

**Article III.—SOME SKULLS OF *PERCHÆRUS* [*THINOHYUS*]  
FROM THE WHITE RIVER AND JOHN DAY FORMATIONS**

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In The American Museum of Natural History there are five primitive suilline skulls from the White River and John Day Oligocene; in all of them the lower jaw is lacking, but otherwise they are nearly complete. Besides these there are the back part of another skull and a variety of jaw fragments.

Two of these skulls have already been described by Cope (1888, Proc. Amer. Phil. Soc., XXV, pp. 70–77) under the names *Bothrolabis pristinus* and *B. rostratus*. Sinclair determined (1905, Univ. of Californ. Publications, Bull. Dept. Geol., (6) IV, p. 135) that Cope's genera *Chænohyus* and *Bothrolabis* were identical and synonymous with Marsh's type *Thinohyus* (Marsh, 1875, Amer. Journ. Sci., (3) IX, pp. 248–249). Peterson expressed a similar opinion (1905, Mem. Carneg. Mus. Pittsburg, (8) II).

In 1907 (Bull. Amer. Mus. Nat. Hist., XXIII, p. 216) Matthew established a new genus, *Desmathyus*, for certain Lower Miocene suillines intermediate in type between the specialized dicotylids of higher levels and the primitive Oligocene genus *Perchærus* Leidy (Leidy, 1869, Journ. Acad. Nat. Sci. Phila., (2) VII, p. 195). He pointed out that Peterson's species "*Thinohyus*" *siouxensis* (Peterson, *loc. cit.*), from the Harrison beds of the Lower Miocene, could more properly be referred to this new genus, whereas the typical *Thinohyus*, from the John Day Oligocene, was apparently not generically distinct from the White River *Perchærus*.

In 1915 Cope's plates of the species described by him for the U. S. Geological Survey were published with descriptions by Matthew, who revised the generic names "*Palæochærus*," "*Bothrolabis*," and "*Thinohyus*" to *Perchærus* ('Hitherto Unpublished Plates of Tertiary Mammalia and Permian Vertebrates,' U. S. Geological Survey and Amer. Mus. Nat. Hist., Monograph Series, No. 2).

Dr. Matthew felt that the Oligocene material in the American Museum needed more detailed description and he very kindly suggested that I might undertake the work. I should like to offer my very best thanks to the following for the help which they have given me in the course of this paper. To Dr. W. K. Gregory for his advice and criticism, for reading the manuscript, and for the privileges which I have enjoyed in his department. To Dr. W. D. Matthew for reading the manu-

script and for the free access which I have had to the material under his charge. To Mrs. Helen Ziska for her valuable suggestions and criticism in drawing. And to Miss Jannette M. Lucas and my other friends of the American Museum library for incalculable assistance, moral and material.

#### THE SKULL OF THE GENUS *PERCHÆRUS*

Stehlin, in his monograph 'Ueber die Geschichte des Suiden Gebisses' (Zurich, 1899), attempted to compare Cope's John Day "Bothrolabidæ" with recent peccaries and to gain some light on the relationships of New World to Old World suillines. He had only Cope's figures and descriptions of the John Day skulls to be guided by and, as he himself pointed out, these were inadequate as regards morphological detail.

Descriptions of the New World Oligocene suillines by American writers would seem to have been so exclusively concerned with allotting them to one or other of the numerous species which have arisen, or with creating new species, that the well-established underlying structure which they have in common has been neglected. In our ignorance as to the degree to which even closely related individuals can vary from one another, a study of such superficial characters as are usually relied upon for separating species is, especially in dealing with fossil material, of very little value in tracing relationships.

It may, therefore, be of some help towards an understanding of the relationship between New World and Old World suillines to give here a description of certain characteristics which seem to have firmly established themselves in a number of the earliest known skulls of the former.

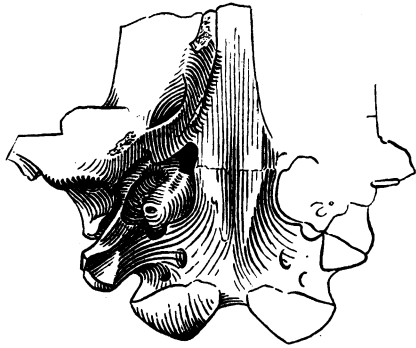
An idea of the general shape and proportions of the skulls and their component parts may best be obtained from the figures. I will, therefore, give a detailed description of only the more interesting regions.

#### BASICRANIAL AND OTIC REGIONS

In the otic region *Perchærus* is already well advanced along the line of specialization peculiar to the suilline group (though paralleled in other widely divergent groups such as the rhinoceroses and certain rodents); that is to say, the post-glenoid and post-tympanic processes of the squamosal have closed around the tubular external auditory meatus, forming a sheath which fuses with the tympanic. In later forms this sheath extends half-way up the side of the occiput, carrying with it the opening of the middle ear, but in *Perchærus* it still does not extend much above the level of the top of the foramen magnum. A clear understand-

ing of this region can best be obtained by tracing its structural evolution from a primitive Eocene artiodactyl through Oligocene forms of other groups which have not in this part of the skull advanced so far on their own peculiar line of specialization as has *Perchærus*.

Fig. 1 is a ventral view of the incomplete and crushed skull of a Bridger bunodont artiodactyl, A. M. N. H. No. 13079, probably referable to the genus *Helohyus* (Sinclair, 1914, Bull. Amer. Mus. Nat. Hist., XXXIII, p. 283). Here the tympanic bone is lacking and was probably, as in the Eocene members of other mammalian groups, ring-shaped, or at any rate not completely flask-shaped, and not firmly ankylosed with the neighboring bones of the skull. The stout paroccipital process is composed of a broad exoccipital portion posteriorly, and anteriorly of a well-developed mastoid, the grooved ventro-mesial surface of which doubtless served as a channel for the facial nerve, though I have been unable to detect the opening of the aqueductus fallopiani in the periotic bone. On the exposed surface of the latter a large fenestra rotunda is evident and just in front of this there is a smaller fenestra ovalis, lying directly opposite the mouth of the deep, empty channel between the post-glenoid and post-tympanic processes of the squamosal. The post-glenoid process, a downwardly-projecting flange at the back of the flat glenoid surface of the squamosal, is penetrated by a large post-glenoid foramen. (This foramen, if it corresponds to the similarly situated one which in most recent mammalian groups closes up during embryonic life, indicates the primitive condition of an external jugular vein communicating anteriorly with the venous sinuses within the cranium.) The post-tympanic process, forming the posterior wall of the channel, is another downwardly-directed flange and is pressed against the anterior surface of the root of the mastoid.



Natural size.

Fig. 1. Basis cranii of ? *Helohyus*, No. 13079.

Fig. 2, of the otic region of *Leptomeryx evansi*, A. M. N. H. No. 1343, represents a type which is primitive and generalized for White River artiodactyls, since they all, except the extremely aberrant entelodonts, can be readily referred to it. The chief advance over the Bridger forms

is in the flask-shaped tympanic, firmly ankylosed to the surrounding bones, with its tubular neck lying wedged into the channel between the post-glenoid and post-tympanic processes of the squamosal; its rounded bulla fails to cover completely the ventral surface of the periotic, the mesial edge of which lies exposed between it and the basi-occipital. The mastoid still forms a considerable portion of the paroccipital process and the groove on its mesial surface is now closed in by the tympanic bulla to form the stylomastoid foramen. The postero-ventral surface of the bulla, just in front of and mesial to this foramen, has a deep pit-like indentation plugged by the small wedge-shaped tympano-hyal. There is apparently no post-glenoid foramen.

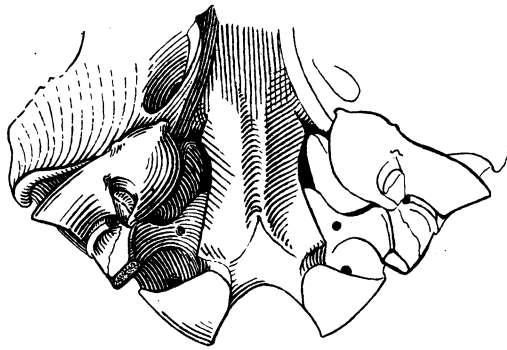


Fig. 2. Basis cranii of *Leptomeryx evansi*, No. 1343.

One and a half natural size.

Returning to the skulls of *Perchaerus*, we find the otic region most completely shown in Nos. 7394 and 7398 (Figs. 3 and 12), though it is sufficiently well preserved in the other skulls and especially in the two young ones from the White River (Fig. 6) to complete the information given by these and to show that all are essentially similar in this region. The tubular external auditory meatus no longer lies freely exposed on the ventral surface of the skull, but the channel in which it rests, between the postglenoid and post-tympanic processes of the squamosal, has become closed in to form a complete tunnel by the fusion of these two processes along its whole length. The floor of the tunnel is formed by the post-tympanic process, which curves forward beneath the bony meatus and laps up against the posterior surface of the post-glenoid process. The two processes have fused with each other and with the enfolded bony ematus itself. Although there is apparently no post-glenoid foramen leading into the brain cavity, the post-glenoid process is pierced by a narrow

tunnel running through it from side to side. This tunnel, which is present in more recent peccaries but not in *Sus*, lies nearly parallel to the auditory meatus, which runs upwards, outwards and backwards from the cavity of the bulla. The lateral opening of this tunnel is by the side of, and just anterior to, the auditory opening itself and lies with the latter at the base of the same shovel-shaped pit at the back of the zygomatic process of the squamosal (Fig. 4). The mesial opening is just above the level of the ventral surface of the bulla and lies two-thirds of the way back along the length of the latter, which is here joined to the postglenoid process by a narrow bridge or bone. In front of this bridge there is a pit-like depression, exceptionally deep in No. 7398, between the

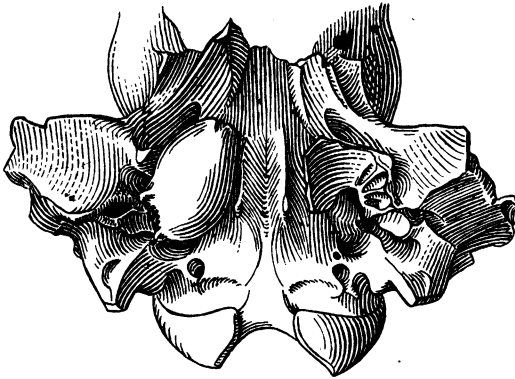


Fig. 3. *Perchærus* species, No. 7398.  
Three-quarters natural size.

side of the bulla and postero-mesial corner of the glenoid surface. A much deeper pit lies directly behind this bridge and, although no tympano-hyal is present, its relation to the surrounding structures indicates that this is where the tympano-hyal was lodged and that the bridge itself and the prominence which projects back from it on the outer side of the pit correspond to that part of the bulla which in *Leptomeryx* (Fig. 2) ensheathes the tympano-hyal plug antero-laterally. Immediately behind this region, again, is the stylomastoid foramen, forming the mouth of a channel which leads upwards into the tympanic cavity.

The mastoid process, as in recent suillines, has disappeared<sup>1</sup> and this channel for the facial nerve, instead of forming a groove on the mesial

<sup>1</sup>Gidley, J. W. (1920, Proc. U. S. Nat. Mus., XLVII, p. 654) appears to mistake the post-tympanic process of the squamosal for a true mastoid. Disarticulated young skulls of *Tayassu* and *Sus* show that the periotic has no pars mastoidea. In this paper Gidley gives definitions of the families Suidæ and Tayassuidæ and of the two recent tayassuid genera *Tayassu* and *Pecari*.

surface of that process in the primitive manner, makes a groove instead on that part of the squamosal which takes its place. That is, the part lying behind the post-tympanic process and abutting against the anterior face of the paroccipital process of the exoccipital (Figs. 6 and 7).

The bulla itself is roughly egg-shaped, its long axis antero-posterior and at only a very slight angle with the plane of the basis cranii, its narrower end rugose and pointing forwards. It completely covers in the periotic bone ventrally, there being but a narrow crack between its mesial wall and the basi-occipital. At its posterior end, however, the edge of the latter bone is scooped out in the usual way to form the foramen lacerum posterius or jugulare; this foramen, in contrast to the condition found in *Tayassu* but in accordance with that in most primitive forms, is completely separated from the stylo-mastoid foramen by a backward projection from the tympanic bulla meeting a forward projection from the root of the paroccipital process.

Although the bulla was apparently not filled with a dense sponge of cancellous bony tissue, as in *Desmathyus* and more recent peccaries, there are traces of bony septa on its inner surface in some of the skulls (Figs. 3 and 6).

The paroccipital process (see especially Figs. 6, 11, and 13) is of the dicotylid type, of moderate length only and with pointed extremity and broad base. It is more flattened antero-posteriorly than in *Tayassu*, however, with strongly ridged edges. The postero-internal edge takes origin in the narrow prominence separating the jugular foramen (f. lacerum posterium) from the condylar foramen. Just below its origin this edge is produced into a small backwardly-directed process.

There is a single condylar foramen only, large and corresponding in position to the anterior one of other forms.

The configuration of the muscle areas on the basi-occipital surface and the prominence of their bounding ridges varies somewhat in the different skulls. I have found this region to be very variable in *Tayassu*, also among skulls of the same sub-species. All the *Perchærus* skulls show, however, two more or less well-marked ridges at the anterior end of the bone, between the tympanic bullæ, for the insertion of the longi capitis muscles; these ridges are best developed in No. 7398 (Fig. 3).

#### OCCIPUT

Fig. 4 is a reconstruction of this region made from the two White River skulls and from the young skull (No. 7396) from the John Day, which corresponds very closely with them.

The supra-occipital region, which in recent suillines is flattened outwards by the extensive parietal sinus within, is here much more deeply hollowed beneath the occipital crest; a median ridge runs up it for some way from the dorsal border of the foramen magnum below. This dorsal border is notched in the mid-line where the supra-occipital is just excluded from it by the two exoccipitals meeting each other.

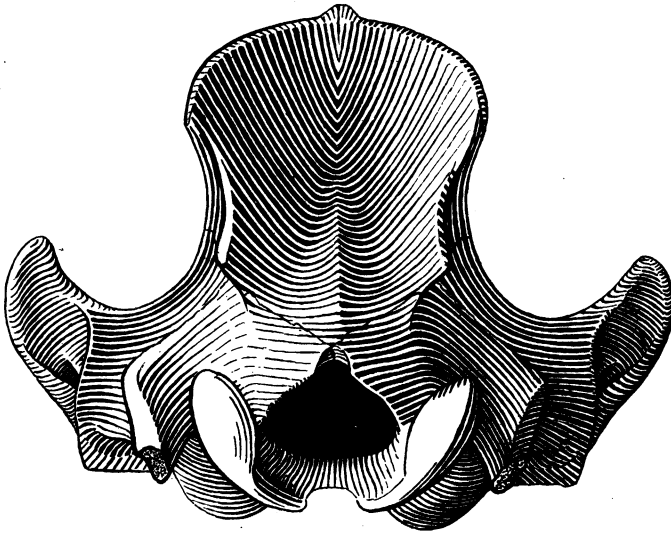


Fig. 4. Occiput of *Perchærus* as reconstructed from the young White River skulls, Nos. 585 and 695.  
Natural size.

The hollowed-out appearance of the back of the occiput is accentuated by the presence on either side of it of a crest which joins the main occipital crest above and runs straight down from the latter to end abruptly in an outward projection about a centimeter above the exoccipital condyle.

The temporal fossa is divided from the occipital surface by the usual sharp ridge. This runs downwards and outwards from the occipital crest to form the postero-dorsal border of the zygomatic wing of the squamosal, and terminates in the cowl-shaped projection of the latter above the external auditory meatus.

#### GLENOID SURFACE AND ZYGOMA

The level of the glenoid surface of the squamosal, in comparison with the basis cranii and the ventral surfaces of the bullæ, appears to

vary with age and with species, but it is never so far depressed as in more recent peccaries (*Desmathyus* seems to have reached an extreme of depression). The surface is directed more from side to side than in these latter and there is not such a well-marked pre-glenoid elevation of the squamosal. Postero-externally this surface is smoothly continuous with a shallow depression which leads round from it up on to the lateral surface of the zygoma, parallel to the suture line between the post-glenoid and post-tympanic processes; there is no such depression in recent peccaries, where the glenoid surface is marked off posteriorly by a definite edge, joining the post-glenoid and pre-glenoid processes.

The zygomatic bar of the jugal has a strongly ridged ventral edge terminating abruptly just in front of the glenoid surface; this is more like the condition in *Sus* than that in later peccaries. Dorsally the jugal has the usual well-marked post-orbital process projecting up towards the post-orbital process of the frontal.

#### PALATE

From in front of each tympanic bulla the pterygoid process of the alisphenoid runs forwards to meet the sphenoid process of the palatine and together they form a long wall joining the palate to the basis cranii. This wall, with its fellow of the opposite side, encloses a long deep "mesopterygoid" fossa into which the posterior nares open anteriorly and the basisphenoid steeply plunges down posteriorly. In the John Day skulls the everted ventral edge of this wall carries a double ridge with a shallow groove between; this is the pterygoid fossa for the internal pterygoid muscle; it leads up to the mouths of the foramen ovale and the foramen lacerum medium under cover of the anterior end of the tympanic bulla. (The foramen ovale is completely encircled by alisphenoid in all the skulls of *Perchærus* which show this region clearly, and is not, as in recent suillines, merely a notch confluent behind with the foramen lacerum medium.)\*

In *Desmathyus* the two well-separated walls of *Perchærus* have been, as it were, pinched together, the posterior nares being thus thrown much farther back. A similar condition is found in the modern genus *Pecari*, whereas in *Tayassu* and most of the Pleistocene forms the position of the nares can better be described as due to the backward extension of the palate.

There is no evidence of the presence of a pterygoid bone.



## ORBIT

*Perchærus pristinus*, No. 7394, is the only skull which shows this region well, so that the description given is mainly from this (see Fig. 5). Such structure as is preserved in the other skulls, however, fits in essentially with this; *P. rostratus*, No. 7395, diverges most in detail from the type, as in all other parts of the skull.

The most conspicuous feature of the orbit of *Perchærus* is, perhaps, its prominent lachrymal bulla. This protrudes into the antero-external corner of the orbit at the root of the zygomatic arch. It is formed by the orbital part of the lachrymal bone and joins the jugal by suture laterally, the maxilla ventrally. A sharply defined ridge curves down its orbital surface from the lachrymal foramen above to the posterior opening of the infra-orbital canal below.

The lachrymal foramen is situated within the anterior edge of the orbit, just above the bulla; it lies in a pit under cover of a small lachrymal tuberosity. Mesial to it, on the mesial border of the lachrymal bone and well within the orbit, lies another pit or depression; this is too much crushed and distorted in all the skulls to lend itself to clear description, but it probably corresponds to the similarly situated pit which in recent suillines gives origin to the interior oblique eye muscle. See Sisson, 'The Anatomy of the Domestic Animals,' 2nd edition, p. 172.

Gregory (Bull. Amer. Mus. Nat. Hist., XLII, p. 193) refers to this pit in the recent peccary as a prominent foramen possibly representing the spheno-palatine foramen and leading into the nasal cavity. The true spheno-palatine foramen in *Tayassu*, however, is that which lies between the vertical plate of the palatine and the orbital expansion of the ethmoid, just below and in front of the latter at the entrance of the infra-orbital canal. The foramen in question would seem to be rather a perforation or break in the very thin bone lining the pit, and is not present in all the skulls in the Museum collection; it is probably always closed up in the living skulls. Since the pit corresponds almost exactly in position with that described by Sisson as housing the inferior oblique muscle in *Sus*, it is presumably homologous with that in both *Tayassu* and *Perchærus*.



Fig. 5. Orbit of *Perchærus pristinus*, No. 7394, as seen from without and behind.

One-half natural size.

The similarity between *Perchærus* and *Sus* in this region is striking, in spite of the absence of a definite lachrymal bulla in the latter. They not only agree in the possession of lachrymal foramina and of the above-discussed pit in the lachrymal, but in *Sus* as in *Perchærus* there is a strong ridge lateral to the pit and curving downwards from the vicinity of the lachrymal foramen to the orbital opening of the infra-orbital canal.

This region differs from that in ruminants, which also possess a lachrymal bulla, owing to the absence of the prominent circum-orbital rim of bone which in these prevents the bulla from appearing in a side view of the skull. The relations of the lachrymal bulla to the alveolar tuberosity of the maxilla also differ in *Perchærus* and the ruminants, because in the former, with its narrower palate, the tuberosity is very close to the sphenoid process of the palatine, whereas in the latter it is widely distant and immediately ventral to the bulla.

In *Perchærus* the alveolar tuberosity, the pointed posterior extremity of which projects back behind the third molar to the region of the palato-alisphenoidal suture, closes in the orbit ventrally, its dorsal surface forming a flat shelf. In the angle between this shelf and the lachrymal bulla is a deep crevice in which lies the entrance to the infra-orbital canal (maxillary foramen). The sphenopalatine foramen appears to be a smaller opening which, as in *Tayassu*, lies just above and mesial to this entrance, but not, as in *Sus*, well forward within the canal itself.

The ethmoidal bone has not the bullate orbital expansion which in *Tayassu* lies postero-dorsally to the sphenopalatine foramen and overhangs the fossa for the external pterygoid muscle. The orbital wall is concave in this region, but more posteriorly. Below the small ethmoidal foramen there is a slight swelling in the orbito-sphenoid, which probably marks the termination of the lateral ethmoid in the sphenoidal sinus.

A ridge runs from the tip of the maxillary tuberosity upwards and backwards towards the foramen sphenorotundum and delimits dorsally the area of origin of the external pterygoid muscle. Sutures are barely traceable in this region but the ethmoidal foramen is distinguishable on some of the skulls and presumably lies, as in recent suillines, in the orbital plate of the frontal, and marks the anterior end of the cerebral hemisphere at the level of the rhinal fissure.

At the back of the orbit there is an abrupt outward projection of the cranial wall, curving downwards from the post-orbital process of the frontal bone above to the root of the pterygoid wing of the alisphenoid below. This projection sharply separates the orbit from the temporal

region of the skull, and roughly marks the division between the anterior and mesial cranial fossæ within. It overhangs the foramen opticum and the f. spheno-rotundum (the latter formed, as in recent suillines, by confluence of the sphenoidal fissure and f. rotundum) situated at the back of the orbit. To the lateral border of the f. spheno-rotundum a ridge runs down the face of this projection, starting just below the entrance to the supra-orbital canal which lies directly under and in front of the post-orbital process. Less than a centimeter behind this ridge, and separated from it by a shallow groove, lies a second ridge, the infra-temporal or "pterygoid" crest, which starts immediately behind the post-orbital process in the region of the fronto-parietal suture; after crossing the suture between alisphenoid and squamosal, it ends perpendicularly to the anterior edge of the glenoid surface, about half a centimeter external to the edge of the pterygoid wing of the former bone. As it passes behind the foramen spheno-rotundum this second ridge is expanded, at the posterior edge of the temporal wing of the alisphenoid, into a pyramidal process (see especially Fig. 3 of No. 7398).

#### SNOUT

On the side of the face in front of the orbit there is absolutely no trace of the fossa in which, in recent suillines, lie the levator labii muscles controlling the mobile snout. The lachrymal bone has a well-developed facial plate which extends forward to a varying degree in the different skulls; it meets the maxilla anteriorly and divides the jugal from the frontal. From its sutures with the jugal and lachrymal the maxilla has a flat surface, smoothly continuous with that of those bones behind and of the frontal and nasal above, and sloping inwards towards the post-canine region. In front of this region, which is the narrowest part of the snout, the maxilla curves outwards again round the root of the canine. Just anterior to the latter it meets the premaxilla and the alveolar borders of the two are pressed upwards, in the adult skull, as though by the tip of a finger, to receive the tip of the lower canine.

The alveolar and palatal regions of the premaxillæ are bent downwards at a slight angle with the plane of the rest of the palate, as in more recent peccaries.

#### UPPER DENTITION

Except for a right upper permanent incisor, with only its tip exposed, in the young White River skull No. 695, the upper incisor teeth are missing in all the American Museum skulls. The only upper incisors preserved in any of the material are those in the type specimen of *P. trichæ-*

*nus* Cope, A. M. N. H. No. 7390 (Fig. 14), a much crushed and battered upper and lower jaw described separately below; it shows, as do the broken roots in *P. probus*, No. 1282, and the empty alveoli in other specimens, that the three incisors were of approximately equal size.

The canines are of the prominent, downwardly-directed dicotyloid type, flattened anteriorly and rounded or with a more or less sharp edge posteriorly. The outer surfaces bear one or more grooves.

P<sup>1</sup> and p<sup>2</sup> are narrow and two-rooted. [In "*Thinohyus*" *subæquans*, according to Cope and Peterson, p<sup>1</sup> is single-rooted.] Each consists of a protocone with a slight posterior heel. P<sup>3</sup> and p<sup>4</sup> are three-rooted and broad. P<sup>3</sup> consists of a stout protocone and a broad postero-internal cingulum expanded and hollowed out posteriorly to form a basin-shaped heel; the anterior and external cingula are reduced or absent. P<sup>4</sup> has a well-developed deuterococone and a larger or smaller tritococone closely joined to the protocone; there is a broad posterior and a narrower anterior cingulum; a crest runs forwards and outwards from the deuterococone to meet the anterior cingulum in front of the protocone.

The deciduous first and second molars are of the same type as their successors. No unworn or unbroken dm<sup>3</sup> is preserved, but it is a three-rooted tooth like its successor, with the protocone over the anterior root; it differs from its successor, however, in being longer in proportion to its breadth and in bearing two cusps over its posterior roots instead of a basin-shaped heel; a narrow basal cingulum is present on all the sides which are unbroken. Dm<sup>4</sup> is four-rooted and quadricuspid, very closely simulating the molars behind it but somewhat smaller; intermediate cuspules simulating proto- and metaconule are present; there is a basal cingulum, interrupted lingually.

M<sup>1</sup> and m<sup>2</sup> are of the conventional bunodont sexi-tubercular type, with two main outer and two main inner cusps, two intermediate cuspules, broad anterior and posterior cingula, a narrow external and no internal cingulum. The posterior cingulum bears a larger or smaller tubercle in the mid-line; other smaller styles are frequently present and the cingula are mammilated. M<sup>3</sup> is referable to this same type, with the addition of a varying number of accessory cuspules and styles which vary also in size and position; the posterior cingulum is very broad, usually forming a prominent heel.

A study of from thirty to forty skulls of recent peccaries of the Colombian species *Tayassu pecari* and of *Tayassu pecari beebei* from British Guiana (for access to which I am indebted to the kindness of the Department of Mammalogy of the American Museum) shows that

even within the same subspecies the molar styles may be very variable; they show every gradation from well-developed cuspules into the usual mammilations of the cingulum; they may even differ in the opposite molars of the same individual. This is especially true of the third molar, and in this tooth the accessory intermediate cuspules also grade from well-developed tubercles into mere ridges on the sides of the main cusps, varying in number and position. In *T. pecari beebei* the two main posterior cusps are usually contiguous at their bases, but the two intermediate cuspules at the anterior end of the valley between them extend back into this valley to a varying extent and may even just touch the tubercle on the cingulum at the posterior end of it. In *T. pecari* these two main posterior cusps may be hardly more separated than in the subspecies or the intermediate cuspules may interpose between them entirely and have a broad contact with the posterior tubercle. These details as to individual variations in recent peccaries are of interest because almost exactly similar variations are found in the third molars of the different genera of fossil forms, and within the genus *Perchaerus* itself. It would seem that they cannot be used in making specific distinctions, and it also makes it almost impossible to establish homologies between the cuspules and styles of the different specimens, or between those of the third molar and those of the more conservative first and second molars.

*Helohyus* Marsh has been mentioned as a possible ancestor for the American Oligocene suillines; (Scott, W. B., 1913, 'Land Mammals of the Western Hemisphere,' pp. 273, 361-365; Matthew, W. D., 1915, 'Climate and Evolution,' Ann. N. Y. Acad. Sci., XXIV, p. 242). This small Bridger artiodactyl has been described by Sinclair and referred by him to the Dichobunidae (1914, Bull. Amer. Mus. Nat. Hist., XXXIII). The skull-back, A. M. N. H. No. 13079, since it comes from one of the lower Bridger formations (B 5), and also on account of its size, even if it is correctly referred to this genus, must have been associated with molar teeth of a type at least as primitive as those of the species *H. plicodon*, so that we would expect to find only the most general indications of suilline ancestry in the skull. What we do find is a structure so primitive and generalized that it is distinguishable in detail only from that of contemporary carnivores<sup>1</sup> and must have been separated by many intermediate stages from the first true suillines such as *Perchaerus*, if these are really to be derived from it.

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<sup>1</sup>*Helohyus* is distinguished by the stronger paroccipital process, the much larger post-glenoid foramen, the broader glenoid surface of the squamosal and a post-glenoid process which does not curve forwards over the latter to the same extent as in Carnivora.

The upper molars of *Helohyus*, and what is preserved of the premolars, are again very much more primitive, but at the same time point very strongly towards the *Perchærus* type (Fig. 15). The hypocone is reduced and the metaconule enlarged to take its place—less so in the Bridger (B 3) *H. plicodon*, more so in the Bridger (C 5) *H. milleri*, which is also larger—suggesting the commencement of the process by which, according to Stehlin, all modern Artiodactyl groups have attained a quadrituberculate molar in which the postero-internal cusp is not the hypocone but the metaconulé. *Helohyus* further possesses a well-developed protoconule and a small intermediate cuspule, again best developed in *H. milleri*, which bears the same relations to the enlarged metaconule as the latter usually bears to the hypocone, and corresponds in position to the intermediate cusp in the first and second molars of *Perchærus*; this increases the probability of Stehlin's view that the Suidæ, as well as other modern artiodactyls, differ from other mammalian groups in their derivation of a sextitubercular molar from the tritubercular prototype.

The third molar of *Helohyus* lacks the enlarged posterior cingulum of that tooth in *Perchærus* and indeed more nearly approaches the tritubercular type than the first two.

In size the molars of *Helohyus milleri* are quite comparable with those of the smallest species of *Perchærus* I have seen, No. 10510 in the Princeton Museum, from the White River Oreodon Beds of South Dakota. In proportions they differ considerably, for in *Helohyus* the transverse diameter of the upper molars considerably exceeds the antero-posterior, whereas in *Perchærus* the reverse is always true of the third molar and to a lesser extent of the second molar, while the first molar varies.

	<i>P. probus</i> Leidy A. M. N. H. No. 1282	<i>Perchærus</i> Princeton No. 10510	<i>Helohyus milleri</i> Sinclair, A. M. N. H. No. 12151
Length of m <sup>1</sup> to m <sup>3</sup> inclusive	41.0 mm.	33.0 mm.	30.0 mm.
Antero-posterior diameter of m <sup>3</sup>	15.5	10.0	10.0
Transverse diameter of m <sup>3</sup>	13.0	7.5	14.5
Antero-posterior diameter of m <sup>2</sup>	14.0	11.8	10.0
Transverse diameter of m <sup>2</sup>	13.5	8.8	13.5

The fourth premolar of *Helohyus* is very comparable with that of *Perchærus*, but there is apparently no trace of a triticocone and the anterior and posterior cingula are not so broad in comparison with the rest of the

tooth; *Helohyus* further possesses a small intermediate cuspule, lacking in *Perchærus*, on the ridge which leads outwards and downwards from the deuterococone to the anterior cingulum.

There is in the American Museum no sufficiently unbattered third premolar certainly referable to *Helohyus* to make a comparison of value.

#### LOWER JAW

There are no complete, well-preserved lower jaws in the American Museum collection. The fragments show that the symphysis was not so long as in recent peccaries and it sloped upwards at a steeper angle to the inferior border of the ramus.

There are three lower incisors, again fully preserved in *P. trichænus* No. 7390 (Fig. 14) alone. The stumps and alveoli in other specimens show that they tend to be very crowded upon each other and on the canine. (Cook, in the *Pan-American Geologist*, June, 1922, describes an extreme case of crowding in a jaw named by him *Perchærus minor*, from the lowermost clays of the Chadron formation.) As in all suillines, the three incisors are worn on their posterior faces and the first two, which are larger and more procumbent than the third, across the tips as well.

The canine is slightly recurved, has a flat posterior surface where it slides against the upper canine, and bears a ridge on its buccal surface.

$P_1$  is a small, laterally-compressed cone, usually single-rooted.  $P_2$  is two-rooted, also simple, trenchant and compressed, with a posterior cingulum forming a small heel.  $P_3$  is similar to  $P_2$  but larger and with a better developed heel. In  $P_4$  a deuterococonid is developed, equal in size and slightly posterior to the protoconid from which it is separated by a shallow valley between their tips alone, the posterior heel is extensive and supports a well-developed basal cusp; there is also a smaller anterior basal cusp.

I am indebted to Dr. Milo Hellman for directing my attention to an interesting condition in the occlusion relationships of the deciduous molars in recent Suidæ. In all recent suillines, both New World and Old World, the fourth deciduous molar is an unusual tooth. It resembles a third permanent molar, being very long and possessing three transverse ridges, each composed of two main cusps. From the occlusion of these cusps with the upper molars, however, it would appear that it is the central pair which correspond to a protoconid and metaconid, whereas the anterior pair are a new acquisition, arising, as it were, from an anterior talonid. These two anterior cusps bite into the transverse valley of the almost molariform  $dm^3$ , and the transverse valley between

these two cusps and the central pair receives the posterior pair of cusps of that tooth. The two new cusps thus functionally replace a hypoconid and entoconid on  $dm_3$ , which has only a small cusplless heel and is thus far less molariform than  $dm^3$ .

Of *Perchærus* I have only been able to find a very fragmentary lower jaw still retaining the milk molars (A. M. N. H. No. 1285, from the White River *Protoceras* Beds). Its  $dm_4$  is split but it still shows that already in the Oligocene this tooth was of the six-cusped type described above.  $Dm_3$  has only one main cusp with a deep dint on its posterior surface and even less heel than in recent peccaries.

$M_1$  and  $m_2$  are rectangular teeth with four main cusps of approximately equal size and a small hypoconulid on the posterior cingulum, closing behind the valley between hypoconid and entoconid; the tips of the latter are at a slightly lower level than those of the protoconid and metaconid; there is a narrow anterior cingulum and a discontinuous external cingulum.

$M_3$  has a very broad heel bearing one main cusp or ridge, or a variable number of smaller ones. The same remarks applied to  $m^3$  as to the variability of these small cusps and their relations to the mammilations on the cingulum, and to the lobules on the sides of the main cusps, apply also to  $m_3$ .

The lower dentition of *Helohyus* again affords a good ancestral type but is considerably more primitive in the possession of a simple  $pm_4$  with no deuteroconid, of a small paraconid in the molars, and of a much narrower heel to  $m_3$ . No  $m_3$  of *H. milleri*, the species with the most advanced upper molars, is preserved, but the single tooth, A. M. N. H. No. 12150, from the Bridger horizon D 3, doubtfully referred to *H. lentus* Marsh, (see Sinclair, *loc. cit.*, p. 283, Fig. 17) is larger than the corresponding tooth in *P. probus*, A. M. N. H. No. 1283, and considerably larger than some of the smaller species of *Perchærus* (Fig. 16). Indeed, it is its smaller heel alone which prevents it from being entirely comparable in size and proportions with the larger species of that genus, such as *P. pristinus* from the John Day and some of the miscellaneous White River teeth in the collection. Its antero-posterior diameter is 1.93, its breadth at the anterior transverse valley 1.0. In spite of its smaller size the heel bears several small tubercles in addition to the hypoconulid in a manner very similar to that in *Perchærus*; there is a small tubercle on the postero-internal slope of the hypoconid very similar to the ridge or tubercle in several unworn teeth of that genus; the paraconid is reduced to a minute excrescence on the anterior slope of the metaconid.



## YOUNG AND PRIMITIVE CHARACTERS IN THE DICOTYLIDÆ

Three of the skulls in the American Museum collection are those of young animals still retaining their milk dentition. Since two of these young skulls are the only skulls from the White River formation (*Protoceras* beds) whereas the third, from the John Day (*Diceratherium* beds), is at a slightly older stage, it was necessary to determine whether any of the more primitive characters which they showed were due, not to youth alone, but to their being in an earlier stage of evolution. The study in this connection of a very good age series of recent peccary skulls kindly lent me by the Department of Mammalogy brought out the following growth changes in these animals.

1.—Increase in size. There is no evidence of a progressive increase in size in post-Eocene suillines. Even in the Bridger we have seen that *?Helohyus lentus* was comparable in size with the larger species of *Perchaerus*. The range of size in *Perchaerus* skulls is very similar to that in the living genera *Tayassu* and *Pecari*.

2.—Development of well-defined temporal ridges, the brain-case in very young peccaries being smooth and rounded. The three young *Perchaerus* skulls already show these ridges well-developed. They unite to form a median sagittal crest as in *Pecari*, but much farther forward than in that genus.

3.—Deepening of lateral depression on snout for the maxillo-labial (*levator labii*) muscles. None of the *Perchaerus* skulls, young or adult, show any indication of this depression. (It is present, though very much less marked than in *Tayassu* or *Pecari*, in the Rosebud genus *Desmathyus*.)

4.—Backward passage of the infraorbital foramen in relation to the cheek teeth.

5.—Backward extension of palate behind the tuberosity of the alveolar portion of the maxilla, and correlated changes in the pterygoid region of the alisphenoid. The true appearance of the posterior end of the palate in the fossil skulls is difficult to determine, owing to the bad preservation of this region. It appears, however, to extend back little, if at all, behind the alveolar tuberosity.

6.—Forward shifting of the posterior palatine foramina to a position in front of the canines. This is effected by a closing in of the grooves which lead forwards from the original foramina along the surface of the palate. The closure is, however, imperfect, and leaves sundry minute foramina scattered along its course; these are presumably for branch vessels from the now enclosed posterior palatine artery to the

mucous membrane of the palate. (Stehlin, 'Geschichte des Suiden-Gebisses,' 1899, p. 412, refers to this character.) In *Perchærus* (and *Desmathys*) the posterior palatine foramina are in their usual posterior position. In the young skulls they are, if anything, farther forward than in the adult (e.g. opposite  $dm^4$  instead of  $m^1$ ).

7.—Formation of a groove in front of the upper canines for reception of the lower. This groove is well-developed in the adult John Day *Perchærus rostratus*, No. 7395, less well in the John Day *P. pristinus*, No. 7394, and still less well in the only fragment of upper jaw of an adult from the White River (*P. probus*, No. 1282). In the young skulls it is barely indicated.

8.—Increase in extent of orbital exposure of the ethmoid. This comes to project beneath the eye as a marked swelling filled with waferous bony tissue. In *Perchærus* this swelling of the ethmoidal region appears to be lacking, but all the skulls are much crushed within the orbit.

9.—Loss of individuality of the very small lachrymal bulla of very young forms as the surrounding parts increase in size. In *Perchærus* the lachrymal bulla is badly crushed in all the young skulls but it is a distinctive feature of the adult John Day forms.

10.—Carrying down of the glenoid surface of the squamosal to a level considerably below that of the basis cranii. This process continues until the tympanic bullæ are nearly hidden in lateral view by the zygomatic wing of the squamosal. This down-carrying takes place in *Perchærus* but to a very much smaller extent.

11.—Development of a more concave glenoid surface, owing to the uprising of a preglenoid ridge. Greater accentuation of the post-glenoid process of the squamosal, which comes to project down beyond the post-tympanic process. In *Perchærus* the glenoid surface remains much flatter and the post-glenoid process projects very little below the post-tympanic.

12.—Lengthening of the tubular external auditory meatus and heightening of the folds of the squamosal which ensheath it. The zygomatic wing of the squamosal comes to extend up as far as the parieto-squamosal suture. The meatus remains comparatively short in the adult *Perchærus*, as in the very young peccary, and the zygomatic wing remains comparatively low.

13.—More marked accentuation of the triangular shape of the bulla. The bulla appears to be larger both actually and proportionally in the young White River skulls than in those from the John Day. It is elliptical in contour and not at all triangular.

14. Loss of sutures. The sutures are more pronounced in the young *Perchærus* skulls but are still traceable in the adult.

These comparisons between youth and age in the individual and in the race showed that all the apparently more primitive characters in the White River skulls could equally well be attributed to youth; there were no obvious evolutionary changes between the first and second phases of the Upper Oligocene. They also established certain characters as primitive in the genus *Perchærus* as a whole and, if to these we add others of an obviously primitive nature or which must be accepted as primitive because they are still shared by recent *Suidæ* in the Old World, we obtain the following list.

#### Primitive Characters in *Perchærus*

1.—Brain development small in comparison with that in recent *Suidæ* and *Tayassuidæ*. In correlation with this are found those conditions of the parietal, squamosal, and orbital regions of the cranium which Matthew in his memoir on 'The Carnivora and Insectivora of the Bridger Basin' (1909. *Mem. Amer. Mus. Nat. Hist.*, IX, part 6, p. 132) indicates as primitive in the early stages of evolution of progressive races. To these may probably be added the close approximation of the supra-orbital canals and the meeting of the ex-occipitals above the foramen magnum to the exclusion of the supra-occipital from its dorsal margin.

2.—Absence of depression, or any clearly defined area of origin. for the levator labii muscles. This depression in *Sus* is not so deep as in recent peccaries but extends much further backward and upward towards the rim of the orbit. The muscles in *Perchærus* were probably much less strongly developed, in correlation with a shorter and less mobile snout and with less powerful canines.

3.—Very slight upturning of maxilla above root of upper canine.

4.—Infra-orbital foramen situated relatively far forward in relation to cheek teeth.

5.—Palate not prolonged backward beyond alveolar border of maxilla. Pterygoid wings of alisphenoids correspondingly long; they are not approximated anteriorly as in *Desmathyus* and *Pecari*.

6.—Posterior palatine foramina in their usual position well back between the cheek teeth (so also in *Sus*).

7.—Foramen ovale completely encircled by the alisphenoid bone. (In all recent suillines there is only a spur of the latter projecting between this foramen and the f. lacerum medium, the two being confluent behind.)

8.—Absence of marked ethmoidal swelling in orbit.

Measurements of the Individual Specimens  
(Corrected to the Nearest Half Millimeter)

Character of Measurements	White River			John Day				
	<i>P. probus</i> No. 1282	Young <i>P.</i> No. 585	Young <i>P.</i> No. 695	<i>P. pristina</i> No. 7394	<i>P. trichin.</i> No. 7390	<i>P. ———</i> No. 7398	Young <i>P.</i> No. 7396	<i>P. rostr.</i> No. 7395
Total length of skull from back of basi-occipital to tips of premaxillae.....	.....	c. 197	.....	229	.....	.....	c. 190	255
Slant length of snout from edge of lachrymal foramen just below tubercle to anterior extremity of premaxilla.....	.....	.....	.....	143	.....	.....	120 (v. approx.)	173
Width of skull at posterior ends of zygomatica level with articular surfaces.....	.....	102	.....	115	.....	.....	95.5	130.5
Distance between top of foramen magnum and foramen rotundum.....	.....	c. 50	.....	c. 56	.....	c. 50 (crushed)	c. 52	c. 55
Length of basis cranii from back of basi-occipital to basisphenoid level with f. rotundum.....	.....	c. 44	.....	c. 48	.....	c. 46	c. 44	c. 48
Distance between condylar foramina.....	.....	19.5	?16.5	21.5	.....	23.5	19.5	24
Length of tympanic bulla.....	.....	25	.....	23	.....	c. 23	?26	21
Total length of dental series, measured along mid-line of palate.....	c. 120	.....	.....	143	.....	.....	.....	152

Width across palate at p <sup>2</sup> (or dm <sup>2</sup> ).....	34	28	.....	28.5	.....	29	c. 28.5
Width across palate at antero-internal roots of first molars.....	?29	21.5	.....	26	.....	24	?29
Length between canine and p <sup>2</sup> (or dm <sup>2</sup> ).....	22	22.5	22	27	c. 21	21.5	37 <sup>1</sup>
Length between canine and m <sup>1</sup> .....	40.5	42	43	47	.....	43.5	55.5 <sup>1</sup>
Length from m <sup>1</sup> to m <sup>3</sup> inclusive.....	41	.....	.....	48	45	.....	43.5
Distance between canine alveolus and alveolus of anterior root of p <sup>1</sup> (or dm <sup>1</sup> ).....	1.5	almost none	1.5	3.5	.....	almost none	c. 12.0 <sup>1</sup>
Distance between p <sup>1</sup> and p <sup>2</sup> (or dm <sup>1</sup> and dm <sup>2</sup> ), measured at borders of alveoli.....	5.5	3	3	7	.....	5	6.5
Distance between p <sup>2</sup> and p <sup>3</sup> (or dm <sup>2</sup> and dm <sup>3</sup> ), measured at borders of alveoli.....	.5	c. .5	c. 1	1	almost none	almost none	4.5
Distance between canine alveolus and alveolus of anterior root of p <sup>2</sup> (or dm <sup>2</sup> ).....	13	10.5	13	17	10 (v. approx.)	12.5	24 <sup>1</sup>
Antero-posterior diameter of m <sup>1</sup> .....	12	14.5	15	13.5	13	13.5	13
" " m <sup>2</sup> .....	14	15.5	.....	16	14.5	16	14
" " m <sup>3</sup> .....	15.5	.....	.....	17.5	16.5	.....	16
" " m <sup>1</sup> .....	12	14	14	14	c. 12	12.5	.....
" " m <sup>2</sup> .....	13.5	.....	.....	15	12.5	13	.....
" " m <sup>3</sup> .....	13	.....	.....	15.5	13	.....	12

<sup>1</sup>This length is much increased by the the downgrowth of a sheath of maxilla round the base of the canine.

# Indices Deduced from the Table Measurements

Nature of Index		<i>P. probus</i> No. 1282	Young <i>P.</i> No. 585	<i>P. prist.</i> No. 7394	Young <i>P.</i> No. 7396	<i>P. rostrat.</i> No. 7395
I	Ratio of length of molar series to total length of dental series, $\times 100$ .....	34	.....	34	.....	29
II	Ratio of length from canine to $p^3$ to total length of dental series, $\times 100$ .....	18	.....	19	.....	24
III	Ratio of slant length of snout to total length of skull, $\times 100$ .....	.....	.....	62	c. 63	68
IV	Ratio of length from foramen magnum to f. rotundum to slant length of snout, $\times 100$ .....	.....	.....	39	c. 43	32
V	Ratio of width of skull at posterior ends of zygomata to total length of skull, $\times 100$ .....	.....	.....	50	c. 50	51
VI	Ratio of length from foramen magnum to f. rotundum to width of skull as above, $\times 100$ .....	.....	c. 49	49	54	42
VII	Ratio of width of skull as above to slant length of snout, $\times 100$ .....	.....	.....	80	c. 80	75
VIII	Ratio of length from foramen magnum to f. rotundum to length of skull, $\times 100$ .....	.....	c. 25	24	c. 27	22
IX	Ratio of width across palate at $p^2$ to total length of dental series, $\times 100$ .....	28	.....	20	.....	19

Specific Reference	Period	Formation	Beds	Locality
No. 1282 <i>P. probus</i> Leidy <sup>1</sup>	Upper Oligocene—1st phase	White River—Protoceras.	Cheyenne River, S. Dakota.	
585 " "				
695 " "				
7394 <i>P. pristinus</i> Leidy <sup>2</sup>	Upper Oligocene—2nd phase	John Day	Diceratherium.	N. fork, John Day River, Oregon.
7390 <i>P. trichænus</i> Cope <sup>3</sup>			?	John Day Valley, Oregon.
7398			?	"The Cove," John Day River, Oregon.
7396			Diceratherium.	John Day Valley, Oregon.
7395 <i>P. rostratus</i> Cope <sup>4</sup>			"	Camp Creek, Crooked River, Oregon.

<sup>1</sup>Leidy, 1869, J. Acad. Nat. Sci. Phil., (2) VII, p. 194.  
<sup>2</sup>Leidy, 1873, Rep. U. S. Geolog. Surv. of the Territories, F. V. Hayden, I, p. 216, "Dicotyles" *pristinus* Cope, 1888, Proc. Amer. Phil. Soc., XXV, pp. 66 and 70, "*Bothrolabis*" *pristinus* (this skull).  
<sup>3</sup>Cope, 1888, loc. cit., pp. 66 and 74, "*Bothrolabis*" *trichænus* (these jaws). Cope and Matthew, 1915, loc. cit., Pl. cxa, fig. 2, *Percherus trichænus* (one of these upper jaws).  
<sup>4</sup>Cope, 1888, loc. cit., pp. 66 and 77, "*Bothrolabis*" *rostratus* (this skull).

- 9.—Well-developed facial portion of lachrymal bone.
- 10.—Lachrymal foramen present under cover of lachrymal protuberance. (*Tayassu* has lost both 9 and 10 but both are retained by *Sus*.)
- 11.—Glenoid surface of squamosal at a level very little below that of the basis cranii.
- 12.—Flat glenoid surface directed more from side to side, less antero-posteriorly.
- 13.—Strongly ridged ventral edge to zygomatic bar of jugal, which comes to an abrupt end just in front of glenoid surface, a condition resembling that in *Sus* more than that in late peccaries.
- 14.—Comparatively short tubular external auditory meatus; zygomatic wing of squamosal not extending up to parieto-squamosal suture.
- 15.—Egg-shaped or ovoid tympanic bullæ with a few septa on inner surface but free from the cancellous bony tissue which fills them in later peccaries and in *Sus*.
- 16.—Retention of sutures.
- 17.—Retention of third upper incisor (so also in *Sus*). All three incisors subequal in size.
- 18.—Retention of first upper and lower premolars and absence of long diastemata behind the canines (so also in *Sus*).
- 19.—Retention of comparatively simple, non-molariform premolars.

#### A CONSIDERATION OF THE ACCOMPANYING TABLE OF MEASUREMENTS, OF THE INDICES DEDUCED FROM IT, AND OF OTHER CHARACTERS

It is impossible to do very much in the way of drawing conclusions from the accompanying measurements. The number of specimens is much too small and within this number corresponding parts are rarely preserved intact. Of moderately intact skulls only two are adult—*Perchaerus pristinus*, No. 7394, and *P. rostratus*, No. 7395—and therefore suitable for comparison. Nos. 585 and 695 from the *Protoceras* beds of the White River and No. 7396 from the *Diceratherium* beds of the John Day still retain their milk dentition and their third molars are uncut. They have not attained their adult size and proportions. The only measurements which will not be subject to further change are those of the first and, where cut, the second molars. In the two White River skulls (Fig. 6) these are rather larger than in the palate, No. 1282, from the same beds, together with which they have been referred to the species (*P. probus* Leidy. (See p. 83 for references. The teeth described

by Leidy under this name are intermediate in size between No. 1282 and Nos. 585 and 659.) That the length between the canine and the molar teeth in these two young skulls is already greater than in No. 1282 may be partly in agreement with a similar condition in young *Tayassu* skulls, where the length seems out of proportion to that in adults; in these it is because the canine alveolus has not yet attained its full dimensions.

Thus, owing to the nature of the material, specific characters distinguishing *P. probus* from the John Day species can only be sought for in the palate and dentition. The most noticeable points are: the short snout, as indicated by the total length of the upper dental series being more than 2 cms. less than that of *P. pristinus*, whereas Index I is the

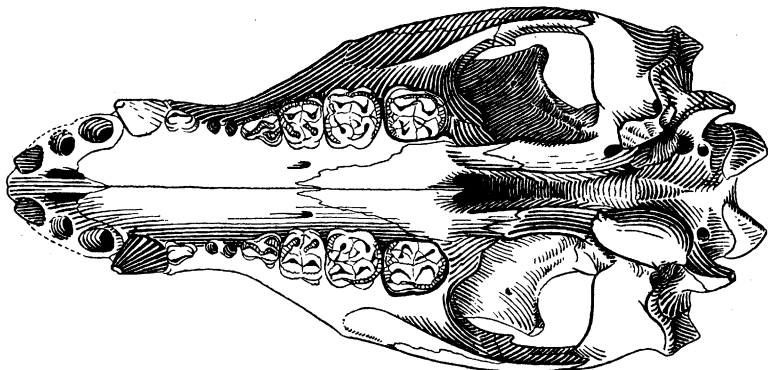


Fig. 6. Reconstruction of the young White River skulls, Nos. 585 and 695.  
One-half natural size.

same; the breadth of palate as brought out by the palate measurements and Index IX (these measurements are not wholly reliable, however, as the palate has been broken and plastered); the slight upturning of the maxillary border in front of the canine; and the narrow posterior cingulum to  $m^3$ , this tooth lacking the definite heel of some of the John Day forms.

Sinclair (1905, *loc. cit.*) in differentiating his species lays considerable stress on the spacing of the premolars. This is evidently in a highly variable condition within the genus. It again is a character influenced by age, but in all the American Museum specimens except *P. rostratus*  $p^1$  (or  $dm^1$ ) is very close to the canine and slightly mesial to it. In *P. rostratus* the apparently wide gap between them is largely due to the excessive downgrowth of the maxilla to form a sheath around the base of the canine, possibly for strengthening a longer tooth. *P. rostratus*



is further distinguished by having a much more pronounced diastema between  $p^2$  and  $p^3$ , where as in *P. pristinus* it is only slightly wider than in *P. probus*. In the diastema between  $p^1$  and  $p^2$  all three species much more nearly approach each other, though in *P. rostratus*, considering the length of its snout, it is short when contrasted with that in *P. pristinus*. An indication of the comparative length occupied by diastemata behind the canine in these three species is given by Index II.

No. 7396 (Figs. 7, 8, and 9) has little but youth to distinguish it from the *P. pristinus* type. Indices III, V, and VII show that, although smaller in absolute size, in proportions of length and breadth of skull it already corresponds very closely with *P. pristinus*; the brain-case has

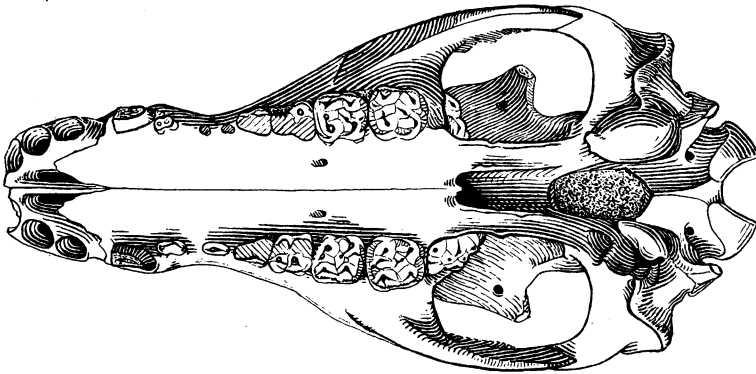


Fig. 7. Young John Day skull, No. 7396.  
One-half natural size.

already attained more nearly adult dimensions, as is brought out by Indices IV and VI. The correspondence between the palatal width at  $p^2$  and that of adult forms is another feature shared by the young *Tayassu*. The antero-posterior diameter of its first two molars corresponds well with those of *P. pristinus*; the transverse diameters are less than in the latter but fall within the 2 mm. range of variation which I found to exist among thirty individuals of the recent species *Tayassu pecari*. (For the antero-posterior diameter of  $m^2$  I found a range of 2 mm. in *Tayassu pecari*, for that of  $m^3$  a range of 4 mm. and for  $m_3$  a range of 6 mm. Though I regrettably had not the time to employ any but the roughest methods of determining these ranges, they were not based on the conditions in rare extremes.) With the pattern of  $m^1$  and  $m^2$  of *P. pristinus* no comparison is possible, for those teeth are quite worn down.

No. 7398 (Fig. 3) consists of a skull-back alone. It closely approaches *P. pristinus* (No. 7394) from which it differs chiefly in the better preservation of its structural details. The difference in the shape of the occipital condyles which comes out in the drawings is probably largely an unreal one, since the ratio of plaster to bone in the condyles of the *P. pristinus* skull is large but not easy to indicate. The ridges for the longi capitis muscles are unusually prominent, especially at their posterior ends,

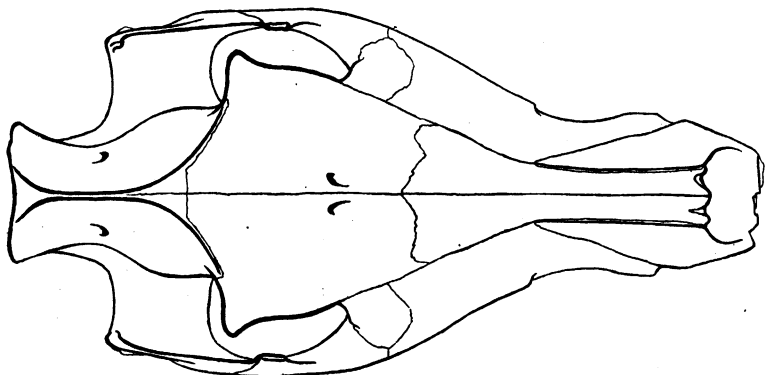


Fig. 8. Young John Day skull, No. 7396.  
One-half natural size.

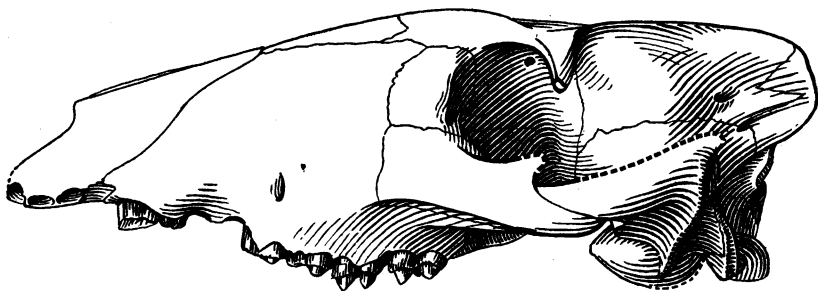
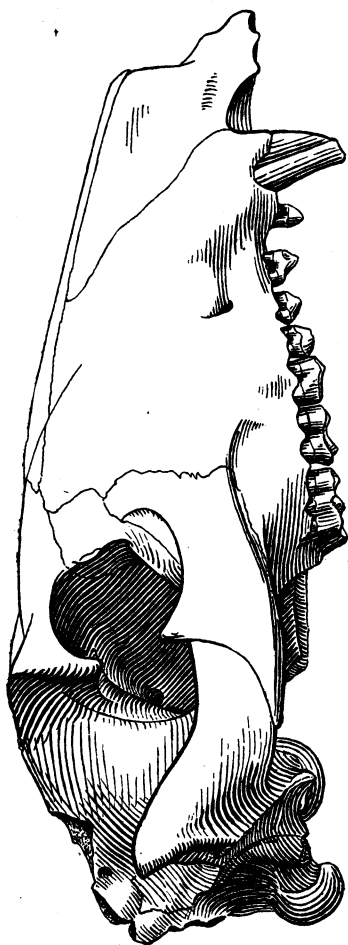


Fig. 9. Young John Day skull, No. 7396.  
One-half natural size.

but very little stress can be laid on this for, as mentioned above, it is a character which varies very greatly within a single species of modern peccary.

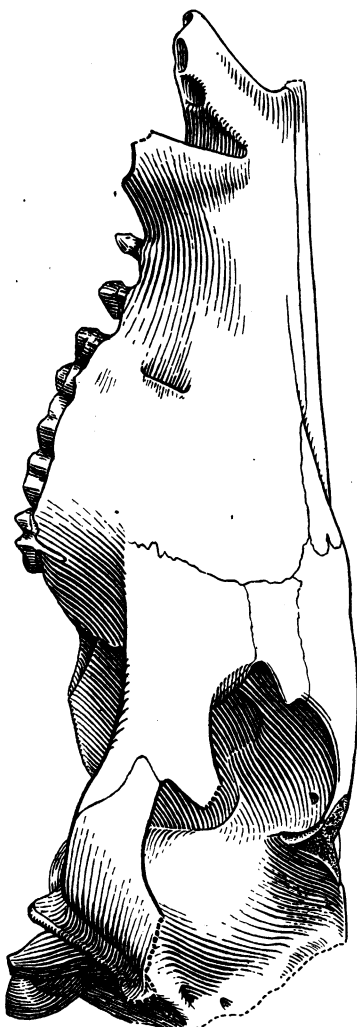
*P. pristinus*, No. 7394 (Figs. 10 and 12), itself was described by Cope in 1888 under the generic name "*Bothrolabis*." He distinguished it from the other four species (including "*Chænohyus decedens*") which he described at that time by the characters of the third molar and by the



One-half natural size.

Fig. 10.

Fig. 10. *Perchærus pristinus*, No. 7394.

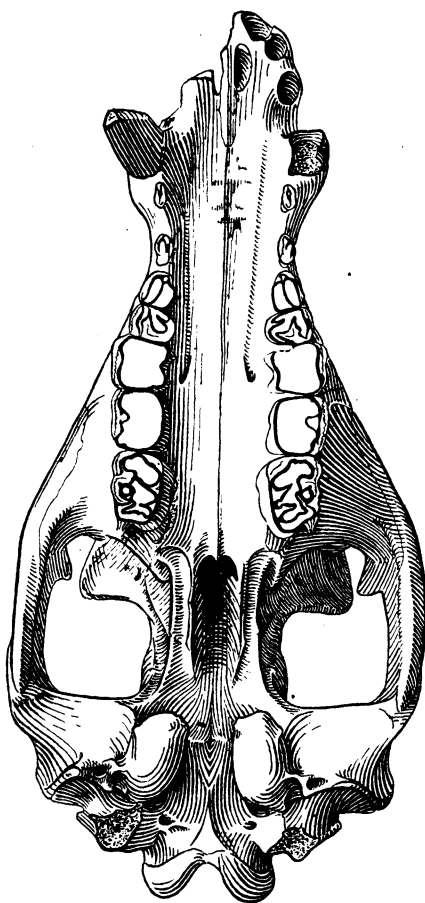


One-half natural size.

Fig. 11.

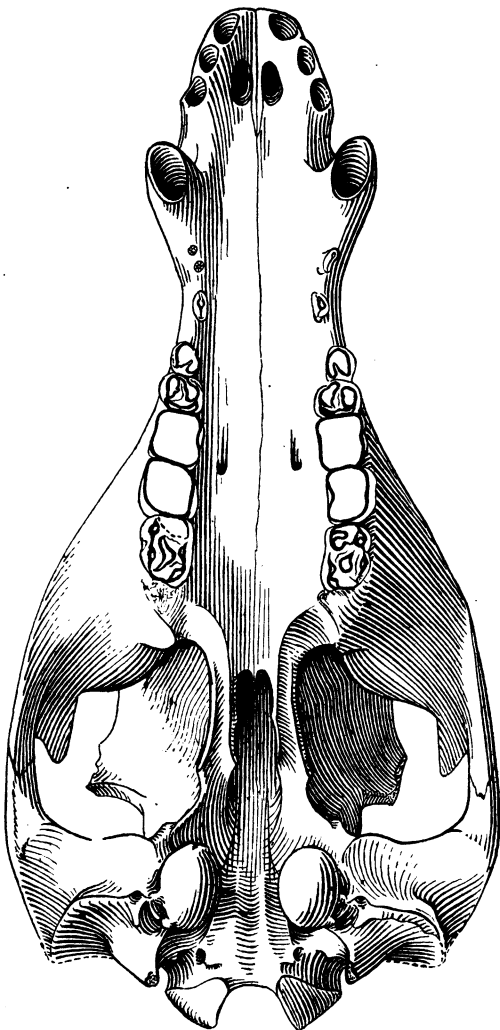
Fig. 11. *Perchærus rostratus*, No. 7395.

length of the molar series compared with the length from the canine to  $m^1$ . Sinclair (*loc. cit.*, p. 140) in comparing this with other species of "*Thinohyus*" also refers to the character of  $m^3$ . This tooth is considerably worn, the details of its cusp arrangement being lost, but it is char-



One-half natural size.

Fig. 12



One-half natural size.

Fig. 13

Fig. 12. *Perchaerus pristinus*, No. 7394.

Fig. 13. *Perchaerus rostratus*, No. 7395.

acterized by its very broad posterior eingulum projecting postero-internally as a prominent heel. The comparatively great length of the molar series when contrasted with *P. rostratus* is brought out by Index I. The premolar teeth are also large. The skull is further characterized by

what Cope called a "median frontal rib"—a low ridge in the mid-line of the frontal region of the skull roof behind the supra-orbital foramina; a similar ridge is faintly indented in No. 7396.

*P. rostratus* Cope, No. 7395 (Figs. 11 and 13), stands out as a distinct type, divergent in size and proportions. It is considerably longer than *P. pristinus*, both in snout and in total length and considerably broader from one zygomatic arch to another. Its basi-occipital is also broader but other measurements of the brain-case are strikingly similar. Indeed, in all the material in which brain-case measurements are possible they are very conservative. Measurements on the outside of the brain-case which will give some idea of the dimensions of the brain are not easy to obtain, but the somewhat approximate ones given of (a) the distance between the top of the foramen magnum and the f. rotundum and (b) the length of the basis cranii from the f. magnum to the basisphenoid level with the f. rotundum are an attempt to approach them, the latter foramen being taken as at the level of the anterior end of the hypophysis and posterior edge of the optic chiasma. Most of the brain-cases are too worn or crushed to make the conventional "greatest width of brain-case" of any comparative value.

That the snout of *P. rostratus* is longer in comparison with the width of the skull at the zygomatic arches than in *P. pristinus* is brought out by Index VII, but that it is at the same time comparatively narrower at the level of  $p^2$  is brought out by Index IX ( $p^2$  is level, or nearly level, with the narrowest part of the snout and palate in all the skulls). The molar teeth are not only comparatively but absolutely very much smaller than in *P. pristinus*;  $m^1$  and  $m^2$  are much worn and much buttressed by plaster and their width and pattern therefore undeterminable;  $m^3$  also has all the smaller details worn away. The spacing of the premolar teeth, which are again smaller than those of *P. pristinus*, and the sheath of maxilla at the base of the canine, have already been referred to. The premaxillæ appear to be bent downwards on the main plane of the palate at a slightly greater angle than in *P. pristinus*; the indentation in front of the upper canine is much deeper; the post-orbital process of the molar is larger; the glenoid surface of the squamosal is carried down to a much lower level with reference to the basis cranii and tympanic bulla. Noticeably distinct from those of all the other skulls are the very small tympanic bullæ, considerably shorter in their absolute length (see table) and apparently without the pointed anterior extremity. Characteristic also is the great antero-posterior breadth of the zygomatic process of the maxilla (compare Fig. 13 with Fig. 12). The palate, though broken

posteriorly, extends back at least as far as the maxillary tuberosity and considerably behind the third molar, whereas in *P. pristinus* it ends considerably in front of the former and only a short distance behind  $m^3$ .

*P. trichænus* Cope, No. 7390, consists of the imperfect jaws alone (Fig. 14). Cope tentatively separated it as a distinct species from *P. pristinus* on account of the smaller molars, the character of  $m^3$  and the possession by  $p_1$  of one root only. Further reference is made to the lower jaw later. The upper molars are certainly considerably smaller than in *P. pristinus* and the prominent postero-internal heel of  $m^3$  in *P. pristinus* and *P. rostratus* is entirely lacking. The molars are narrow in proportion to their length.  $M^3$ , when compared with that of *P. probus*, No. 1282

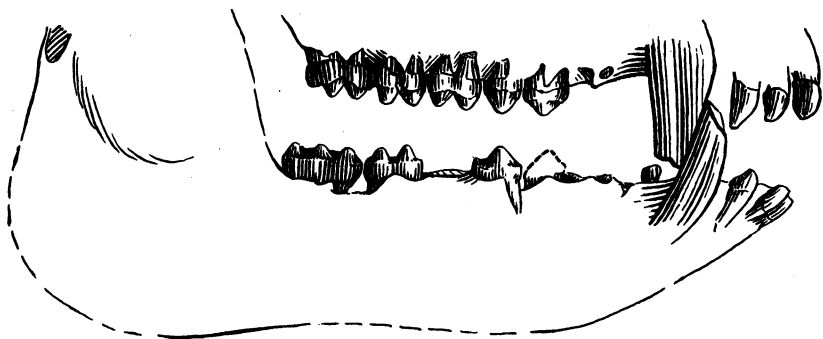


Fig. 14. *Perchærus trichænus*, No. 7390 (partly restored from the opposite side).  
One-half natural size.

(Fig. 15), shows a lack of the large intermediate cusp which in that form separates the two main posterior cusps, unless, indeed, it is the main postero-internal cusp itself which is lacking in *P. trichænus*, as is suggested by the narrow posterior end of the tooth and by the relations of the existing cusp to the cingulum and to the intermediate cuspsule in the transverse valley. (See, however, remarks on pp. 72, 73 as to conditions in recent peccaries.) The tritocone on  $p^4$  is very poorly developed and not differentiated from the protocone by a groove on the outer surface of the tooth. The jaw is much battered in the canine region and  $p^1$  and  $p^2$  are lacking on both sides, but the canine appears to have been nearer to  $p^2$  than in any of the other skulls; the alveoli  $p^1$  are not distinguishable, but were probably situated close behind the canine and rather mesial to it, as in the other species.  $I^1$  l.,  $i^2$  and  $i^3$  r. are preserved;  $i^1$  and  $i^2$  are more shovel-shaped and worn on their posterior surfaces,  $i^3$  is more pointed.

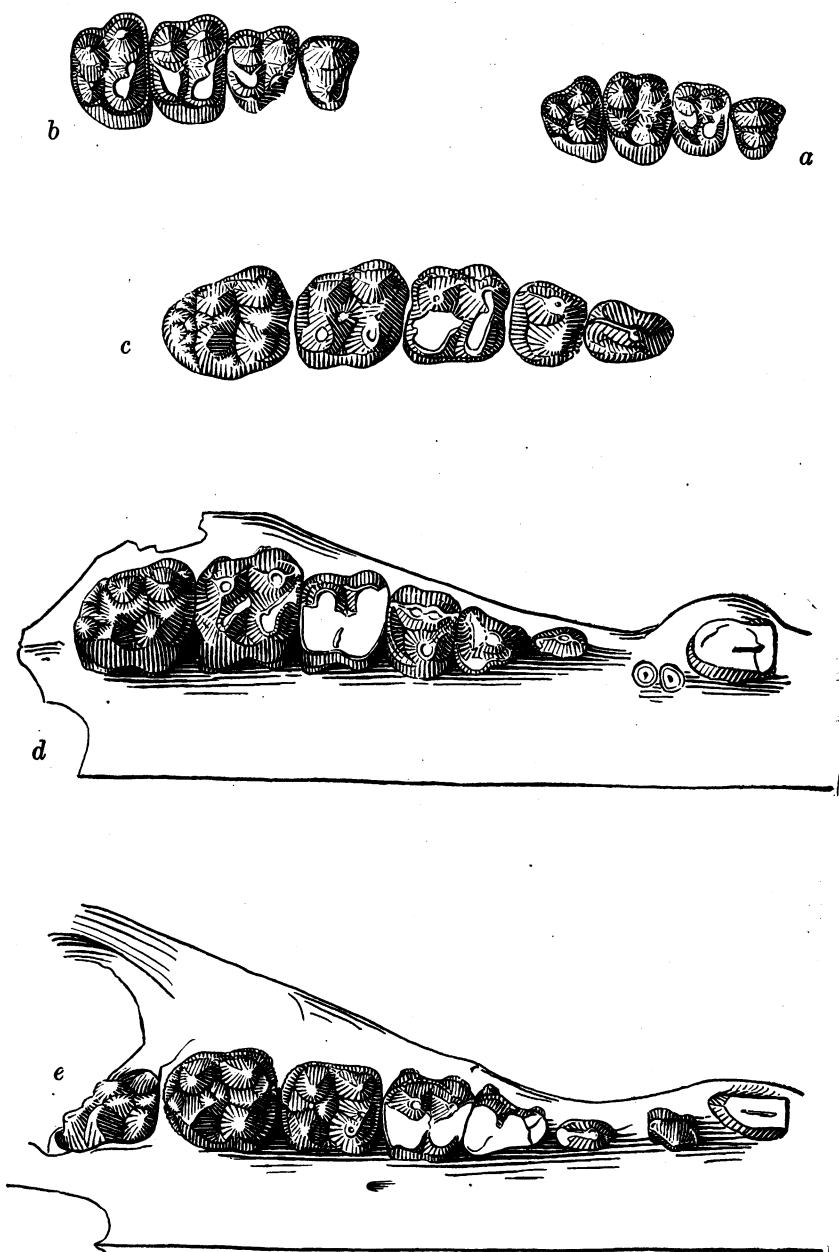


Fig. 15. Right upper dentitions of Bridger and Upper Oligocene suillines (in some cases partly restored from opposite side).

Natural size.

(a) *Helohyus plicodon* No. 12147; (b) *Helohyus milleri*, No. 12151; (c) *Perchaerus trichænus*, No. 7390; (d) *Perchaerus probus*, No. 1282; (e) *Perchaerus* species, No. 7396 (Milk dentition).

# Measurements of Lower Jaw Fragments and Teeth (Corrected to the Nearest Half Millimeter)

	American Museum Nos.									
	12314	1283	1015B	1200	1286	×	9812	7391	7392	7393
Depth of mandible below p <sup>3</sup> .....	.....	?26	.....	26	.....	.....	.....	32	.....	.....
Depth of mandible below entoconid of m <sup>3</sup> .....	.....	28	.....	30.5	.....	.....	44	30.5	.....	c. 38
Antero-posterior diameter of m <sub>1</sub> .....	.....	12	.....	11.5	.....	.....	13.5	13	.....	c. 37
Antero-posterior diameter of m <sub>2</sub> .....	.....	13.5	.....	12	15	.....	15.5	14.5	15.5	11.5
Antero-posterior diameter of m <sub>3</sub> .....	.....	17	.....	15	20.5	.....	22.5	20.5	21	12
Length from m <sub>1</sub> to m <sub>3</sub> , inclusive.....	.....	42	.....	38	.....	21.5	50.5	47.5	49.5	.....
Transverse diameter of m <sub>1</sub> .....	.....	8	.....	8	.....	.....	8	7.5	7.5	.....
Transverse diameter of m <sub>2</sub> .....	.....	9.5	.....	9	11	.....	9.5	9	10	.....
Transverse diameter of m <sub>3</sub> (at anterior transverse valley).....	7.5	8.5	12	8	10.5	10	11	9	9.5	8
Breadth of heel of m <sub>3</sub> .....	.....	7.5	9.5	5.5	8	9	9.5	8	8.5	9.5

Specific Reference	Period	Formation	Beds		Locality	
			Mid. Titanotherium	Mid. Oreodon	Cheyenne River, S. Dak.	Cheyenne River, S. Dak.
No. 12314.....	Lower Oligocene	.....				
1283 <i>P. probus</i> Leidy <sup>1</sup> .....	Middle Oligocene	.....	Oreodon	Metamynodon	S. Dakota	Cheyenne River, S. Dak.
1015B.....		.....				
1200.....		White River				
1286.....	Upper Oligocene	.....	Protoceras	"Top"	Cheyenne River, S. Dak.	Cheyenne River, S. Dak.
×		.....				
9812.....	1st phase	.....	?	Diceratherium	Little White River, S. Dak.	Camp Creek, Crooked River
7391 <i>P. pristinus</i> Leidy <sup>2</sup> .....	?	? White River				
7392 <i>P. pristinus</i> Leidy <sup>2</sup> .....	Upper Oligocene	.....	Diceratherium	Diceratherium	John Day Basin	Camp Creek, Crooked River
7390 <i>P. trichaeus</i> Cope <sup>3</sup> .....		John Day				
7393 ? <i>P. socialis</i> Marsh <sup>4</sup> .....		.....				

<sup>1</sup>Leidy, 1869, J. Acad. Nat. Sci. Phil., (2) VII, p. 194. ? Marsh, 1894, Amer. J. Sci., XLVIII, p. 271. "*Thinohyus nanus*."

<sup>2</sup>Leidy, 1873, Rep. U. S. Geol. Surv. of the Territories, F. V. Hayden, I, p. 216. "*Dicotyles*" *pristinus*. Cope, 1888, Proc. Amer. Phil. Soc., XXV, pp. 66-74, "*Bothrolabis*" *pristinus*. Cope and Matthew, 1915, Hitherto unpublished list of Tertiary Mammalia, Pl. cxi, fig. 2, *Percherus pristinus* (jaw, No. 7392).

<sup>3</sup>Cope, 1888, loc. cit., pp. 66 and 75. "*Bothrolabis*" *trichaeus*. Cope and Matthew, 1915, loc. cit., Pl. cxa, *Percherus trichaeus* (upper jaw of this specimen).

<sup>4</sup>Marsh, 1875 and 1894, Amer. J. Sci. and Arts, IX, p. 249, XLVIII, p. 271. "*Thinohyus*" *socialis*. Cope and Matthew, 1915, loc. cit., Pl. cxi, fig. 3, *Percherus socialis* (this jaw fragment).



## LOWER JAW FRAGMENTS

Little of importance in species-determination can be added to the accompanying table of measurements; the material is too fragmentary and the teeth in most cases much worn. The table gives some idea of the range of variation, however. It indicates that the animals represented may be divided into two types, a large type and a small type, existing side by side during the Oligocene; the large type was possibly already foreshadowed in the Bridger by *Helohyus lentus* Marsh (see above, p. 76). *Perchærus probus* Leidy, No. 1283, of the White River, forms an intermediate between these two types but more nearly approaches the smaller of them. It is possibly synonymous with "*Thinohyus*" *nanus* Marsh, (1894, Amer. Journ. Sci., XLVIII, p. 271) and the following comparison has been made by O. P. Hay<sup>1</sup>:

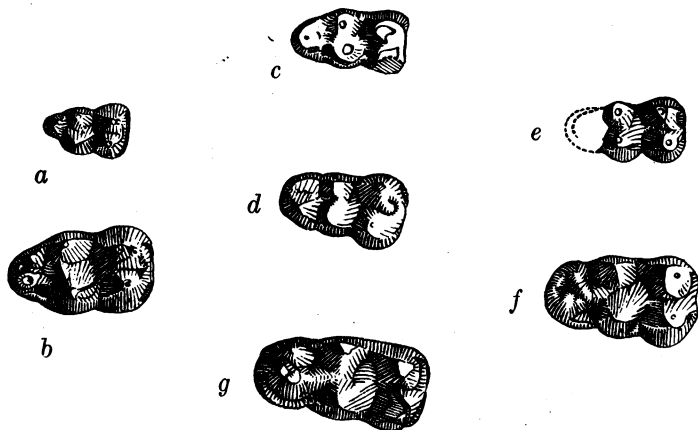


Fig. 16. Right third lower molars of Bridges and Upper Oligocene suillines.

Natural size.

(a) *Helohyus validus*, No. 12694; (b) *Helohyus lentus*, No. 12150; (c) *Perchærus probus*, No. 1200; (d) *Perchærus probus*, No. 1283; (e) ? *Perchærus socialis*, No. 7393; (f) *Perchærus trichænus*, No. 7390; (g) *Perchoerus* sp., undetermined, No. 9812.

On making a comparison of this jaw No. 1283 with the type *T. nanus* at Yale the following may be said: No. 1283 is extremely like the type, except that 1283 is larger. The teeth are longer and the width is somewhat disproportionately greater;  $m_1$  is longer and broader;  $m_2$  is longer and broader and especially across its anterior part. The jaw is deeper; under  $m_2$  *T. nanus* 21 mm., No. 1283 28 mm. The latter is possibly a male jaw.

The exact horizon of the Marsh specimen in South Dakota is unknown.

<sup>1</sup>Manuscript note in the American Museum.

To the smaller type belong:

(1.) No. 1200, a jaw fragment with  $p_3$  to  $m_3$ ;  $m_3$  is characterized by a very narrow heel supporting, as in No. 1283, a single main cusp. Compared with the other species the jaw is deep in proportion to the size of the teeth.

(2.) No. 12314, a broken anterior molar and a broken  $m_3$ , each worn and in a broken fragment of jaw; these are the smallest of all the teeth in the collection.

(3.) No. 7393, a jaw fragment with  $p_3$  to  $m_3$ , the latter with its heel broken off. This is the only specimen of the small type from the John Day. The teeth are almost exactly comparable with those of No. 1200 from the White River but not so much worn;  $m_1$  and  $m_2$  are very slightly narrower. It has been assigned by Cope and Matthew (1915, *loc. cit.*) to the species *T. socialis* Marsh, the type specimen of which comes from Oregon, presumably also from the John Day, and consists of two upper molars.

To the larger type belong:

A.—From the White River Formation (for exact horizons, where known, see p. 92).

(1.) No. 9812, a jaw fragment with  $m_1$  to  $m_3$ ;  $m_1$  and  $m_2$  very worn.  $M_3$  has a broad heel with three main cusps and an external cingulum; the antero-buccal of the three cusps is connected with an intermediate cusp or bridge which lies behind and between the entoconid and hypoconid in the posterior transverse valley. The jaw is stout and deep.

(2.) An unnumbered specimen marked X in the table. Part of both rami and the symphysis are present. The alveolar border is much battered and all the teeth except  $m_3$  r. are split and broken off near the roots.  $M_3$  is very much worn; in size it corresponds well with No. 9812; the external cingulum on the heel does not extend to the back of the latter as in that form, and the cusps on the heel appear to have been arranged rather differently.

(3.) No. 1015B, an isolated  $m_3$ , the largest in the collection. The details of its structure are obscured by attrition, but they appear to have been very similar to those in the last two specimens; the trigonid is broader in proportion to the rest of the tooth than in these.

(4.) No. 1284, not included in the table, consists of the symphysial end of a jaw with the broken roots of the incisors, canines and first three premolars of either side, and the worn and broken remains of  $p_4$ - $m_1$  r. In general proportions it is evidently entirely comparable with the last three specimens, though no comparative measurements are possible.

The roots of the incisors, sub-equal in size, are closely crowded on one another and on those of the canines, with only the narrowest alveolar borders between them.  $P_1$  r. has a single root in a large alveolus 4 mm. directly posterior to the canine. No similar alveolus is present on the left side; this appears to be an anomaly or due to an accident rather than an indication of future evolutionary changes. The distance between  $p_1$  r. and  $p_2$  r. is 6.5 mm. The heel of  $p_4$  has an unusually broad cingulum on either side of the central cusp.

(5.) No. 1286, consisting of  $m_3$ , a broken  $m_2$  and the broken symphysis, is slightly smaller than the others of this series from the White River. The roots of its incisors again show crowding, though not quite so extreme as in No. 1284.  $P_1$  is again single-rooted and directly behind the canine but only 2 mm. from it.  $M_3$  is unworn and shows a heel covered with small tubercles instead of supporting two or three larger cusps as in the forms described above. It is closely comparable with  $m_3$  of *P. trichænus*, No. 7390, from the John Day, which is also little worn and with which it agrees in most of those smaller details of tubercle arrangement, so highly variable in recent peccaries, which distinguish the *P. trichænus* molar from that of *P. pristinus*.

B.—From the John Day.

(1.) *P. pristinus* Leidy, No. 7392 (Fig. 17), the tooth-bearing portions of two rami connected by a battered symphysis,  $p_3$  r.,  $p_4$  l.,  $m_1$  to  $m_3$  of both sides, and the roots of  $p_2$  r. These may be compared with (2.) *P. pristinus*, No. 7391, a right jaw fragments with  $p_3$  to  $m_3$ , rather worn, and with (3.) *P. trichænus*, No. 7390 (Fig. 14), battered jaws with  $i_1$  to  $c$  of both sides, the stump of  $p_1$  r., a battered  $p_3$  r.,  $p_4$  r. and a broken  $m_2$



Fig. 17. *Perchaerus pristinus*, No. 7392. Left Lower dentition,  $p_3$  to  $m_3$ , ( $p_3$  restored from partly broken tooth on right side).

Natural size.

and an  $m_3$  of both sides; the other teeth are mostly represented by roots; it is associated with the upper jaws described above.

These three constitute a very closely connected group, the larger specimen of *P. pristinus* (No. 7392) forming an intermediate link as regards size between the smaller specimen and *P. trichænus*. The jaw of the latter appears to be somewhat deeper and its ventral border to curve down less at the angle than in *P. pristinus*, but this may be in-

fluenced by crush.  $M_3$  of *P. trichænus* is distinguished by the anterior cingulum not curving up into the anterior rib of the metaconid, and by the slightly greater prominence of the intermediate cuspules in the transverse valleys and of the numerous tubercles on the heel.  $M_2$  of *P. trichænus* has a less extensive posterior cingulum than  $m_2$  of No. 7392.  $P_4$  and  $p_3$  are closely similar in both species. In the premolar region of both there are diastemata between  $p_1$  and  $p_2$ ,  $p_2$  and  $p_3$ ; the first of these diastemata measures 7 mm. in *P. trichænus*, the second 4 mm.; in *P. pristinus* the first is not determinable, the second 5.5 mm. According to Cope the jaw of *P. pristinus* in the Condon collection, University of Oregon, has a two-rooted  $p_1$ ; this character is not determinable in the American Museum jaws No. 7391 and 7293; in *P. trichænus*  $p_1$  is single-rooted.

The lower canines of *P. trichænus* have a broad, shallow groove on their lateral surface, separated by a broad rib from a second shallow groove on the antero-buccal surface.  $I_1$  and  $i_2$  are spade-shaped and procumbent, their tips cut off abruptly by wear.  $I_3$  is separated from them at its tip by being less procumbent; the tip is pointed and the crown worn on the edge which faces posteriorly; the tooth corresponds closely in shape with the  $i_3$  of a fragmentary jaw from the Upper Oreodon beds of White River (A. M. N. H. No. 9813), which is probably referable to *P. probus*.