specimen which vary from those of *H. boöps* may ultimately be regarded as only representing individual variation. In that case *Helaletes nanus* becomes the type of the genus and *H. boöps* Marsh and "*Hyrachyus*" *nanus* Leidy hypotypes." (p. 113)

Troxell (1922b, p. 68) distinguished *Helaletes boops* from *H. nanus* by the lack of distinctly separated lingual cusps on the premolars and a supposed difference in the configuration of the dorsal edge of the maxilla. The maxilla in *H. nanus*, according to Troxell curves strongly inward above the premolars, while in *H. boops* it rises vertically. Reexamination of the specimens has failed to substantiate Troxell's observations. The maxilla

in the type of *H. boops* is damaged and partly missing immediately above the premolars. Also, the specimen was crushed and somewhat distorted. When these factors are taken into account, the maxillae in *H. boops* and *H. nanus* actually appear very similar in structure.

YPM 11080, the type of *Helaletes nanus*, has a distinct hypocone beside the protocone on P^3 , while YPM 11807, the type of *H. boops*, has only a protocone lingually on P^3 . However, other specimens of *Helaletes* provide a gradational series of intermediate stages in premolar molarization with YPM 11080 and YPM 11807 at the opposite extremes (see fig. 10). This and the other more minor differences between the two specimens appear to be those of individual variation. Thus, Peterson (1919, p. 113) was right in his prediction. *Helaletes boops* is a synonym of *Helaletes nanus*, and *Helaletes nanus* becomes the type of the genus.

The type of *Hyrachyus nanus* Leidy, ANSP 10313, comes from Grizzly Buttes, Wyoming (= Bridger B). It consists of fragments of left lower jaw with P_3 - M_3 . ANSP 10313 differs from most specimens of *Helaletes nanus* (Marsh) in two features: the hypoconulid on M_3 is very small, and P_2 - M_3 are small. In these respects ANSP 10313 approaches *Dilophodon minusculus*. Scott (1883, p. 51) considered Leidy's *nanus* a species of *Dilophodon*. However, ANSP 10313 is closer to *Helaletes nanus* than *Dilophodon minusculus* in size of teeth and M_3 hypoconulid. Also, it was found in Bridger B beds. *Helaletes nanus* is mainly confined to lower Bridger beds (B), with only a few specimens recorded from Bridger C-D. On the other hand, *Dilophodon minusculus* is found in upper Bridger beds (C-D), and is not definitely known from Bridger B. Therefore, the stratigraphic evidence supports the assignment of ANSP 10313 to *Helaletes nanus* (Marsh). ANSP 10313 may well represent the population of *Helaletes nanus* which evolved into the animal called *Dilophodon minusculus* of later Bridger time.

There is no evidence at present for recognizing more than one species of *Helaletes* in the Bridger B fauna. Statistical analysis of length-width measurements of all Bridger B *Helaletes* yields coefficients of variation as low as might be expected in one contemporaneous species (see Table 6). No discontinuous variation in any morphological feature has been discerned. No correlation between size and degree of molarization of premolars, or any other features is evident. Therefore, all specimens of *Helaletes* known from Bridger B beds are assigned to *H. nanus*.

Helaletes nanus is fairly common in the lower part of the Bridger formation (Bridger B) but is rare elsewhere. About sixty specimens are known from Bridger B beds, while only five individuals are recorded from Bridger C-D. Therefore, *Helaletes nanus* may be considered a fairly good index fossil for early Bridgerian time.

The few specimens of *Helaletes* from Bridger C-D (YPM 15241, 15242, USNM 17820, USNM 17824, UC 55612) do not differ consistently or significantly in size or other morphological features from Bridger B *Helaletes nanus*.

Specimens referred to *Helaletes* have been found at a few localities outside of the Bridger Basin, Wyoming. P. Robinson (unpublished dissertation) listed four specimens from the Gardner Butte local fauna, Huerfano formation, Colorado, as *Helaletes* sp. cf. *boops*. YPM 16457 (P_2 - M_3) more closely resembles *Heptodon* than *Helaletes nanus* in the robust character of the teeth and the unprogressive P_3 . P_1 is absent, a feature more characteristic of *Helaletes* than *Heptodon*, but not definitely diagnostic. AMNH 17503 (P_2 - M_3) could belong to *Heptodon* or *Helaletes* on the basis of cusp configuration. Its dimensions, however, are more suggestive of *Heptodon*. AMNH 55262 (M_1 - DP_1) and YPM 16464 (M_3) could be either *Heptodon* or *Helaletes*. The Gardner Butte tapiroid may represent a form intermediate between *Heptodon* and *Helaletes*, but more material, preferably including the nasal incision, is necessary for more definite diagnosis.

A specimen in the collections of the University of Wyoming, with P^3 , M^2 - 3 , from Horse Track Anticline, (sec. 22, T27N, R97W, Fremont Co.) Wyoming, is referable to *Helaletes nanus*. The protoloph of P^3 extends posteriorly for a short distance past the metaloph (a feature which distinguishes it from *Heptodon*). The teeth are as large as the largest known from *Helaletes nanus* in the Bridger Basin.

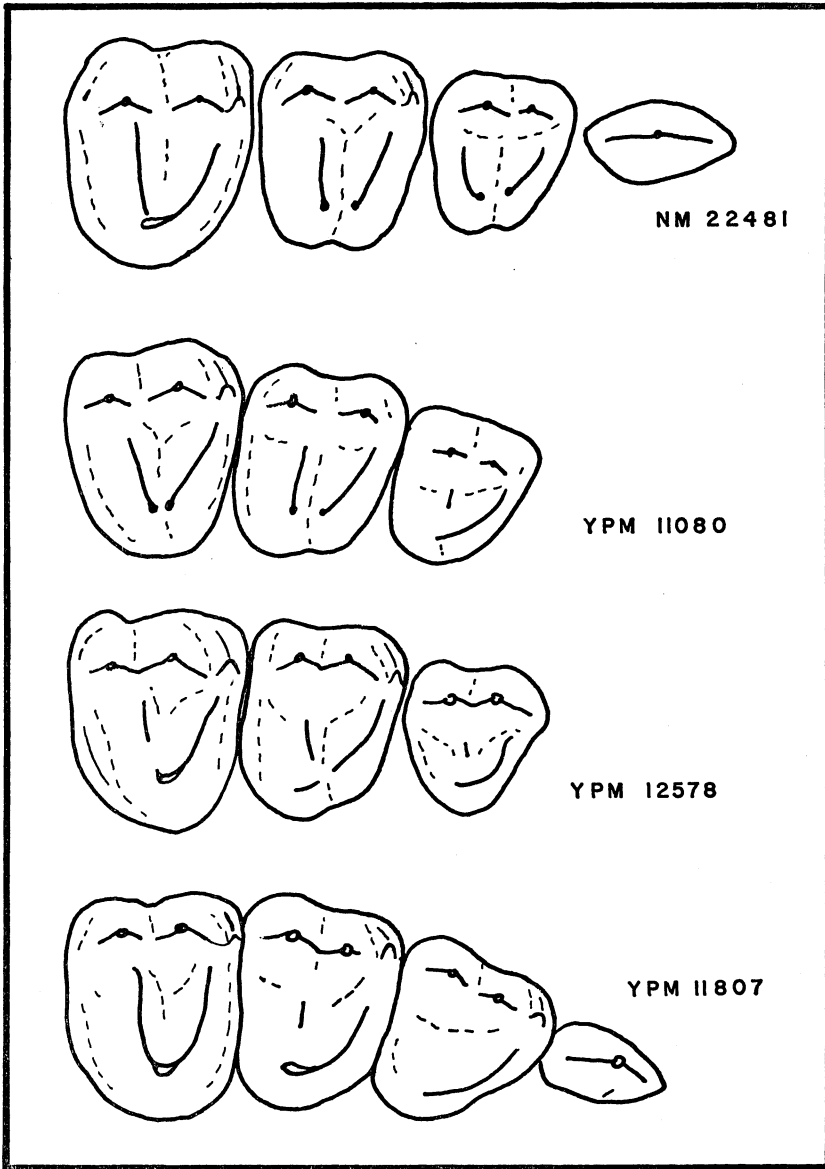


Fig. 10. Diagrammatic drawings of *Helaletes nanus* premolars showing range of variation in degree of molarization. All $\times 3$. (YPM 12578 reversed.)

Matthew (1899, p. 45) listed an unrecorded specimen of *Helaletes boops* from Dug Springs, Washakie Basin, Wyoming. The specimen on which the record was based has not been located by the present investigator, and, therefore, the validity of the claim cannot be substantiated.

Helaletes intermedius (Osborn, Scott and Speir), 1878

Plate 2, figs. 4-5.

Hyrachyus intermedius Osborn, Scott and Speir, 1878, p. 51.

Desmatotherium guyotii Scott, 1883, p. 46.

Chasmotheroides intermedius, Wood, 1934, p. 187.

TABLE 6
Statistical Data on Teeth of *Helaletes nanus*

| | N | OR | SR | M | σ | V |
|------------------|----|-----------|-----|--------------|-------------|--------------|
| P ¹ L | 8 | 5.2- 6.5 | 3.5 | 5.72 ± 0.19 | 0.54 ± 0.14 | 9.52 ± 2.38 |
| W | 8 | 3.2- 4.2 | 2.7 | 3.70 ± 0.14 | 0.41 ± 0.10 | 11.19 ± 2.80 |
| P ² L | 9 | 6.2- 7.3 | 2.4 | 6.83 ± 0.12 | 0.37 ± 0.09 | 5.39 ± 1.27 |
| W | 9 | 6.4- 8.2 | 4.2 | 7.06 ± 0.21 | 0.64 ± 0.15 | 9.01 ± 2.12 |
| P ³ L | 11 | 7.0- 8.0 | 2.6 | 7.53 ± 0.12 | 0.40 ± 0.09 | 5.27 ± 1.12 |
| W | 11 | 8.4-10.3 | 3.8 | 9.25 ± 0.17 | 0.58 ± 0.12 | 6.30 ± 1.34 |
| P ⁴ L | 12 | 7.7- 8.8 | 2.1 | 8.16 ± 0.10 | 0.33 ± 0.07 | 4.07 ± 0.83 |
| W | 12 | 8.7-11.0 | 4.1 | 9.97 ± 0.18 | 0.63 ± 0.13 | 6.34 ± 1.29 |
| M ¹ L | 13 | 8.3-10.6 | 4.6 | 9.60 ± 0.20 | 0.71 ± 0.14 | 7.37 ± 1.45 |
| W | 13 | 10.0-12.0 | 5.1 | 10.95 ± 0.22 | 0.78 ± 0.15 | 7.09 ± 1.39 |
| M ² L | 15 | 10.4-11.6 | 2.7 | 10.95 ± 0.11 | 0.41 ± 0.07 | 3.72 ± 0.68 |
| W | 15 | 10.8-13.4 | 5.6 | 11.89 ± 0.22 | 0.86 ± 0.16 | 7.27 ± 1.33 |
| M ³ L | 19 | 10.1-12.3 | 4.3 | 11.09 ± 0.15 | 0.67 ± 0.11 | 6.03 ± 0.98 |
| W | 19 | 10.7-13.3 | 5.4 | 11.79 ± 0.19 | 0.83 ± 0.13 | 7.05 ± 1.14 |
| P ₂ L | 7 | 6.2- 7.4 | 2.3 | 6.67 ± 0.13 | 0.35 ± 0.09 | 5.18 ± 1.39 |
| W | 7 | 3.6- 4.6 | 2.3 | 3.94 ± 0.13 | 0.35 ± 0.09 | 8.76 ± 2.34 |
| P ₃ L | 21 | 6.8- 8.7 | 3.0 | 7.67 ± 0.10 | 0.46 ± 0.07 | 5.96 ± 0.92 |
| W | 21 | 4.5- 5.9 | 2.3 | 5.24 ± 0.08 | 0.35 ± 0.05 | 6.59 ± 1.02 |
| P ₄ L | 27 | 7.5- 8.8 | 3.4 | 8.14 ± 0.10 | 0.52 ± 0.07 | 6.37 ± 0.87 |
| W | 27 | 5.1- 7.0 | 3.1 | 6.01 ± 0.09 | 0.48 ± 0.07 | 7.91 ± 1.08 |
| M ₁ L | 31 | 8.4-10.8 | 3.6 | 9.34 ± 0.10 | 0.55 ± 0.07 | 5.88 ± 0.75 |
| W | 31 | 5.3- 7.3 | 2.7 | 6.35 ± 0.08 | 0.42 ± 0.05 | 6.57 ± 0.83 |
| M ₂ L | 27 | 9.9-11.8 | 3.7 | 10.71 ± 0.11 | 0.57 ± 0.08 | 5.37 ± 0.73 |
| W | 27 | 6.3- 7.9 | 2.8 | 7.20 ± 0.08 | 0.43 ± 0.06 | 5.95 ± 0.81 |
| M ₃ L | 26 | 11.5-15.1 | 5.8 | 13.37 ± 0.18 | 0.90 ± 0.12 | 6.70 ± 0.93 |
| W | 26 | 6.5- 8.3 | 2.7 | 7.55 ± 0.08 | 0.42 ± 0.06 | 5.50 ± 0.76 |

TYPE: PU 10095: right M¹⁻³.

HYPODIGM: type and PU 10166 (type of *D. guyotti*), YPM 15233.

KNOWN DISTRIBUTION: Late Bridgerian: Bridger C-D, Bridger Basin, Wyoming; ? Washakie Basin, Wyoming.

DIAGNOSIS: Size large: mean length M¹⁻³ = 44.4 mm. P³⁻⁴ metaloph extends towards protocone, bypassing the hypocone. See Table 7.

DISCUSSION: The type of *Helaletes intermedius*, PU 10095, was collected in the Bridger Basin, Wyoming, by the Princeton Scientific Expedition of 1877. Osborn, Scott, and Speir (1878, p. 52) listed for the locality "Cottonwood Creek," which suggests a Bridger B horizon. However, the catalogue card for the specimens reads "Henry's Fork," a locality in Bridger C or D beds. Matthew (*in* Osborn, 1909, p. 97) records *Hyrachyus intermedius* as from the upper Bridger (horizons C-D). It seems more reasonable to assume a mistake in the 1878 publication than in the catalogue, so, following Matthew (*loc. cit.*), the horizon for PU 10095 is considered to be Bridger C-D.

TABLE 7
Measurements of Teeth of *Heleletes intermedius*

| | PU10095 | PU10166 | YPM15233 | M |
|------------------|---------|---------|----------|-------|
| P ² L | — | 9.0 | — | 9.0 |
| W | — | 9.0 | — | 9.0 |
| P ³ L | — | 11.0 | 9.4 | 10.20 |
| W | — | 12.2 | 11.6 | 11.90 |
| P ⁴ L | — | 11.2 | 10.6 | 10.90 |
| W | — | 14.1 | 13.3 | 13.70 |
| M ¹ L | 12.7 | 13.6 | 13.8 | 13.37 |
| W | 15.0 | 15.6 | 15.1 | 15.23 |
| M ² L | 14.5 | 15.3 | 15.8 | 15.20 |
| W | 16.7 | 16.4 | 16.8 | 16.63 |
| M ³ L | 15.4 | 16.5 | 15.6 | 15.83 |
| W | 16.7 | 17.0 | 17.0 | 16.90 |

The type of *Desmatotherium guyotii*, PU 10166, was recorded by Scott (1883, p. 46) as coming from "the Bridger Eocene of Wyoming Territory." However, Matthew (*in* Osborn, 1909, p. 98) listed the specimen as from the late middle Eocene of the Washakie Basin (= Washakie A). Granger (1909, p. 22) recorded *D. guyotii* as questionably from the Washakie A faunal zone. Matthew and Granger (1925a, p. 4) considered the locality of *D. guyotii* as ? Washakie, and referred to PU 10166 in a footnote on the same as follows:

"Recorded as Bridger, but it may have come from the Washakie. It has not been recognized in any of the subsequent collections from the Bridger and appears to be decidedly later in type than the Bridger lophiodonts."

Gazin (1956, p. 15) wrote:

"Originally described by Scott as coming from the Bridger Eocene, it is now understood that the type of *Desmatotherium guyotii* came from the Washakie beds (see Granger, 1909, p. 22) and is in all likelihood upper Eocene rather than Bridgerian in age."

The reasons Gazin gives for considering *D. guyotii* upper rather than middle Eocene (see p. 20, *loc. cit.*) are that *Desmatotherium* has been found in upper Eocene deposits elsewhere but has not been found in Bridgerian beds.

Gazin cited Granger (1909, p. 22) as the authority for locating the type of *D. guyotii* in the Washakie Basin. However, Granger merely listed the species as from "? Washakie A," and gave no explanation for that assignment. The other late Eocene species Gazin referred to *Desmatotherium* (*D. kayi* Hough, 1955, and *D. woodi* Gazin, 1956) more closely resemble the early Oligocene *Colodon*, while *D. guyotii* is more similar to the middle Eocene genus *Heleletes*. The type of *Heleletes intermedius*, PU 10095, here considered conspecific with *D. guyotii*, comes from late Bridgerian beds in the Bridger Basin. Also, a third specimen, YPM 15233, appears conspecific with *D. guyotii*, and probably comes from the Bridger Basin. This argument is further supported by locality evidence from *Dilophodon minusculus* (see below, p. 56), another species of tapiroid, the type of which presumably came from the same locality as *Desmatotherium guyotii*; several specimens of *Dilophodon minusculus* have been found in the Bridger Basin, in late Bridgerian strata.

Morphological evidence thus suggests a late Bridgerian age for *D. guyotii*. If the type did come from the Washakie Basin, it seems more probable that the horizon was Washakie A (= Bridger D) rather than Washakie B.

The type of *Heleletes intermedius* (PU 10095) consists of M¹⁻³; that of *Desmatotherium*

guyotii (PU 10166) includes P²-M³. On the basis of the upper molars, the former is specifically inseparable from the latter. M³ in the type of *D. guyotii* is anteroposteriorly longer than in PU 10095, but the difference in proportions is no greater than that observed between individuals of the same species, *inter alia*, *Helaletes nanus*, and is therefore considered intraspecific or individual variation. M¹⁻² exhibit no significant differences between the two types; both specimens have in common features characteristic of *Helaletes* (see generic diagnosis and discussion). Unfortunately no premolars were preserved with PU 10095, so comparison is limited to the molar teeth.

Since *Helaletes intermedius* and *Desmatotherium guyotii* cannot be separated morphologically or stratigraphically there seems no alternative but to consider them conspecific. *D. guyotii* is the more familiar name, but *intermedius* is older and therefore has priority.

The wisdom of this decision may be questioned, since the species involved are so poorly known. One might argue that it would be better to await collection of more specimens before disrupting existing taxonomy. Thus a more conservative approach would maintain *intermedius* and *guyotii* as distinct species, assigning both to *Helaletes*, or perhaps even keep them generically distinct.

However, the types of *intermedius* and *guyotii* were collected over seventy-five years ago, and subsequent intensive collecting, especially in the Bridger Basin, has failed to yield further pertinent material. Apparently they were rare animals at the sites of deposition. It is possible that unidentified or misidentified (probably called *Hyrachyus*) specimens in various museum collections actually pertain to *Helaletes intermedius*. This may account for the lack of lower dentitions, which probably greatly resembled those of *Hyrachyus*. However, examination by the author of some of the largest collections of Bridgerian mammals (AMNH, YPM, USNM) revealed only one additional specimen referable to *H. intermedius* (YPM 15233, to be discussed below; see also footnote p. 44). Therefore, availability of new material does not appear imminent.

Maintaining *intermedius* and *guyotii* as distinct species would imply a greater diversity in middle Eocene helaletids than available (although admittedly scanty) evidence suggests. Also, it would not be possible to write a specific diagnosis separating the types on more than an individual basis. Thus, after due consideration of both the inconveniences and advantages involved, it seems desirable to take positive action and modify the existing taxonomy to best reflect the morphological and stratigraphic evidence now available. Therefore, *D. guyotii* is here placed into synonymy with *H. intermedius*.

A previously undescribed specimen referable to *Helaletes intermedius* was found in the extensive Bridger collection at Yale Peabody Museum. YPM 15233 consists of a pair of maxillae, with P²-M³, and a fragment of the back of the skull. Locality data for the specimen unfortunately are poor. The accession number indicates that it arrived on September 28, 1872, from Fort Bridger, Wyoming, sent by B. D. Smith, one of Marsh's itinerant collectors. Examination of Smith's letters to Marsh revealed that in August of that year he had collected both in the Bridger Basin and at Bitter Creek in the Washakie Basin. However, on September 19, 1872, YPM received a shipment from Smith sent from Bitter Creek. It seems reasonable to assume that this accounted for the Washakie Basin specimens Smith collected, and that the later shipment, including YPM 15233, sent from Fort Bridger, probably included only Bridger Basin specimens. A Bridger Basin locality for YPM 15233 agrees with the locality date of PU 10095 and lends further weight to the suggestion that PU 10166 may also have come from the Bridger Basin.

YPM 15233 is important because it is the only specimen of *Helaletes intermedius* other than PU 10166 with premolars preserved. In P³⁻⁴ the hypocone is not as well separated from the protocone as in PU 10166, but, as in the latter specimen, the metaloph is very small and extends towards the protocone. Without more material or better stratigraphic data it is not possible to determine whether the difference in degree of premolar molarization is due to evolutionary change, PU 10166 being more recent and of a more advanced character, or to individual variation within a synchronous population. The great amount of individual variation seen in premolars of *Helaletes nanus* and other tapiroid species suggests that the latter may be the case.

M¹⁻³ of YPM 15233 differ in no significant way from those of PU 10095 and PU 10196.

The ascending walls of both maxillae of YPM 15233 are preserved and indicate that *Helaletes intermedius*, like *H. nanus*, had greatly enlarged nasal incisions. The infra-orbital canal opens on the cheek above M¹ and is only about seven mm long. This discovery supports the decision, based on similarities in dentition, that *H. nanus* and *H. intermedius* should be placed in the same genus.

Wood, Seton and Hares (1936, p. 394-5) recorded a specimen of *Desmatotherium guyotii* (= *Helaletes intermedius*) from lower Bridgerian strata in the northwestern part of the Wind River Basin, Wyoming. The specimen, presumed to be in the collections of the Museum of Comparative Zoology at Harvard, was not located for examination so the record cannot be substantiated.

Helaletes sp.

REFERRED SPECIMENS: YPM 18775-18802.

KNOWN DISTRIBUTION: Late Lostcabinian or early Bridgerian. Carter Mountain local fauna, Bighorn Basin, Wyoming.

DISCUSSION: Several isolated tapiroid teeth from the Carter Mountain local fauna exhibit cusp configurations characteristic of *Helaletes*. The teeth correspond to *H. intermedius* in size, but the upper molar metacones appear slightly more convex than in the three specimens now known for that species. Eight M³'s average somewhat relatively shorter and wider than is typical for *Helaletes nanus* or *intermedius* (see fig. 11). Several P³⁻⁴'s exhibit the same degree of molarization as in *H. intermedius*, with the hypocone budding off from the protocone and metaloph extending toward the protocone. However, several other upper premolars are less molariform than in *H. intermedius* and resemble teeth seen in some individuals of *Helaletes nanus*, or even *Hyrachyus*, with the protoloph extending around the lingual end of the tooth and the metaloph a small ridge between the metacone and protocone.

The lower teeth resemble those of *Helaletes nanus* except for larger size. Small entocoids are present on all of the P₃₋₄'s. A possible distinguishing feature may lie in the fact that not one of the eleven lower molars preserved has a hypoconulid such as occurs on M₃ of *H. nanus*. Without this posterior cusp it seems impossible to determine what jaw position an isolated lower molar occupied. A study of wear facets did not solve this problem. If any of the teeth are M₃, the lack of a hypoconulid would distinguish this species from *Helaletes nanus*, and suggest affinities to *H. intermedius* (see footnote p. 44).

The Carter Mountain tapiroid is referred to the family Helaletidae on the basis of the molar structure (metacone flattened but not lengthened, and with an external cingulum). Assignment to the genus *Helaletes* is based on molar structure (metacone flatter than in most *Heptodon*, but not as reduced as in *Colodon*), and the submolariform premolars (more molariform than in *Heptodon*, less than in *Colodon*). Resemblance to *Helaletes intermedius* is seen in the large size and some of the more molariform premolars. However, affinities to *H. nanus* are suggested by the early age (not later than early Bridgerian), some of the less molariform premolars, and perhaps the slightly convex upper molar metacones.

Present data is insufficient for adequate assessment of the relationships between the Carter Mountain tapiroid and species of *Helaletes* and *Hyrachyus*. Therefore, naming and formal diagnosis of the species will await collection of additional and more complete material.

GENUS DILOPHODON Scott, 1883

Heteraletes Peterson, 1931.

TYPE: *Dilophodon minusculus* Scott, 1883.

INCLUDED SPECIES: *Dilophodon minusculus*, *D. leotanus*.

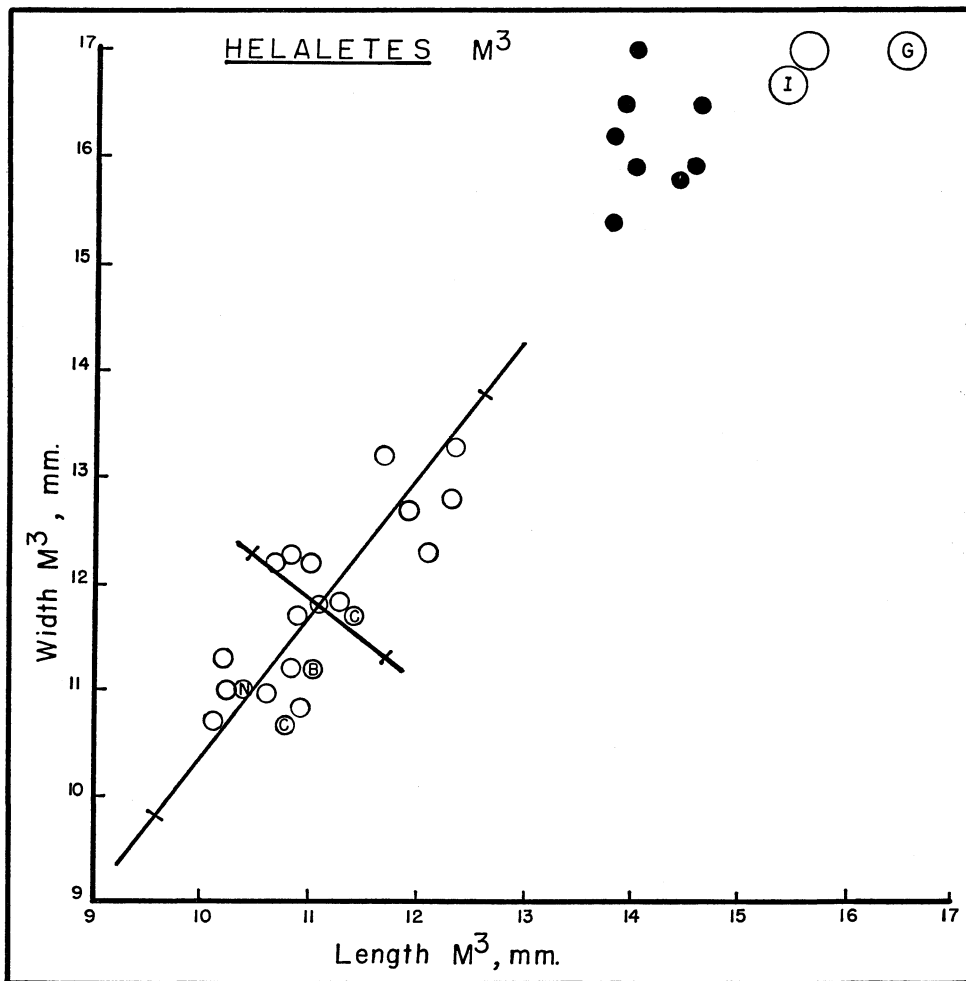


Fig. 11. Scatter diagram of length-width measurements of *Helaletes* M³'s, with 95% and 99% equiprobability ellipse axes calculated for *H. nanus*. Small circles = *H. nanus*: N = type of *H. nanus*, B = type of "H. boops," C = Bridger C; all others from Bridger B. Large circles = *H. intermedius*: I = type of *H. intermedius*, G = type of "Desmatherium guyotii." Solid circles = Carter Mountain specimens.

DISTRIBUTION: Middle to late Eocene of North America.

DIAGNOSIS: Very small helaletids. Molarization of premolars retarded relative to *Helaletes-Colodon* line. M²⁻³ metacone lingually displaced, with small labial cingulum, but slightly convex labially. Relatively short post-canine lower diastema. P₁ absent. M₃ without hypoconulid.

HISTORY OF TAXONOMY: *Dilophodon minusculus* was erected by Scott (1883, p. 51) as a new genus and species closely allied to *Hyrachyus*. Scott distinguished *Dilophodon* from *Hyrachyus* by the absence of P₁, and from *Helaletes* by the absence of a hypoconulid on M₃. He also noted the relatively short lower post-canine diastema in *Dilophodon*.

Osborn (*in* Scott and Osborn, 1889, p. 505) without explanation noted that *Dilophodon* was synonymous with *Helaletes*. Osborn and Wortman (1892, p. 131), Wortman and

Earle (1893, p. 180), and Matthew (1899, p. 45) recognized *minusculus*, but as a species of *Heleletes*.

Matthew (in Osborn, 1909, p. 98) without explanation resurrected the genus *Dilophodon* and subsequent writers have followed this usage. Peterson (1919, p. 113) considered the shorter diastema and absence of a hypoconulid on M_3 as indicative of generic separation of *Dilophodon* from *Heleletes*. Troxell (1922b, p. 365) likewise considered *Dilophodon* quite different from *Heleletes*, due to the lack of an M_3 hypoconulid, and believed it to be closer to *Hyrachyus*. In Troxell's opinion, only smaller size and absence of P_1 distinguished *Dilophodon* from *Hyrachyus*, but these differences he thought indicative of at least subgeneric separation.

Peterson (1931, p. 68) named a new genus and species of late Eocene tapiroid *Heteraletes leotanus*, basing generic characters on the molariform condition of the lower premolars. He distinguished it from *Dilophodon* by its more advanced premolars and smaller size.

Scott (1945, p. 246-247), in a review of Duchesnean mammals, quoted verbatim Peterson's (*loc. cit.*) description of *Heteraletes*.

Hough (1955, p. 29-30) pointed out that *Heteraletes leotanus* Peterson was based on a deciduous dentition, and that permanent teeth of that species did not differ generically from *Dilophodon*. She therefore placed *Heteraletes* in synonymy with *Dilophodon*, but maintained *leotanus* as a species of *Dilophodon*.

Subsequently Gazin (1956, p. 20) confirmed Hough's conclusion that *Heteraletes* was not generically distinct from *Dilophodon*, and referred *leotanus* to the latter genus.

Dilophodon minusculus dentition so closely resembles that of *Heleletes nanus* that were no younger successors to *D. minusculus* known (i.e. *leotanus*), the present reviewer would have followed earlier workers and made *Dilophodon* a synonym of *Heleletes*, referring *minusculus* to the latter genus as a somewhat aberrant short-lived offshoot. However, late Eocene tapiroids referred to *D. leotanus* exhibit increasingly smaller size, retarded premolar molarization, and convex M^{1-2} metacones, features divergent from major evolutionary trends seen in the *Heleletes-Colodon* stock. In order to express adequately the magnitude of this divergence taxonomically, the *minusculus-leotanus* line should be distinguished generically from species evolving in the *Heleletes-Colodon* group. Therefore, the genus *Dilophodon* is retained here.

DENTITION: I_1^1-3 and C_1^1 are not preserved in any *Dilophodon* specimens. C_1 roots in PU 10019 suggest a small fang.

P^1 in *D. minusculus*, preserved in YPM 16361, is relatively small, roughly oval in outline, with a low, apparently undifferentiated ectoloph, a small crista developing from the lingual cingulum, and the beginning of a posterolingual shelf. In CM 11992 (*D. leotanus*) P^1 is triangular, with a small parastyle, sharp paracone, small metastyle, and a prominent posterolingual shelf bounded by an anterolingual cingulum.

P^2 in YPM 16361 (*D. minusculus*) is triangular in outline, with small parastyle and metastyle, broad paracone and possibly a small metacone (details obscured by wear) comprising the ectoloph, a prominent protoloph and a barely discernible metaloph which trends towards the middle of the protoloph. Behind the metaloph, a broad slope and prominent cingulum form a posterior shelf. In CM 11992 (*D. leotanus*) P^2 differs in the more advanced ectoloph, with metacone prominent and distinct from paracone, and in the more prominent posterior cingulum, which bounds a relatively larger posterior shelf.

In *D. minusculus* (YPM 16361 and AMNH 1634a) P^3 is subrectangular in outline, with small parastyle and metastyle, distinct metacone and paracone, prominent protoloph which extends posteriorly for a short distance at the lingual apex, and very small metaloph extending anterolingually. In AMNH 1634a a faint groove is discernible on the anterolingual corner of the protoloph. In *D. leotanus* (CM 11992 and USNM 21098) P^3 differs by being more rectangular, with paracone and metacone more conical and distinct from the ectoloph, the posterior extension of the protoloph (or protocone) longer, with a

lingual groove isolating the posterior end as a hypocone (less obvious in the more worn USNM 21098). The small metaloph extends towards the protocone. Cingula are present on all sides.

P⁴ in *D. minusculus* (ANSP 10317) is subrectangular, with prominent paracone and slightly lingually depressed but convex metacone, prominent protoloph with very short posterolingual extension, metaloph just a small lingual crista between paracone and metacone, and wide posterior cingulum. In *D. leotanus* (CM 11992) P⁴ is slightly smaller, with a faint lingual groove indicating separation of hypocone (not seen in lingual P⁴ fragment in USNM 21098). The small metaloph is relatively more prominent than in *D. minusculus* and extends towards the protocone.

M¹⁻² resemble those of *Helalestes* in cusp pattern, differing in smaller size and less flattened metacones. *D. leotanus* differs from *D. minusculus* in smaller size and more convex metacones.

M³ in *D. minusculus* and *D. leotanus* differs from that of *Helalestes* mainly in progressively smaller size.

C₁-P₂ diastema in *D. minusculus* is shorter than in *Helalestes* and the symphysis begins anterior to P₂. In *D. leotanus* diastema length apparently is not decreased but the symphysis begins posterior to P₂, suggesting a shortening of the lower jaw.

P₂-M₃ in *D. minusculus* differ from those of *Helalestes* only in smaller size, slightly more basined premolar talonids, and absence of M₃ hypoconulid. In *D. leotanus* P₂₋₄ are advanced over those of *D. minusculus* in reduced paralophids and shortened trigonids, most noticeable in P₂. Entoconids however are still small. *D. leotanus* M₁₋₃ differ from those of *D. minusculus* in smaller size.

DECIDUOUS DENTITION: Upper milk teeth are unknown for *Dilophodon*. A complete lower deciduous dentition is preserved in CM 11849, the type of *D. leotanus*.

In CM 11849, DI₁₋₃ are small, broad, spatulate and procumbent, with DI₁ largest and DI₃ smallest. DC₁ is a small, slightly labiolingually compressed sharp fang, situated immediately posterior to DI₃.

DP₂, preserved on the right side in CM 11849, is relatively longer and narrower than P₂ in *D. leotanus*, with a longer paralophid, distinct paraconid, metaconid not distinct from protoconid, and narrower talonid.

DP₃ has the same pattern as in *Helalestes*, but is progressively smaller in *D. minusculus* and *D. leotanus*.

DP₄ is a smaller, relatively longer and narrower duplicate of M₁.

Permanent teeth of *Dilophodon minusculus* may be distinguished from those of *Helalestes nanus*, the species it most closely resembles, by the following features: smaller size; less progressive upper premolars; shorter C₁-P₂ diastema; slightly more basined lower premolar talonids; lack of M₃ hypoconulid.

Dilophodon minusculus Scott, 1883

Plate 3, fig. 3.

TYPE: PU 10019: right ramus with P₂-M₃, and symphysis.

HYPODIGM: Type and YPM 15227-15231, 16354, 16356, 16361; AMNH 1634a, 2343, 12131; USNM 17826; CM 9930; ANSP 10317.

KNOWN DISTRIBUTION: Late Bridgerian: Bridger C-D, Bridger Basin, Wyoming; Washakie Basin, Wyoming.

DIAGNOSIS: Slightly larger than *D. leotanus*. Mean length M₁₋₃ = 28.0 mm; P² with one labial cusp; P²⁻⁴ relatively unmolariform, with prominent, unnotched protoloph and very small metaloph. Symphysis begins anterior to P₂. P₂₋₄ relatively long and narrow. See Table 8.

DISCUSSION: Scott (1883, p. 51) recorded PU 10019 (the type of *D. minusculus*) as from "the Bridger Eocene of Wyoming Territory." As in the case of *Desmatotherium guyotii*,

TABLE 8

Statistical Data on Teeth of *Dilophodon minusculus* and *Dilophodon leotanus*

| | <i>D. minusculus</i> | | | <i>D. leotanus</i> | | |
|------------------|----------------------|------------|-------|--------------------|-----------|-------|
| | N | OR | M | N | OR | M |
| P ¹ L | 1 | — | 4.0 | 1 | — | 4.1 |
| W | 1 | — | 3.3 | 1 | — | 3.5 |
| P ² L | 1 | — | 5.2 | 1 | — | 4.8 |
| W | 1 | — | 5.9 | 1 | — | 5.8 |
| P ³ L | 2 | 6.0– 6.3 | 6.15 | 2 | 5.4– 5.9 | 5.65 |
| W | 2 | 7.4– 7.8 | 7.60 | 2 | 7.3– 8.0 | 7.65 |
| P ⁴ L | 2 | 6.7– 6.8 | 6.75 | 1 | — | 5.8 |
| W | 2 | 8.0– 8.4 | 8.20 | 1 | — | 7.8 |
| M ¹ L | 2 | 7.6– 8.6 | 8.10 | 1 | — | 7.0 |
| W | 2 | 9.1– 9.5 | 9.30 | 1 | — | 8.4 |
| M ² L | 1 | — | 9.5 | 0 | — | — |
| W | 1 | — | 10.2 | 0 | — | — |
| M ³ L | 2 | 9.0– 9.3 | 9.15 | 5 | 8.6– 9.1 | 8.86 |
| W | 2 | 10.2– 10.4 | 10.30 | 5 | 9.3– 10.4 | 10.10 |
| P ₂ L | 1 | — | 5.5 | 2 | 4.1– 4.8 | 4.45 |
| W | 1 | — | 3.5 | 2 | 3.1– 3.6 | 3.35 |
| P ₃ L | 4 | 6.5– 7.5 | 6.92 | 2 | 5.1– 5.8 | 5.45 |
| W | 4 | 4.5– 5.3 | 4.78 | 2 | 4.1– 4.6 | 4.35 |
| P ₄ L | 5 | 6.9– 7.2 | 7.06 | 2 | 5.7– 6.0 | 5.85 |
| W | 5 | 5.2– 5.8 | 5.56 | 2 | 4.7– 5.1 | 4.90 |
| M ₁ L | 4 | 7.8– 8.5 | 8.15 | 3 | 6.9– 7.2 | 7.10 |
| W | 4 | 5.3– 5.7 | 5.43 | 3 | 4.8– 5.2 | 4.93 |
| M ₂ L | 6 | 8.6– 9.5 | 9.12 | 3 | 7.4– 8.6 | 8.00 |
| W | 6 | 5.9– 6.3 | 6.18 | 3 | 5.1– 6.0 | 5.57 |
| M ₃ L | 6 | 10.5– 11.2 | 10.78 | 3 | 9.6– 10.6 | 10.07 |
| W | 6 | 6.3– 6.8 | 6.52 | 3 | 6.1– 6.7 | 6.43 |

most later writers, including Matthew (*in* Osborn, 1909, p. 98), Granger (1909, p. 22), and Gazin (1956, p. 20), considered the locality Washakie Basin. Gazin (*loc. cit.*) wrote:

“It is clear that Scott regarded the Washakie beds as Bridger and it is from the Washakie Basin rather than the Bridger Basin, as indicated by Granger (1909, p. 22) that the *D. minusculus* type originated. Granger has the species listed as representing Washakie A, but I suspect that the horizon for this, as well as *D. guyotii*, is B, particularly since both are known from the upper Eocene elsewhere and neither has turned up in the rather extensive collections known from the Bridger proper.”

According to Scott's memoirs (1939, p. 77), in 1878, when the *D. minusculus* type was found, he regarded the Washakie beds as part of the Bridger formation. However, the 1878 expedition collected both in the Washakie and Bridger Basins (*loc. cit.* p. 77, 81). Granger (1909, p. 22) gave no evidence or reasons for assigning *D. minusculus* to the Washakie rather than the Bridger Basin. The locality is important because the Bridger Basin contains only middle Eocene strata, while the Washakie beds range from middle to late Eocene.

In the course of the present investigation, thirteen previously undescribed specimens of *Dilophodon* were found in Bridger Basin collections (see hypodigm), with available locality data indicating Bridger C-D horizons. One specimen (AMNH 2343) is recorded from the Washakie Basin. PU 10019 closely resembles the middle Eocene specimens and is clearly distinct from the late Eocene *Dilophodon leotanus* (see specific diagnoses). Therefore, morphological evidence suggests a late Bridgerian age for *D. minusculus*. If PU 10019 was collected in the Washakie Basin, the horizon probably was Washakie A (= Bridger D) rather than Washakie B, as Gazin suggested.

All available stratigraphic data for *Dilophodon minusculus* confine the species to late Bridgerian (Bridger C-D) horizons. Interestingly enough, *Heteralestes nanus*, the most closely related species (= possible competitor) and probable ancestor, is virtually confined to early Bridgerian (Bridger B) strata, so the two species were essentially allochronous.

Dilophodon leotanus (Peterson), 1931

Plate 3, figs. 1-2.

Heteralestes leotanus Peterson, 1931, p. 68.

TYPE: CM 11849: lower jaw with deciduous dentition.

HYPODIGM: Type and USNM 20207, 20208, 21098, 22894, 22895; CM 9560, 11772, 11992.

KNOWN DISTRIBUTION: Late Uintan: Uinta C and Randlett horizons, Uinta Basin, Utah; Badwater area, Wind River Basin, Wyoming; Sage Creek, Montana.

DIAGNOSIS: Slightly smaller than *D. minusculus*. Mean length $M_{1-3} = 25.1$ mm. P^3 with 2 labial cusps; P^{3-4} submolariform, with hypocone barely separate from protocone, and metaloph directed towards protocone. Symphysis begins posterior to P_2 . P_{2-4} relatively shorter and wider than in *D. minusculus*. See Table 8.

DISCUSSION: Peterson (1931, p. 68) based generic characters of *Heteralestes leotanus* on molariform premolars of CM 11849, actually a deciduous dentition. In describing permanent teeth of *D. leotanus*, Hough (1955, p. 30) noted:

"They show no differences of generic rank either in size or character of the premolars from *Dilophodon*. In fact, they are barely separable specifically from *D. minusculus* on the basis of the lower jaw. Peterson's species is retained, however, because of the difference in age and locality and the fact that upper dentition is not certainly known. . . ."

Dilophodon leotanus averages smaller than *D. minusculus*, but the size difference is within possible specific limits (see fig. 12). The more molariform upper premolars of *D. leotanus*, however, confirm the evidence of shortened lower premolar trigonids (especially P_2) indicating specific distinction from *D. minusculus*.

The exact stratigraphic position of CM 9560, the only Sage Creek *Dilophodon* specimen (excluding the problematical CM 717), is uncertain. Hough (1955, p. 29) considered it late Eocene, and, with the Badwater Creek specimens, synchronous with the Randlett early Duchesnean *D. leotanus* type. Gazin (1956, p. 5-7) suggested that the Randlett fauna was Uintan, close to, if not correlative with, Uinta C. Comparisons between *Dilophodon* specimens from Uinta C, Randlett, Badwater, and Sage Creek faunas suggest that all are conspecific. The admittedly few specimens provide no evidence for evolutionary change between the above-mentioned faunas and therefore do not confirm a relatively later age for any one of them. Thus, available evidence suggests only a late Uintan age for *Dilophodon leotanus*.

Dilophodon sp. indet.

An isolated M^1 or M^2 from the Tapo Ranch fauna (CIT locality 180) of the Sespe late Eocene in California was referred by Stock (1936, p. 260) to *Dilophodon*. CIT no. 1949 corresponds in size to *Dilophodon minusculus* and, from the photograph (*loc. cit.*, pl. 1,

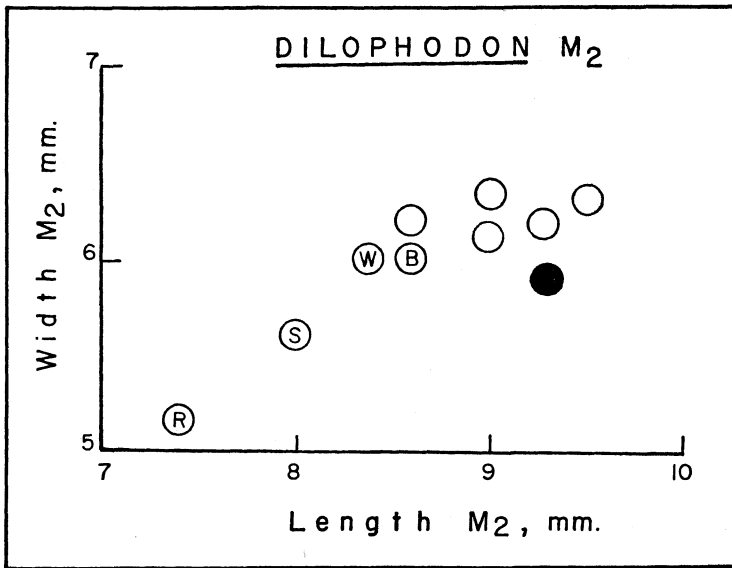


Fig. 12. Scatter diagrams of length-width measurements of *Dilophodon* M₂'s. Open circles = *D. minusculus* from Bridger C-D; solid circle = type of *D. minusculus*; W = *D. minusculus*, Washakie horizon unknown. All others = *D. leotanus*: B = Badwater; S = Sage Creek; R = type of *D. leotanus*, Randlett horizon.

fig. 1) appears to have an unshortened slightly convex metacone, as in *D. minusculus*, but less reduced than in *D. leotanus*. Conspecificity with *D. minusculus* is unlikely in view of the later age of CIT no. 1949; more definite specific allocation should await collection of further material.

Gazin (1956, p. 7) correlated the Tapo Ranch horizon with the Badwater beds as late Uintan. CIT no 1949 serves to extend the geographic range of *Dilophodon* to the West Coast in late Eocene time.

GENUS COLODON Marsh, 1890

Lophiodon Leidy, 1868 (nec Cuvier)

Desmatotherium Hough, 1955 (nec Scott)

Desmatotherium Gazin, 1956 (nec Scott)

TYPE: *Colodon luxatus* Marsh, 1890 = *Colodon occidentalis* (Leidy), 1868.

INCLUDED SPECIES: *Colodon kayi*, *C. woodi*, *C. occidentalis*, *C.?* *cingulatus*, *C.?* *hancocki*, Asiatic forms.

DISTRIBUTION: Late Eocene to late Oligocene of North America. Late Eocene to early Oligocene* of Asia.

REVISED DIAGNOSIS: Medium-sized to large helaleitids with relatively short, wide cheek teeth. Canines small or absent. P¹ with lingual loph or cusp; P²⁻⁴ essentially molariform, protocone and hypocone more or less well separated, metaloph as prominent as proto-loph and extending to hypocone. M¹⁻³ metacone flat to concave, more lingually displaced and shortened than in *Helaletes*. P₁ absent. P₂₋₄ with wide talonids and relatively large entoconids. Greatly enlarged nasal incisions with reduced nasals.

HISTORY OF TAXONOMY: Leidy (1868, p. 232) established the species *Lophiodon occidentalis* on an isolated M₃ from early Oligocene beds in Nebraska or South Dakota. Sev-

* Ardyn Obo fauna, Mongolia.

eral years later, Marsh (1890, p. 524) named a new genus and species of early Oligocene tapiroid, *Colodon luxatus*, describing it as follows:

"The present genus (*Colodon*) appears to be nearly allied to *Lophiodon* but may be distinguished from it by the upper premolars having two inner cones, and by the absence of canines in the lower jaws. The upper and lower true molars are of the same general structure as those of *Lophiodon*. From *Hyrachyus*, of the Eocene, the upper premolars, the absence of canines below, and the last lower molar with a posterior lobe, will separate it."

Shortly thereafter, Wortman and Earle (1893, p. 173-4) referred *Lophiodon occidentalis* Leidy to *Colodon*. Later writers erected several Oligocene species of *Colodon*, most of which have been relegated to synonymy.

Hough (1955, p. 31) proposed the species *Desmatotherium kayi* for several specimens of a late Eocene helaetid. In distinguishing *Desmatotherium* from *Colodon*, Hough mainly cited features of *Desmatotherium guyotii*, a species in the present work considered synonymous with *Helaletes intermedius*. In referring to *D. kayi*, Hough wrote:

"It is a question . . . into which genus (*Desmatotherium* or *Colodon*) the species falls, but from the very incomplete material on hand the Sage Creek species seems near *Desmatotherium*." (p. 32)

The following year, Gazin (1956, p. 17) proposed another species of late Eocene helaetid, *Desmatotherium woodi*, distinguishing it from *D. kayi* by its smaller size. In contrasting *Desmatotherium* with *Colodon*, Gazin also used mainly features of *Desmatotherium guyotii* (= *Helaletes intermedius*).

As discussed in the section on *Helaletes* (p. 42), recent examination of all pertinent specimens suggests that *D. kayi* and *D. woodi* more closely resemble *Colodon* than *Helaletes intermedius*. The upper molars of *kayi* and *woodi* essentially duplicate in miniature those of *Colodon occidentalis*, but are relatively shorter and wider, and have shorter and more depressed metacones than M^{1-3} of *Helaletes*. P^{3-4} (and probably also P^2) of *kayi* and *woodi* are also relatively shorter and wider than those of *Helaletes*, and essentially molariform, with metaloph as long and prominent as protoloph, and extending to hypcone, as in *Colodon*, but advanced over the condition in *Helaletes*. The portion of P^2 crucial for classification, the lingual half, is not preserved in *woodi* or *kayi*. However, the P^2 parastyle seen in *woodi* seems as prominent as in *Colodon*, and more so than in *Helaletes intermedius*. P^1 in the type of *D. woodi* is less molariform than the corresponding tooth in Oligocene *Colodon*, having only one labial cusp and no prominent lingual cone. P^1 roots preserved in *Helaletes intermedius* suggest a still less molariform tooth than in *D. woodi*.

A lower dentition here referred to *D. kayi* looks like a smaller replica of the corresponding teeth in *Colodon*, with resemblance most striking in the short, broad premolars. Lower dentitions of *Helaletes*, on the other hand, display relatively longer and narrower molars and premolars.

Thus dentitions of *Desmatotherium kayi* and *D. woodi* display features characteristic of *Colodon*; the main difference is that of size. *D. kayi* and *D. woodi* are certainly closer to *Colodon* than to *Helaletes*. To better express these relationships the genus *Colodon* is here expanded to include the late Eocene species *Desmatotherium kayi* and *D. woodi*. In any event, the genus *Desmatotherium* is no longer valid, inasmuch as the type species (*D. guyotii*) is here transferred to the genus *Helaletes*.

DENTITION: Scott (in Scott and Jepsen, 1941, p. 764-766) described in detail the dentition of *Colodon occidentalis*. For the sake of completeness, dental morphology of all *Colodon* species will here be briefly reviewed.

I^{1-3} have large, low, wide, subequal spatulate crowns, close-set in a semicircle, each with a prominent lingual cingulum. I_1^1 slightly exceed in size I_2^2 , which in turn are larger than I_3^3 .

In *C. occidentalis*, C^1 is vestigial (PU 13595: Chadronian) or absent (PU 12700: Orel-

lan). However, a small C^1 is preserved in late Eocene and Oligocene Mongolian species of *Colodon* (AMNH 19161, 20355). Also, two species questionably referred to *Colodon*, *C.?* *cingulatus* and *C.?* *hancocki*, retain C^1 .

In the late Eocene *C. kayi*, a referred lower dentition (CM 8930) displays a small, low, almost wedge-shaped canine immediately behind I_3 , with a short anterior and long posterior edge. In *C. occidentalis*, however, both Chadronian (YPM 11830) and Orellan (AMNH 9979) specimens lack any trace of C_1 . *C.?* *cingulatus*, however, retains C_1 . Loss of canines, once considered a generic character of *Colodon*, appears rather to be a specialized feature of one species only, *C. occidentalis*.

Moderately long diastemata precede P_2^1 .

P^1 in *C. Woodi* is relatively narrow, with only a crista or very small cuspule located posterolingually, and a low loph or prominent cingulum bounding the anterolingual edge. In *C. occidentalis* P^1 is triangular in outline, with a small parastyle, or anterolabial cuspule, prominent paracone, small metastyle or posterolabial cuspule, large posterolingual cusp and small cuspule or loph between the posterolingual cusp and parastyle.

In *C. occidentalis* P^2 is molariform, with parastyle and well-separated paracone and metacone comprising the ectoloph, and a protoloph and slightly longer metaloph extending to distinct protocone and hypocone. Degree of separation of protocone and hypocone, relative length of protoloph to metaloph, and prominence of anterior and posterior cingula varied in observed specimens. The labial half of P^2 preserved in *C. woodi* corresponds to this pattern; the crucial lingual portion is missing.

P^3 is molariform, with protoloph and metaloph of equal prominence and usually equal length, and hypocone and protocone distinct but still close together. In *C. occidentalis* paracone and metacone seem flatter and less distinct from the ectoloph than in *C. woodi* or *C. kayi*. Anterior, lingual, posterior and posterolabial cingula vary in prominence.

P^4 is larger than P^3 and has a slightly flatter, more depressed metacone, and less well-separated protocone and hypocone.

In M^1 the metacone is shortened, flattened, very lingually depressed and bounded by a prominent posterolabial cingulum. The protoloph, paracone, and metaloph form a lingually open U-shaped wall, with the metacone a short posterior extension almost half-way between paracone and hypocone. The parastyle is prominent, close to and slightly labial to the paracone. Anterior, lingual, and posterior cingula vary greatly in size.

M^2 is like M^1 but larger, and with a more depressed and reduced metacone and more prominent posterolabial cingulum. Metacone reduction reaches an extreme in *C. occidentalis*, where the cusp is exceptionally short and concave.

M^3 is like M^2 but longer lingually and shorter labially, with a smaller parastyle, even shorter metacone, and a greatly reduced posterolabial cingulum.

P_1 is absent.

P_2 is broadly triangular, with prominent paralophid, metaconid close to but separate from protoconid, low metalophid, very wide talonid with large hypoconid and slightly smaller entoconid.

P_3 is roughly rectangular in outline, with a long but low paralophid bounding the trigonid labially and anteriorly, well developed protolophid, very wide talonid with low metalophid and parallel lingual lophid extending anteriorly from the large hypoconid and entoconid respectively. A short crest extends from the hypoconid lingually towards the entoconid, but ends half-way across the talonid.

P_4 is like P_3 , but with paralophid more reduced, trigonid relatively wider, and protolophid more prominent.

M_{1-3} are essentially as in *Helalestes*, but with paralophid and metalophid somewhat more reduced, so that protolophid and hypolophid are virtually bilaterally symmetrical, with the valley between them open at both ends. M_3 hypoconulid varies greatly in length and width and is unreliable as a taxonomic criterion.

DECIDUOUS DENTITION: Deciduous incisors are unknown in *Colodon*.

Teeth preserved immediately anterior to DP²⁻⁴ in AMNH 39454 and CM 6526 correspond to the cusp pattern described for P¹. Although DP¹ is replaced in the living genus *Tapirus*, possibly it was not in *Colodon*. This would account for the great amount of wear observed on all P¹'s in *C. occidentalis* permanent dentitions.

DP² has a small parastyle, closely-spaced but distinct paracone and metacone, small metastyle, and a short protoloph and longer metaloph.

DP³ is essentially molariform, except that the hypocone is more lingual than the protocone. The metacone is slightly flattened and lingually displaced, with a prominent labial cingulum.

DP⁴ is like M¹, but relatively longer and narrower.

DP₂ has a narrow trigonid, with a prominent paralophid and metaconid close to protoconid, and a long, narrow talonid, with a short hypolophid, and low metalophid and parallel lingual lophid projecting anteriorly from the entoconid.

DP₃ is like M₃, except relatively longer and narrower, and with a longer paralophid.

DP₄ is a relatively longer, narrower, and smaller replica of M₁.

Colodon dentitions may be distinguished from those of contemporaneous species of the tapirid *Protapirus* by the following features: premolars more molariform, with P²⁻⁴ metalophs as well developed as protolophs, and lingual cusps more distinct; P₂ shorter, P₂₋₄ entoconids relatively larger; M²⁻³ metacones flatter, more lingually displaced, more reduced; small M₃ hypoconulid retained. Also, loss of canines is distinctive of *Colodon occidentalis*.

Colodon kayi (Hough), 1955

Plate 4, figs. 1, 5

Desmatotherium kayi Hough, 1955, p. 31.

TYPE: CM 9561: maxilla with P³-M³.

HYPODIGM: type and USNM 20203, 20199; CM 12088, 8930, 12003.

KNOWN DISTRIBUTION: Late Uintan: Sage Creek, Montana.

DIAGNOSIS: Larger than *C. woodi* and smaller than *C. occidentalis*: length M¹⁻³ = 43.3 mm. Small canines present. See Table 9.

DISCUSSION: In the original diagnosis Hough (1955, p. 32) was primarily concerned with differentiating *Desmatotherium* [= *Colodon*] *kayi* from *Desmatotherium* [= *Helaletes*] *guyotii*. The relationship between these two forms has already been discussed in detail (see p. 58); distinguishing features are given in the respective generic diagnoses. The present revision assigns *kayi* to *Colodon*, thereby necessitating distinctive comparison with other species of that genus.

The upper dentition of *Colodon kayi* is known mainly from the P³-M³ preserved in the type. Except for somewhat smaller size, these teeth are nearly indistinguishable from those of the Oligocene *Colodon occidentalis*. The somewhat less reduced M² metacone and slightly more labially convex P³⁻⁴ metacones suggest a slightly more primitive dentition than that of most specimens of *C. occidentalis*, but more specimens must be observed to determine whether these features are specifically diagnostic or merely indicative of individual variation.

Projecting evolutionary trends backward, the early age of *C. kayi* suggests that C¹ may have been better developed and P¹⁻² less molariform than in the later species of *Colodon*; substantiation of these hypotheses must await discovery of the unknown teeth.

CM 12088, from the same locality as the type, and CM 8930, from near the type locality, represent the only known lower dentitions of *C. kayi*. CM 12088, a ramus with P₃-M₃, is a smaller replica of *C. occidentalis*; P₂₋₄ with short trigonids, wide talonids, and large entoconids, duplicate in miniature the degree of molarization seen in the later species. M₃ hypoconulid is extremely short, hardly more than a large posterior cingulum. However, because this feature varies greatly within *Colodon*, its validity as a specific

TABLE 9

Statistical Data and Measurements of Teeth of *Colodon woodi* and *Colodon kayi*

| | | <i>C. woodi</i> | | <i>C. kayi</i> | |
|----------------|---|-----------------|-----------|----------------|----------|
| N | | OR | M | | |
| P ¹ | L | 1 | — | 7.4 | |
| | W | 1 | — | 6.0 | |
| P ² | L | 1 | — | 8.3 | |
| | W | | — | — | CM 9561 |
| P ³ | L | 4 | 8.7–9.0 | 8.85 | 9.4 |
| | W | 4 | 11.7–12.5 | 11.98 | 13.1 |
| P ⁴ | L | 4 | 9.1–9.5 | 9.30 | 10.0 |
| | W | 4 | 12.6–13.0 | 12.78 | 14.5 |
| M ¹ | L | 3 | 10.8–11.1 | 10.97 | 12.5 |
| | W | 3 | 13.7–14.2 | 13.93 | 15.1 |
| M ² | L | 2 | 12.9–13.0 | 12.95 | 14.9 |
| | W | 2 | 15.0–15.8 | 15.40 | 17.3 |
| M ³ | L | 3 | 12.8–13.6 | 13.07 | 15.9 |
| | W | 3 | 14.8–15.7 | 15.17 | 17.9 |
| | | | | CM 8930 | CM 12088 |
| P ₂ | L | | | 9.4 | 8.3 |
| | W | | | 7.7 | 7.2 |
| P ₃ | L | | | 9.7 | 8.7 |
| | W | | | 9.2 | 8.5 |
| P ₄ | L | | | 10.0 | 9.2 |
| | W | | | 9.7 | 9.5 |
| M ₁ | L | | | 12.0 | 11.4 |
| | W | | | 9.0 | 9.6 |
| M ₂ | L | | | 14.0 | 14.3 |
| | W | | | 10.6 | 10.6 |
| M ₃ | L | | | — | 17.3 |
| | W | | | — | 11.6 |

criterion is questionable. Anteriorly, shattered roots of I₁₋₃ are wedged in a semicircle. Immediately posterior to I₃ root, on one side only, a small fragment of dentine may indicate a very small canine root.

CM 8930, an exceptionally unworn mature lower dentition (Hough, 1955, p. 31, erred in calling it immature), with only M₃ unerupted, corresponds in size to CM 12088, and duplicates in miniature the cusp patterns of *Colodon occidentalis*. A deep labial fold on P₂₋₄, accentuated somewhat by lack of wear but apparently more distinct than in *C. occidentalis*, may be a characteristic distinguishing feature. The worn P₂₋₄ in CM 12088 show traces of it. I₁₋₃ are small replicas of those in the later species. Immediately posterior to I₃, a small, low, incisiform (i.e., spatulate) canine presents an obvious difference from *C. occidentalis*, where C₁ is absent. This difference is considered indicative of specific differentiation only.

In summary, the two lower Sage Creek dentitions confirm evidence seen in the type: upper dentition suggesting conspecific relationship with Oligocene *Colodon*.

Stratigraphic control at the Sage Creek locality leaves much to be desired. Hough (1955, p. 29) considered the fauna equivalent to that of the Randlett (late Eocene), partly on the basis of correlation with the tapiroid *Dilophodon leotanus*. Gazin (1956, p. 7) correlated the Sage Creek fauna with the better known Badwater assemblage, which suggested a late Uintan age. Close resemblance between *C. kayi* and the Badwater *Colodon woodi* supports correlation of the two faunas. The absence of *Colodon* in the Uinta Basin neither supports nor contradicts correlation with Uinta C or Randlett faunas. *Colodon kayi* and *C. woodi* more closely approximate the Chadronian (early Oligocene) *Colodon occidentalis* than they do the late Bridgerian (middle Eocene) *Heleletes intermedius*. The somewhat more primitive dentition of the Sage Creek and Badwater species of *Colodon* accords well with the suggested late Uintan age.

Colodon woodi (Gazin), 1956

Desmatotherium kayi Hough, 1955, p. 31 (in part)

Desmatotherium woodi Gazin, 1956, p. 17

HYPODIGM: Type and USNM 20201, 20202, 20204, 22896-22898.

KNOWN DISTRIBUTION: Late Uintan: Badwater fauna, Wind River Basin, Wyoming.

DIAGNOSIS: Size small: mean length $M^{1-3} = 37.6$ mm. P^1 with small posterolingual cusp. See Table 9.

DISCUSSION: Gazin (1956, p. 17) noted that Badwater specimens referred by Hough (1955, p. 31) to the species *Desmatotherium* (= *Colodon*) *kayi* were discontinuously smaller (the molars by about 20 per cent) than the type Sage Creek material. He therefore proposed the species *Desmatotherium* (= *Colodon*) *woodi*, distinguished on the basis of small size.

Lack of lower dentitions for *C. woodi* limits comparisons with *C. kayi* to P^3 - M^3 . Except for slightly larger size in *C. kayi*, these teeth are virtually indistinguishable. M^3 of CM 9561, the type of *C. kayi*, is about 15 per cent larger than M^3 of USNM 20200, the *C. woodi* type, and about 20 per cent larger than two isolated Badwater M^3 's. A second Sage Creek M^3 (USNM 20199) is intermediate in size between CM 9561 and the Badwater material. Size differences between M^2 - P^3 of *C. woodi* and *C. kayi* progressively decrease, and fall within possible range of variation of a single species. However, larger samples are needed for more precise definition of size limits; such data when gathered may suggest conspecificity of *C. kayi* and *woodi*.

Like *Colodon kayi*, *C. woodi* apparently differs from *C. occidentalis* in having a less reduced M^2 metacone and slightly more convex P^{3-4} metacones. In addition, P^1 preserved in USNM 20202 has a much smaller posterolingual cusp than P^1 in *C. occidentalis* (resembling that tooth in *C. cingulatus*). The labial half of P^2 present in USNM 20202 offers no distinguishing features; examination of the lingual half is essential for comparison of degree of molarization with that of Oligocene *Colodon*.

The presence of *C. woodi* in the Badwater fauna supports correlation of that fauna with the Sage Creek collection, which includes *C. kayi*. *Dilophodon leotanus* is also common to both faunas, and occurs in the Randlett and Uinta C assemblages as well. Analysis of the entire Badwater assemblage by Gazin (1956, p. 5) suggested a late Uintan age for the fauna.

? *Colodon*

Douglass (1903, p. 158) referred an isolated M^3 (CM 718) found near the type locality of *Colodon kayi* in the Sage Creek beds, Montana, to *Hyrachyus* (= *Heleletes*) *intermedius*. Several years later Wood (1934, p. 187) designated the type of *Hyrachyus intermedius* as a new genus, *Chasmotherooides* and referred Douglass' specimen to *Chasmotherooides* cf. *intermedius* (*loc. cit.*, p. 249).

CM 718 resembles M^3 's in both the middle Eocene *Heleletes intermedius* and the late Eocene *Colodon kayi* and *woodi*. It is more like *H. intermedius* in the relatively short

metaloph, but approximates the *Colodon* species in the degree of ectoloph reduction. The tooth apparently came from slightly lower in the section than the type of *C. kayi* but still from beds of late Eocene age (see Hough, 1955, p. 28). Since *Helaletes* is not known from the late Eocene, stratigraphic evidence supports assignment of CM 718 to *Colodon*.

CM 718 corresponds in size to M³'s of the Badwater *Colodon woodi* and is about 15 per cent smaller than comparable teeth in the Sage Creek *C. kayi*. More information is needed to determine whether it was contemporaneous with *C. kayi* and a small representative of that species, or occurred earlier, and represented another, smaller species, perhaps *C. woodi*. The third possibility, that CM 718 was sympatric with *C. kayi* and yet belonged to another species, seems unlikely in light of the similarities in size and cusp pattern.

Colodon occidentalis (Leidy), 1868

Plate 4, figs. 2, 6

Lophiodon occidentalis Leidy, 1868, p. 232

Colodon luxatus Marsh, 1890, p. 524

Colodon dakotensis Osborn and Wortman, 1895, p. 362

Colodon procuspидatus Osborn and Wortman, 1895, p. 364

TYPE: an isolated M₃, presumably at the Academy of Natural Sciences of Philadelphia but now apparently missing (personal communication, H. Richards, 1962). Figured by Leidy, 1869, pl. 21, figs. 28-30.

HYPODGM: Type and YPM 11830, 16582, 16583; PU 10507, 13595; AMNH 1044, 1044a (all Chadronian); AMNH 658, 1045, 1212-1216, 9779, 22455, 38854, 39010, 39126; PU 10953, 11066-11068, 12683, 12700; F:A.M. 42890, 42892, 42894, 42896, 42900; YPM 14247; CNHM P25465; SDSM 3045 (all Orellan); PU 10506, 11159, 11166, 12733; AMNH 1217, 39009, 39454; F:A.M. 42895 (horizon unknown).

KNOWN DISTRIBUTION: Chadronian through Whitneyan, White River Group, western South Dakota, and (rarely) Nebraska.

DIAGNOSIS: Size large: mean length M¹⁻³ = 49.4 mm. Canines vestigial to absent. P¹ submolariform, with large posterolingual cusp. M² metacone flat to concave, and much reduced. See Table 10.

DISCUSSION: In 1868 Leidy (p. 232) proposed the species *Lophiodon occidentalis* for an isolated M₃ brought back by Hayden "from the Mauvaises Terres of Nebraska or South Dakota." Concerning the stratigraphic horizon, Leidy wrote:

"I have a suspicion that this specimen belonged to the lowest bed of the White River tertiary formations, and with associated remains of *Hyopotamus* and *Titanotherium*, probably indicates the end of the eocene. . . ." (p. 232-233)

(Association with titanotheres would indicate Chadronian age.)

Marsh (1890, p. 524) described the species *Colodon luxatus*, based on the type, YPM 11830 (an almost complete lower dentition), YPM 16582 (P²-M²), and YPM 16583 (lower teeth of at least three individuals). However, no mention of *Lophiodon occidentalis* Leidy was included in this paper. According to the YPM accession catalogue, the type of *C. luxatus* was collected in the White River Oligocene of South Dakota, and YPM 16582 and 16583 were purchased from L. W. Stillwood at Deadwood, South Dakota. Marsh (*loc. cit.*, p. 523) considered all specimens to be from "the *Brontotherium* beds of Dakota" (= Chadronian).

Three years later Wortman and Earle (1893, p. 175) referred *Lophiodon occidentalis* Leidy to *Colodon*, placing *C. luxatus* Marsh in synonymy with *occidentalis*. In discussing *Colodon* specimens from the American Museum, Princeton, and Yale collections, these writers (*loc. cit.*, p. 174) noted that at least two species were represented. However, they described and discussed only *Colodon occidentalis*.

Osborn and Wortman (1895, p. 362) named two new species of *Colodon*, *C. dakotensis*

TABLE 10
Statistical Data on Teeth of *Colodon occidentalis*

| | N | OR | SR | M | σ | V |
|------------------|----|-----------|------|--------------|-------------|--------------|
| P ¹ L | 5 | 7.8-9.5 | 4.7 | 8.64 ± 0.32 | 0.72 ± 0.23 | 8.37 ± 2.65 |
| W | 5 | 7.4-10.0 | 7.0 | 9.20 ± 0.48 | 1.08 ± 0.34 | 11.73 ± 3.71 |
| P ² L | 6 | 9.9-11.0 | 2.3 | 10.45 ± 0.14 | 0.35 ± 0.10 | 3.36 ± 0.97 |
| W | 6 | 12.2-14.3 | 5.3 | 13.23 ± 0.33 | 0.82 ± 0.24 | 6.20 ± 1.79 |
| P ³ L | 5 | 10.9-12.0 | 3.0 | 11.26 ± 0.21 | 0.46 ± 0.15 | 4.05 ± 1.28 |
| W | 5 | 15.0-16.2 | 3.1 | 15.52 ± 0.21 | 0.48 ± 0.15 | 3.10 ± 0.98 |
| P ⁴ L | 7 | 11.1-12.2 | 3.1 | 11.63 ± 0.18 | 0.48 ± 0.13 | 4.11 ± 1.10 |
| W | 7 | 15.5-17.4 | 4.0 | 16.40 ± 0.23 | 0.61 ± 0.16 | 3.69 ± 1.00 |
| M ¹ L | 6 | 13.6-14.9 | 3.4 | 14.15 ± 0.21 | 0.52 ± 0.15 | 3.65 ± 1.05 |
| W | 6 | 16.6-18.3 | 4.3 | 17.22 ± 0.27 | 0.67 ± 0.19 | 3.89 ± 1.12 |
| M ² L | 6 | 16.0-19.0 | 7.1 | 17.32 ± 0.45 | 1.10 ± 0.32 | 6.33 ± 1.83 |
| W | 6 | 18.1-20.7 | 6.4 | 19.40 ± 0.40 | 0.99 ± 0.29 | 5.09 ± 1.47 |
| M ³ L | 8 | 17.2-20.0 | 6.3 | 18.20 ± 0.34 | 0.96 ± 0.24 | 5.29 ± 1.32 |
| W | 8 | 18.2-21.8 | 7.5 | 20.11 ± 0.40 | 1.14 ± 0.28 | 5.65 ± 1.41 |
| P ₂ L | 9 | 9.9-11.9 | 4.2 | 10.53 ± 0.22 | 0.65 ± 0.15 | 6.16 ± 1.45 |
| W | 9 | 8.2-10.2 | 4.9 | 9.31 ± 0.25 | 0.76 ± 0.18 | 8.14 ± 1.92 |
| P ₃ L | 14 | 10.4-13.5 | 6.3 | 11.69 ± 0.26 | 0.97 ± 0.18 | 8.31 ± 1.57 |
| W | 14 | 10.1-12.4 | 4.1 | 11.27 ± 0.17 | 0.63 ± 0.12 | 5.59 ± 1.06 |
| P ₄ L | 16 | 10.7-13.9 | 6.3 | 11.94 ± 0.24 | 0.97 ± 0.17 | 8.13 ± 1.44 |
| W | 16 | 10.7-14.2 | 6.2 | 12.21 ± 0.24 | 0.96 ± 0.17 | 7.85 ± 1.39 |
| M ₁ L | 19 | 12.0-16.0 | 7.6 | 14.32 ± 0.27 | 1.17 ± 0.19 | 8.14 ± 1.32 |
| W | 19 | 10.1-13.3 | 6.0 | 11.43 ± 0.21 | 0.93 ± 0.15 | 8.10 ± 1.31 |
| M ₂ L | 16 | 14.5-19.7 | 10.1 | 16.94 ± 0.39 | 1.56 ± 0.28 | 9.19 ± 1.62 |
| W | 16 | 11.4-15.4 | 6.8 | 13.39 ± 0.26 | 1.05 ± 0.19 | 7.86 ± 1.39 |
| M ₃ L | 18 | 18.2-24.2 | 9.1 | 21.57 ± 0.33 | 1.41 ± 0.24 | 6.52 ± 1.09 |
| W | 18 | 12.7-15.1 | 4.7 | 13.93 ± 0.17 | 0.72 ± 0.12 | 5.18 ± 0.86 |

and *C. proscupidatus*, both from middle Oligocene strata. *Colodon dakotensis* (type AMNH 1212; P¹-M³; cotype AMNH 1213; P₃₋₄, M₂₋₃) was distinguished from *C. occidentalis* by its larger size and double P₄ posterointernal cusp, and from *C. proscupidatus* (type AMNH 1215; P¹-M³) by lack of premolar internal and external cingula and less well separated P²⁻⁴ lingual cusps. These authors distinguished *C. proscupidatus* from *C. occidentalis* by its larger size and more robust character.

After studying individual variations in modern tapir teeth, Hatcher (1896, p. 170-173) noted that such features as relative size of entoconid and degree of separation of metaconid on P₂₋₄, double P₄ postero-internal cusps, and development of basal cingula were probably of little importance as specific criteria. As a consequence of such observations, he synonymized *C. luxatus* and *C. proscupidatus* with *C. occidentalis*, which he distinguished from *C. dakotensis* by less molariform (*sic*) superior premolars and generally smaller, less robust teeth.

Scott (*in* Scott and Jepsen, 1941, p. 763-775) discussed in considerable detail the postcranial anatomy and specific taxonomy of *Colodon*, and recognized two species, the Chadronian *C. occidentalis* (Leidy), including *C. luxatus* Marsh, and the Orellan *C. dako-*

tensis Osborn and Wortman, including *C. procrispidatus* Osborn and Wortman. (The supposed differences in degree of premolar molarization between the latter two species he considered largely due to different stages of abrasion in the types.) *Colodon dakotensis* was distinguished from *C. occidentalis* "by its larger size, by the absence of the upper canine [considered minute and vestigial in *C. occidentalis*], by the more distinct separation of the internal cones of the upper premolars and by the more reduced talon of the last molar." (*loc. cit.*, p. 773)

This suggests a temptingly simple picture—that of a smaller and more primitive species (*C. occidentalis*) succeeded by a larger, more advanced one (*C. dakotensis*); but study of all *Colodon* specimens now available casts doubt on such an interpretation. Scott's description of *C. occidentalis* is based on PU 13595, one of the smallest Oligocene *Colodon* specimens, with a minute vestigial C¹ and barely separated hypocone and protocone on P⁴. The absence of the upper canine in *C. dakotensis* can be ascertained in only one specimen, PU 12700. The presence or absence of an admittedly vestigial tooth is a variable feature and should not be used as a specific criterion, especially when based on only two specimens.

The only other known White River Chadronian *Colodon* upper dentition, YPM 16582, has premolars about as molariform as in most Orellan *Colodon* specimens. Degree of premolar molarization varies in *Colodon*, with the specimens examined displaying a complete gradation between primitive and advanced extremes. Larger samples than those available at present are needed to establish the usefulness of such a variable character as a specific criterion.

Size of M₃ hypoconulid varies greatly and apparently does not differ consistently between Chadronian and Orellan specimens.

The remaining criterion used to separate White River species of *Colodon* is size. The *C. dakotensis* type, AMNH 1212, is one of the largest South Dakota *Colodon* specimens known. However, all White River *Colodon* upper dentitions fall within the possible size range of a single species, and the Chadronian YPM 16582 is near the mean. Lower teeth exhibit a wider range of variation in length and width than the uppers. Most Chadronian lower dentitions are small, and the types of *C. occidentalis* and *C. luxatus* fall slightly below the mean, but Orellan specimens grade uniformly from the smallest known lower dentitions to the largest (AMNH 1213, the cotype of *C. dakotensis*), with no apparent discontinuities or clustering. (It should be noted that AMNH 658, the measurements of which were included by Scott (*in* Scott and Jepsen, 1941, p. 773) under *C. occidentalis*, comes from an Orellan horizon.) Larger collections may show Chadronian samples to average smaller than Orellan, but since there is such an extensive overlap, on the basis of data now available, size cannot be used as a criterion to separate White River species of *Colodon*.

Due to lack of adequate samples from single horizons statistical data on *C. occidentalis* tooth dimensions were calculated from combined Chadron-Orella collections. Despite the obviously long time range spanned by included specimens, coefficients of variation are not much higher than would be expected for a single species—the mean of all V's = 6.30 (see Table 10).

Since no other characters were found which distinguished Chadronian from Orellan specimens or indicated bimodality or discontinuity in any feature within samples from one horizon, *C. dakotensis* is here synonymized with *C. occidentalis*.

An isolated DP⁴ (AMNH 1217a) is recorded as coming from the *Protoceras* beds (= Whitneyan) of South Dakota. In size and cusp pattern it corresponds to *Colodon occidentalis*; if this assignment is correct, AMNH 1217a apparently represents a late survivor and extends the chronologic range of *Colodon occidentalis* to the late Oligocene.

Colodon was rare in White River Oligocene faunas, especially compared with the great abundance of similarly built cursorial hyracodonts and horses. About forty specimens, many consisting of only one or two teeth, make up the total number of *Colodon occidentalis* specimens available in museum collections. Except for one individual (F:A.M. 42896, from Nebraska), all known specimens of this species were collected in South Dakota.

Colodon cf. *C. occidentalis*

Three *Colodon* specimens from the Whitneyan *Protoceras* beds of South Dakota correspond in cusp pattern to *C. occidentalis* but in tooth size slightly exceed the upper 99 per cent size limits for that species. F:A.M. 42891, 42893, and SDSM 4013, confirm the record of AMNH 1217a (see p. 65) that *Colodon* ranged into the late Oligocene in South Dakota and support the hypothesis that evolutionary size increase occurred in the *C. occidentalis* line during the Oligocene. Assignment to *C. occidentalis* is tentative since larger collections may well allow specific separation, at least on the basis of size, of Whitneyan from earlier specimens.

F:A.M. 42891 is of additional importance because it is the most complete *Colodon* skull yet discovered.

Colodon? *cingulatus* Douglass, 1901
Plate 4, figs. 3-4

Colodon cingulatus Douglass, 1901, p. 255.

TYPE: CM 722: maxillary fragment with P² roots and P³-M¹.

HYPODIGM: type and CM 715 (Toston beds, type locality); CM 299, 300, 1088, 1154, 1157, 2016, 6526, 9990, 12001, 12002; F:A.M. 42897-42899 (McCarty's Mt.); CM 773, 1059, 9815-9817 (Thompson's Creek).

KNOWN DISTRIBUTION: Chadronian through Orellan, southwestern Montana.

REVISED DIAGNOSIS: Larger than *C. occidentalis*: mean length M¹⁻³ = 57.6 mm. Small canines present. Upper teeth relatively slightly wider and lower premolars relatively narrower than those of *C. occidentalis*. P¹ with small posterolingual cusp. Some individuals with P²⁻⁴ hypocones not differentiated from protocones and P₃₋₄ with small entoconids. M² metacone flat to slightly convex, not as shortened and concave as in *C. occidentalis*. See Table 11.

DISCUSSION: The type of *Colodon?* *cingulatus* may be distinguished from specimens of *Colodon occidentalis* only by its larger size. However, other more complete specimens referable to *cingulatus* exhibit differences of greater significance, including: retention of canines, less molariform P¹, P²⁻⁴ hypocone not always distinct from protocone (F:A.M. 42898 and 42899), more convex and less reduced molar metacones, and very small P₃₋₄ entoconids (noted in F:A.M. 42897). On the other hand, a basic similarity between *cingulatus* and *occidentalis* is the occurrence in both species of greatly enlarged nasal incisions and shortened nasals (seen in *cingulatus* in CM 6526 and 9815).

The F:A.M. specimens with relatively nonmolariform premolars suggest that the *cingulatus* line was separate from the other known species of *Colodon* before late Eocene time, since by then *C. woodi* and *C. kayi* already had molariform premolars. This suggestion is supported by the lesser degree of depression and reduction of molar metacones in *cingulatus*, another unprogressive or retarded feature. These differences suggest that further information, perhaps of postcranial anatomy, may show *cingulatus* to be generically distinct from other species of *Colodon*. However, since present knowledge of advanced helaletids is so incomplete it seems best at this time to postpone a more definite generic assignment and to leave *cingulatus* questionably referred to *Colodon*.

Colodon? *cingulatus* occurs in Chadronian deposits at Thompson's Creek and McCarty's Mt. and in Orellan levels at the type locality near Toston. As was the case with *C. occidentalis*, no consistent differences are apparent between early and late specimens of *C.?* *cingulatus*. Unfortunately, detailed stratigraphic data are not available for McCarty's Mt. specimens. If the specimens with less molariform premolars (F:A.M. 42898 and 42899) came from a lower horizon than those with fully molariform premolars (CM 299 and 300), it might be possible to recognize two distinct species.

Differences between Oligocene faunas from South Dakota and Montana led White (1954, p. 435) to suggest the existence of environmental differences between the plains and

TABLE 11
 Statistical Data on Teeth of *Colodon? cingulatus*

| | N | OR | M |
|------------------|---|-----------|--------|
| P ¹ L | 4 | 10.8-11.4 | 11.00 |
| W | 4 | 8.6-11.0 | 9.75 |
| P ² L | 5 | 11.2-12.4 | 11.74 |
| W | 5 | 14.5-16.2 | 15.34 |
| P ³ L | 4 | 11.2-13.0 | 12.18 |
| W | 4 | 17.0-18.9 | 17.98 |
| P ⁴ L | 6 | 11.8-13.5 | 12.87 |
| W | 6 | 18.3-20.4 | 19.56 |
| M ¹ L | 3 | 15.5-18.6 | 17.10 |
| W | 3 | 20.5-21.7 | 21.03 |
| M ² L | 4 | 19.2-20.7 | 20.10 |
| W | 4 | 23.3-25.6 | 24.28 |
| M ³ L | 2 | 19.9-21.0 | 20.45 |
| W | 2 | 22.2-25.4 | 23.80 |
| P ₂ L | 1 | — | 12.0 |
| W | 1 | — | 10.0 |
| P ₃ L | 5 | 11.3-14.2 | 12.30* |
| W | | | |
| P ₄ L | 5 | 12.0-13.0 | 12.58* |
| W | | | |
| M ₁ L | 5 | 14.0-17.0 | 15.14* |
| W | | | |
| M ₂ L | 4 | 16.5-20.0 | 18.10* |
| W | | | |
| M ₃ L | 4 | 22.7-25.9 | 24.42 |
| W | 4 | 14.2-16.2 | 15.28 |

* Measurements taken from roots.

mountains in early Oligocene time. The allopatry of *C.? cingulatus* and *C. occidentalis* supports this hypothesis, as may also the apparent allopatry of *C. woodi* and *C. kayi* in late Eocene time.

Colodon? hancocki, sp. nov.*

Plate 3, figs. 4, 5

TYPE: UOMNH 20377: anterior part of a skull with left P¹-M³.

HYPODIGM: Type and UOMNH 20376, 20378-20381.

KNOWN DISTRIBUTION: Late Eocene or early Oligocene** : Clarno formation, John Day Basin, Oregon.

* Named for the late A. W. Hancock, who was the first to discover a fossil mammal in the Clarno formation.

** Personal communications from J. A. Shotwell and M. C. McKenna suggest late Eocene and early Oligocene ages respectively for the Clarno fauna.

DIAGNOSIS: Medium-sized helaletids: length $M^{1-3} = 44.4$ mm. Small canines present. P^1 narrow with only a cingulum lingually. P^{2-4} relatively short and wide, but barely submolariform, with at most only a shallow anterolingual groove indicating incipient separation of protocone and hypocone; metaloph slightly less prominent than protoloph. M^{1-2} metacones shortened and lingually displaced, but convex labially. P_2 relatively short but without entoconid. P_{3-4} with small entoconids. See Table 12 for measurements.

DISCUSSION: An advanced helaletid in the hitherto undescribed Clarno fauna resembles species of *Colodon* in general tooth proportions and greatly enlarged nasal incision and reduced nasals. Basic differences from *C. kayi*, *C. woodi* and *C. occidentalis* include less molariform premolars and more convex molar metacones; in these features *hancocki* approaches *C.?* *cingulatus*, from which it may be distinguished by its smaller size, less molariform upper premolars, and more depressed M^{1-2} metacones.

TABLE 12
Measurements of Teeth of *Colodon?* *hancocki*

| | UOMNH 20377 | UOMNH 20379 | UOMNH 20380 |
|---------|----------------|----------------|----------------|
| P^1 L | — | — | — |
| W | — | — | — |
| P^2 L | 9.6 | — | — |
| W | 11.2 | — | — |
| P^3 L | 10.0 | 10.9 | — |
| W | 14.2 | — | — |
| P^4 L | 10.6 | 10.9 | 11.1 |
| W | 15.0 | — | 16.0 |
| M^1 L | 13.6 | 13.9 | — |
| W | 16.5 | — | — |
| M^2 L | 15.5 | 14.9 | — |
| W | 17.7 | — | — |
| M^3 L | 15.3 | — | — |
| W | 16.4 | — | — |
| | UOMNH 20376 | UOMNH 20378 | |
| P_2 L | — | 7.9 | |
| W | — | 6.5 | |
| P_3 L | — | — | |
| W | — | — | |
| P_4 L | 9.7 | — | |
| W | 8.4 | — | |
| M_1 L | 13.0 | — | |
| W | (10.5) | — | |
| M_2 L | 14.5 | 15.4 | |
| W | 11.3 | 11.6 | |
| M_3 L | 17.5 | — | |
| W | 11.3 | 11.2 | |

Dentition of the Clarno tapiroid closely resembles the few teeth known of the Asiatic late Eocene *Desmatotherium grangeri* Tokunaga, 1933 (see also Takai, 1939, p. 211), which exhibits relatively nonmolariform premolars and convex molar metacones. The illustrations in the works cited above are, however, insufficient for adequate comparison.

Phylogenetic relationships between *C.?* *hancocki* and the other late Eocene and Oligocene tapiroids are difficult to interpret. In dental morphology the Clarno tapiroid is intermediate between *Helaletes* and *Colodon occidentalis* and *C.?* *cingulatus*. Late stratigraphic occurrence coupled with retarded premolar molarization and convex M^{1-2} metacones remove *hancocki* from the main *Helaletes-Colodon* line, since the contemporaneous or older *C. kayi* and *C. woodi* are more advanced in those features. Should *C.?* *hancocki* prove to be older than the earliest *C.?* *cingulatus* (of Chadronian age), the former would be a possible ancestor for the latter.

C.? *hancocki* is also intermediate in morphology between *Helaletes* and *Protapirus*, the earliest tapirid. The necessary changes from *C.?* *hancocki* to *Protapirus* would involve size increase, labial displacement and increase in convexity of molar metacones, relative lengthening of P_2 , and loss of M_3 hypoconulid, all of which would have to be accomplished by middle Oligocene (Orellan) time. Here again, age of the Clarno tapiroid is a critical factor for interpreting phylogenetic relationships.

Taxonomic assignment of the Clarno tapiroid raises problems. Classifying it as generically distinct from *Colodon* would necessitate the naming of a new genus and perhaps imply too great a degree of morphological divergence in view of similarities in dentition and anterior skull structure. However, placing it in *Colodon* would necessitate expansion of the concept of that genus to include a lineage with retarded premolar molarization and perhaps a trend towards increasing molar metacone convexity. This would make the *Colodon* group disproportionately diverse in morphology compared with other genera in the family. Since advanced helaletid phylogeny is still obscure, and since nothing is known of the postcranial anatomy of the Clarno tapiroid, it seems best at this time to postpone a more definite taxonomic decision and for the present leave *hancocki* questionably referred to *Colodon*.

Size relationships between the above discussed species of *Colodon* are shown in fig. 13.

Colodon spp. indet.

An upper and lower deciduous dentition (CM 892) and a P^{2-3} (CM 890) from the Chadronian Prickley Pear Creek local fauna, Canyon Ferry Reservoir area, southwestern Montana, correspond in size to *C. occidentalis*, averaging smaller than the few specimens known of *C.?* *cingulatus*. Cusp configuration does not favor reference to one species rather than the other. The apparent confinement of *C. occidentalis* to the South Dakota area, and inclusion of all other Oligocene helaletids from southwestern Montana in *C.?* *cingulatus* suggests that the Prickley Pear Creek specimens may represent small *C.?* *cingulatus* rather than far-ranging members of *C. occidentalis*. However, since size differences between the two species are not very great, and relatively few specimens are known, specific assignment of CM 890 and 892 should await collection of further, more complete, material.

Russell (1936, p. 77) referred to *Colodon occidentalis* a P^2 (GSC 8871) and P_{3-4} (GSC 8872) from the Chadronian Cypress Hills fauna of Saskatchewan. On the basis of size these specimens could represent small *C.?* *cingulatus* or large *C. occidentalis*. No features are preserved which would justify assignment to one species rather than the other. Therefore, in the absence of more diagnostic evidence, it is suggested that GSC 8871 and 8872 be referred to *Colodon* sp. indet. This record marks the northernmost occurrence of the genus in North America.

An incomplete ramus with damaged M_{1-3} from the Chadronian Titus Canyon fauna of California was assigned by Stock (1949, p. 236-237) to *Colodon* sp. The excellent illustrations (*loc. cit.*, pl. 2, figs. 4, 4a) show LACM-CIT no. 3567 to be an advanced helaletid, but cusp patterns of M_{1-3} do not allow more specific diagnosis. M_3 length corresponds to small *C. occidentalis*, slightly exceeding in size the one M_3 known for *C.?* *hancocki*; M_{1-2} could

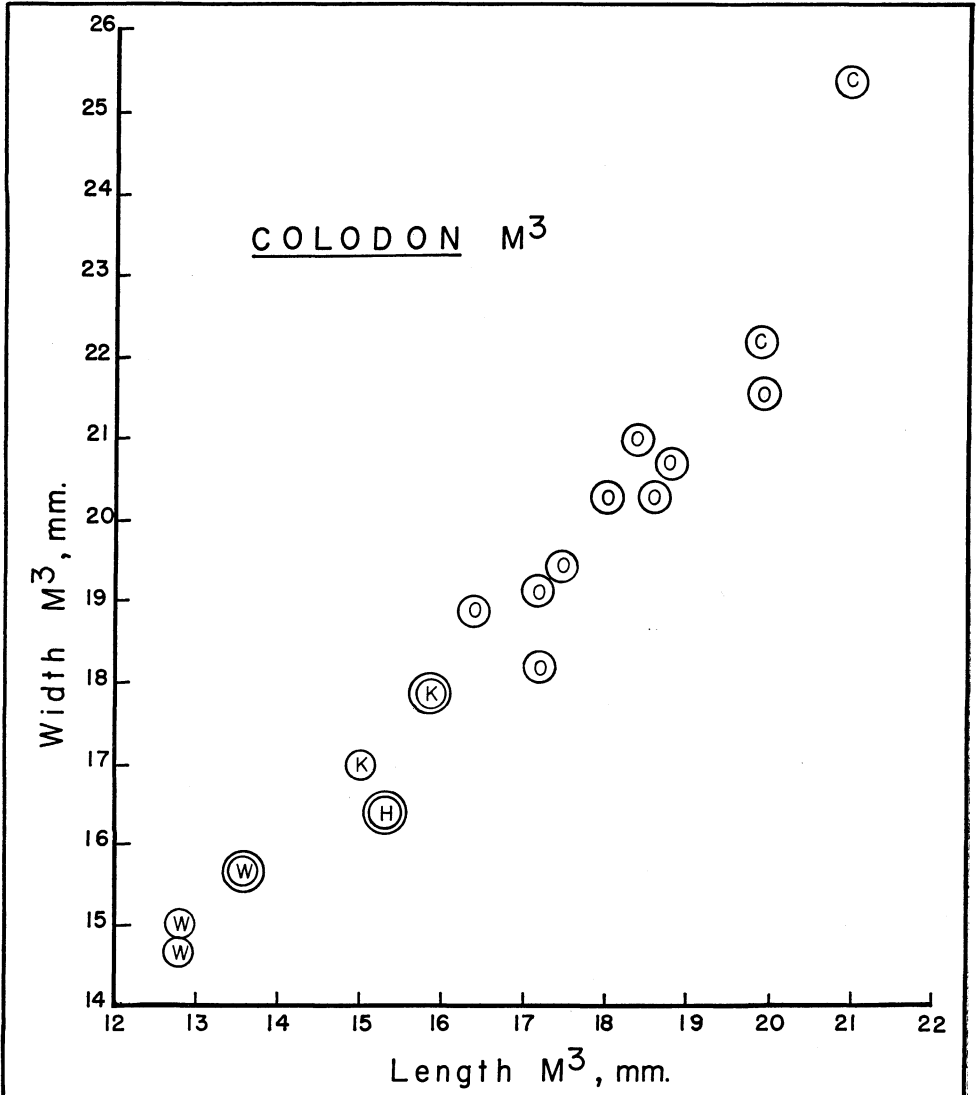


Fig. 13. Scatter diagram of length-width measurements of *Colodon* M³s showing size relationships between species. W = *C. woodi*; H = *C. hancocki*; K = *C. kayi*; O = *C. occidentalis*; C = *C. cingulatus*. Double circles indicate types.

belong to either species. Since there is no other diagnostic evidence, LACM-CIT no. 3567 is here referred to *Colodon* sp. indet.

Russell and Wickenden (1933, p. 62) referred to *Hyrachyus* (= *Helaletes*) *intermedius* and isolated M³ from the late Eocene Swift Current fauna, Saskatchewan, Canada. National Museum of Canada No. 8659 more closely resembles M³s in *Colodon* than *Helaletes*, which well accords with its late Eocene age. The tooth is slightly larger than known M³s in *Colodon kayi*, corresponding in size to small *Colodon occidentalis*. More material is necessary for further specific analysis.

? HELALETIDAE, gen. indet.

Douglass (1903, p. 155-156; fig. 1, p. 155) referred to *Heptodon*? a maxillary with worn P⁴-M³ (CM 717) from the Sage Creek beds northeast of Lima, Montana. Matthew (in Osborn, 1909, p. 99) assigned the specimen to ?*Helaletes*. Wood (1934, p. 251-2) noted that CM 717 was smaller than *Heptodon* and larger than *Dilophodon*, but that it agreed in size and character with *Helaletes* in general and was inseparable from *H. boops* (= *H. nanus*) in particular.

Hough (1955, p. 31; pl. 8, fig. 2) maintained that CM 717 was distinctly different from *Helaletes boops* and was, in fact, representative of a species of *Dilophodon* similar to *D. leotanus* but specifically distinct. Hough's comparisons involved mainly M³, and emphasized the rounded parastyle and paracone, the depressed and flattened metacone, elevation of internal cusps, shortening of cross crests, and truncation of ectoloph immediately posterior to metacone. In these features, in Hough's opinion, CM 717 resembled *Dilophodon leotanus* and was radically unlike *H. boops*. Hough also mentioned oblique, parallel, and uncurved cross crests on M¹⁻² and two internal cusps on P⁴ of CM 717 as further differences from *H. boops*.

Hough has pointed out differences between only the type specimen of *H. boops* (YPM 11807) and CM 717. When the Sage Creek specimen is compared with several other *H. nanus* dentitions many of the differences she cited are encompassed within the range of individual variation of that species. (Hough herself noted that CM 717 was more similar to *H. nanus*, probably Marsh's type, YPM 11080, than to *H. boops*).

Gazin (1956, p. 7) stated that CM 717 represented an advanced dilophodont distinct from *Dilophodon leotanus*. He suggested that possibly it had weathered out of overlying Oligocene beds and was perhaps a small and unprogressive species of *Protapirus*. Gazin gave no evidence to support this suggestion nor did he give reasons for considering CM 717 "unprogressive" compared to *Protapirus* or more advanced than *Dilophodon*.

Comparison of CM 717 with all available specimens of *Helaletes* and *Dilophodon* has yielded the following information. In size, CM 717 is about average for *Helaletes nanus* but larger than any known *Dilophodon*. P⁴ is too worn to yield any pertinent information (it is not possible to determine whether or not it had two lingual cusps, as Hough suggested). The metacone of M¹ is more convex than in most *Helaletes*; in this respect it resembles *Dilophodon*. M² yields no significant evidence as to affinities. M³, however, deviates from both *Helaletes nanus* and *Dilophodon leotanus*. Lingually the metaloph diverges markedly from the protoloph, placing the hypocone more posterior relative to the paracone than in *D. leotanus*. Also, the metaloph is shortened relative to the protoloph, and the lingual edge of the tooth trends posterolabially, with the angle between lingual and anterior edges almost as small as that between labial and anterior edges—a feature noted neither in *Helaletes* nor in *Dilophodon*. In fact, this peculiar relative shortening and lingual divergence of the M³ metaloph was observed only in two specimens of *Heptodon posticus* and, interestingly enough, in *Protapirus*.

Besides the unusual M³ metaloph, the main factors excluding CM 717 from *Helaletes* are its stratigraphic position and M¹ metacone convexity. The Sage Creek beds in which the specimen in question was found are late Eocene in age (early Duchesnean according to Hough, 1955, p. 28-29, late Uintan according to Gazin, 1956, p. 5-7). *Helaletes* has never been recorded from strata younger than late Bridgerian (Middle Eocene), and by late Eocene time the *Helaletes-Colodon* line had developed very flat and depressed M¹⁻² metacones.

The main differences between CM 717 and *Dilophodon leotanus* are larger size and shortened, divergent M³ metaloph in the former. Derived from *Helaletes nanus*, the *Dilophodon minusculus*-*D. leotanus* line appears to decrease in size with time. Therefore, it is unlikely that CM 717, which is larger than *D. minusculus*, would belong to that lineage. Of course, it is possible that CM 717 may be the only known representative of a line which diverged from *Helaletes* and paralleled *Dilophodon* in maintaining convex M¹⁻² metacones, but not in decreasing size. This, however, is pure speculation and does not account for the peculiar M³.

CM 717 differs from the newly described *Colodon? hancocki* in the more convex, less lingually depressed M¹ metacone, shortened, posterolingually directed M³ metaloph and smaller size.

Much smaller size distinguishes CM 717, as far as it is known, from *Protapirus*, the discrepancy in size being so great as to seemingly outweigh the apparent cusp pattern similarities of convex M¹ metacone and divergent shortened M³ metaloph.

Uncertainty as to stratigraphic horizon, incompleteness of the specimen, and heavy wear obscuring cusp detail, preclude generic or even definite familial assignment of CM 717. The present revision has shown middle and late Eocene tapiroid phylogeny to be more complex than heretofore realized. Discovery of a new and previously undescribed species (*Colodon? hancocki*) cautions against excluding the possibility of still more unknown tapiroid lineages in North America. Therefore, in the light of present knowledge, it seems best not to 'force' CM 717 into any preexisting genus, or to construct an almost completely hypothetical phylogenetic lineage on the basis of so little evidence. The Sage Creek tapiroid CM 717 should, for the time being, remain *incertae sedis*, probably helatid, but possibly some sort of prototapirid.

PHYLOGENY

Suggested phylogenetic relationships of North American Eocene and Oligocene tapiroids are summarized in figure 14. The earliest tapiroid, *Homogalax*, is so similar to the contemporaneous earliest equoid, *Hyracotherium angustidens*, that immediate common ancestry seems quite probable. This suggestion is supported by the presence of hyracothere-like features in the dentition of the most primitive species of *Homogalax*, from the Four Mile fauna. Also, *Hyracotherium angustidens* resembles *Homogalax* in the absence of long anterior diastemata (Kitts, 1956, p. 10), the development of which in more advanced hyracothere species marks divergence from *Homogalax*.

The undifferentiated *Hyracotherium-Homogalax* early perissodactyl stock probably arose from a Paleocene phenacodontid. Dental patterns within this condylarth family display basic features one would expect to find in perissodactyl ancestry, including relatively primitive premolars, quadrate, bunodont sextubercular upper molars, and quadrate, four-cusped lower molars.

Tiffanian and Clarkforkian (late Paleocene) phenacodonts are more specialized than early perissodactyls in possession of a mesostyle on M^{1-3} , a feature which appears in descendants of *Hyracotherium*. Derivation of perissodactyls from a phenacodont with a mesostyle would require evolutionary oscillation of that flexure, disappearing in *Hyracotherium* and appearing again in the middle Eocene *Orohippus*. It would, therefore, seem more probable that perissodactyls evolved from a phenacodont which had not yet developed a mesostyle, such as some species of Torrejonian (middle Paleocene) *Tetraclaenodon*. (Kitts [1956, p. 13] erred in considering the early Paleocene *Dematoclaenus* the only phenacodont without a mesostyle; Matthew [1937, p. 188] notes its absence in *Tetraclaenodon*.)

The absence of forms intermediate in morphology between phenacodonts and perissodactyls in later Paleocene deposits in North America led Kitts (*loc. cit.*, p. 14) to suggest that the transition had taken place in some other continent. This conclusion, in the opinion of the present author, greatly overestimates the scope of our knowledge of early Tertiary vertebrate faunas. Only an infinitesimally small percentage of animals living during Paleocene time were fossilized, and only a very small fraction of these are in beds now accessible to collectors. North American Paleocene mammals have been found in a few limited geographic areas, mainly in the Rocky Mountain region, and therefore, cannot be said to represent fully the fauna of the entire continent. Virtually nothing is known of early Tertiary mammals of eastern North America. Even in areas where faunas of appropriate age are known, the present study has revealed unaccountable gaps in chronologic and geographic ranges of almost all tapiroid genera, such as Lysitean *Homogalax*, New Mexican *Heptodon*, Uinta Basin *Colodon*, etc. Therefore present paleozoogeographic data are here considered much too inadequate for definite exclusion of North America as the possible area of origin of the Perissodactyla.

Homogalax appears to have been directly ancestral to all later tapiroids. With *Isectolophus* it forms a single conservative lineage, the Isectolophidae, known from three successive species, *Homogalax protapirinus*, *Isectolophus latidens*, and *I. annectens*, from early, middle, and late Eocene respectively.

The earliest helaletid, *Heptodon*, also may be derived from *Homogalax*, although the transition is not yet well documented. Some *Homogalax protapirinus* teeth from the Bighorn Basin Gray Bull beds show features approximating *Heptodon* dentition (see p. 16) and some *Heptodon calciculus* individuals resemble *Homogalax* in possession of somewhat trapezoidal M³'s (see p. 30). However, intermediate stages in one of the most noticeable morphological changes between these two genera, the development of long post-canine diastemata, have not been observed. In the Bighorn Basin of Wyoming, one of the few areas containing an almost continuous record of early Eocene deposition, *Heptodon* appears abruptly a considerable distance above the base of the Willwood formation, with no antecedent forms known from underlying strata and no apparent hiatuses. It is therefore suggested that *Heptodon* evolved from an as yet unknown *Homogalax* population elsewhere and migrated into the Bighorn Basin, where its first appearance has been used to mark the beginning of Lysitean time.

Similarities in dentition suggest close relationship between *Hyrachyus*, the earliest rhinocerotoid, and the helaletid tapiroids (see p. 44 for details). *Heptodon* is well-suited, both morphologically and chronologically (hyrachyids first appear in Lostcabinian faunas), to have been ancestral to *Hyrachyus*. The transition from tapiroid to rhinocerotoid, involving mainly increase in size, lengthening of M¹⁻² metacone, and loss of M₃ hypoconulid, may have occurred not long after *Heptodon* branched off from *Homogalax*, perhaps in late Graybullian or early Lysitean time.

Wind River Basin Lost Cabin *Heptodon calciculus* specimens approach early Bridgerian *Helaletes nanus* in small size, tendency towards loss of P₁, and molar cusp pattern; one specimen, AMNH 294, may even show beginnings of nasal incision retraction. Thus the smallest *Heptodon calciculus* appears to represent (at least morphologically) the ancestral form which evolved into *Helaletes nanus*.

During the middle Eocene a major helaletid radiation occurred, originating primarily from *Helaletes*. Small size, unprogressive premolars, and reduced M₃ hypoconulid in several specimens of early Bridgerian *Helaletes nanus* suggest that species as the probable ancestor of the diminutive *Dilophodon* line, which may be traced through the late Bridgerian *D. minusculus* to the late Uintan *D. leotanus*.

Similarities in dentition and nasal incision enlargement indicate that *Colodon* also arose from *Helaletes*, although the transition is not as well documented as that leading to *Dilophodon*. Available evidence is insufficient to indicate definitely which species of *Helaletes*, *H. nanus* or *H. intermedius* was nearest the ancestry of *Colodon*, but premolar morphology suggests the former.

Phylogenetic relationships between species included in the *Colodon* group are open to conjecture. The late Eocene *C. kayi* and *C. woodi* apparently were closely related contemporaneous allopatric species, differing so far as is known only in size. In Oligocene time *C. occidentalis* shows increase in size and dental specialization in loss of canines, greater degree of P¹ molarization, and further reduction of molar metacones; the contemporaneous but geographically separated *Colodon? cingulatus* was larger but somewhat less specialized in dentition than *C. occidentalis*. Occurrence of relatively nonmolariform premolars in some individuals of *C.? cingulatus* suggests that it was separated from the *kayi-woodi-occidentalis* line by late Eocene time.

The combination of enlarged nasal incision and comparatively unmolarized premolars suggests that the late Eocene or early Oligocene *Colodon? hancocki* may represent an independent lineage which diverged early from the main *Hela-*

letes-Colodon stock. *C.?* *hancocki* is well suited, chronologically and morphologically, to have given rise to the earliest tapirid, *Protapirus*.

An offshoot from the *Helaletes-Colodon* line is represented in Asia by several late Eocene and Oligocene species referred to the latter genus (see review on p. 93).

More information is required, not only about dentition, but also about the cranial and postcranial anatomy of species of *Colodon* before details of evolution within this group may be worked out.

Little is known of the origins of *Helaletes intermedius*. Since it possesses in common with *H. nanus* a greatly enlarged nasal incision, it seems likely that both species descended from a common ancestor which had already developed that feature; otherwise one would have to postulate independent acquisition of an unusual cranial modification. Since the probable late Lostcabinian ancestor of *H. nanus*, *Heptodon calciculus*, did not have unusually enlarged nasal excavations, *Helaletes nanus* and *H. intermedius* probably diverged after Lostcabinian time. *H. intermedius* might have evolved from a Bridger B *H. nanus* stock with relatively simple premolars, or the two species might have been distinct during early Bridgerian time, having separated between Lostcabinian and Bridger B time.

Evolutionary radiations are usually initiated by the appearance of a basic adaptation which allows expansion into new environmental niches or increases efficiency in competition. A possible key to the middle Eocene helaletid radiation may be the greatly enlarged nasal incision which first appears in early Bridgerian *Helaletes*, suggesting an incipient proboscis. The development of this feature will be discussed in more detail in a later section (p. 89).

One may also speculate on reasons for the extinction of the Helaletidae. The last species, *Colodon occidentalis*, persisted until the end of the Oligocene in North America. Cursorial skeletal modifications (see Wortman and Earle, 1893 and Scott in Scott and Jepsen, 1941) and association with lightly-built hyracodonts and horses (Matthew, 1901) suggest that *Colodon occidentalis* inhabited the open plains or uplands. Extinction may have been due to an inability to compete with other cursorial perissodactyls or artiodactyls. (It is interesting to note that the hyracodont rhinoceroses also became extinct at this time.) The contemporaneous brachydont tapirid *Protapirus* was mediportal and probably lived in swampy forested lowlands; this ecological difference may account for its survival.

STRATIGRAPHIC DISTRIBUTION

Isectolophid tapiroids first appear in deposits of early Wasatchian (early Eocene) age and are last found in late Uintan (late Eocene) beds. Helaletids are known from the middle of Wasatchian time to the end of the Oligocene. The stratigraphic distribution of both families is summarized in fig. 14.

Several Eocene tapiroid genera have restricted time ranges and therefore may serve as guide fossils to provincial ages or faunal zones (although their usefulness in such a capacity is limited by their general scarcity in most faunas).

Homogalax and *Heptodon* are confined to and fairly common in early Eocene faunas and are listed by Wood, *et al.*, (1941, p. 10) as index fossils for Wasatchian time. The restricted vertical ranges of these genera are further diagnostic of faunas which apparently represent subdivisions of Wasatchian time.

Homogalax serves as a guide fossil for the early Wasatchian Gray Bull faunal zone. Granger (1914, p. 203) originally delimited the Gray Bull beds by the presence of *Homogalax*, which in the Bighorn Basin is extremely abundant in these beds but strikingly absent from lower and higher strata. Discovery of *Homogalax* in the immediately underlying Sand Coulee beds, which have a somewhat similar fauna, led Jepsen (1930, p. 474) to redefine the Gray Bull to include the Sand Coulee beds. Other workers (*inter alia* Simpson, 1937, p. 1; 1955, p. 424; Kitts, 1956, p. 42) have found it taxonomically useful to distinguish Sand Coulee fossils from those of the later Gray Bull fauna.

Absence of *Homogalax* and presence of *Heptodon* has been used to determine the boundary between the Gray Bull and overlying Lysite beds (Sinclair and Granger, 1911, p. 104; Granger, 1914, p. 203). In the summer of 1961, a Yale Peabody Museum expedition discovered *Homogalax* (YPM 17082) at the same horizon and locality as *Heptodon*, about fifty feet above the lowest *Heptodon* recovered by that party in the Bighorn Basin. Such an overlap in chronologic ranges should not be surprising for two reasons: first, appearance of isectolophid descendants of *Homogalax* in middle Eocene faunas indicates that intermediate forms must have existed somewhere during middle and late Wasatchian time; secondly, *Heptodon* appears to have migrated into the Bighorn Basin, rather than evolved in place (see p. 75) so its sudden appearance does not necessarily indicate a long time lapse between Gray Bull and Lysite faunal zones.

The great abundance of *Homogalax* in Graybullian faunas makes it a good guide fossil for early Wasatchian time. The occurrence of *Homogalax* in older or younger faunas is not a sufficient reason of itself for vertical extension of the Gray Bull zone, since faunal zones should be based on composition of total faunal assemblages rather than presence or absence of only one genus.

Occurrence of *Heptodon* without *Homogalax* or *Lambdotherium* has been used to define the middle Wasatchian Lysite beds (Sinclair and Granger, 1911, p. 104); in the overlying Lost Cabin beds *Heptodon* occurs with *Lambdotherium*. Van Houten (1945, p. 428) noted the difficulty of identifying Lysitean assemblages since the zone is defined mainly on negative grounds and lacks distinctive genera. Unfortunately, the lack of clear and successive species differences in *Heptodon* provides no help in distinguishing Lysite from Lost Cabin zones. In the Wind

River Basin, Lostcabinian specimens of *H. calciculus* average slightly smaller than those from the underlying Lysite and exhibit in some individuals a precocious trend towards loss of P_1 . These differences could be used to determine stratigraphic horizon of large samples of Wind River Basin *Heptodon* but do not distinguish the usual collections of only a few isolated teeth. Also, large size of specimens from other localities in Wyoming complicates the picture in a way not yet fully understood. The rare *H. posticus* apparently occurred in both Lysite and Lost Cabin faunal zones. Thus on the basis of available evidence occurrence of *Heptodon* appears equally indicative of either middle or late Wasatchian time.

Helaletes and *Isectolophus latidens* may be used as guide fossils for strata of Bridgerian (middle Eocene) age. The relatively great abundance of *Helaletes nanus* in Bridger B beds and its scarcity in Bridger C-D beds make that species a fairly good guide to early Bridgerian time.

Isectolophus annectens is diagnostic of Uintan (late Eocene) faunas. Analysis of larger samples than are available at present may allow use of that species to differentiate between faunas from Uinta B and Uinta C beds.

The occurrence of *Dilophodon* is indicative of a late Bridgerian or late Eocene age. The presence of *Colodon* indicates late Eocene or Oligocene time.

GEOGRAPHIC DISTRIBUTION

Representatives of either Isectolophidae or Helaletidae are found in most North American mammal-bearing deposits of appropriate age (see figs. 15-17). Unusual exceptions like the absence of *Heptodon* from the well-known early Eocene Largo fauna, San Juan Basin, New Mexico, apparently reflect paleoecological factors which are not yet fully understood (see p. 39).

So far as is known, isectolophids were confined to North America, but helaletids apparently migrated to Asia and occur in late Eocene and Oligocene faunas of Mongolia and Korea (see discussion of Asiatic tapiroids, p. 93).

Probably the most interesting feature of isectolophid and helaletid geographic distribution is allopatry: contemporaneous representatives of each family rarely occur at the same localities. In the early Eocene, *Homogalax* is absent from the numerous Lysitean and Lostcabinian *Heptodon* localities, except for slight stratigraphic overlap in the Bighorn Basin (see p. 77) and a possible rare occurrence of *Homogalax* at the Dad locality (see p. 17).

Helaletes nanus is common in early middle Eocene deposits and rare later, while the reciprocal situation is true for *Isectolophus latidens*. In the late Eocene, *Colodon* occurs at the Sage Creek and Badwater localities but is absent from the well-known contemporaneous Uinta Basin faunas; *Isectolophus annectens*, on the other hand, is common in the Uinta Basin but missing from other late Eocene localities.

The main exception to this disjunct distribution pattern is the sympatry of *Dilophodon* and *Isectolophus*. *Dilophodon minusculus* and *Isectolophus latidens* occur together and are both most common in late Bridgerian (middle Eocene) faunas; *D. leotanus* is found with *I. annectens* in Uintan (late Eocene) beds. It should be noted that *Dilophodon* differs from all other helaletids in very small size and loss of M_3 hypoconulid. (The latter feature taken by itself is not highly significant but may reflect more basic genetic differences.)

The apparent allopatry between isectolophid and helaletid tapiroids is a phenomenon worth some careful speculation. Differences in dentition (such as presence of post-canine diastemata, more molariform premolars) and the development of a proboscis in the Helaletidae, suggest basically different feeding habits (these differences are discussed in more detail in following sections). Contemporaries in both groups are about the same size, lightly built and cursorial. The allopatry might have been due to interfamilial competition or to adaptation to different environments. Further speculation should be based on a thorough analysis of the total faunal assemblages involved, review of all pertinent geological evidence, and a detailed study of helaletid and isectolophid skeletal anatomy. These will be investigated by me in the near future but are beyond the scope of the present project.

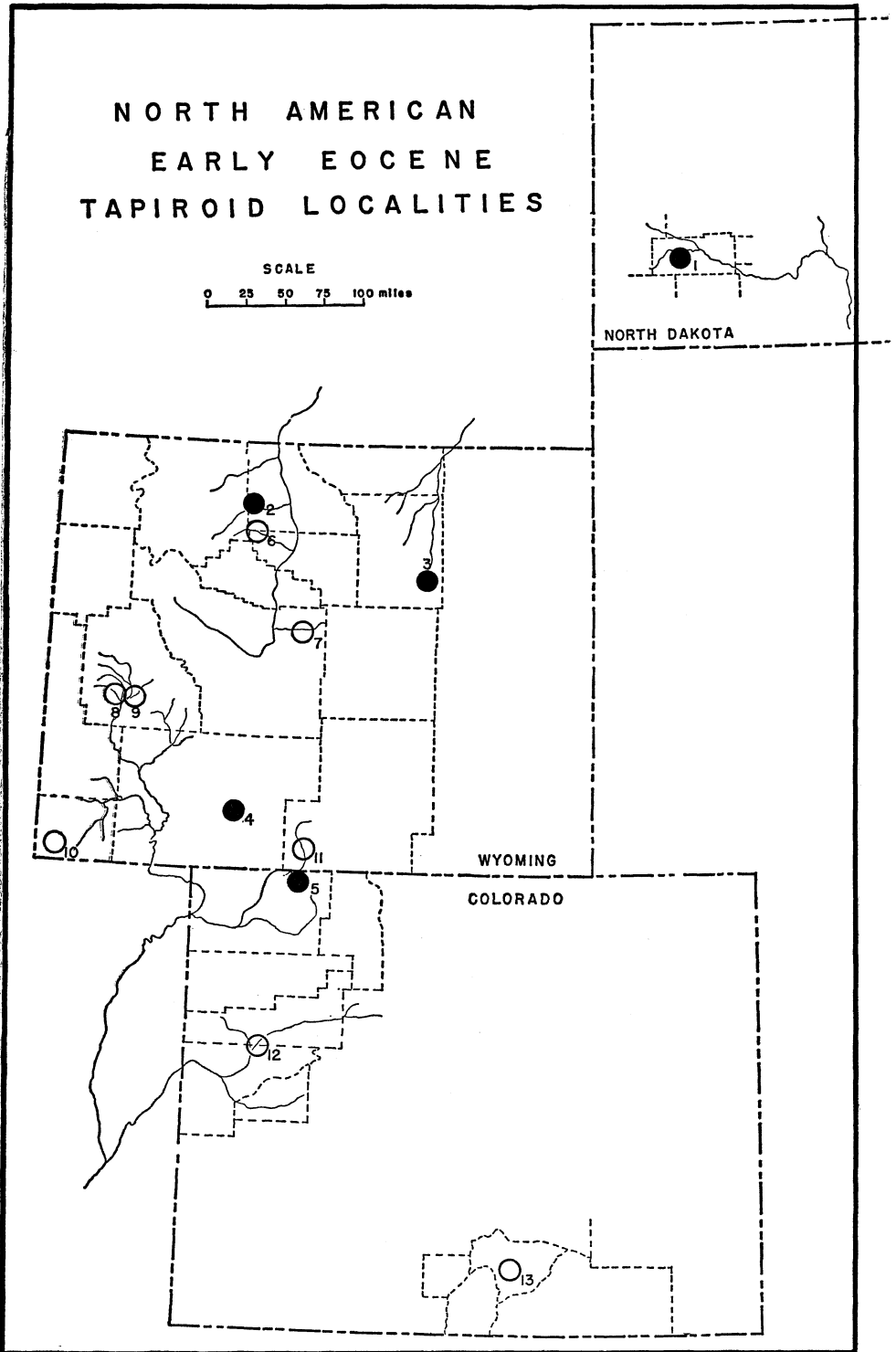


FIG. 15. Map showing localities where early Eocene tapiroids have been found in North America. Solid circles = *Homogalax*: 1 = Golden Valley; 2 = Bighorn Basin; 3 = Sussex, Powder River Basin; 4 = Bitter Creek, Washakie Basin; 5 = Four Mile. Open circles = *Heptodon*: 6 = Bighorn Basin; 7 = Wind River Basin; 8 = La Barge; 9 = New Fork; 10 = Knight Station; 11 = Dad; 12 = DeBeque; 13 = Huerfano.

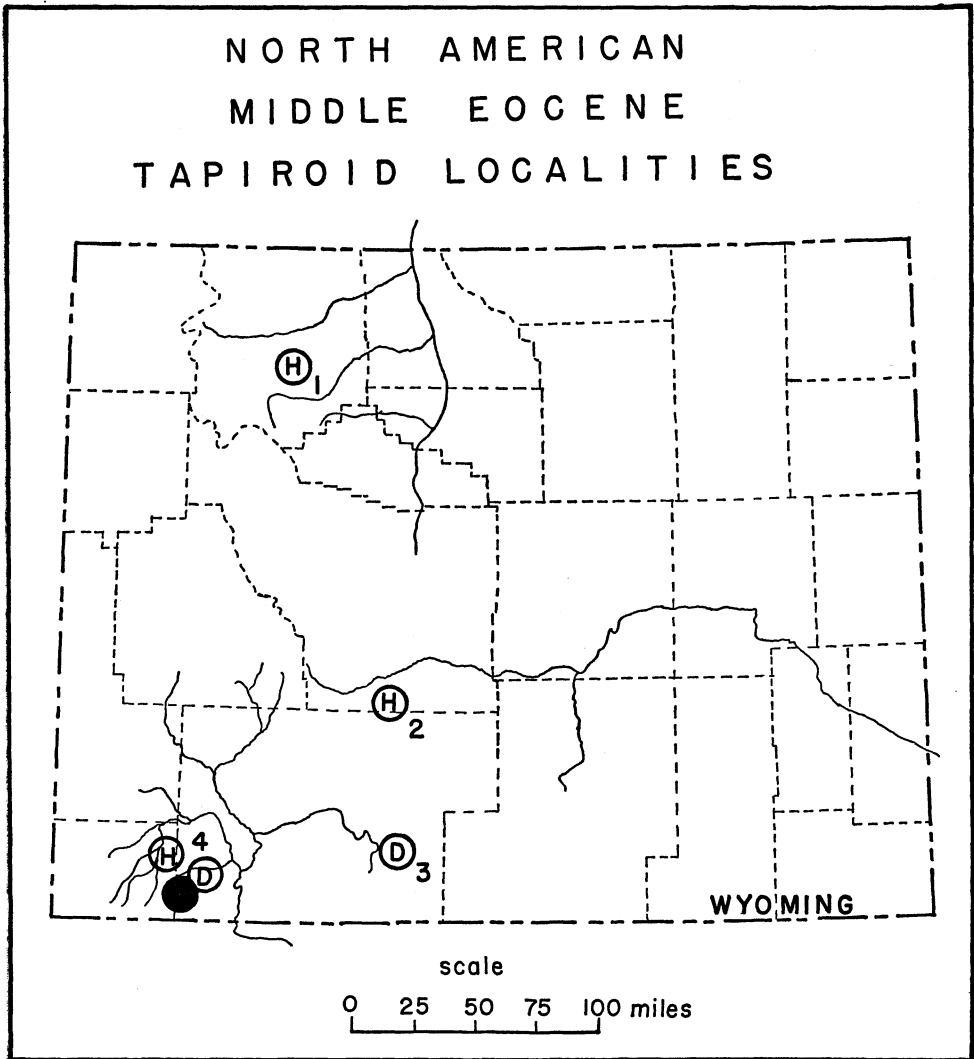


Fig. 16. Map showing localities where middle Eocene tapiroids have been found in North America. Solid circles = *Isectolophus*; H = *Helaletes*; D = *Dilophodon*. 1 = Carter Mountain; 2 = Horsetrack Anticline; 3 = Washakie Basin; 4 = Bridger Basin.

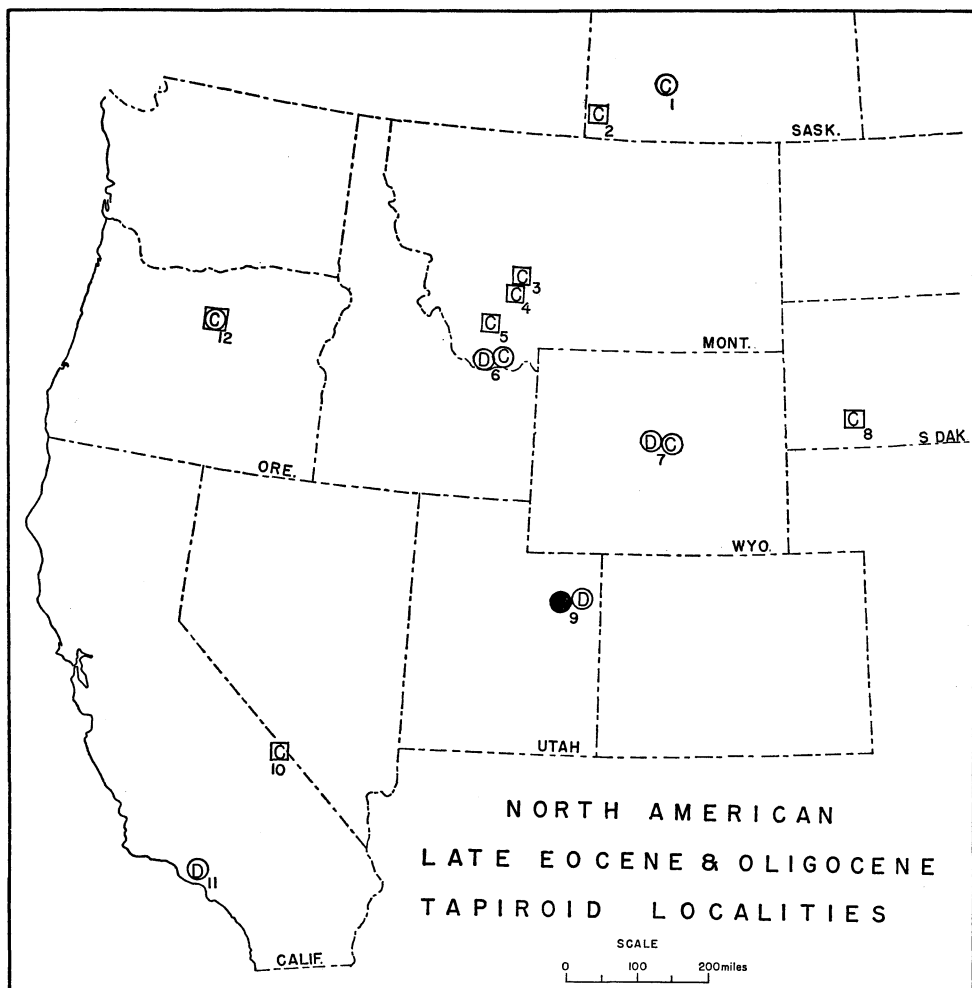


Fig. 17. Map showing localities where late Eocene and Oligocene tapiroids have been found in North America. Circles = late Eocene; squares = Oligocene. Solid circle = *Isectolophus*; C = *Colodon*; D = *Dilophodon*. 1 = Swift Current; 2 = Cypress Hills; 3 = Toston; 4 = Thompson's Creek; 5 = McCarty's Mountain; 6 = Sage Creek; 7 = Badwater Creek, Wind River Basin; 8 = White River group; 9 = Uinta Basin; 10 = Titus Canyon; 11 = Sespe; 12 = Clarno.

EVOLUTION OF TAPIROID DENTITION

Detailed descriptions of isectolophid and helaetid dentition have been given in the taxonomic section. The following discussion will summarize evolutionary trends in tapiroid dental morphology with emphasis on functional interpretation.

PERISSODACTYL ORIGINS: The middle Paleocene condylarth *Tetraclaenodon* seems a suitable morphological antecedent for all Perissodactyla. Its molars bear broad, low, bunodont cusps, apparently mainly suited for crushing. Primitive perissodactyls, such as *Hyracotherium angustidens*, show the following advances in dentition over *Tetraclaenodon*: relatively higher, sharper, and more lophodont molar cusp patterns, with more prominent ectoloph; protocone and protoconule, hypocone and metaconule approximately aligned into transverse shearing lophs; entoconid increased in size until equal to hypoconid, and M_{1-2} hypoconulids reduced and posteriorly displaced, allowing transverse shear across entoconid and hypoconid. In addition, M_3^3 , relatively reduced posteriorly in condylarths, become about as large and molariform as the anterior molars, with the M_3 hypoconulid greatly lengthened. These changes suggest that the transition from condylarth to perissodactyl involved a shift in dental function from mainly crushing to shearing.

Previous analysis of molar wear facets has provided significant information on occlusal relationships and jaw movements which appears to substantiate the above suggestion. Detailed studies of wear surfaces on *Hyracotherium* teeth enabled Butler (1952 p. 801) to divide jaw motion of that primitive perissodactyl into three major phases or components of motion. Starting with the lower jaw most buccally located, labial sides of paralophid, protoconid, metalophid and hypoconid shear upward and somewhat lingually against lingual surfaces of the ectoloph. In the second phase, shear is mainly transverse, with posterior sides of first protoconid and hypoconid, then metaconid and entoconid, sliding lingually across anterior faces of protoconule and metaconule, and protocone and hypocone, respectively. Anterior faces of entoconid and metaconid brush past posterior sides of protocone and preceding hypocone. Finally, anterolingual sides of hypoconid and protoconid slide lingually past posterolabial faces of protocone and preceding hypocone. The large M_3 hypoconulid shears against the posterolingual face of M^3 metacone and posterior side of M^3 metaloph in phases 1 and 2 respectively.

Premolar occlusal contacts consist largely of vertical shear between lingual sides of ectolophs and labial sides of paralophids and metalophids (first phase of jaw motion). Some transverse shear occurs between anterior sides of P^{3-4} protolophs and posterior sides of P_{3-4} protolophids. Contacts also occur between P_4 hypoconid lingually and P^4 protocone labially, and P_4 paralophid and P_3 hypoconid lingually and P^3 protocone labially.

Butler interpreted the jaw motion of *Hyracotherium* to be rotary in a transverse vertical plane. Consideration of his diagrams (*loc. cit.*, p. 800, fig. 13) and manipulation of actual specimens suggest that some rotary motion in a horizontal plane may also be involved, with contacts behind protocone and hypocone occurring 180 degrees out of phase from shear in front of protoloph and metaloph.

ISECTOLOPHIDAE: Dentition of *Homogalax*, the earliest tapiroid, closely resem-

bles that of *Hyracotherium angustidens*, and occlusal relationships were probably essentially similar (see fig. 18). *Homogalax* differs from *Hyracotherium* mainly in emphasis of upper and lower molar cross lophs, with protoconule and metaconule merged into protoloph and metaloph, and protolophid and hypolophid more complete. These changes, which mark the initial divergence of ceratomorph and hippomorph perissodactyls, allow a more continuous transverse shear between anterior faces of protoloph and metaloph and posterior sides of protolophid and hypolophid. The relatively larger parastyle in *Homogalax* provides a longer surface for shear against the labial side of the protoconid, in line with the transverse shear. Trapezoidal M^3 outline, an isectolophid characteristic, results from relative increase in tooth width, with metaloph about as long as protoloph, and slight shortening of the metacone; these changes increase length of transverse shear across protoloph and especially metaloph, but reduce vertical shear of M^3 hypoconulid against M^3 metacone.

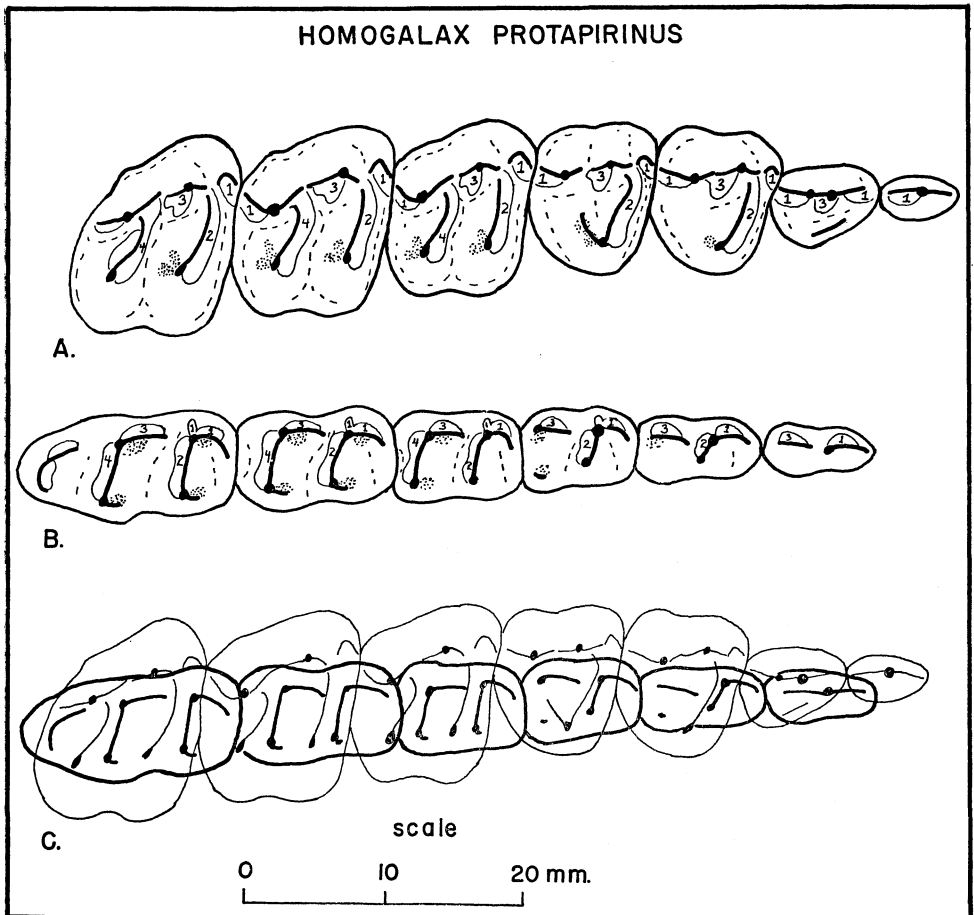


Fig. 18. Wear facets and occlusal relations in *Homogalax protapirinus*. A = upper dentition, B = lower dentition. Numbers refer to corresponding wear facets. Stippled areas indicate less important contacts. C = upper and lower dentitions superimposed to show occlusal relations.

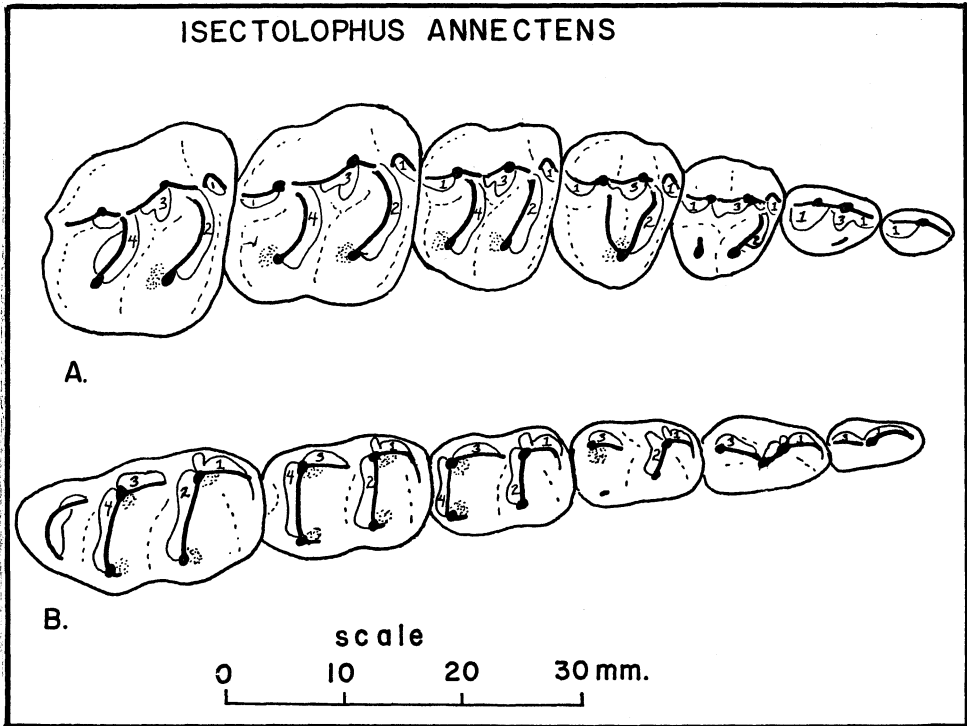


Fig. 19. Wear facets in *Isectolophus annectens*. A = upper dentition, B = lower dentition. Numbers refer to corresponding wear facets. Stippled areas indicate less important contacts. See text for discussion.

Isectolophid dentitions, from early Eocene *Homogalax* through middle Eocene *Isectolophus latidens* to late Eocene *Isectolophus annectens* show general increase in size with time and lengthening of molar series relative to premolars. This latter trend perhaps indicates increasing importance of molars in mastication. M^{1-3} become slightly longer relative to width, but M_{1-3} exhibit no change in proportions. Molarization of P^3 begins in the middle Eocene, with the hypocone appearing as a small, isolated posterolingual cuspsule, present in some specimens of *I. latidens*; by late Eocene time it is found in all individuals of *I. annectens*. However, even in the most advanced specimens, protocone and hypocone are small and low, and occlusal relationships are essentially as in *Homogalax*, with lingual sides of P_4 paralophid and P_3 hypoconid sweeping against labial and posterolabial faces of P^3 hypocone and protocone, instead of only against the protocone (see fig. 19).

Isectolophus cusp morphology is more specialized than that of *Homogalax* in the following relatively minor features: metaloph attached higher up on a more complete ectoloph, protoconule and metaconule completely merged into proto-loph and metaloph, metastylid no longer present, and protolophid and hypolophid somewhat better developed—changes which primarily allow freer transverse shear along cross lophs and somewhat more extensive vertical shear on ectolophs; P_{2-4} trigonids relatively lower and metalophids relatively higher, with P_{2-3} paralophid and metalophid aligned as an essentially continuous low medial blade, evidently adapted for increased vertical shear against P^{2-4} ectolophs.

HELALETIDAE: Dental evolution from *Homogalax* to *Heptodon*, the earliest representative of the Helaletidae, involved development of several features which became characteristic of that family. Canines become somewhat smaller. A long post-canine diastema, present in most perissodactyls and artiodactyls but never developed in the Isectolophidae, occurs in *Heptodon*. This separation allows functionally dissimilar dental areas (nipping incisors and masticatory cheek teeth) to act independently, thereby increasing efficiency of operation. P_1 becomes reduced in size and is lost entirely in some specimens of *Heptodon*. As in *Isectolophus*, the molar series increases in length relative to the premolars, suggesting perhaps relative increase in importance of molars in mastication. M^2 and M^3 become relatively longer, the latter tooth assuming the long, narrow, squat outline characteristic of helaletids. This change in proportions of M^3 involves reduction and lingual depression of the metacone and shortening of the metaloph, with the portion of the ectoloph between metacone and paracone shifted into line with the metaloph. This increases length of transverse shear between posterior hypolophid face and anterior metaloph surface, while decreasing the area of ectoloph involved in vertical shear. Reduction of M_3 metalophid, which occludes against the ectoloph, supports this suggestion. Apparently in conjunction with M^3 metaloph shortening, the M_3 hypoconulid, which in isectolophids shears against the rear of that crest, undergoes drastic reduction in length, width, and height.

M^2 , and to a lesser degree M^1 , also exhibits flattening and lingual depression of metacones, with anterior metacone edge brought more into line with metaloph. This indication of increasing emphasis of transverse shear and decreasing importance of vertical (ectoloph) shear is supported by the better development of upper and lower molar cross lophs, relative increase in width of lower molars, and reduction of metalophids in dental evolution from *Homogalax* to *Heptodon*.

Heptodon premolars exhibit the following trends towards molarization not seen in *Homogalax* or later isectolophids: P_{2-4}^2 become progressively relatively shorter and wider, P^2 protoloph and P^{3-4} metalophs more prominent, and P_{2-4} trigonids lower. These changes in proportions suggest increased emphasis on transverse shear (along protolophids).

Major evolutionary changes in helaletid dentition, from early Eocene *Heptodon* through middle Eocene *Helaletes* to late Eocene and Oligocene *Colodon*, result from continuation of trends initiated in *Heptodon*, as described above. Canines become smaller and are lost entirely in *Colodon occidentalis*. P_1 is lost in *Helaletes* and later forms. M^{1-3} metacones become increasingly lingually depressed and reduced, reaching an extreme in the Oligocene *Colodon occidentalis*, where protoloph, paracone, metacone and metaloph form a continuous inverted U-shaped crest, with the posterior metacone ridge a short extension between paracone and hypocone. Reduction of $M_{1,3}$ paralophids and metalophids results in bilaterally symmetrical protolophids and hypolophids in *Colodon*. These alterations seem to indicate increasing importance of transverse shear along cross lophs and decreasing emphasis of vertical ectoloph shear. *Helaletes* molars exhibit a slight relative increase in length compared to those of *Heptodon*, but in *Colodon* molars relative shortening and widening is marked (see fig. 20).

Molarization of premolars is a major evolutionary trend in helaletid dentition. In the early Eocene, *Heptodon* P^{2-4} 's have only one lingual cusp, a conical protocone; in the middle Eocene genus *Helaletes*, a short low ridge runs posteriorly from the protocone and a more or less prominent lingual or anterolingual groove marks incipient separation of hypocone from protocone. This contrasts with the

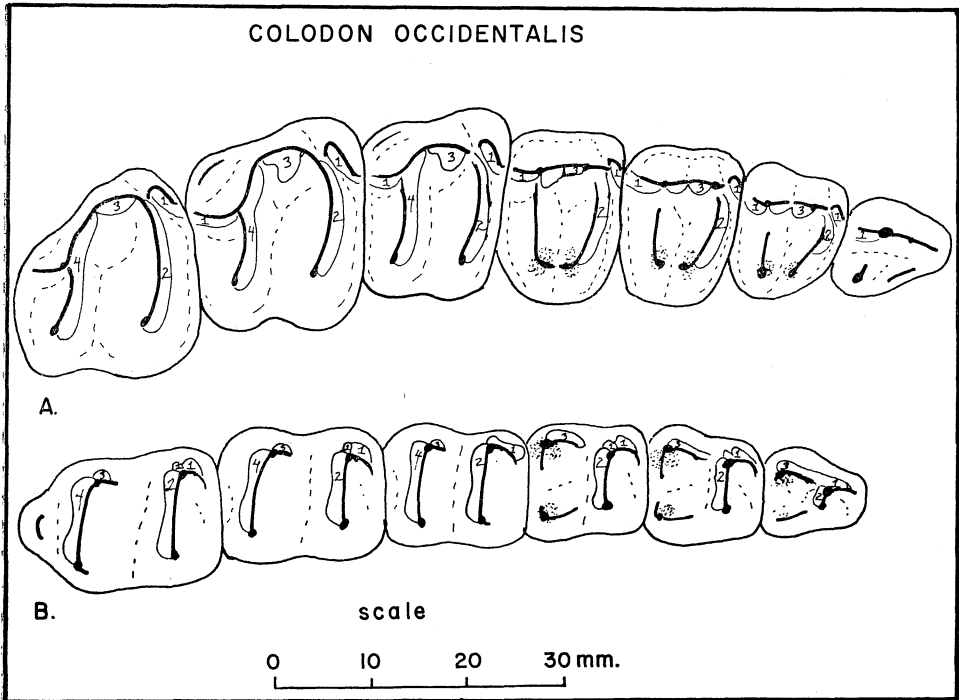


Fig. 20. Wear facets in *Colodon occidentalis*. A = upper dentition, B = lower dentition. Numbers refer to corresponding wear facets. Stippled areas indicate less important contacts. See text for discussion.

method of molarization of P^3 in *Isectolophus*, where the hypocone appears as an independent, isolated cusp. In *Heleletes* the metaloph is smaller than the protoloph and extends either towards the incipient hypocone (*H. nanus*) or anterolingually, to the protocone (*H. intermedius*). Lower premolar talonids are somewhat better developed than in *Heptodon*, and an entoconid always occurs on P_3 .

By the late Eocene, *Colodon* exhibits short, wide, virtually molariform P^{2-4} , with protocone and hypocone distinct but close together, and metaloph as prominent as protoloph. P^1 is advanced over that in *Heleletes* in development of a lingual loph. P_{2-4} are very short and wide, with reduced paralophids, long protolophids, and wide talonids with entoconids as large as hypoconids but not connected by a hypolophid.

Premolar occlusal relationships differ from those of the molars in several features. Most important, close proximity of protocone and hypocone block the lingual valley between protoloph and metaloph, so that hypoconid and entoconid cannot shear transversely between upper cross lochs. The dorsolingual side of the hypoconid grinds almost horizontally across the ventrolabial surfaces of protocone and hypocone, while at the other end of the transverse jaw motion, the labial side of the entoconid occludes against the lingual edge of the protocone. Since metacones lie almost directly posterior to paracones, P^{2-4} ectolophs are straight; as might be predicted, P_{2-4} metalophids and paralophids are relatively prominent. Thus vertical shear between lingual ectoloph surfaces and labial sides of lower premolars remains unreduced and is more important in the anterior cheek

teeth than in the molars. Transverse shear between protoloph and protolophids occurs as in the molars, and becomes relatively more effective with time through the Eocene as premolars become relatively wider.

Retarded premolar molarization is the basic feature by which *Helaletes-Colodon? hancocki* dental evolution diverges from that of the main *Helaletes-Colodon* line. Relatively short and wide premolars in the late Eocene *C.? hancocki* suggest occlusal relationships similar to those described for *Colodon*. However, lesser degree of protocone-hypocone differentiation and relatively small size of entoconid indicate that in *C.? hancocki* grinding contacts between P²⁻⁴ lingual cusps and P₂₋₄ talonids were less extensive than in *Colodon*, and more like the condition in *Helaletes*.

Dental evolution in the *Helaletes-Dilophodon minusculus-Dilophodon leotanus* lineage differs from that in the *Helaletes-Colodon* line in several features, the most evident of which is lesser degree of premolar molarization. Premolars in the late Eocene *D. leotanus*, although relatively short and wide as in *Colodon*, exhibit submolariform cusp patterns, no more advanced than in *Helaletes*, with hypocone at most barely distinct from protocone, metaloph minute compared to protoloph and directed anterolingually, towards protocone, and entoconid much smaller than hypoconid. M¹⁻² metacones in *D. leotanus*, although lingually depressed, are convex labially and not much reduced. This suggests that in *Dilophodon* importance of vertical ectoloph shear did not decrease with time. *Dilophodon* dentition is more advanced than that of *Helaletes* or *Colodon* in one feature—loss of M₃ hypoconulid—which had already been attained in the middle Eocene *D. minusculus*. The *Helaletes-Dilophodon* line exhibits decreasing size with time, in contrast to the size increase seen in *Colodon*.

DECIDUOUS DENTITION: Evolution of deciduous dentition in isectolophids and helaletids parallels changes in the permanent teeth. In *Homogalax*, DP⁴ and DP⁸ are fully molariform, although relatively longer and narrower than permanent molars. DP², like P², is very narrow, with only a cingulum lingual to paracone and metacone. DP₄ is fully molariform; DP₃ is less molariform only in the more posterior position of the metaconid.

Advances seen in the deciduous dentition of the late Eocene *Isectolophus* include posterior widening of DP², with enlargement of its anterolingual cingulum into a low protoloph, and appearance of a tiny isolated hypocone in the posterolingual corner; with these modifications DP² comes to resemble P³. DP₃ in *Isectolophus* is advanced over the corresponding tooth in *Homogalax* by the more anterior placement of the metaconid.

In the helaletid line, evolution of the deciduous dentition involves molarization of DP¹⁻²⁻³. In the middle Eocene *Helaletes* DP² is submolariform like P² or P³; DP₃ is molariform and DP₂ is like P₂. By Oligocene time, *Colodon* exhibits fully molariform DP₂² and submolariform DP¹. In addition, metacones of DP⁴ and, to a lesser degree, DP³ are lingually depressed, paralleling trends in the molars.

These observations substantiate the work of Butler (1952b) which demonstrated the correlation between molarization patterns of premolars and milk molars within given groups of perissodactyls. The mechanism of molarization of both premolars and deciduous dentition of isectolophid and helaletid tapiroids seems best explained by the molarization field theory of Butler (1939, p. 2; 1952a, p. 812) which accounts for the correlation of changes in upper and lower teeth, and for the appearance of cusps which at first are too small to occlude.

EVOLUTION OF THE TAPIROID PROBOSCIS

Although a detailed description of cranial anatomy is beyond the scope of this work, certain skull modifications in the Helaletidae have important taxonomic implications and therefore warrant discussion at this point.

The earliest helaletid, *Heptodon*, exhibits typical primitive perissodactyl skull morphology. In the two complete skulls known (MCZ 17670 and LACM 2343) the nasal incision, a relatively small, somewhat V-shaped notch, ends over the post-canine diastemata. The long nasals extend as far anteriorly as the tips of the premaxillae, have a short premaxillae contact and a long horizontal maxilla suture. The infraorbital foramen lies above P²⁻³, while the anterior orbital wall rises above M¹⁻², leaving a relatively long infraorbital canal. In AMNH 294, a maxillary fragment indicates further extension of the nasal incision back to a point over P¹, completely separating nasals from premaxillae—a condition suggestive of future modifications.

In the middle Eocene genus *Helaletes* the nasal incision is greatly expanded as a large, posteriorly rounded excavation extending back to a point over P³⁻⁴. The premaxillae lose the ascending process, no longer contact the nasals, and share a shortened suture with the maxillae. The nasals have been reduced to long, narrow, splint-like bones, which nevertheless extend as far forward as the anterior tips of the premaxillae. The nasal-maxilla contact is limited to a short, mainly vertical suture at the posterior end of the nasal incision. The maxillae do not reach to the nasals to form lateral walls of the snout along most of the cheek tooth series, isolated from the nasal incision by the ascending portion of the premaxilla. Instead, for some distance between premaxilla and nasal sutures the maxilla forms a smooth-edged posteroventral border to the enlarged nasal incision. The ascending portion of the maxilla, between orbit and nasal incision, bears a broad, shallow, almost vertical groove, which terminates immediately anterior to the infraorbital foramen. This latter opening appears above P⁴, while the anterior wall of the orbit extends over M¹, leaving a very short infraorbital canal.

Further modifications seen in late Eocene and Oligocene *Colodon* include shortening of the nasals, which only extend as far forward as C¹. This is essentially the condition of the skull in the earliest tapirid, *Protapirus*.

Illustrations of the cranial modifications discussed above are shown in fig. 21.

The functional significance of the great maxillary excavations in *Helaletes* is open to speculation. Extension of the nasals to tip of snout seems to preclude development of a lengthy flexible proboscis, since those bones would limit mobility of such an organ. Gregory (1920) noted that a maxillary depression (pre-orbital fossa) in many groups of perissodactyls is occupied by a nasal diverticulum, a cartilaginous sac which opens into the nasal passage near the external nares. Perhaps maxillary reduction and enlargement of the nasal incision in *Helaletes* resulted from the necessity to accommodate greatly expanded nasal diverticula, the adaptive significance of which is as yet unknown.

Reduction of the nasals in *Colodon*, so similar to that in modern tapirs, surely indicates by analogy the development of a proboscis. As far as is known, the Helaletidae were the only Eocene tapiroids to acquire this feature, the taxonomic implications of which are discussed on page 95.

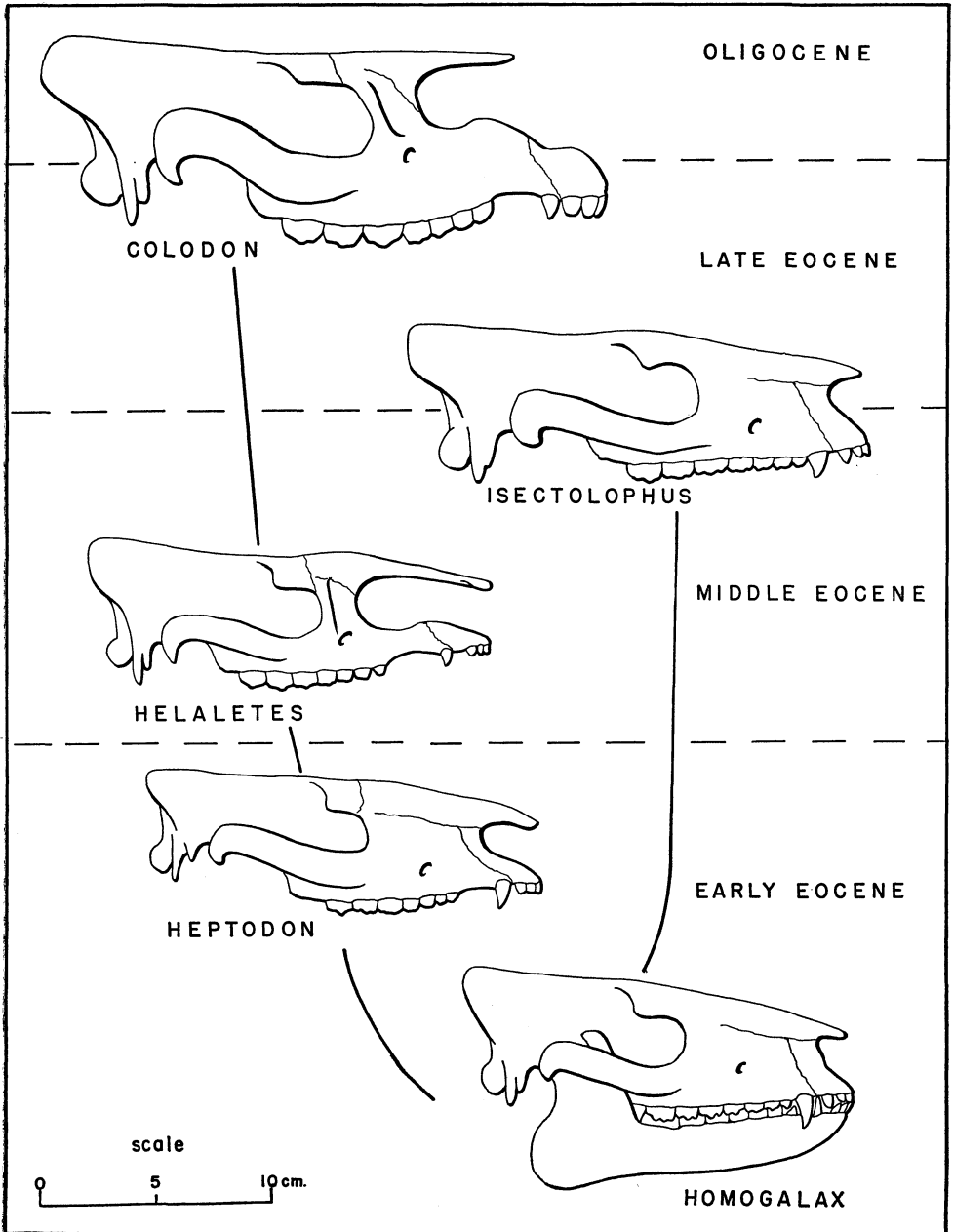


Fig. 21. Evolution of tapiroid skulls. Note progressive enlargement of nasal incision in the Helaletidae. All $\times 1/3$.

EARLY TERTIARY TAPIROIDEA OF EUROPE AND ASIA

Consideration of the record of early Tertiary tapiroids of Eurasia gives one better perspective on evolution of North American isectolophids and helaletids. The following brief review is based mainly on published descriptions and illustrations.

Eocene European Tapiroidea comprise the family Lophiodontidae, for which Simpson (1945, p. 140) lists five genera: *Lophiodon*, *Lophiaspis*, *Atalonodon*, *Chasmothorium*, and *Lophiodochoerus*.

Lophiodon Cuvier, 1822, abundant in middle and late Eocene European mammalian faunas, includes several species of medium-sized to large, primarily mediportal tapiroids, which range in age from late Ypresian (= late Wasatchian or early Bridgerian) to Bartonian (= approximately Uintan). A study of descriptions and figures in, *inter alia*, Filhol, 1888; Depéret, 1903; Stehlin, 1903, 1906, indicates the following as significant features of *Lophiodon* dentitions: large canines; long post-canine diastemata; P_1^1 lost; P^{2-4} nonmolariform to submolariform, with prominent protoloph, short, usually incomplete metaloph, small hypocone distinct in posterolingual corner in advanced forms; M^{1-2} with prominent parastyle, convex paracone, metacone as long as paracone but flattened and slightly lingually displaced; M^3 similar to M^{1-2} except metacone shortened; P_2 a labiolingually compressed central cusp with small talonid; P_{3-4} with prominent paralophid, short, high protolophid, low metalophid to the hypoconid, small entoconid variably developed; M_{1-3} with low metalophid variably developed; M_3 with narrow hypoconulid. No enlarged nasal incisions. Evolutionary changes in *Lophiodon* apparently consisted chiefly of size increase and slight premolar molarization. No Oligocene descendants are known.

Lophiaspis Depéret, 1910a (see also Depéret, 1910b, 1921) was distinguished from *Lophiodon* mainly by the presence of a low distinct protoconule on M^{1-3} . Three species, represented by very few specimens, parallel *Lophiodon* in stratigraphic range and evolutionary size increase. *Lophiaspis*, if indeed it is generically distinct (Heller, 1934, p. 42, gives it subgeneric rank), appears to be closely related to the *Lophiodon* group.

Atalonodon Dal Piaz, 1929, based on a single mandible from the Lutetian (= approximately Bridgerian) of Sardinia, differs from *Lophiodon* primarily in lacking an M_3 hypoconulid. Pending further information, *Atalonodon* may be considered to be not far removed from the *Lophiodon* line.

Chasmothorium Rüttimeyer, 1862 (see Stehlin, 1903, 1906, and Depéret, 1904), includes three evidently successive species in a single lineage which ranges from late Ypresian to Bartonian. Distinguishing characteristics of this genus include: full placental dentition; no upper diastemata; I^{1-3} and C^1 low, sharply conical, with thin leading and trailing ridges; P^1 with prominent paracone, much smaller metacone, posterolingual shelf; P^{2-4} fully molariform, with small parastyle, convex paracone and metacone, complete protoloph and metaloph, with protocone and hypocone more or less well separated; M^{1-3} as in *Lophiodon*; I_{1-3} and C_1 unknown; short post-canine gap; P_1 a simple, labiolingually compressed blade; P_2 with single main cusp and narrow talonid; P_{3-4} with prominent paralophid, short protolophid, prominent metalophid, and hypolophid complete in advanced species; M_{1-3} as in

Lophiodon except M_3 without hypoconulid. Nasal incision not enlarged. Evolutionary trends include perfection of premolar molarization and increase in size (the largest species was slightly smaller than *Tapirus terrestris*).

Chasmothorium represents a tapiroid evolutionary lineage distinct—perhaps on the family level—from that of *Lophiodon*. (Viret [1958, p. 466] placed *Chasmothorium* in a separate subfamily.) The premolars are more molariform than in any other early Bridgerian perissodactyl and, together with the molars, are specialized for transverse grinding of vegetation. One would expect such cheek teeth to be separated from spatulate nipping incisors by a diastema. The combination of sharp conical piercing incisors, no diastemata, and precociously molariform grinding premolars is indeed incongruous and difficult to explain functionally.

Lophiodochoerus Lemoine, 1880, from the late Sparnacian (= approximately early or middle Wasatchian) was originally considered an artiodactyl, with M_{1-3} described as having “quatre pointes surbaissées réunies par une ligne diagonale,” and the cuboid and calcaneum as being “bien caractéristique du groupe des pachydermes doigts pairs” (*loc. cit.*, p. 9). Eleven years later, Lemoine (1891, p. 287, pl. 11, figs. 128-130) first figured *Lophiodochoerus*, now listing it as a perissodactyl. M_{2-3} resemble low-cusped *Hyracotherium* molars; examination of the figures, however, does not allow adequate taxonomic assessment. Stehlin (1903, p. 69) mentioned *Lophiodochoerus* in discussing possible ancestors of *Chasmothorium* but noted that from Lemoine's illustrations (*loc. cit.*) it was impossible to form an impression of the genus. Thus evaluation of the taxonomic position of *Lophiodochoerus* and possibly more information on the ancestry of the Lophiodontidae must await reexamination of the specimens and/or collection of further early Eocene European tapiroid material.

In summary, two main tapiroid stocks appear to be represented in Europe during the middle and late Eocene: the *Lophiodon-Lophiaspis-Atalonodon* group, characterized by nipping incisors, post-canine diastemata, loss of P_1 , and submolariform premolars; and the less common *Chasmothorium* lineage, with conical incisors, no diastemata, complete placental dentition, and precociously molariform premolars. Molar cusp patterns in both groups resemble those of *Heptodon* and indicate similar occlusal relationships. Slightly longer metacones and paralophids in lophiodontids compared to helaletids suggest greater importance of vertical ectoloph shear in mastication in the European group. Neither lophiodontid line developed enlarged nasal incisions. Both lines exhibit size increase (late Eocene forms approximating modern tapirs in bulk) and slight advance in premolar molarization from middle to late Eocene—evolutionary changes similar to those which occurred in North American isctolophids, but less in magnitude than those observed for helaletids. Like isctolophids, lophiodontids apparently became extinct at the end of the Eocene, leaving no known Oligocene descendants.

European early Eocene mammalian faunas are poorly known, and lophiodontid origins obscure. *Lophiodon* could have been derived from a form similar to *Heptodon*, but the ancestor of *Chasmothorium* probably lacked post-canine diastemata (unless one would postulate secondary loss of that feature). If similarities in molar pattern between these two genera are indicative of immediate common ancestry, and if tapiroids originated as suggested in the previous section, then the Lophiodontidae probably arose from tapiroids somewhat more primitive than *Heptodon* (which already had post-canine diastemata). This would suggest an early Wasatchian origin for the Lophiodontidae.

Knowledge of early Tertiary tapiroids in Asia is poor, most of the named genera being known from very few specimens. *Indolophus* Pilgrim, 1925, from the

late Eocene of Burma does not belong to the Isectolophidae (see p. 10, this paper) and cannot be assigned at present to any other known tapiroid family.

The family Helaletidae is represented in Asia by several late Eocene and Oligocene species apparently referable to *Colodon*, including *Colodon orientalis* Boris- siak, 1918; *Colodon inceptus* Matthew and Granger, 1925a; *Paracolodon curtus* Matthew and Granger, 1925a; *Desmatotherium fissum* Matthew and Granger 1925b; *Colodon hodosimai* Takai, 1939, and probably *Desmatotherium mongoliense* Osborn, 1923. The types of *Desmatotherium mongoliense* and *Paracolodon curtus* exhibit the enlarged nasal incisions characteristic of advanced helaletids. *Desmatotherium grangeri* Tokunaga, 1933, in illustrations of Takai, 1939, pl. IV, figs. 5b, 6b, displays nonmolariform premolars and convex M² metacone reminiscent of *Colodon? hancocki*.

Deperetella Matthew and Granger, 1925a, and *Teleolophus* Matthew and Granger 1925b, from late Eocene Shara Murun and Irdin Manha beds respectively, resemble *Colodon* in basic molar cusp pattern, but show more specialization in having higher, sharper cross lophs, more reduced metacones, loss of M₃ hypoconulid, and, in *Deperetella*, possession of hypolophids on P₃₋₄. Retention of P₁ in both *Teleolophus* and *Deperetella* precludes the possibility of common ancestry with any helaletid genus later than the early Eocene *Heptodon*.

Cristidentinus Zdansky, 1930, from the late Eocene of China, is based on a lower jaw with P₃-M₃, which resemble in cusp pattern dentition of *Deperetella* (the type of which includes P₃₋₄ with hypolophids). *Diplolophodon* Zdansky, 1930, from the same locality as *Cristidentinus*, is known from a maxilla with worn teeth, which also shows closest affinities to *Deperetella*.

Schlosseria Matthew and Granger, 1926, from the Arshanto formation, and *Lophialetes* Matthew and Granger, 1925b, from the overlying late Eocene Irdin Manha formation, Mongolia, resemble *Lophiodon* in lower dentition but differ in the upper dental series in these features: P¹ retained, P²⁻⁴ metaloph and proto- loph lingually convergent in a U- or V-shaped loop, M¹⁻³ ectoloph (especially in *Lophialetes*) lengthened as in rhinocerotoids. *Schlosseria* also differs from *Lophiodon* in possessing a tridactyl manus. *Lunania* Chow, 1957, resembles *Schlosseria* and *Lophialetes* in prominence of metalophid and long narrow M₃ hypoconulid.

Gromova (1952, p. 99) proposed a new tapiroid genus, *Ergilia*, for a few limb bones from early Oligocene deposits of Ergil-Obo (= Ardin-Obo), Mongolia. Detailed comparisons with corresponding osteological elements of other perissodactyls are given in a later paper (Gromova, 1960). It is impossible to determine adequately the relationship of *Ergilia* to other tapiroids, since most genera of this superfamily are known primarily from teeth, with little information available on postcranial anatomy. As Gromova herself noted (1960, p. 105) new material may show *Ergilia* to be synonymous with a previously named tapiroid genus.

From the scanty evidence now available, early Tertiary Asiatic tapiroids appear to represent at least four major groups. *Indolophus* apparently belongs to an otherwise unknown lineage. Several species referred to *Desmatotherium*, *Paracolodon*, and *Colodon* are surely closely related to, if not congeneric with, North American *Colodon*, and represent Asian advanced helaletids. *Teleolophus*, *Deperetella*, *Cristidentinus*, and *Diplolophodon* seem to comprise an independent tapiroid family, with dentition specialized for transverse shear almost to the exclusion of vertical ectoloph shear. *Schlosseria*, *Lophialetes*, and *Lunania* represent another independent tapiroid family that may be related to lophiodontids but with dentition suggesting evolutionary emphasis on vertical ectoloph shear, as in rhinocerotoids.

ON THE ORIGIN OF THE TAPIRIDAE

HISTORICAL RESUMÉ: Beginning with Leidy's publication of 1868, reports of early Tertiary fossil tapiroids discovered in North America stimulated a great deal of speculation on the origin of true tapirs. In 1877 (p. 361) Marsh wrote: "The Tapir is clearly an old American type, and we have seen that, in the Eocene, the genera *Helaletes* and *Hyrachyus* were so strongly tapiroid in their principal characters, that the main line of descent probably passed through them." Scott (1883, p. 50) followed Marsh in deriving *Tapirus* from *Hyrachyus*, with *Desmatotherium guyotii* (= *Helaletes intermedius*) as an intermediate form.

Isectolophus annectens, discovered in the Uinta Basin in 1886, seemed to Scott and Osborn (1887, p. 260-261) a more probable ancestor of true tapirs. Stressing similarities in metacone convexity and M_3 hypoconulid, they derived *Tapirus* from what they called *Helaletes* (which was surely *Isectolophus latidens*) through *Isectolophus annectens* and *Colodon occidentalis*, then known only from a single trilobed M_3 . Two years later Osborn (in Scott and Osborn, 1889, p. 523) extended the tapiroid lineage back to *Homogalax*, including *Isectolophus latidens*, *I. annectens*, and *Colodon occidentalis*. He noted as characteristic of the lineage possession throughout of convex molar metacones, lack of post-canine diastemata, trilobed M_3 , and a few foot characters. (His reasoning is difficult to follow since tapiroids have a post-canine diastema and a bilobed M_3 .)

In spite of these conclusions, Marsh (1890, p. 524) still considered *Helaletes* ancestral to true tapirs, with *Colodon* as an intermediate form. Two years later, Osborn (in Osborn and Wortman, 1892) reiterated his earlier opinion that the dentition of *Helaletes* removed it entirely from any relationship to the Tapiridae.

Prompted by the discovery of American species of *Protapirus* to reexamine tapiroid ancestry, Wortman and Earle (1893, p. 169-173) followed Scott and Osborn in deriving *Protapirus*, the earliest true tapir, from *Homogalax* through *Isectolophus latidens* and *I. annectens*. Noting the nonmolariform premolars of *Protapirus simplex*, the earliest American species, they cautioned that discovery of molariform P^{3-4} in *Isectolophus annectens* would exclude it from the tapirine line.

Hatcher (1896, p. 176-178) observed that the molar metacone in *Protapirus* was less convex than in both the earlier *Isectolophus* and later *Tapirus*, and therefore placing the three genera in ancestor-descendant relationship would involve a reversal in evolutionary trend of that feature. Nevertheless, he considered such a shift plausible and supported the *Isectolophus-Protapirus* origin of the true tapirs suggested by Wortman and Earle.

In a comprehensive study of middle and late Eocene North American tapiroids Peterson (1919, p. 114, 124-126) rejected both *Helaletes* and *Isectolophus* as possible ancestors of *Protapirus*, citing among other points their possession of more molariform P^3 's than are found in early tapiroids. He considered the enlarged nasal incisions of *Helaletes* "specializations of an early origin . . . in all likelihood . . . also extended to the true ancestors of the recent tapirs . . ." (*loc. cit.*, p. 114). Peterson was the first to suggest that *Dilophodon* might be closer to the true tapirs than to *Helaletes*.

Troxell (1922b, p. 371), in a redefinition of *Helaletes*, suggested that relation-

ship to the modern tapir was indicated by "the position of the antorbital foramen, the rising of the sagittal crest, the trend toward molariformity in the premolars, the low maxillaries, and especially the presence of a pit in front of the orbit, which may have given rise to the receded nasal aperture of the modern animal."

In a description of a new genus of Miocene tapir, Schlaikjer (1937, p. 244) considered *Homogalax*, as well as *Helaletes* and *Isectolophus*, too specialized in dentition to have given rise to *Protapirus*. He suggested *Heptodon* instead as a possible ancestor, since it possessed no characters which would exclude it from tapirid origins.

More recently, Gazin (1956, p. 22), after describing new material pertaining to the late Eocene *Dilophodon leotanus*, noted that it possessed all the dental features to be expected in the ancestor of *Protapirus*.

DISCUSSION: Speculation on the ancestry of a group should be guided by consideration of its most primitive morphology. The earliest known tapirid genus, *Protapirus*, first appears in early Oligocene cave deposits in Europe (Quercy phosphorites, reported to be of Stampian provincial age) (Filhol, 1877, p. 131) and in middle Oligocene (Orellan) strata in North America (Wortman and Earle, 1893, p. 168). The most primitive North American tapirid species, *Protapirus simplex*, is based on a maxillary fragment with P¹ roots and P²⁻⁴, which are relatively short and wide but nonmolariform, with only a protocone lingually. Other Oligocene specimens of *Protapirus* indicate the following additional pertinent dental features: small canines; post-canine diastemata; M¹⁻³ cusp pattern similar to that of advanced helaletids, except metacone convex and more labially located; P₂ with relatively long trigonid; P₂₋₄ entoconids smaller than hypoconids; M₁₋₃ as in helaletids except for loss of M₃ hypoconulid.

Retention of P¹ and retarded premolar molarization in *Protapirus* clearly exclude from its ancestry the European *Lophiodon* group and *Chasmotherium*. These features plus short but unreduced and convex molar metacones eliminate as possible ancestors the Asiatic *Teleolophus*, *Deperetella*, *Cristidentinus*, *Diplolophodon*, and *Schlosseria*, *Lophialetes*, and *Lunania* groups. In North American tapiroids, full placental dentition unbroken by diastemata, emphasis on vertical shear in P₂₋₃, P³ with two lingual cusps, M¹⁻³ metalophs almost as long as proto-lophs, and large M₃ hypoconulid indicate dental specializations which exclude *Isectolophus* from tapirid ancestry. Thus by a process of elimination only the Helaletidae, or an as yet unknown group of tapiroids, remain as possible ancestors of the Tapiridae.

The hypothesis that tapiroids arose from an unknown tapiroid stock seems unlikely because *Protapirus* (and later tapirs) possessed greatly enlarged nasal incisions and shortened nasals, similar to those in advanced helaletids (see fig. 21). These peculiar cranial modifications indicate development of a proboscis, an organ so rarely occurring in mammals that its independent appearance in two groups of tapiroids seems extremely improbable. Similar proboscis development in *Protapirus* and advanced helaletids strongly suggests that both were derived from a common ancestor which possessed at least incipient manifestations of this feature. The fact that enlarged nasal incisions first appeared in the middle Eocene *Helaletes* (see p. 89) suggests inclusion of at least some species of that genus in tapirid ancestry.

Small size, shortened P₂₋₄, and submolariform P²⁻⁴, with metaloph bypassing hypocone, in *Dilophodon leotanus* indicate evolutionary trends which remove the

Dilophodon lineage from tapirid origins. The molariform premolars of *Colodon* exclude all known species of that genus from the ancestry of *Protapirus*. In the Clarno helaletid questionably referred to *Colodon*, however, relatively nonmolariform premolars and convex M^{1-3} metacones suggest close relationship to the tapirid line. The small M_3 hypoconulid of *Colodon? hancocki* indicates helaletid affinities but could easily be lost (as in *Dilophodon*). Only the shortened P_2 trigonid would seem to weaken the suggestion that *hancocki* was a tapirid ancestor. However, allometric growth could account for alteration of a small short P_2 into a large, relatively long one.

An additional point not discussed above and yet critical for phylogenetic interpretations, is the fact that *Protapirus* had a tetradactyl manus. *Colodon occidentalis* apparently had lost mc V and had an elongate tridactyl manus (see Scott in Scott and Jepsen, 1941, for anatomical details). No postcranial remains are yet known for *Colodon? hancocki*; should it also prove to have lost mc V, it must be removed from the direct line of ancestry of the Tapiridae. However, in any event, similarities in dentition between *C.? hancocki* and *Protapirus* are so great that the former must almost certainly lie near the ancestry of the latter.

In conclusion, consideration of dentition and skull morphology suggests derivation of tapirids from the Helaletidae some time after the beginning of the middle Eocene, with the late Eocene or early Oligocene *Colodon? hancocki* representative of the transitional morphology.

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APPENDIX

TABLE 13
Selected Indices of Tapiroid Teeth

| | M ³ | M ² | 100 × Length | | | 100 × Length P ¹⁻⁴ | |
|-------------------------|----------------|----------------|--------------|-----|----------------|-------------------------------|-------------------------|
| | | | Width | | P ³ | P ² | Length M ¹⁻³ |
| | M ¹ | P ⁴ | | | | | |
| <i>H. protapirinus</i> | 78 | 83 | 83 | 83 | 94 | 128 | 100 |
| <i>I. latidens</i> | 84 | 90 | 89 | 84 | 97 | 131* | 86 |
| <i>I. annectens</i> | 86 | 88 | 88 | 85 | 90 | 118 | 83 |
| <i>Hept. calciculus</i> | 88 | 87 | 84 | 75 | 82 | 93 | 87 |
| <i>Hept. posticus</i> | 89* | 90 | 94* | 76* | 81* | 106* | 74 |
| <i>Hel. nanus</i> | 94 | 92 | 88 | 82 | 81 | 97 | 89 |
| <i>Hel. intermedius</i> | 94 | 91 | 88 | 80* | 86* | 100* | 82 |
| <i>D. minusculus</i> | 89* | 93* | 87* | 82* | 81* | 88* | 83 |
| <i>D. leotanus</i> | 88 | — | 83* | 74* | 74* | 83* | — |
| <i>C. woodi</i> | 86 | 84* | 79 | 73 | 74 | — | 92 |
| <i>C. kayi</i> | 89* | 86* | 83* | 69* | 72* | — | — |
| <i>C. occidentalis</i> | 91 | 89 | 82 | 71 | 73 | 79 | 84 |
| <i>C.? cingulatus</i> | 86* | 83 | 81 | 66 | 68 | 77 | 83 |
| <i>C.? hancocki</i> | 93* | 88* | 82* | 70* | 70* | 86* | 84 |

* Based on 1 or 2 specimens only.

TABLE 14
Selected Indices of Tapiroid Teeth

| | M ₃ | M ₂ | 100 × Width | | | 100 × Length P ₂₋₄ | |
|-------------------------|----------------|----------------|-------------|------|----------------|-------------------------------|-------------------------|
| | | | Length | | P ₃ | P ₂ | Length M ₁₋₃ |
| | M ₁ | P ₄ | | | | | |
| <i>H. protapirinus</i> | 51 | 67 | 66 | 68 | 61 | 58 | 71 |
| <i>I. latidens</i> | 49 | 68 | 65 | 71 | 62* | 51* | 64 |
| <i>I. annectens</i> | 50 | 67 | 67 | 67 | 62 | 56* | 64 |
| <i>Hept. calciculus</i> | 55 | 70 | 72 | 75 | 70 | 73 | 63 |
| <i>Hept. posticus</i> | 50 | 69 | 69 | 72* | 66* | 65* | 57 |
| <i>Hel. nanus</i> | 57 | 67 | 68 | 74 | 68 | 59 | 67 |
| <i>D. minusculus</i> | 60 | 68 | 67 | 79 | 69 | 64* | 69 |
| <i>D. leotanus</i> | 64 | 70 | 69 | 84* | 80* | 75* | 63 |
| <i>C. kayi</i> | 67* | 75* | 80* | 100* | 97* | 85* | 64 |
| <i>C. occidentalis</i> | 65 | 79 | 80 | 102 | 96 | 88 | 65 |
| <i>C.? cingulatus</i> | 63 | — | — | 92* | 80* | 83* | 64 |
| <i>C.? hancocki</i> | 65* | 78* | — | 87 | — | 82* | — |

* Based on 1 or 2 specimens only.

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PLATES

PLATE 1

All figures $\times 1.5$

Figs. 1, 5. *Homogalax protapirinus* (Wortman).

1. Type, AMNH 4460. P^1-M^3 .

5. AMNH 15371. Right P_2-M_3 .

Fig. 2-4, 6. *Isectolophus latidens* (Osborn, Scott, and Speir)

2. YPM 12563, type of "Homogalax bridgerensis." C^1-M^3 .

3. YPM 16854. P^2-M^2 (reversed). Note minute hypocone on P^3 .

4. Type, PU 10251. P^3-M^3 .

6. YPM 12563, type of "Homogalax bridgerensis." Right P_1-M_3 (P_{1-3} reversed from left side).



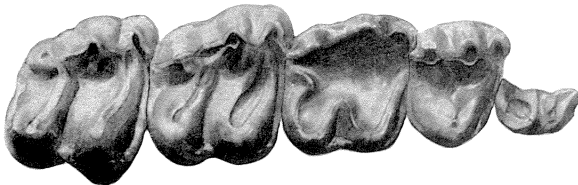
1. *H. protapirinus*



2. *I. latidens*



3. *I. latidens*



4. *I. latidens*



5. *H. protapirinus*



6. *I. latidens*



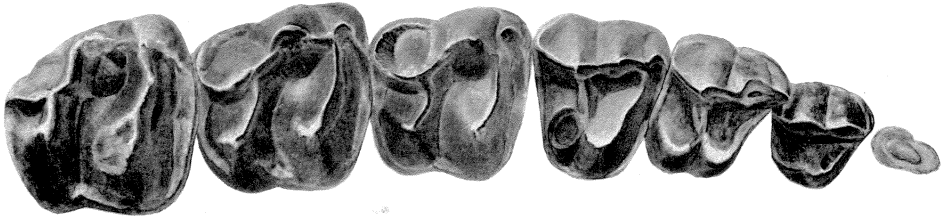
1. Hept. calciculus



2. Hel. nanus



3. Hel. nanus



4. Hel. intermedius



5. Hel. intermedius



6. Hept. calciculus



7. Hel. nanus

PLATE 2

All figures $\times 1.5$

Figs. 1, 6. *Heptodon calciculus* (Cope)

1. AMNH 14884. P²-M³

6. Type, AMNH 4858. Right P₃-M₃ (M₃ reversed from left side).

Figs. 2-3, 7. *Helaletes nanus* (Marsh)

2. YPM 11807, type of "Helaletes boops." P¹-M³.

3. Type, YPM 11080. P²-M³.

7. YPM 16363. Right P₃-M₃ (reversed from left side).

Figs. 4-5. *Helaletes intermedius* (Osborn, Scott and Speir)

4. PU 10166, type of "Desmatotherium guyotii." P²-M³.

5. Type, PU 10095. M¹⁻³ (taken from cast).

PLATE 3

Figs. 1-2. *Dilophodon leotanus* (Peterson)

1. CM 11992. P¹-M¹ (P¹ reversed from left side). × 2
2. CM 9560. Right P₂-M₈ (P₂₋₄ reversed from left side). × 2

Fig. 3. *Dilophodon minusculus* Scott

3. Type, PU 10019. Right P₂-M₈. × 2

Figs. 4-5. *Colodon? hancocki* sp. nov.

4. Type, UOMNH 20377. P¹-M⁸. × 1.13
5. UOMNH 20376. Left P₄-M₈. × 1.13



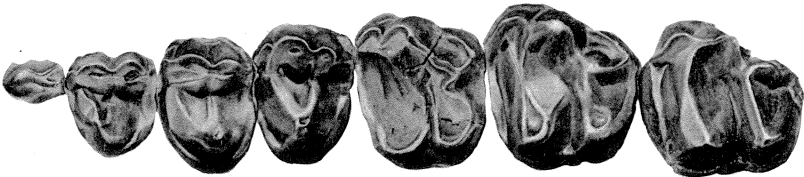
1. *D. leotanus*



2. *D. leotanus*



3. *D. minusculus*



4.

C.? *hancocki*



5.



1. *C. kayi*



2. *C. occidentalis*



3. *C.? cingulatus*



4. *C.? cingulatus*



5. *C. kayi*



6. *C. occidentalis*

PLATE 4

All figures $\times 1$

Figs. 1, 5. *Colodon kayi* (Hough)

1. Type, CM 9561. P³-M³ (reversed).
5. CM 8930. Left P₂-M₂.

Figs. 2, 6. *Colodon occidentalis* Leidy

2. YPM 16582. P²-M³. M³ taken from YPM 14247 (reversed).
6. AMNH 658. Left P₂-M₃.

Figs. 3-4. *Colodon? cingulatus* Douglass

3. Type, CM 722. P³-M¹. M¹ protoloph restored.
4. CM 9815. P¹-M³.