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ART. XVII.—*Recent and Fossil Tapirs*; by J. B. HATCHER.  
(With Plates II-V.)

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The existing *Tapirs* present many characters of peculiar interest, and in some respects, as for example, geographical distribution and conservativeness in accomplishing anatomical changes, they are unique among living Perissodactyls. Remains of fossil *Tapirs* and closely allied forms, though comparatively rare, have been found in Tertiary deposits belonging to nearly every period, from the Wahsatch, of the lower Eocene, up to, and including, the Quaternary, and in widely separated localities.

It is the purpose of this article to describe a new species of *Protapirus* from the *Protoceras beds* of the White River (*Oligocene*) of S. Dakota; and to add something to our knowledge of the osteology of this genus, especially in regard to the skull and fore limb; to give some additional characters diagnostic of the various species of *Protapirus* and *Colodon* already described by Leidy, Marsh, Wortman, Earle and Osborn; to point out distinctive osteological and dental characters in the skulls of the five generally accepted species of recent *Tapirs*; and to review previous work of others on the phylogeny of the *Tapiridæ* and *Helaletidæ*.

*Protapirus* (Filhol).

Wortman and Earle\* have recently described, from the Oligocene of S. Dakota, remains of two species of *Tapiroids*,

\* See Bull. Am. Mus. Nat. Hist., vol. v, pp. 159-180.

at present not distinguishable from the genus *Protapirus*, described by Fillhol from the *Phosphorites du Quercy*, France. The species described by these authors are *P. obliquidens*, based on a nearly complete superior dentition (*No. 659 Am. Mus. Col.*). The authors do not give the horizon in which it was found, but from the matrix enclosing it I am led to believe that it is from the *Protoceras beds*. The other species is *P. simplex*, based upon a series of superior premolars and fragments of the lower jaw (*No. 660 Am. Mus. Coll.*) found in the *Oreodon beds*.

The Princeton Scientific Expedition of 1894 was fortunate in securing material, representing a third American species of this genus, besides other material which will increase our knowledge of the known species of *Protapirus* and the somewhat similar genus *Colodon*.

The following is given as a key to the *American* species of *Protapirus*.

1. Internal cone of all the superior premolars absolutely simple, showing no signs of division, with very rudimentary posterior cross-crests, especially in pms. 3 and 4. . . . . *P. simplex*.
2. Internal cone of the fourth superior premolar just commencing to divide, posterior cross-crests moderately developed on all of the last three superior premolars. . . . . *P. validus*.
3. Internal cones of last two superior premolars commencing to divide, posterior cross-crests of the last three superior premolars like intermediate tubercles. . . . . *P. obliquidens*.

*Protapirus validus*, sp. nov.

The type of the present species (*No. 10899 Princ. Coll.*) consists of a nearly complete skull, without the lower jaw and a complete atlas, humerus, radius, ulna and parts of other bones. It is from the *Protoceras sandstones*, about four miles south of White river and five miles below the mouth of Porcupine creek in S. Dakota; about one mile from the spot where the type of *Protoceras celer* was secured. It was found by Mr. H. F. Wells of Sturgis, S. Dakota, a most energetic collector of vertebrate fossils, who was the first to distinguish the *Protoceras beds* and the rich vertebrate fauna contained in them. These beds were shown by Mr. Wells to Dr. J. L. Wortman, who was the first to name and describe them.\*

In most of the more important characters, *Protapirus validus* is intermediate between *P. simplex* and *P. obliquidens*, as for example, the structure of the internal cone of the sup. pms., but in some respects, notably, the development of the posterior cross-crests of these teeth, it is in advance

\* See Am. Mus. Bull., vol. v, pp. 95-105.

of both of these species. (Compare fig. 3, plate II, of the present paper with A. & B., fig. 1, of Wortman and Earle.) From these and other characters *P. simplex* appears to have been the ancestor of *P. validus* and *P. obliquidens*. There seems to be little doubt that the former is a direct successor of *P. simplex*, while the latter has been derived from that species either directly through *P. validus* or some other as yet unknown form with all its characters intermediate.

*The Skull*: In many respects the skull of *Protapirus* resembles that of the recent Tapir, especially of *Tapirus roulini*, the least specialized of all the species of modern Tapirs. In the type specimen of *P. validus* the occipital condyles are sessile and as deep as broad. The condylar foramen is placed well forward and inward just opposite the base of the paroccipital process, which is a slender, styliform bone directed straight downward much as in *Tapirus roulini*, but quite different from *T. indicus*, in which species this process is broad and flat with its distal end curving inward. The post-tympanic process is low and broad and is confluent but not coössified with the paroccipital process; its lower extremity is curved forward, abutting against the post-glenoid and entirely enclosing the *meatus auditorius externus*, a condition not present in any of the living Tapirs. The post-glenoid process is low, broad and thin, and curves forward inferiorly; it is set obliquely to the longer axis of the skull, at an angle of about 45 degrees, much as in all the species of recent Tapirs. The zygoma is slender, only slightly expanded, and nearly parallel with the longer axis of the skull. There is no post-orbital process on the malar. The floor of the orbit is much deeper than in *Tapirus*, but not quite so deep as in some specimens of *Elasmognathus*. The infraorbital foramen is situated well in front of the orbit, and directly above pm. 4, at the bottom of a deep groove, which commences just above pm. 2 and runs obliquely backward and upward, from this point, until reaching the fronto-maxillary suture, where it turns abruptly backward and terminates at the post-orbital process of the frontal. This groove is, perhaps, homologous with a similar excavation on the surface of the skulls of modern species of Tapir. In recent Tapirs it is deepest at, or near, the base of the nasals, and its function, as has been shown by Parker,\* is the lodgment of a cartilaginous air sinus; it very likely served the same purpose in *Protapirus*; the apparent and actual change in its position having been accomplished by the shifting of the nasals to a more posterior position in recent forms. The greatest depth of this groove, in *Protapirus*, is at a point just opposite the

\* See: Some Points in the Anatomy of the Indian Tapir, by W. N. Parker, P. Z. S., 1882, pp. 768-777.

base of the nasals, where it attains a depth of 8<sup>mm</sup>, and a width at the top of 12<sup>mm</sup>. The premaxillaries in the present specimen are broken off at the base of the canines; they were strong, and had an extended contact with the maxillaries.

The most striking differences between the skull of *Protapirus* and that of the recent Tapirs are to be seen in the conformation of the superior aspect of the skull, and in the position of the frontals and nasals, relative to the other elements of the skull. In *Protapirus* the top of the skull, from the tip of the nasals to the occipital crest, is a nearly straight line, while in most recent Tapirs it is somewhat convex, and in *T. terrestris* (*Americanus*) it is strongly convex, especially in the region of the parietals and frontals. In the characters just mentioned *T. roulini*, among modern Tapirs, is most like *Protapirus*. In recent Tapirs the nasals occupy a position considerably posterior to that of the nasals in *Protapirus*, in which the posterior border of the nasal opening is directly above the anterior border of the orbit; while in recent Tapirs it is always back of the posterior constriction of the orbit.

The nasals are slightly injured in the present specimen, and it is impossible to determine their exact length, they could hardly have reached much in front of the posterior border of the premaxillaries; they are applied closely to each other, but are not coössified. They are narrow, deep, and triangular in cross-section anteriorly, but gradually expand and present a greatly thickened lateral edge, posteriorly. On the upper surface, and a little in front of the middle of the nasals, there is a ridge, running from the inner margin obliquely forward to the outer, and giving to these bones a peculiar twisted appearance. The frontals are low and broad, with distinct postorbital processes; from which temporal ridges extend obliquely backward and inward and unite to form a low, sharp, sagittal crest. The lateral edges of the frontals, above the orbits, are thickened and bent upward so as to form the external wall of the groove above described. The fronto-parietal suture marks the point of greatest constriction in the temporal fossa. The parietals are moderately expanded, and unite superiorly in a low, sharp, sagittal crest; which becomes broader in the region of the supra-occipitals, and gradually expands into the occipital crest, which is deeply emarginate, and considerably overhangs the occipital condyles. The combined length of the parietals and frontals in *Protapirus* is considerably greater than that of the same bones in *Tapirus indicus* or *Elasmognathus bairdii*, the two largest species of recent Tapirs, notwithstanding that skulls of either of the latter are fully two-thirds longer than the skull of *Protapirus*; from this comparison the remarkable reduction of the length of those bones, in modern Tapirs, becomes apparent.

In *Protapirus*, the anterior border of the posterior nares is opposite the middle of m. 2. The pterygoids are slightly bifid and rather strong. The *post-glenoid foramen*, *foramen lacrum medium* and *foramen lacrum posterius* are confluent, much as in recent Tapirs. The petrosal is deeply inserted. The tympanic is not present in our specimen; it probably was of the nature of that element in recent Tapirs, in which, according to Parker,\* it is small, and does not become ankylosed to the surrounding bones, so that it is usually lost in the process of maceration, and rarely seen in dry skulls. I have never seen it, although I have examined about fifty skulls. The foramen ovale is in the alisphenoid, at the base of the pterygoid.

*The teeth:* The incisors are wanting and only the roots of the canines are present; they indicate that this tooth was rather small. The crown of pm. 1 is gone from both sides, and the roots indicate that there was a considerable individual variation in the size of this tooth. In the present specimen, the one on the left side was much the larger, and was fixed in the jaw by two roots; while that on the right was quite small, and had only one root. The succeeding superior premolars gradually increase in size, from before backwards; they all have external, and anterior and posterior basal cingula, and anterior and posterior cross-crests. The internal cone of pm. 4 shows a shallow, median groove, on its inner surface; an indication of division, which is absent in pms. 2 and 3. The posterior cross-crest in pms. 2 and 3 is rather better developed than in pm. 4. The latter tooth has a somewhat prominent parastyle, and its postero-external cone is situated a trifle farther in than the antero-external. Molar 1 is very much worn and its characters, consequently, not well defined: there is a pronounced basal cingulum, and the postero-external cone is situated farther in than the same element in pm. 4. In ms. 2 and 3, which are both well preserved, and scarcely at all worn, the antero-external cone is much larger than the postero-external, and the latter is placed far in from the former. The parastyle is nearly as high as the antero-external cone, and is continuous with the anterior basal cingulum. The anterior cross-crest is much larger than the posterior, and is united with the antero-external cone and not with the parastyle. Both of the external cones are convex externally. There is a deep median sinus which opens internally, but is closed externally. At the head of the median sinus there is a buttress. For an illustration of the more important characters of the skull and sup. dentition see figs. 1, 2, 3, plate II.

*The lower jaw:* No lower jaw was found with the type specimen, but a lower jaw (*No.* 10,900 *Princ. Coll.*), found in

\* P. Z. S. 1882, p. 776:

the same locality and the same horizon, agrees perfectly, in size, with the type, and I have referred it to the same species, and made it a collateral type, figuring it in position in fig. 1, plate II. The inferior border is gently convex, the angle is slightly deflected, and its border turned inward, as in recent Tapirs. The mental foramen is a little in front of pm. 2. The symphysis is long and much constricted, as in *Tapirus*.

*The teeth:* Incisors 1 and 2 are of about equal size and much larger than I. 3, which is quite small, they are all spatulate and slightly cupped. The canine is small, conical and placed close to I. 3. The number of the inferior premolars is reduced to three. There is a long diastema between the canine and pm. 2. All of the pms. have two anterior cones, united by cross-crests notched in the middle; these cross crests are better developed in pms. 2 and 3 than in pm. 4, as has been shown to be the case in the posterior cross-crests of the sup. pms. The antero-external cone is situated farther forward than the antero-internal. There are also two posterior cones, but no posterior cross-crest; the postero-internal is the smaller and there is a low ridge running obliquely forward and inward from the postero-external cone and uniting with the base of the cross-crest. In addition to the elements already described there is a fifth cusp on the anterior border of pm. 2. The true molars each have two anterior and two posterior cones connected by high, sharp cross-crests. There are anterior and posterior basal cingula on all the inf. molars and premolars, but no external or internal cingula. The principal characters of the inf. dentition are well shown in fig. 4, plate II.

*The Atlas:* The articular surfaces for the occipital condyles are deep; those for the axis are of only moderate extent and curve inward exteriorly. There is a short dorsal spine, and a small posterior protuberance on the inferior arch. The transverse processes are only moderately expanded laterally, and posteriorly they extend but little beyond the articular surfaces for the axis. There is a vertebral canal, and foramina, for the inferior and superior branches of the first spinal nerve. The present specimen agrees in every essential character with the atlas of *Elasmognathus bairdii*.\*

*The fore limb:* The humerus is proportionately rather strong and does not differ materially from that bone in recent Tapirs. The head is broad and sub-triangular in cross-section; the articular surface is continued upon the inner surface of the greater tuberosity, which is much larger than the lesser, and is produced, anteriorly, into an obtuse point which overhangs the bicapital groove. The deltoid ridge is prominent,

\* An atlas of *E. bairdii* in the Princ. Coll. has the vertebral canal present on one side and absent on the other.

and without the hook seen in recent Tapirs. The supinator ridge is rather more prominent than in recent Tapirs. The internal condyle is broader and stronger than the external. The anconeal fossa is deep and the supratrochlear shallow: there is no intercondylar foramen. The axis of the trochlea is at nearly right angles to that of the shaft. The intercondylar ridge is prominent and situated well outward, the ulnar articulation being much larger than the radial.

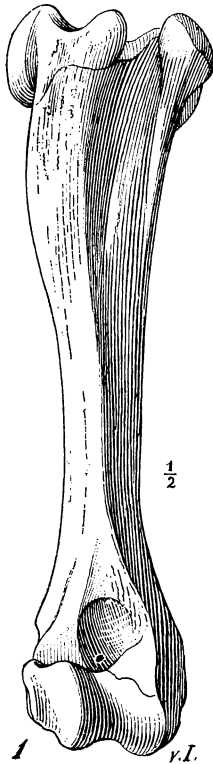


FIG. 1. Humerus of *Protapirus validus*.

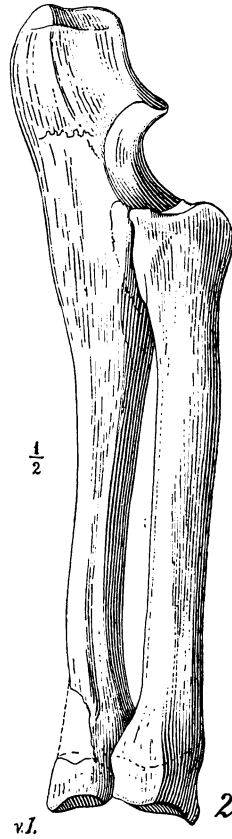


FIG. 2. Radius and ulna of *Protapirus validus*.

The radius and ulna are proportionally rather more slender than the humerus. The olecranon is not pointed superiorly as in *Elasmognathus*, but is of nearly equal breadth from top to bottom. The proximal articulations of the radius and ulna bear about the same relations to each other, and to the

humerus as those of *Elasmognathus*. Our material does not enable me to add anything to what Wortman and Earle have already made known respecting the structure of the carpus.

*Measurements of Protapirus validus.*

Length of skull from base of canine to occipital condyle..	242 <sup>mm</sup>
Length of frontals and parietals .....	151
Distance between postorbital processes of frontals .....	73
Greatest length of lower jaw .....	227
Depth of jaw below pm. 2 .....	33
“ “ “ 4 .....	46
Length of inferior diastema .....	32
“ superior “ .....	27
“ “ premolar molar series .....	102
“ “ molar series .....	53
“ inferior premolar-molar series .....	102
“ “ molar series .....	57
“ humerus .....	203
Breadth of distal end of humerus .....	41
Length of radius .....	158
Breadth of proximal end of radius .....	32
Breadth of distal end of radius .....	29
Length of ulna .....	216
Height of olecranon process above articular surface .....	40

*Protapirus simplex* W. & E.

This species is known only from the superior premolars and fragments of the lower jaw. There is in our collection a lower jaw (11165), with the inferior dentition and both rami nearly complete, found by Mr. H. F. Wells in the *Protoceras beds*, in the same locality as the material just described. Notwithstanding the horizon in which this specimen was found on account of its size and the structure of the premolars I refer it to *Protapirus simplex*. It is smaller than the jaw referred to *P. validus*, and the premolars are in a less advanced stage, the postero-internal cone being quite rudimentary. It differs, also, from *P. validus* in that the cross-crest on pm. 4 is in advance of the same element in pms. 2 and 3, while just the opposite is the case in the latter species. A further structural difference is noticeable in pm. 2; in this tooth in *P. validus* the ridge, which runs forward from the postero-external cone, unites with the antero-external, while in the present specimen it unites with the antero-internal. The principal dental characters of this specimen are shown in figs. 5 and 5a, plate III; the last molar is dropped down in each to accommodate the figures to the size of the plate.

## Measurements.

Greatest length of jaw .....	220 <sup>mm</sup>
Depth of jaw below pm. 2 .....	31
“ “ “ m. 3 .....	40
Length of diastema .....	30
Length of premolar-molar series .....	98
“ molar series .....	55

*Colodon* (Marsh).\*

The present genus is distinguished from *Protapirus*, which it most resembles, by the presence of a fifth cusp on the last inferior molar; by the reduction of the number of lower incisors to two on either side; by the more molariform superior premolars and by the shape of the postero-external cone of the superior molars, which in the present genus is concave on its external surface. The inferior premolars of *Colodon* are distinct from those of *Protapirus*, in that the postero-external cone is always connected with the antero-external by a low ridge. The second inferior premolar is proportionately very much shorter in *Colodon* than in *Protapirus*.

Although remains of *Colodon* are rarely found, yet five species have already been proposed, viz: *C. (Lophiodon) occidentalis* (Leidy)†, founded on a last inferior molar; *C. luxatus* (Marsh)‡, founded on a lower jaw in which pm. 2 is absent; *C. dakotensis* (O. and W.)§, founded on a complete superior dentition, with a portion of an inferior dentition and sup. pm. 4, from another individual as a collateral type; *C. proCUSpidatus* (O. and W.)||, founded on a superior dentition from one side in which m. 3 is wanting and pm. 1 is injured, and *C. (Mesohippus) longipes* (O. and W.)¶, founded on a hind foot now provisionally referred to *Colodon* although first described as *Mesohippus longipes*. Prof. Marsh's type of *C. luxatus* agrees, in size and all essential characters, with Leidy's *occidentalis* in so far as we are able to determine those of the latter, from Leidy's description and figures, and both apparently belong to the same species.

Osborn and Wortman remark, in closing their description of *C. proCUSpidatus*, that "the only means at present known of distinguishing *C. proCUSpidatus* from *C. occidentale* (spelling theirs) is by the smaller size and generally less robust character of the latter." They give the horizon as the Metamyno-

\* See this Journal, June, 1890, p. 524, and Nov., 1893, p. 411.

† See Extinct Mam. Fauna, Dak. and Neb., p. 239.

‡ Loc. cit.

§ See Bull. Am. Mus. Nat. Hist., vol. vii, p. 362.

|| See Bull. Am. Mus. Nat. Hist., vol. vii, p. 364.

¶ See Bull. Am. Mus. Nat. Hist., vol. vii, p. 366, and vol. vi, p. 214.

don layer. Mr. Gidley, who found the specimen, informs me that it is from the *Oreodon beds* below the *Metamynodon layer*. No measurements of the type are given, except to say that, "so far as the measurements are concerned, it agrees very closely in size with *C. dakotensis*." In giving the measurements of the latter species they place in another column, for comparison, corresponding measurements of *C. occidentalis*, but they do not give the measurements of Leidy's type, but those of a smaller individual, referred by Wortman and Earle\* to that species; in this way they obtain as the comparative length of the last lower molar of *C. procuspidatus* and *C. occidentalis* .025 of a meter for the former and .019 for the latter, while the natural size figure of that tooth in *C. occidentalis*, published by Leidy in his description of the species, measures a little more than .022 of a meter, showing, that both the smaller measurements and the larger are well within the limits of specific variation. I have therefore considered it best to regard *procuspidatus* as also a synonym of *occidentalis*.

Disregarding *C. longipes*, which may or may not belong to the genus *Colodon*, and which, if it should prove to belong to that genus will quite likely be found to pertain to one of the previously known species, the following is submitted as a key to the species of *Colodon*.

1. The internal cusps of sup. pms. 2, 3, 4, showing signs of division.  
Postero-internal cone of inferior pms. smaller than postero-external  
*C. dakotensis*.
2. Two distinct internal cusps on sup. pms. 2, 3, 4. Postero-internal cone of inf. pms. as large or nearly as large as postero-external  
*C. occidentalis*.

*Colodon (Lophiodon) occidentalis* Leidy.

*Syn. C. luxatus, C. procuspidatus, and C. longipes?*

There are in our collections several jaws and groups of teeth referable to this species, a crown view of the inf. dentition of one of these (No. 10953) is shown in fig. 6, plate III. It is peculiar in the structure of pm. 2, in which tooth there is but one anterior cusp, a character not seen in any other specimen of *Colodon*. The postero-internal cone on all the premolars in the present specimen equals in size the postero-external. These characters might be regarded as of specific importance, but I prefer to consider them as only individual variations, after studying, with some care, the individual variations in the structure of the teeth of modern Tapirs. In all of the jaws in our collection referred to *C. occidentalis*, the teeth are propor-

\* Bull. Am. Mus. Nat. Hist., vol. v, p. 178.

tionately narrower than in those referred to *C. dakotensis*. The present specimen is from the Oreodon beds, below the *Metamynodon* layer.

*Milk dentition:* Portions of two lower jaws (Nos. 10507 and 10506, fig. 2 and 7, plate III) in our collection are of interest, inasmuch as they show successive stages in the eruption of the milk and permanent dentitions. In 10507 the first milk molar has been broken off and lost, but the second and third are still in place, and immediately behind them is the first permanent molar fully erupted and behind it m. 2 may be seen just commencing to cut the gum. Beneath the deciduous molars and the anterior half of the first permanent molar, the bone from the inside of the jaw has been removed, exposing the unborn premolars in position. By a glance at fig. 2, plate III, it will at once be seen that these teeth, as well as permanent molar 2, occupy a position in the ramus considerably posterior to that which they will assume when fully erupted. In other words, in the process of eruption they will move forward and upward. No. 10506 has all the deciduous molars in place and the first permanent molar just coming into place. As has been remarked by O. & W., the last two milk molars closely resemble the permanent set, while the first is like the corresponding premolar. These specimens were found by Mr. J. W. Gidley in the upper Titanotherium beds.

*Measurements of C. occidentalis (No. 10953 Princ. Coll.)*

Length of inf. premolar-molar series .....	82 <sup>mm</sup>
“ “ “ series .....	32
“ “ molar “ .....	50
“ last inferior molar .....	21

*Colodon dakotensis, O. & W.*

In describing this species, Osborn and Wortman have described the postero-internal cusp of the last lower premolar as double, placing considerable importance upon this character, and the absence of external and internal basal cingula on the superior premolars. The double character of the postero-internal cusp of the last lower premolar is, probably, of little importance, since in their collateral type specimen it is very faint, and has more the nature of a basal cingulum than of a cusp, and moreover, a similar state of affairs is noticeable on some of the smallest of our specimens, referred to *C. occidentalis*. Too much importance should not be given to the presence or absence of basal cingula, which have been shown by Nathusius\* to depend, in living animals, largely upon the abundance or

\* See Der Schweinschadel.

scarcity of nourishment. The more molariform superior premolars and the usually larger size and more robust character of all the teeth of *C. dakotensis* at once distinguish it from *C. occidentalis*. Several specimens in the Princ. Coll. are referred to this species, one of which (No. 11159) consists of a median unguinal phalanx, found associated with a fragmentary lower-jaw, in which the inferior dentition, excepting the canine and m. 3, is complete and in a splendid state of preservation. The unguinal phalanx and a crown view of the teeth are shown in figs. 3 and 3a, plate III. This specimen was found by Mr. Wells, and no record was kept as to the horizon; from the nature of the matrix it appears to be from the Oreodon beds below the Metamynodon layer. There may be some doubt as to whether the unguinal found associated with the teeth really belongs with them, but from the texture of the bone, color, etc., I believe they pertain to the same individual; it is in shape remarkably like the same bone in *Mesohippus*, but much larger than that in any species of that genus known from the lower Oreodon beds. It also resembles the same bone in the third digit of *Elasmognathus* and like that bone in this genus and in *Mesohippus* it is notched in front.

The incisors in the present specimen are very large, chisel shaped and their crowns are slightly excavated or cupped. The premolars and molars are very strong.

*Measurements of C. dakotensis (No. 11159 Princ. Coll.)*

Length of inf. pms. and ms. 1 and 2 .....	75 <sup>mm</sup>
“ “ .....	40
Depth of ramus below m. 1 .....	35
Length of unguinal phalanx .....	24
Breadth “ “ .....	22

*Recent Tapirs.*

I do not expect to be able to add much to our present knowledge of recent Tapirs, but rather to collect and condense a part of what is already known of the dental characters, and the osteology of the skull, in the five now generally accepted species; with a list of the synonymy of each, complete, in so far as the literature available will permit. The following key to genera and species is submitted.

A. *Maxillaries greatly expanded superiorly and embracing the mesethmoid cartilage, which in adult specimens is ossified and extends as a bony plate far in front of the nasals. Premaxillaries short and obtuse posteriorly* ..... *Elasmognathus*.

1. Nasals longer than their combined width, and applied to one another throughout the greater part of their length, each usually ossified from a single center..... *E. bairdii*.
2. Nasals broader than long, more or less separated by an anterior prolongation of the frontals, each usually ossified from two separate centers ..... *E. dowi*.

B. *Ossification of mesethmoid cartilage never extending much in front of middle of nasals. Superior border of maxillaries low, and widely separated from each other. Premaxillaries long and acute posteriorly* ..... *Tapirus*.

1. Premaxillo-maxillary suture bisecting alveole for canine. Premaxillary deeply embraced by superior and inferior branches of the maxillary. Sagittal crest broad and low. Nasals broad and long, sup. pm. 2 molariform .. *T. indicus*.
2. Premaxillo-maxillary suture passing in front of alveole for canine. Premaxillary not deeply embraced by superior branch of maxillary. Sagittal crest sharp and high. Nasals broad and short. Sup. pm. 2 molariform..... *T. terrestris*.
3. Premaxillo-maxillary suture passing in front of alveole for canine. Premaxillary scarcely at all embraced by superior branch of maxillary. Sagittal crest sharp and low. Nasals long and narrow. Sup. pm. 2 submolariform .. *T. roulini*.

*Tapirus*, Brisson (1756) *Regne Anim.*, p. 118.

*Syn. Rhinocœrus (Gray), Rhinocœrus (Wagner) in part, Hydrocœrus (Erxleben) in part, Sys. Reg. An., 1777, p. 191.*

*Tapirus roulini* Fischer.\*

*Syn. T. pinchacus, T. villosus, T. leucogenys, T. ænigmaticus and Tapir pinchaque.*

A skull and the sup. dentition of the present species are shown in fig. 2, plate V, and figs. 2 and 2a, plate IV, drawn from No. 204 in the Yale osteological collection. *T. roulini* is the smallest and least specialized of all the recent Tapirs. The skull is low, narrow and flat, the nasals are long, pointed, coössified, and posteriorly, they are but little lower than the frontals. The premaxillaries are scarcely at all embraced by a superior arm of the maxillaries and the latter projection is not higher than the embraced portion of the premaxillary. The ossified septum does not extend in front of pos. border of nasal opening. The cavity for lodgment of cartilaginous air sinus is deep, but extends but slightly upon the base of the nasals. The floor of the orbit is shallow but deeper than in *T. indicus*. The foramen magnum is absolutely and relatively larger than in any of the other species. Sup. pm. 1

\* Fischer's Synops. Mam. Add., p. 406.

is much longer than broad and the internal cone is situated on the extreme postero-internal angle and is quite rudimentary. The antero-internal cone in sup. pm. 2 is a mere tubercle and the anterior cross-crest is absent.

*Tapirus (Hippopotamus) terrestris*, Linn.\*

*Syn. T. americanus, T. anta, T. suillus, T. laurillardii, T. equadorensis.*

The principal characters of the skull and sup. dentition of this species are shown in fig. 1, plate V, and I and 1a, plate IV, which have been drawn from No. 157 in the Yale Coll. The present species seems to be most closely related to the preceding; the skull, like that of the former, is compressed and there is a sharp sagittal crest in both; but in the present species the sagittal crest is convex antero-posteriorly and elevated far above the nasals, which are short and broad in marked contrast to those conditions which have been found in *T. roulini*. The premaxillaries have an extended contact with the maxillaries and are slightly embraced posteriorly by a superior branch of the latter which is not elevated above the premaxillary. The excavation for the air sinus is mainly in the frontals and maxillaries, near the base of nasals and does not encroach much upon the latter. The first sup. premolar is nearly as broad as long and the internal cone is near the middle of the tooth. Sup. pm. 2 is entirely molariform.

*Tapirus indicus* Desm.†

*Syn. T. sumatranus, T. maylayanus, T. bicolor, T. me.*

A skull and sup. dentition of *T. indicus* are shown in figs. 3, plate V, and 3 and 3a, plate IV, drawn from No. 200 in the Yale Coll. As has been noticed by Gill the present species more nearly resembles species of *Elasmognathus* than do either of the other species of *Tapirus*, among the points of resemblance the following are noteworthy. The premaxillaries are embraced by the maxillaries and the superior branches of the latter are produced above the premaxillaries and approach each other medially. The mesethmoid cartilage is ossified as far forward as the middle of the nasals in adult specimens. The frontals are broad and abruptly elevated above the base of the nasals, precisely as in *Elasmognathus*. The premaxillo-maxillary suture bisects the alveole for the canine, in this respect *T. indicus* is unique among modern Tapirs, and I have found this character absolutely constant in

\* Sys. Nat., 10th ed., 1758.

† Desm. Mam., p. 411.

all the skulls I have been able to examine and in the published figures of them. The nasals are long, broad posteriorly, narrow anteriorly and separated throughout their entire length, near their base there is a deep excavation for the lodgment of the cartilaginous air sinus. Sup. pm. 1 is longer than broad, the internal cone is placed farther forward than in *T. roulini*. The cross-crests in sup. pm. 2 are not complete in the present specimen, but I notice that in other specimens they are quite complete.

*Elasmognathus* Gill.\*

This genus has not been generally accepted, but the characters assigned to it by Dr. Gill are constant and seem to be of generic importance. In addition to the characters already pointed out. I may mention the extreme breadth of the top of the skull which may almost be described as without a sagittal crest, and the invariably complete molariform condition of sup. pm. 2. Species of the present genus rival in size *T. indicus*, the largest of the species of *Tapirus*, and include the most specialized forms belonging to the Tapiridae.

*Elasmognathus bairdii* Gill.†

The principal characters of the skull and sup. dentition of this species are shown in figs. 4, plate V, and 4 and 4a, plate IV, drawn from No. 515 in the Yale Coll. The ascending posterior arm of the maxillaries, which articulate with the lacrymals and frontals is much compressed and entirely concealed by the latter bones, when the skull is viewed from the side. The premaxillary is short and obtusely pointed, posteriorly. The post-tympanic and postglenoid processes approach each other inferiorly but do not meet. The nasals are longer than broad, are closely applied throughout their entire length and coössified in old individuals; they usually ossify, each, from a single center, and posteriorly, they are but little separated by the anterior median prolongation of the frontals.

*Elasmognathus dowi* Gill.‡

In general, the skull and dentition of the present species resembles so closely those of the preceding that it is not necessary to figure the latter. Alston§ has shown that most of the specific characters ascribed to *E. dowi* are quite variable, and hardly of specific importance. He says on page 98 of the work

\* See Proc. Phil. Acad. Sci., 1865, p. 183.

† See Proc. Phil. Acad. Sci., 1865, p. 183.

‡ See this Journal, 1870, p. 142.

§ See Biologia Centrali-Americana, Mammalia by Edward R. Alston, 1879-1882.

just cited: "The comparison of a sufficient series of skulls in any species of Tapir shows the existence of a very remarkable extent of individual variation in minor dental and cranial characters; and I have not found any of the differences pointed out by Dr. Gill as distinguishing *T. dowi* from *T. bairdii* to be constant, except the extraordinary modification of the fronto-nasal region." After figuring and describing at some length the different characters in the region of the nasals, on page 100, Alston summarizes these characters as follows:

- "1. *T. bairdii*. Nasals well developed, each ossified from a single center, separate throughout life, thick at their base, and articulated with one another for the greater part of their length."
- "2. *T. dowi*. Nasals very small, each ossified from two centers, thin, more or less separated from one another by an anterior prolongation of the frontals, with which they become partially or entirely ankylosed before the animal reaches maturity."

Had Alston had more material he would doubtless have arrived at the same conclusion regarding the nasal characters that he did in regard to those of other parts of the skull. I find these characters exceedingly variable, and in the very extensive collection of skulls of *Elasmognathus* in the National Museum, which I have had the privilege of examining and figuring, every gradation between these two types of nasals is shown. I have selected a series of five of these skulls, showing as many different degrees of variation, and have had the fronto-nasal region in each drawn, and they are shown here in pl. III, figs. A, B, C, D, E. From an examination of these figures in connection with what has already been said, it will at once be seen that as yet no character has been found by which it is possible always to distinguish *E. dowi* from *E. bairdii*, and they might be considered synonyms, although I have preferred to retain both, and consider the former as the less specialized of the two, and the direct ancestor of the latter, which has not as yet been fully differentiated from it. It might better be considered as a sub-species.

#### *Phylogeny.*

Wortman\* and Earle in their most excellent paper entitled "*Ancestors of the Tapir from the Lower Miocene of Dakota*," have reviewed very fully the work done by Marsh, Cope, Scott and Osborn on the phylogeny of the Tapirs. They (Wortman and Earle) derive the true tapirs from the Wind River genus.

\* See Bull. Am. Mus. Nat. Hist., vol. v, pp. 159-180.

*Systemodon* through the intermediate forms *Isectolophus* (*Helaletes*) *latidens* of the Bridger, *Isectolophus annectens* from the Uinta, *Protapirus simplex* and *P. olivoidens* from the White River and perhaps *Tapiravus* from the Loup Fork. They cite as evidences against this line of descent, the union of the protoloph with the parastyle instead of the paracone in both species of *Isectolophus* and the submolariform character of sup. pms. 3 and 4 in that genus as described by Osborn.\* I have carefully examined both of these types and can say that the union of the protoloph is with the paracone rather than the parastyle, the real union being with the ectoloph a little in front of the paracone. In regard to the sup. pms. Prof. Osborn says (on page 519 of the paper just cited): "These are wanting in the Uinta specimens, but the Bridger species which was formerly referred by us to *Helaletes* (*H. latidens*) is closely related to *Isectolophus*, if not generically the same, and shows double internal lobes upon both pm. 3 and pm. 4;" and just below on the same page in his *Generic characters* he says, "Fourth and probably third premolars in both jaws submolariform or with double internal cones." These are certainly errors of observation and description, since in sup. pm. 4, which is the only superior premolar complete and in position in the type of *H. latidens*, the internal cone is absolutely simple and without the faintest signs of division, the same may be said of the only sup. pm. at present known of *Isectolophus annectens*. Prof. Osborn further states on page 521 that the first inferior premolar abuts against the canine; and on page 519, that there is no diastema behind the canine, these are characters not shown in any of the type specimens of the genus; and if we stop to consider the characters which obtain in this region of the skull in the White River Tapiroids, together with the extreme conservativeness of this entire group in accomplishing any dental or other changes, we may infer that it is quite probable, that in the Uinta Tapiroids, there was a considerable post-canine diastema, with a marked constriction of the symphysis of the lower jaw, otherwise we shall have to conclude that the Tapirs, toward the close of the Uinta, began to progress very rapidly, and in the interim between that and the beginning of White River times they outstripped all other Perissodactyls in accomplishing anatomical changes, a very improbable assumption.

After studying carefully all the material referable to *Isectolophus annectens* I can only substantiate the views of Scott, Osborn, Wortman and Earle in referring *Isectolophus* to the *Tapiridæ*. I do not consider *Isectolophus* (*Helaletes*) *latidens* from the Bridger as belonging to the genus *Isectolophus*.

\* The Mam. of the Uinta Form. Trans. Am. Phil. Soc., 1889, pp. 461-572.

There are marked differences in the structure of the sup. true molars in the two species and when the complete dentition of the Uinta species is known, the dental formula and arrangement of the teeth will doubtless be found to differ in the two. If *Isectolophus* (*Helalaetes*) *latidens* can be shown to differ generically from *Helalaetes* it should be made the type of a new genus. I have never seen any of Prof. Marsh's types of *Helalaetes* and his descriptions do not permit of an identification of other material.

The discovery of a nearly complete skull of *Protapirus* with characteristic tapirine characters, already pointed out, may be considered as additional evidence in favor of Wortman and Earle's views in considering that genus as the White River ancestor of the *Tapirs*. In taking this view of the question, however, the fact must not be lost sight of, that in *Protapirus* the character of the metacone of the sup. molars is not what we should expect to find in a White River *Tapir*, and the inferior, external, lateral incisor is much smaller than we should expect it to be, since it persists in recent *Tapirs* and is even proportionately larger than in *Protapirus*. The metacone in *Protapirus* is placed farther in, and is less prominent and not so convex externally as in *Isectolophus*, while the same element in recent *Tapirs* is more prominent and has a more external position than in *Isectolophus*. Thus, according to our present phylogenetic arrangement we should have to allow for first a gradual shifting inward of the position of this cone followed by a period when it commenced to move outward to its normal position in modern *Tapirs*; a rather extreme case of oscillation but not entirely inconsistent with what Scott has shown to have taken place in the Equine series.

Very little is known of the American Miocene representatives of the Tapir line. Prof. Marsh has mentioned the occurrence of two Miocene species of Tapiroids which he considers as standing ancestral to the Tapirs. One of these is from the Miocene of New Jersey and the other is from the Loup Fork or late Miocene (early Pliocene of Marsh) from east of the Rocky Mountains, no more definite locality being given by Marsh. These specimens are made the type of a new genus *Tapiravus*; the one from New Jersey is described as *Tapiravus validus*, while the one from the west is called *T. rarus*. I have never seen either of these specimens and they have not been figured, and are only very briefly described by Prof. Marsh. There would seem to be little doubt that they belong to the direct line leading to the recent Tapirs.

In Europe the paucity of Tapir remains in the Miocene is almost as marked as in America. In *Tapirus helveticus* of Meyer, from the lower Miocene of Eselsberg near Ulm, we

doubtless have one of the direct ancestors of the modern Tapir. In this species sup. pm. 4 is entirely molariform except that the posterior cross-crest is not complete. Sup. pm. 3 is in the same stage as sup. pm. 2 in *T. roulini* of recent Tapirs. *Tapirus helveticus* Meyer is perhaps the European equivalent of *Tapiravus validus* Marsh, from New Jersey. The European species should be referred to the latter genus rather than to *Tapirus*. In regard to the American species at present referred to *Protapirus*, there may be considerable doubt as to whether they should not be referred to a distinct genus; from Filhol's description and figures there would seem to be a considerable difference in the relations of the protoloph to the parastyle in the sup. true molars and in the structure of the posterior cross-crest in sup. pm. 4. The importance of these differences can only be determined by an actual comparison of the specimens.

Of recent Tapirs it can be pretty well demonstrated that *Elasmognathus bairdii*, the most specialized of all, has been derived from *T. roulini* directly through *T. terrestris* and *E. dowi*; while *T. indicus* had a common ancestry and became separated from the others, probably in late Miocene times, since when it has paralleled *Elasmognathus* in some of its characters though not showing the same degree of specialization.

In regard to *Colodon* and the earlier genera of *pseudo-tapirs*, I cannot agree with Osborn and Wortman that their line of descent has been entirely distinct from that of the true *Tapirs*. On account of the, in many respects, very similar tooth and foot structure of the two, it would seem that they were both derived from a common Bridger ancestor, most likely some one of the species now referred to *Helaletes* and which had its immediate ancestor in *Systemodon*. The true genus *Helaletes* with sup. pms. 3 and 4, already molariform according to W. and E., terminates a third line, and is descended directly from Heptodon of the Wind River.

The figures in the plates accompanying this paper were drawn by Mr. Rudolph Weber. I wish here to express my thanks to Prof. Scott for his kindness in allowing me to describe the important and rare skull of *Protapirus* as well as the other fossil material. To Prof. Marsh I am especially indebted for the free use of the very complete collection of skulls and skeletons of recent Tapirs in the Yale Museum. I wish also to thank Mr. F. A. Lucas of the National Museum and Prof. Osborn and Dr. Wortman of the Am. Mus. of Nat. Hist. for the use of material in their charge.

Princeton, N. J., Jan. 13, 1896.

## EXPLANATION OF PLATES.

## PLATE II.

- FIGURE 1.—Side view of skull of *Protapirus validus*,  $\frac{1}{2}$  natural size.  
 FIGURE 2.—Top “ “ “ “ “ “  
 FIGURE 3.—Bottom “ “ “ “ “ “  
 FIGURE 4.—Crown view of inf. dentition of same,  $\frac{3}{4}$  natural size.

## PLATE III.

- FIGURES A, B, C, D, E.—Comparative series of nasals of *E. dowi* and *E. bairdii*  
 FIGURE 2.—Inside view of young lower jaw of *Colodon occidentalis*, showing  
 milk and permanent teeth.  
 FIGURE 3.—Crown view of inf. dentition of *Colodon dakotensis*.  
 FIGURE 3a.—Ungual phalanx of *Colodon dakotensis*.  
 FIGURE 4.—Crown view of sup. m. 3 of *Colodon* sp.  
 FIGURE 5&5a.—Side and crown view of inf. dentition of *Protapirus simplex*. M.  
 3 dropped down in each to accommodate size of plate.  
 FIGURE 6.—Crown view of inf. dentition of *Colodon occidentalis*.  
 FIGURE 7.—Crown “ “ milk dentition of “ “

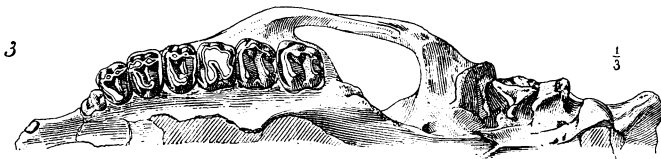
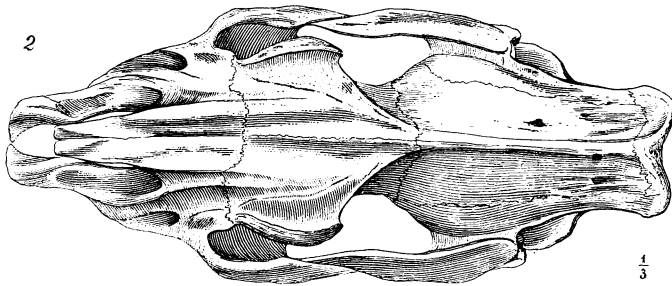
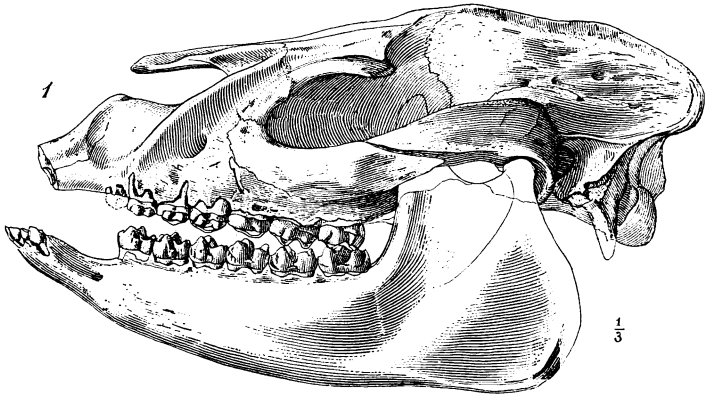
## PLATE IV.

- FIGURE 1.—Crown view of sup. dentition of *Tapirus terrestris*,  $\frac{3}{4}$  nat. size.  
 FIGURE 2.— “ “ “ “ *roulini*, “ “  
 FIGURE 3.— “ “ “ “ *indicus*, “ “  
 FIGURE 4.— “ “ of *Elasmognathus bairdii*, “ “  
 FIGURE 1a.—Top view of nasals and crest of *Tapirus terrestris*,  $\frac{3}{4}$  nat. size.  
 FIGURE 2a.— “ “ “ “ *roulini*, “ “  
 FIGURE 3a.— “ “ “ “ *indicus*, “ “  
 FIGURE 4a.— “ “ “ “ *Elasmognathus bairdii*,  $\frac{3}{4}$  nat. size.

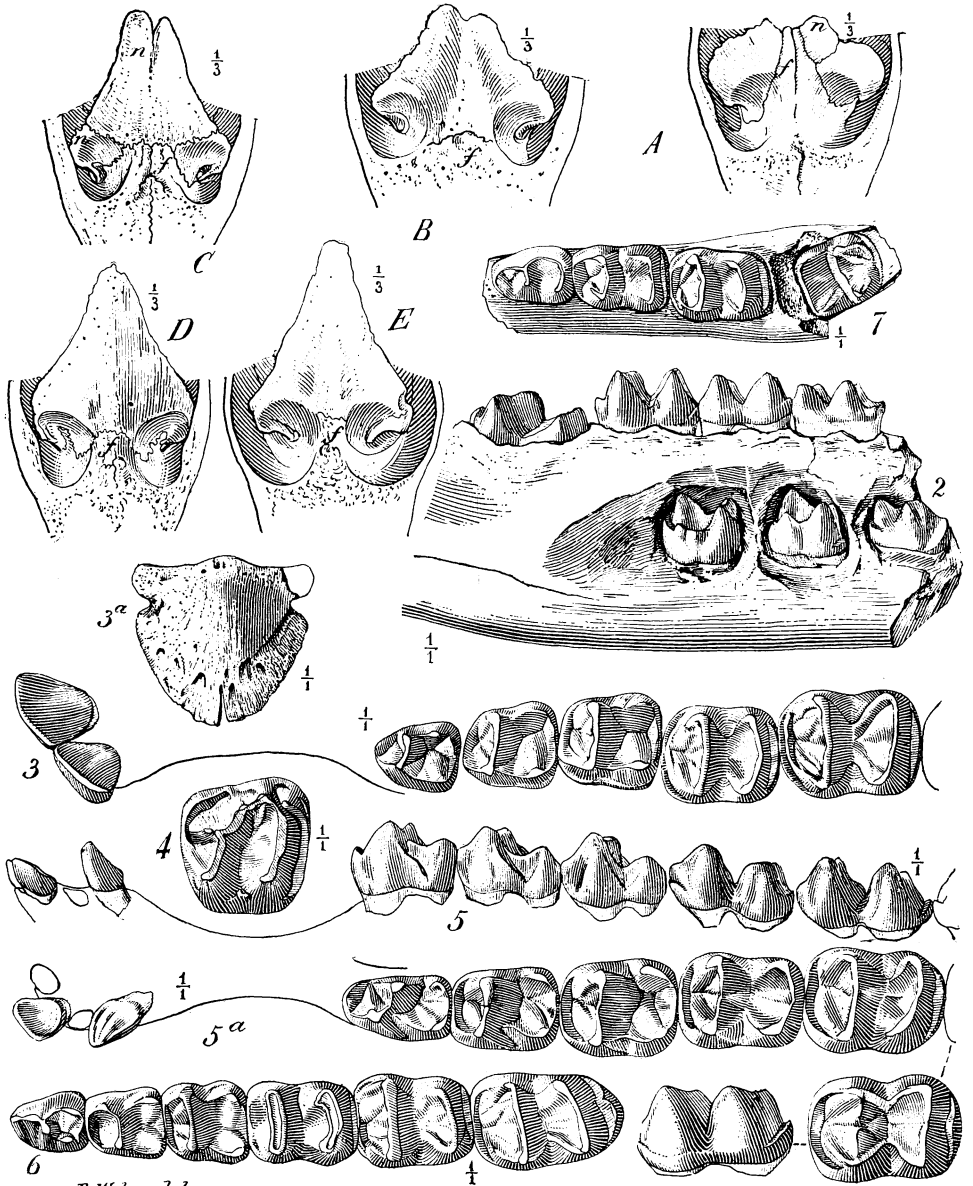
## PLATE V.

[All figs.  $\frac{1}{4}$  nat. size.]

- FIGURE 1.—Side view of *Tapirus terrestris*.  
 FIGURE 2.— “ “ *roulini*.  
 FIGURE 3.— “ “ *indicus*.  
 FIGURE 4.— “ *Elasmognathus bairdii*.



R. Weber, del.



R. Weber. del.

