

Article XI.—ANCESTORS OF THE TAPIR FROM THE LOWER MIOCENE OF DAKOTA.

BY J. L. WORTMAN and CHARLES EARLE.

In the present paper we propose to describe a genus of Perissodactyla new to America, namely, *Protapirus* Filhol, and also to add considerable knowledge respecting the structure of the genus *Colodon* Marsh.

The discovery of the occurrence of *Protapirus* in the upper part of the White River Miocene may be considered as one of the most interesting made by the expedition of 1892. It places the origin of the true tapirs, in this country at least, below the 'Oreodon Beds' of the White River Miocene, and nearly parallel stratigraphically with the European species of *Protapirus*.

In this paper we shall offer, first, a discussion of the various attempts which have been made to solve the problem of the origin of the tapir in America; second, a systematic description of the material relating to the American species of *Protapirus* and *Colodon*; and lastly, a review of the relationship between the American species of *Protapirus* and those found in Europe; including a *résumé* of the principal characters of the supposed Eocene ancestors of both the Tapiridæ and Helaletidæ.

Historical.—Prof. Marsh in his paper of 1877 on the 'Succession of Vertebrate Life in America' remarks: "The tapir is clearly an old American type;" he derives the genus *Tapirus* from *Hyrachyus*, saying that the tapir also passed in its evolution through the genus *Helaletes*. We shall show that at the present time these latter views have proved to be erroneous.

Prof. Scott¹ early attempted the solution of this problem; he also derived the tapir from *Hyrachyus*, placing the genus *Helaletes* (*Desmatotherium*) as a later stage in the evolution of this form. Profs. Scott and Osborn, in the 'Preliminary Report upon the Fossil Mammals of the White River Formation' removed the genera *Hyrachyus* and *Helaletes* from the line of the true tapir, and stated that this line has come down through

¹ E. M. Museum Bulletin of Princeton College, 1883, p. 46.

genera with a trilobed last lower molar. They further remarked that the species of tapiroid called by Leidy *Lophiodon occidentalis* should be placed in the tapir line, and intermediate between the genera *Isectolophus* and *Tapiravus*; they described *Isectolophus*, which they considered as one of the direct ancestors of the tapir.

Prof. Cope¹ followed Prof. Osborn in his derivation of the tapir from *Isectolophus*, but he does not state definitely what he considers to be the earliest ancestor of the tapir.

In the 'Uinta Mammalia' Prof. Osborn more fully explained his reasons for placing *Isectolophus* in the line of descent leading to *Tapirus*, and also definitely stated that he believed *Systemodon* to be the earliest ancestor of the tapir in America. In one of the latest numbers of the Bulletin of this Museum,² Prof. Osborn gives more in detail his views as to the phylogeny of the Eocene Perissodactyla in America, and describes the various characters of the upper molars in the principal Perissodactyle phyla and how they may be distinguished from each other. These lines are considered by him to be: first, the *Systemodon-Isectolophus-Tapirus*; second, the *Heptodon-Helaletes* (to which we may add *Colodon*); and lastly, the *Hyrachyus-Triplopus-Hyracodon*.

In Europe Dr. H. Filhol has contributed greatly to our knowledge of the phylogeny of the modern tapir, through his discovery of the genus *Protapirus*, occurring as early as the Upper Eocene, in the Phosphorites of Quercy. We, however, strongly dissent from the view held by him, that *Protapirus* is identical with the American genus *Hyrachyus*. The conformation of the premolars, and of the external lobes of the superior true molars is very different in these two genera, and they belong in two entirely different lines of descent.

Lastly, another advance in the early history of the tapir in Europe has been made by Prof. Osborn,³ who suggests that the species of *Lophiodon*, called by Rutimeyer *L. annectens*, is really a species of the American genus *Isectolophus*. If this supposition be correct, this will be the earliest European form known to belong in the line of the true tapirs.

¹ American Naturalist, 1888, p. 994.

² Bull. Am. Mus. Nat. Hist., IV, 1892, p. 124.

³ American Naturalist, 1892, p. 763.

TABLE SHOWING THE DISTRIBUTION OF THE TAPIRIDÆ AND HELALETIDÆ.

		AMERICA.	EUROPE.
LOWER MIOCENE.	Upper.	{ Protapirus obliquidens. Colodon occidentalis.	Protapirus douvillei.
	Middle.	Protapirus simplex.	
	Lower.		
EOCENE.	Upper.	Isectolophus annectens.	Protapirus priscus.
	Middle.	{ Helaletes boops. Isectolophus latidens. Heptodon calciculus.	Lophiodon (Isectolophus ?) annectens.
	Lower.	Systemodon tapirinus.	Palæotapirus.

Family TAPIRIDÆ.

Dentition : I $\frac{3}{8}$, C $\frac{1}{1}$, PM $\frac{4}{4}$ or $\frac{3}{3}$, M $\frac{3}{3}$. Premolars molariform or simpler in structure than true molars. Superior true molars with external lobes conical and equal in length ; metacone not flattened. Inferior true molars with crests transverse or oblique. Last lower molar with or without hypoconulid. Digits four-three.

The family Tapiridæ may be divided into two subfamilies ; in the earlier subdivision, or Systemodontinæ, the premolars are simpler in structure than the true molars, whereas in the later forms, the Tapirinæ, or true tapirs, some or all of the premolars are molariform. The genus *Isectolophus* forms the transition stage between these subfamilies, as in it we have an increase in complexity of the posterior premolars ; but *Isectolophus* still retains the large third lobe of the last lower molar, which is lost in the true tapirs.

Subfamily TAPIRINÆ.

Genus **Protapirus** *Filhol.*

Superior premolars with only one internal lobe. Inferior premolars with posterior crest undeveloped, tetartoconid distinct. Superior molars with metacone oblique and shorter than protocone.

The upper premolars in this genus are in some cases in a transitional stage of development as to the division of the internal lobes, but in no case are these teeth as complex as the true molars. A very distinctive character of *Protapirus*, separating it [August, 1893.]

from *Tapirus*, is the fact that the posterior crest of the inferior premolars is wanting, the talon having retained its primitive condition as to the separation of the internal from the external cone. The foot structure of the manus at least is nearly identical with that of the modern tapir.

***Protapirus obliquidens*, sp. nov.**

Last two superior premolars with internal lobes notched at apex, first and second superior premolars with internal cone single. Second superior true molar with metaloph very short and oblique. Median valley of superior true molars not opening externally as in *P. priscus*.

The type specimen in the American Museum collection (No. 659) is a portion of a crushed skull which belongs to a young animal. In this specimen the maxillary dentition is partially preserved, but the individual was so young that the permanent dentition had not yet cut through. In the other specimens in the collection (Nos. 662 and 661), which we refer to this species, the lower jaw with nearly the complete dentition is present, and associated with it, is an upper true molar. Found in close proximity to these specimens was a complete manus; this latter specimen without doubt belongs to the same individual as the jaw.

Dentition.—The type specimen includes the four upper premolars and the second upper true molar. The first superior premolar consists of two external lobes, which are scarcely separated from each other. The internal lobe is single, and anteriorly this lobe is slightly extended transversely. As compared with the recent tapir this tooth has the internal lobe more developed than the external. In the tapir the external part of the first premolar is much extended transversely, and projects far beyond the limit of the internal lobe, whereas in *P. obliquidens* this extension of the external part of the tooth is not present. The three succeeding premolars have two well-developed external lobes; these are more flattened than in the recent tapir. In the type specimen of *Protapirus priscus* the internal lobe of the fourth superior premolar shows no sign of division; the case is otherwise with the species *P. douvillei* figured by Filhol.¹ In the type specimen of *P. obliquidens* the

¹ Ann. Sci. Geol., XVII, Art. 2.

shape of the internal lobes of premolar 3 and 4 agrees with that of *P. douvillei*; and in these teeth we observe that the deutocones are just commencing to indicate signs of division; the slight separation of this cone, however, is confined to the

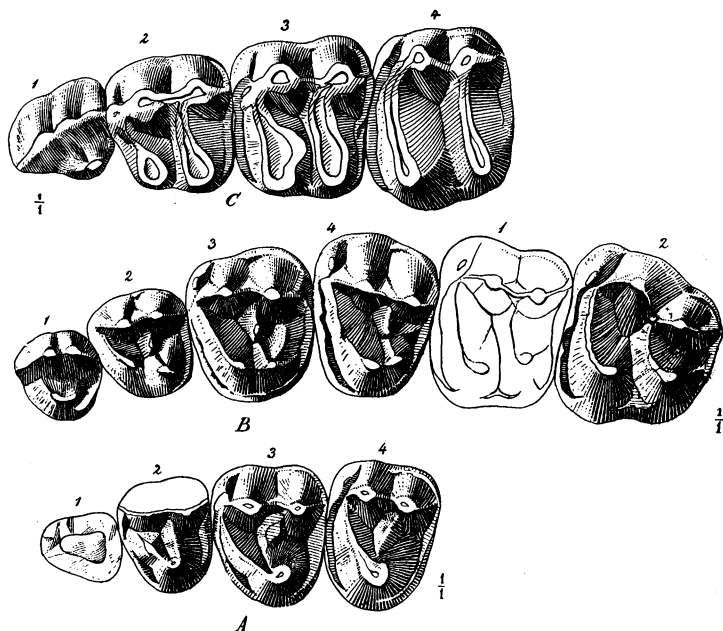


Fig. 1. Evolution of the premolars in *Protapirus* and *Tapirus*. A, *Protapirus simplex*, type; B, *Protapirus obliquidens*, type; C, *Tapirus americanus*.

summit of the lobe. The second superior premolar in *P. obliquidens* has only one internal lobe, and this is not divided as in the two following teeth in this series. It has two small crests running outwards from the deutocone. This tooth in the European species, *P. douvillei*, is more complex than in the White River form. In the former species pm. 2 has two small internal lobes, and from M. Filhol's figure we would conclude that these lobes are well separated. In the third and fourth superior premolars the anterior transverse crest is oblique, and abuts externally at the junction of the protocone with the protostyle. The posterior transverse crest of these teeth is straight and extends completely across the crown from

the deuterococone to a point opposite the tritococone. The parastyle is not well developed on the superior promolars, and in only the last premolar is this lobe large; but in this case it is not separated from the anterior extension of the protocone.

In all the known species of *Protapirus* the posterior crest of the premolars is much shorter and straighter than the anterior. However, the anterior transverse crest is the first to appear; this is shown in the first premolar of *P. obliquidens*. In the second superior premolar of this species this crest is small, but increases much in size in the other premolars. It is interesting to note, that when we go back to the early ancestors of the tapir, we observe that the posterior crest of the posterior premolars arises by a transverse extension of the posterior intermediate tubercle. This conule first extends externally and joins the internal base of the tritococone; and then develops inwards and coalesces with the deuterococone. After complete fusion with this cone the latter begins to divide, and it is in this stage that we find all the deuterococones of the posterior superior premolars of *Protapirus obliquidens*. A better understanding of the growth of the posterior crest may be gained by studying the dentition of the early relatives of both the tapirs and rhinoceroses (*Systemodon* and ? *Hyrachyus*).

The second superior molar of *P. obliquidens* is peculiar in having the posterior portion of the tooth much shorter transversely than the anterior part; this applies particularly to the metaloph, which is considerably shorter than the protoloph. The external part of the crown, or ectoloph, is oblique instead of straight as in the recent tapir; in this character the *P. obliquidens* agrees with the European species of *Protapirus*. The parastyle of the second superior molar is as high as the paracone and is very heavy; it abuts against the external convexity of the protoloph, although the latter is directly connected with the paracone and not with the parastyle. This is an important character in this species, as in the *P. priscus* of the Phosphorites, Filhol states that the anterior transverse crest is in contact externally with the parastyle. We may say, as a rule in the true tapirs, that the protoloph touches externally the paracone, but the *P. priscus* presents an exception to the rule. M. Filhol

compares this character in the latter species with that of *Hyrachyus agrarius*, and concludes from the worn series of teeth, which he figures of *Hyrachyus*, that the protoloph in this genus is also continuous with the parastyle, but in this statement we believe he is mistaken. In all known species of *Hyrachyus* this crest touches the paracone.



Fig. 2. *Protapirus obliquidens*. Crown view of lower dentition.

In the upper true molars of the tapir the parastyle is very large and well separated from the paracone, in contrast with that of *P. obliquidens* the summit of the paracone is high above the parastyle and is connected with the protoloph. This is the typical relation of these two elements of the crown in the modern tapir. The ectoloph of the second upper molar is oblique and has only a faint trace of a cingulum, agreeing in this respect with the European species from St. Gérard-le-Puy. The median valley is deep and its external termination has a prominent buttress. This portion of the valley does not open externally as in the Brazilian tapir and in the *P. priscus*, but is shut off by the crest connecting the paracone with the metacone. In contrast with the upper true molars of the tapir, we observe in this species the further extension of the metacone, and also the great development of the cingulum running externally from the hypocone. The last upper molar is somewhat larger than the second; otherwise its characters are similar. We note in this tooth a great shortening of its metaloph as compared with the length of the protoloph.

The lower jaw in the collection which we refer to *P. obliquidens* has the incisors smaller and more flattened than in *Tapirus americanus*; the crown of the median incisor is much depressed, and this tooth is larger than the others. The canine is a very small tooth as compared with that of the recent tapir. The length of the diastema behind the canine is large, being about two-thirds of that in the American tapir.

The inferior molar series, as compared with the size of the jaw, is larger than in the recent tapir. The three inferior premolars have large and heavy crowns. In the specimen being described these teeth are much worn; however, the general form is the same as in the recent tapir, differing somewhat in the fact that the posterior crest on all the teeth is incomplete, the metaconid being distinct from the tetartoconid. The paraconid of the premolars was very large in the unworn tooth, and in front of this lobe was a small tubercle. The inferior true molars, like the premolars, have broad crowns; the transverse crests of the same are low, the anterior having a prominent crest running inwards. As compared with the recent tapir the internal and external elements of the transverse crest are more strongly marked, and the interval on the crest connecting these latter is thinner than in the tapir's molars. None of the lower teeth have external cingula. The posterior cingulum of the last lower molar is small and limited to the median portion of the tooth.

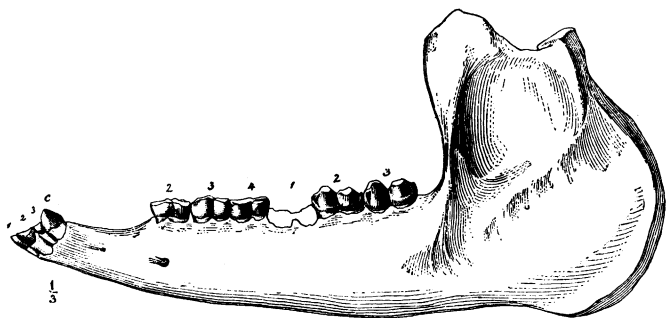


Fig. 3. *Protapirus obliquidens*. Side view of lower jaw.

Jaw.—The lower jaw of *P. obliquidens*, as compared with that of *T. americanus*, is more slender and elongated. The symphyseal portion is shorter and strongly contracted at the diastema. The part of the horizontal ramus below the last molar is the heaviest portion of the jaw, and from this point the jaw tapers gradually to the incisive border. In the American tapir there is an angle of the jaw at the lower border of the ramus, just below the second premolar, and the symphyseal portion is bent upwards from this point. The angle of the mandible is

more pronounced than in the tapir's jaw, and is separated from the horizontal ramus by a concavity which is not present in the tapir. The mental foramina are two and are placed below the diastema.

Measurements of Protapirus obliquidens.

	M.
Length of superior premolars.....	.063
Superior premolar 4 { trans.....	.021
{ antero-post.....	.016
Superior molar 2.. { trans.....	.022
{ antero-post.....	.020
Length of jaw.....	.260
“ diastema.....	.038
“ inferior molar series.....	.108
“ true inferior molars.....	.060

Foot Structure.—The manus of *P. obliquidens* closely resembles in its general form and structure that of *Tapirus*, but it differs in some of the relations of the carpal elements, and the length of the digits to each other. The proportions of the carpus are the same as in the Brazilian tapir; the breadth being slightly greater than the height. It is surprising to find the manus of so early a form as *Protapirus* in such an advanced stage of displacement, and in this respect it resembles

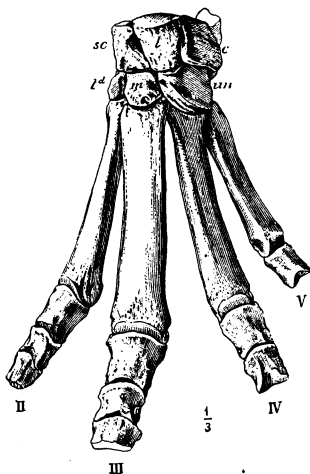


Fig. 4. *Protapirus obliquidens*.
Anterior view of left manus.

the foot of the existing American tapir. The lunar has only a small contact anteriorly with the magnum. The scaphoid nearly covers the whole superior surface of the magnum. The latter bone is higher and narrower than in the recent tapir. The unciform has the characteristic tapiroid shape, its height is greater than the breadth, and it has a large contact with the lunar. The trapezoid is high and narrow. The form of the trapezium is quite different from that of the American tapir. In *Protapirus obliquidens* it is a thick and heavy bone, having a triangular form; while in *Tapirus* this bone is elongate and slender. As we should expect

to find in an early form like *Protapirus*, the proportionate lengths of the metacarpals are different from those of the recent tapir.

The length of the fifth metacarpal as compared with the third is greater than in the recent forms.

The phalanges of the digits in this species are shorter than in the Brazilian tapir, giving the digits a short and heavy appearance. Two of the ungual phalanges are partially preserved, and these have the terminal portion incomplete. Earle has described elsewhere¹ the comparative evolution in the foot structure of the Brazilian and Malayan tapirs, and we will finally remark in closing the description of the manus of *Protapirus obliquidens*, that it is in about the same stage in reduction of the fifth digit as that of the *Tapirus indicus*, but more primitive than the foot of *T. americanus*.

Measurements of manus.

	M.
Total length of manus.....	.175
Breadth of carpus.....	.040
Length of carpus through magnum036
Length of metacarpal III.....	.100
“ “ V.....	.073
Lunar-unciform contact, trans.....	.011

***Protapirus simplex*, sp. nov.**

Internal lobes of all the superior premolars absolutely simple, showing no signs of division. Posterior transverse crest of all the superior premolars rudimentary.

This species of *Protapirus* is from an horizon of the White River formation lower down than that in which the *P. obliquidens* occurs. This division of the White River formation is called the ‘Oreodon Beds,’ and is separated from the upper, or ‘Protoceras Beds’ by a thick layer of barren clay. The character of the dentition of this species, as far as known, is much more primitive than that of the *P. obliquidens*. The type specimen of *Protapirus simplex* (No. 660) contains only the upper premolars of one side, and fragments of the lower jaw.

Dentition.—The crown of the first superior premolar is absent, its roots indicate that it must have closely resembled that of *P. obliquidens*. The internal cones of the remaining premolars are round and obtuse. These lobes are perfectly simple in struc-

¹ Science, March, 1893, p. 118.

ture, and are connected in front with an oblique transverse crest. In the second premolar the anterior crest is rudimentary; this tooth has however the posterior crest more developed than in the succeeding premolars. The external lobes of the last two premolars are round and obtuse, the protostyle is small and not as high as the protocone. In both these teeth there is a faint trace of an external cingulum at the postero-external border.

The first two premolars of the lower jaw are partially preserved. These teeth are much smaller than those of *P. obliquidens*; they have elevated anterior crests. The posterior crest of the first premolar is nearly complete, but the tetartoconid is low and not well developed. Another fragment of the jaw of *P. simplex* contains the injured crowns of the first two molars. These teeth are of the same size as those of *P. obliquidens*. The depth of the jaw at m. 2 is equal to that of the larger species.

Measurements of Protapirus simplex.

	M.
Length of superior premolars.....	.054
Premolar 4 { antero-post.....	.015
{ trans.....	.020
Length of first two inferior premolars.....	.025

THE PHYLOGENY OF THE TAPIRIDÆ.

The earliest representative of the tapir line in the Eocene of America is the genus *Systemodon*. In the Wind River we see the first known departure toward the rhinoceros molar type in the genus *Heptodon*, which has a concave metacone; but in the latter genus this lobe is short and not longer than the paracone, as it is in the true rhinoceroses.

In *Systemodon* the inner lobes of all the superior premolars are absolutely simple. In the second premolar of this genus we see the first indication of the separation of the external lobes. The third and fourth upper premolars have a well-marked anterior transverse crest, but only on the last are there signs of the origin of the posterior crest. The characters of the superior molars in *Systemodon* are well adapted for further evolution into the true tapirine pattern; both external lobes are conical and of equal size, the parastyle being a very prominent element of the crown

as in the tapir's molar. The shortening and obliquity of the metaloph is wanting, which is such a marked character of the upper molars of *Protapirus*. As pointed out by Prof. Osborn, the first inferior premolar in *Systemodon tapirinus* is placed just behind the canine, there being no diastema as in *Hyracotherium*; this point he considers highly characteristic of the tapirs. The third and last inferior premolars in *S. tapirinus* have a deuteroconid, but the talon of the fourth is still in its primitive condition, in lacking the tetartoconid, which is so typical of the Bridger tapirs. The last lower molar has a large hypoconulid, and the crest of the inferior true molars are oblique, instead of straight as in the later forms.

There is a fragmentary example of the skeleton of *Systemodon tapirinus* in the American Museum collection, which indicates that this species was an exceedingly slender and agile form. The character of the pes is not exactly what we should expect to find in an ancestral form of the tapir. The calcaneum has a fibulocalcaneal facet. The astragalus has a deep trochlear surface, with high condyles on each side. There is only a very slight contact between this bone and the cuboid. The metatarsals are long and slender. The internal and upper edge of the fourth metatarsal has a well-marked facet, which extends nearly across the surface of the bone. This facet is bordered above by the superior surface of the metapodial for the cuboid. The presence of this facet proves that *S. tapirinus* had a rudiment at least of a fifth digit.

We would suggest that the pes described by Marsh as belonging to *Eohippus* is possibly that of *Systemodon*.

The next stage in the evolution of the tapir is represented in the Bridger by *Isectolophus latidens* S. & O. The skeleton of this form is as yet unknown. The type was formerly referred by Scott and Osborn¹ to *Helaletes*, but is now placed in the genus *Isectolophus*. The above authors state in their first description of *I. latidens*, that the superior premolars are provided with only one internal cone, "which is joined by transverse ridges from the two outer cusps." In the type specimen of *I. latidens* the fourth inferior premolar is absent; it was however probably nearly

¹ Bull. E. M. Mus. of Princeton College, 1878, p. 54.

molariform in structure. One of the characters by which the upper true molars of *I. latidens* differ from those of the modern tapir, is that the protoloph is continuous with the parastyle and not with the paracone, as in the tapir's molar. The relations of this crest and tubercle are also variable in the European species of *Protapirus*, as shown by Filhol.

The Uinta tapir is the *Isectolophus annectens*. It is very possible that the Bridger species referred by Scott and Osborn to *Isectolophus* may represent a different genus from the latter. In the type of *I. annectens* the upper premolars are wanting. The molars are exceedingly like those of the tapir, and they have the oblique ectoloph so characteristic of *Protapirus*. The shortening of the metaloph has not yet commenced in *Isectolophus*. The last inferior premolar of *I. annectens* is nearly molariform but still lacks the tetartoconid. The crests of the inferior true molars are nearly crescentoid in form, which character we should not expect to find in a Uinta tapir. The last lower molar has also a very large third lobe. Some of the characters above adduced as to the teeth of *I. annectens* may show by later discoveries that this species is not in the direct line leading to the true tapir. If the last two superior premolars are as complex in structure as the true molars, it will certainly have to be removed from the true tapirine line, as the earliest species of *Protapirus* in America has the internal cones of pm. 3 and 4 absolutely simple.

The structure of the carpus in *I. annectens* is exactly what we should expect to meet with in an early ancestor of the tapir. The distal facets of the lunar are nearly equal in extent, and as a result the lunar-magnum contact is much larger than in later forms of this line. The unciform is strongly tapiroid in its characters. The fifth digit of the manus is larger compared with the others than in the recent tapir. The cuboid of *I. annectens* is rectangular in form, closely resembling that of the tapir. The cuboid had a considerable contact with the astragalus.

We may add that the members of the subfamily Tapirinae, or true tapirs, are found earlier in Europe than in America. The type species of the genus *Protapirus* was discovered by Filhol in the Phosphorites of Quercy; these beds correspond approximately with the uppermost or Uinta series of America. The

genus *Palæotapirus* (which is very doubtful as to validity) comes from the Middle Eocene (Buchsweller, Elsass). This formation is below the Phosphorites. The Phosphorite form of *Protapirus* is the most primitive in its dental characters; the last upper premolar in the type specimen has a simple internal cone, and shows no sign of division. The *Protapirus douvillei* is from the Lower Miocene of France (St. Gérard-le-Puy). This form exhibits a decided advance in the complication of the premolars, over the species from the Phosphorites. In the second upper premolar the two internal cones are complete; however, the third and fourth premolars are in a transition stage.

Turning now to the true tapirs in America we find, as already stated, that the earliest species is our *Protapirus simplex* from the Oreodon Beds of the White River Miocene. The structure of the last upper premolar in this species agrees closely with that of the tapir from the Phosphorites, but the development of the posterior transverse crest of the premolars is not as far advanced as in the European species. The latest known species of tapir in the Lower Miocene of America is our *P. obliquidens*; this form agrees closely in the structure of its superior premolars with that from St. Gérard-le-Puy, although the second premolar is not as much differentiated as in the latter species. The inferior premolars of *P. obliquidens* have not as yet completed their posterior crest; and the diastema of the jaw is still much smaller than in the recent tapir. As already shown in the description of the manus of *P. obliquidens*, it had become nearly as much specialized as in the American tapir.

The stages in the evolution of the tapir in America after the White River epoch are as yet not fully known. The genus described by Marsh called *Tapiravus* is from the Lower Pliocene. We have been unable to examine the specimen referred to this genus by Prof. Marsh, and cannot therefore state whether it is a true tapir, or an outcome of the family Helaletidæ.

SUMMARY.—The principal points brought out in the preceding description may be summarized as follows:

1. We consider the genus *Systemodon* as standing in ancestral relation to the Tapiridæ.

2. *Isectolophus latidens* is probably in the line leading to the true tapirs.
3. If further discovery shows that *I. annectens* has both the last two premolars as complex as the true molars, it must be removed from the main tapir line.
4. The earliest member of the subfamily Tapirinæ, or true tapirs, is found in the Phosphorites of France, there being a considerable interval between the latter formation and the Oreodon Beds of the White River Miocene.
5. In contrast with the other Perissodactyla of the White River formation, the premolars of *Protapirus* have not assumed the complexity of the true molars.
6. The foot structure of *Protapirus* is nearly as far advanced in its evolution as that of the existing American tapir.

Family HELALETIDÆ.

Superior molars lophodont, with metacone concave, and placed internal to paracone. External lobes of superior molars separated, with transverse crests of same complete.

This family, like the Tapiridæ, may be divided into the Helaletinæ and Colodontinæ. In the first subfamily the inferior dentition is complete, and the premolars are either simple in structure, or some of them have become molariform. In the Colodontinæ the lower external incisor is absent, and in this subfamily the feet are tending to monodactylism; which is proved by the increase in size of the median digit of the manus in *Colodon*, and the reduction in size of the fifth digit.

In contrast to the Tapiridæ, the Helaletidæ are confined to America, their nearest relatives in Europe being the family Lophiodontidæ. This group ranges in time from the Wind River Eocene (*Heptodon*) to the upper beds of the White River Miocene (*Colodon*).

Genus *Colodon* Marsh.

SYN.—*Lophiodon*, in part; *Mesotapirus* S. & O.

Dentition: I $\frac{1}{2}$, C $\frac{1}{1}$, PM $\frac{1}{3}$, M $\frac{3}{3}$. Last three superior premolars molariform; external lobes of superior true molars equal in size. Inferior premolars with two posterior cusps, but not connected by crests. Last lower molar with a third lobe.

The earliest notice of this genus is to be found in Dr. Leidy's Monograph on the 'Extinct Mammalia of Nebraska.'¹ The material upon which this description was based consist of a last lower molar which this author was unable to distinguish from that of *Lophiodon*, and therefore referred this specimen to that genus. Later Profs. Scott and Osborn,² in describing the affinities of the tapiroid genus *Isectolophus*, suggested that its Miocene successor was to be found in the species described by Leidy under the name of *Lophiodon occidentalis*, and that when the dentition was fully known it would be found to have two premolars like the molars. Upon this supposition they proposed the hypothetical name *Mesotapirus*, which proves to be invalid. In 1890 Prof. Marsh³ attained additional material, by means of which he was enabled to point out the generic rank of this species, as well as the more important characters in which it differs from its nearest ally, *Helaletes*. As regards the species there appear to be at least two if not more represented in the material now known.

Colodon occidentalis Leidy.

SYN.—*C. luxatus* Marsh.

Root of lower canine round in section and placed close to incisor. Inferior premolars short and broad, with faint external cingula. Third lobe of last lower molar very small and conical in form.

Prof. Marsh's type specimen of *Colodon luxatus*, which he has permitted us to examine, is unfortunately not associated with any superior molars. Other specimens, however, in which parts of both series are present, render it quite certain that the upper premolars are complex like the molars. The specimens in the American Museum collection from the White River, which we refer to this species, consist of a finely-preserved lower jaw with all the molars intact, but lacking the crowns of the incisors and canines. Associated with this specimen and belonging to the same individual are parts of the skeleton, and also a beautifully preserved manus. A fragment of the superior maxillary bone bearing two molars is in the collection of Princeton College, and

¹ P. 239, pl. xxi, figs. 28-30.

² *Uinta Mammalia*, p. 523.

³ *Am. Jour. Sci. and Arts*, Vol. XXXIX, 1890, p. 524.

may represent another species. These teeth are rather small to be associated with the lower teeth above referred to.

Dentition.—The most striking character of the upper true molars in *Colodon* is that the metacone is pushed in as it were, its external surface being concave, and placed well in from the paracone. The shape of the paracone is like that of the tapir's molar, and it has a small internal buttress. Both the paracone and metacone are of the same size longitudinally; the latter element is not so much drawn out as in the forms related to rhinoceros (*Hyrachyus*). The parastyle is strongly developed, and continuous internally with a slight anterior cingulum. The protoloph and metaloph are high and sharp. The anterior extension of the paracone is relatively much less in *C. occidentalis* than in *Protapirus obliquidens*. The obliquity of the metaloph is less than in the latter form. In contrast to the teeth of the true tapirs, we observe that the internal cones of the molars are not higher than the external. There is a slight postero-external cingulum on the superior molars in this species. In Prof. Marsh's description of *Colodon luxatus* he considers it to be without a lower canine. We think it more probable that the external incisor has been lost, and therefore believe that the outer tooth of this series is a canine. We may add that in the forms leading to *Titanotherium* (namely, *Palæosyops* and *Diplacodon*), the canine is retained while the external incisor is lost.



Fig. 5. *Colodon* (sp. indet.). Crown view of a second superior molar. Natural size.



Fig. 6. *Colodon occidentalis*. Crown view of inferior dentition.

The roots of the incisors are much extended antero-posteriorly and larger than those for the canines. The latter teeth were smaller than the external incisors, and were separated by a large diastema from the second premolar. The inferior premolars are short and broad, with their posterior portion much

wider than the anterior. The anterior crest of the second is notched. In the third and fourth premolars this crest is complete, but thick and depressed in the middle. The cusps of the talon of the inferior premolars are equal in height but unconnected, as in *Protapirus*. The transverse crest of the lower true molars is thinner and more slender than in *Protapirus*, and the spur extending inwards from the metalophid is less developed. The last lower true molar is larger than the others, its hypoconulid is small, and of a conical form. This lobe is situated at the postero-median part of the crown, and extends upwards nearly on a level with the posterior crest. Both the first and second lower true molars have a well-marked posterior cingulum. The lower jaw at the diastema is much contracted, the superior portion of the same is narrower than the margin bordering on the mental foramina.

Skeleton.—A nearly complete radius with the proximal part of an ulna is preserved. The former closely resembles that of the tapir, but it is shorter and more slender. The proximal trochlear surfaces are deep, that for the internal condyle of the humerus, as is usually the case with early forms, is oblique in position. The distal facets of the radius for the scaphoid and lunar are rather more pronounced than in the recent tapir. A distal portion of an ulna, showing a section of its shaft, is associated with this specimen. It is of great interest to note that the ulna is much reduced in size in *Colodon*, and agrees with the specialization in the manus of approaching monodactylism. The manus is much elongated and slender. The carpus is longer than broad, with its elements highly displaced. The lunar is high and narrow, with a large facet for the unciform which takes up its whole inferior face. The lunar-magnum facet is vertical in position and is continuous with that for the scaphoid. Anteriorly the lunar has a small contact with the magnum. Compared with the lunar of *Heptodon*, that of *Colodon* has its distal facets more unequal in size. In *Heptodon* these facets are nearly equal in dimensions, and the beak of the lunar is largely developed in that genus. The magnum of *C. occidentalis* is high and narrow, and it has a large articulation with the unciform. The shape of

the latter bone is much like that of the true tapir, with its vertical axis greater than the transverse.

As compared with *Heptodon calciculus* the median metacarpal of *C. occidentalis* is larger than the others; proximally it has a large contact with the unciform, but its articulation with mc. IV is reduced. The lateral metacarpals are very long and slender, and the diameter of their shafts, as compared with that of the third metacarpal, is much less. A peculiarity in the manus of this species in contrast with that of its supposed Eocene ancestor, *Heptodon*, is the great abbreviation of the length of the phalanges. In *Heptodon calciculus* the total length of the phalanges of the middle digit of the manus is fully three-fourths as long as their metacarpal, whereas in *Colodon occidentalis* the phalanges are very short, and their length is about three-eighths that of the median metacarpal. A marked character of the

feet of *Heptodon* is the great elongation of the proximal phalanges. The fifth digit is not preserved; however, from the size of the facet on the unciform for this metapodial, we estimate that it was much reduced, as compared with this digit in the Eocene ancestor of *Colodon*. There is only one podial element of the tarsus preserved, the astragalus. This bone closely resembles that of the tapir in its general form. The trochlear surface is rather broad and shallow; the navicular face is much extended from above downwards, and convex. The astragalo-cuboid facet, unlike that of *Heptodon*, is elongated and extends anteriorly all across the anterior external margin of the bone. In this character the astragalus of *Colodon* resembles that of the true tapirs. The sustentacular and inferior

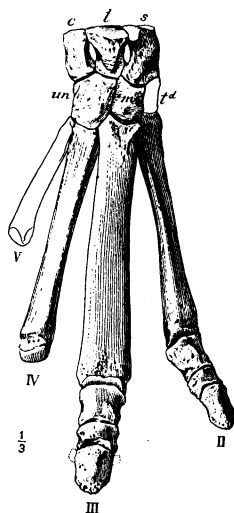


Fig. 7. *Colodon occidentalis*.
Anterior view of right manus.

facets of the astragalus differ from those of the tapir in being continuous, and at the junction of these two facets with that for the cuboid there is a prominent ridge. In *Heptodon* these facets are continuous, but in *Helaletes boops* Marsh they are discontinuous.

We may say that, as a whole, the foot structure, especially of the manus of *Colodon occidentalis*, is more specialized than its contemporary *Protapirus obliquidens*; this is shown by the small size of the lateral digits, and the reduction of the ulna.

Measurements of Colodon occidentalis.

	M.
Total length of radius.....	.195
Breadth of distal extremity.....	.031
" " " of ulna.....	.013
Total length of manus183
Length of lunar.....	.021
Breadth of unciform—mc. V facet007
Length of astragalus036
Breadth of trochlear of same....	.026
Total length of inferior molar series.....	.080
Length of inferior premolars032
" last inferior molar019
Breadth of jaw between canines.....	.016

ANCESTORS OF COLODON.

The earliest known genus in the Eocene, which can be referred to the ancestor of *Colodon*, is considered by Prof. Osborn to be *Heptodon*. This genus was first placed by Prof. Cope as ancestral to the Rhinoceros series. The species of *Heptodon* whose structure is best known is the *H. calciculus* from the Wind River. The osteology of this species has been quite fully described by Osborn and Wortman,¹ and it remains for us to compare the characters of *H. calciculus* with those of *Colodon occidentalis*, and also with the Bridger representative of this line, namely, *Heleletes*.

In both the upper and lower dentition of *Heptodon calciculus* there is a long diastema behind the canines. The first premolar in both jaws is placed close to the second; while in the true tapirine line this tooth, as shown by Prof. Osborn, is situated next to the canine. The internal lobes of the superior premolars show no signs of division, the second superior premolar has only one external lobe, whereas in *Systemodon* this lobe is nearly double. The characters of the external lobes of the superior true molars in *Heptodon* are very important in diagnosing this line of descent. In *Systemodon* we have seen that both the external

¹ Bull. Am. Mus. Nat. Hist., Vol. IV, 1892, p. 127.

lobes of the ectoloph are equal in size, and conical in form. In *Heptodon* the metacone has become strongly bent inwards and lengthened; the extent of this lobe however is not greater than the paracone. The separation of the external elements of the crown of the upper true molars in *Heptodon* is nearly as great as in *Systemodon*. The inferior premolars of *Heptodon calciculus* are very primitive in form; the first and second are simply slender cones. The third and fourth lower premolars have low and broad heels, and the fourth has a well-marked anterior crest. The lower true molars are high and compressed, their crests are slightly oblique; the spur extending from the anterior crest is not as well marked as in *Systemodon*. The last lower molar has a small conical hypoconulid.

The foot structure of *Heptodon calciculus* is rather more specialized than that we should expect to find in an ancestor of *Colodon*. The great compression and elongation of the manus and pes is a marked character of *Heptodon*. However, there is a close resemblance between the form of the lunar of *Heptodon* and that of *Colodon*. The enlargement of the median digit of the manus of both of these genera is to be observed, but in *Colodon* the phalanges are short and heavy; whereas in *Heptodon* they are very long and slender. Comparing the astragalus of *H. calciculus* with that of *C. occidentalis*, we find some difference in the relations of this bone with the cuboid. In the former genus, as we have seen, the astragalo-cuboid contact is very small and confined to the posterior aspect of the tarsus, but in *Colodon* this contact is a large one, and extends all across the antero-external surface of the bone, as in *Tapirus*. We must therefore suppose a great spreading and widening of the tarsus of *Heptodon* and as a result a large astragalo-cuboid contact, to lead up to the condition found in *Colodon*.

The connecting type between *Heptodon* and *Colodon* is now considered to be the genus *Helaletes*. In this form the last two superior premolars have become molariform in structure. In the second superior premolar we remark that the external lobe is double, an advance in structure over the condition of this tooth in *Heptodon*. The internal buttress of the upper true molars of *Helaletes* is large, and the parastyle has increased in size in con-

trast to that of *Heptodon*. In the lower jaw of *Helaletes* the first premolar has been lost, and the third and fourth are nearly as complex in structure as the true molars. The diastema of the jaw is long in this genus, and shows a marked increase in size over that of *Heptodon*. Prof. Osborn has shown that the presence of the hypoconulid on the last lower molar of the different species of *Helaletes* is a variable character. Now in *Colodon* this lobe is small, but well marked. In *Helaletes boops* Marsh there is a small hypoconulid, whereas in *H. (Dilophodon) minusculus* Scott this lobe is absent. We believe, therefore, the *H. boops* was probably ancestor of *Colodon*, but that the *H. minusculus* approaches *Hyrachyus* in the loss of the hypoconulid.

The known material pertaining to the genus *Helaletes* is too insufficient to enable us to trace the stages in the reduction of the lateral incisor of *Colodon*. In *H. boops* (syn. *H. nanus* Leidy) the alveoli for the lower incisors are all nearly equal in size. The canines in this species were much larger than the incisors, this being in marked contrast with those of *Colodon occidentalis*. In conclusion, we think that the discovery of more material referable to *Helaletes* will clear up many points in the evolution of the *Heptodon-Colodon* line which are now in obscurity. In fact all the known species of both *Systemodon* and *Heptodon* are extremely slender forms as compared with their supposed Miocene successors, and if we derive the true tapirs and pseudo tapirs from any of the known species of either of these genera we must suppose a considerable modification of their foot structure to reach the condition found in their Miocene relatives. The dentition of these early Wahsatch and Wind River tapiroids, however, is well adapted for further evolution into later Miocene types, but in their foot structure we find it otherwise.