Principal characters of the Protoceratidae / by O.C. Marsh.

[From the American Journal of Science, Vol. IV, September, 1897.]

PRINCIPAL CHARACTERS OF THE PROTOCERATIDÆ.

By O. C. Marsh.

WITH SIX PLATES.

[From the American Journal of Science, Vol. IV, September, 1897.]

Principal Characters of the Protoceratidæ; by O. C. Marsh.

Part I. (With Plates II–VII.)

The genus *Protoceras*, described by the writer in 1891, from the Miocene of South Dakota, is now known to include some of the most interesting extinct mammals yet discovered. It likewise represents a distinct family, and thus deserves careful investigation and description.* Before this discovery, no horned artiodactyles were known to have lived during Miocene time, and *Protoceras* is thus the earliest one described. The type specimen, moreover, had a pair of horn-cores on the parietals, and not on the frontals as in modern forms of this group. The animal was apparently a true ruminant, nearly as large as a sheep, but of more delicate proportions.

The first skull found, the type specimen of the genus *Protoceras*, belonged to a female, as later discoveries demonstrated. The skull of the male proved still more remarkable, and especially resembles the male skull of the Eocene *Dinocerata* in having several pairs of horn-cores or protuberances upon the head, a feature hitherto unknown among the *Artiodactyla*. It is an interesting fact, moreover, that one pair of these horn-cores of *Protoceras* is on the maxillaries, as in *Dinoceras*, while the posterior pair, as in that genus, is on the parietals.

* This Journal, vol. xli, p. 81, January, 1891; and also, vol. xlvi, p. 407, November, 1893.

The resemblance in the two skulls is further enhanced by the absence of upper incisors and the presence of large canine tusks, forming together a striking similarity in important features, between skulls pertaining to animals of two distinct orders, and from widely different geological horizons. The skull of the male *Protoceras* is shown in Plate II, and that of *Dinoceras* in the text below.

1.

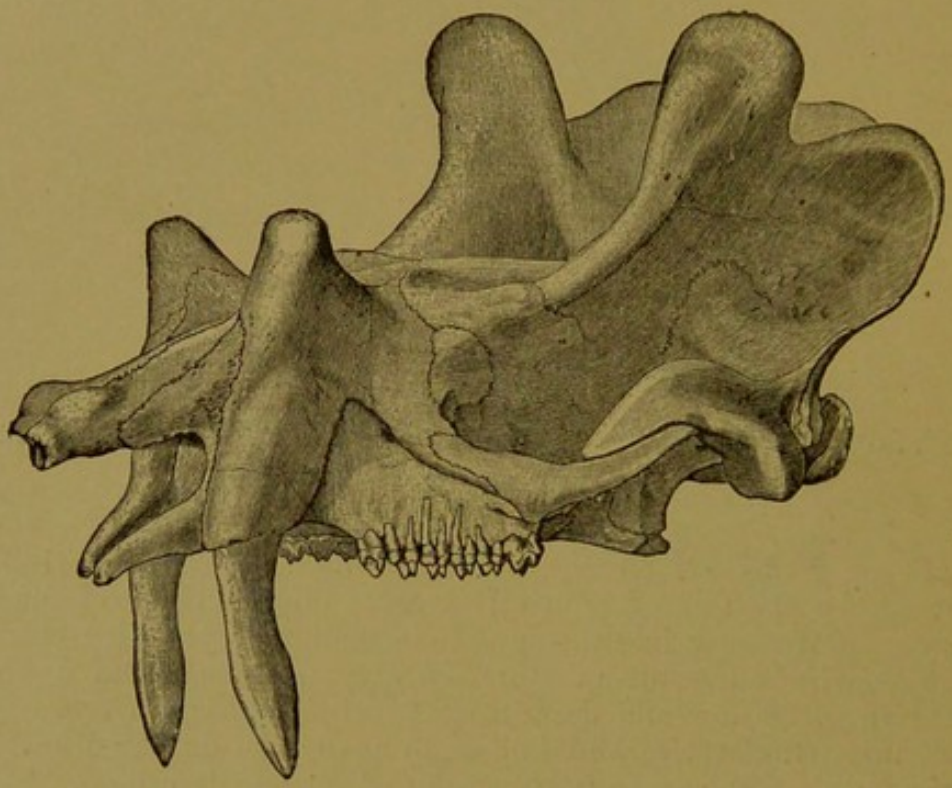


FIGURE 1.—Skull of *Dinoceras mirabile*, Marsh; type; seen from the side. One-seventh natural size. Eocene.

It is a noteworthy fact, that in still another order of ungulate mammals, the *Perissodactyla*, horn-cores in pairs early made their appearance, although none are known in the recent forms. One of the earliest instances is seen in the genus *Colonoceras* from the middle Eocene, which had rudimentary protuberances upon its nasal bones, as represented below, in figure 2. The gigantic *Brontotheridæ* of the lower Miocene all had prominent horn-cores on the maxillary bones, somewhat like those of the male *Protoceras*. One of the most unexpected examples, however, in this order, appears in the Miocene genus *Diceratherium*, the type specimen of which is shown in figure 3. This animal, although a true rhinoceros, had a pair of horn-cores on the nasal bones, while all other rhinoceroses, living and extinct, are either without horns or have them on the median line. In short, horns in pairs are unknown in existing mammals, except in the artiodactyles, an order of later development, but now the dominant group of ungulate mammals.

The Male Skull.

The skull of the male *Protoceras*, in addition to the marked characters above mentioned, has others of equal interest, if not of still greater taxonomic value.* The general appearance of the adult male skull is well shown in Plate II, accompanying the present article, and the special anatomical characters are represented more clearly in the different views on Plates III, IV, V, and VI.

2. 3.

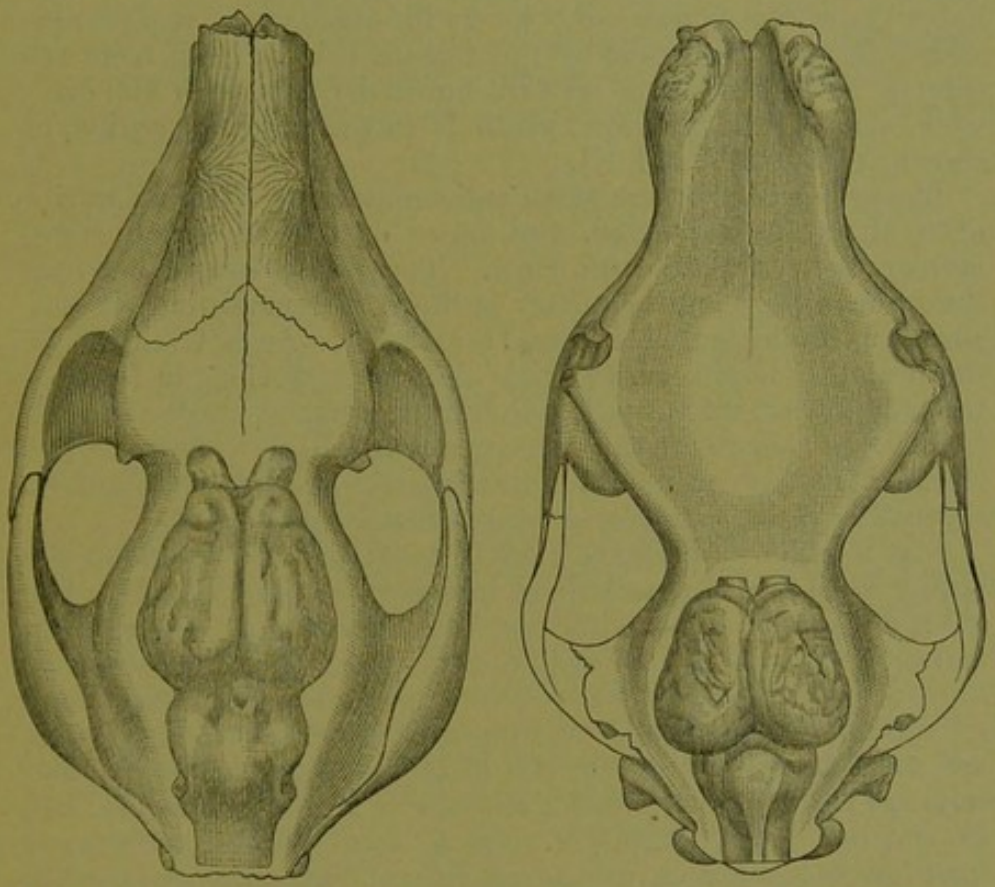


FIGURE 2.—Skull of *Colonoceras agrestis*, Marsh; type, with brain cast; seen from above. About one-half natural size. Eocene.

FIGURE 3.—Skull of *Diceratherium advenum*, Marsh; type, with brain cast; seen from above. One-sixth natural size. Miocene.

Aside from the various horn-cores and protuberances upon the skull, the next most notable feature is the very large, open nasal cavity, a character which pertains to both sexes, and to the entire family of the *Protoceratidæ*. This peculiar feature is of even more importance than the horn-cores, judging from its functional significance, and its rarity in more recent forms of artiodactyles. It indicates clearly in the living animal a

* Osborn and Wortman, Bulletin, Amer. Mus. Nat. Hist., vol. iv, p. 351, 1892. See also Scott, Jour. Morph., vol. xi, p. 303, 1895.

long flexible nose, if not a true proboscis. The only existing ruminant thus equipped, known to the writer, is the rare Saiga antelope (*Saiga Tartarica*, Gray) from the steppes of Siberia. A comparison of a *Protoceras* skull with that of the Saiga antelope plainly indicates, in the nasal region, an identity of function doubtless accompanied by a similar nasal appendage, and it is of interest to find such evidence of this feature in a representative from the Miocene of North America.

The general form of the male skull of *Protoceras* is long and narrow, with the facial portion much produced. The prominent horn-cores, however, serve to obscure its real shape, which is more apparent in the female skull. Seen from the side, as in Plate III, it appears unusually low, with the orbit well behind. Its greatest width is in the posterior region, as shown in Plates V and VI.

The premaxillaries are small and edentulous. Their anterior extremities are depressed, and more or less expanded transversely, as in typical ruminants. The outer suture between the premaxillary and maxillary is short, and persistent even in adults, as indicated in Plates II and III. Seen from below, the premaxillaries form together the palatal surface in front of the maxillaries, each sending backward a narrow process which is inserted between the divergent maxillary plates. The anterior palatine, or incisive, foramina are situated on the sutures separating the two bones, as represented in Plate V.

The maxillary bones are greatly developed, being much the largest elements of the skull, as is well shown in Plate II. The anterior extremity supports the large descending canine tusk, and is hollowed out to contain its base. The high anterior horn-cores are formed entirely of the maxillary bones, which are greatly strengthened to support them. These horn-cores are more or less recurved, and in the type species, their summits are triangular in outline, as seen in Plates II and III, and in the cut below, figure 4. In a new species, *Protoceras nasutus*, the summits of the maxillary horn-cores are oval in section, as shown in cut 5. Another characteristic feature of the genus *Protoceras*, which is seen in both sexes, is a strong lateral ridge extending nearly horizontally across the outer face of the maxillary bone, and continuing backward to the orbit. It is also present in the other members of this family. In the male skull here described, this ridge begins near the base of the maxillary horn-core, and, expanding into a prominent tubercle, just above the antorbital foramen, continues backward by an upward curve, and passes into the ridge of the malar bone extending beneath the orbit. In both sexes, the anterior portion of this lateral ridge, with its characteristic tubercle, forms the lower border of a deep, well-marked

depression, which probably contained a gland. In Plate II, this cavity is well shown behind the maxillary horn-cores, just below the point where the superior border of the skull is lowest.

The nasal bones join the maxillaries above, and complete the posterior border of the large narial opening. They are of moderate length on the median line, and their free anterior extremities are quite short. These bones are much expanded transversely, and at their widest part articulate with the lachrymals. All the sutures surrounding the nasals are distinct, and this is true, also, of their median suture. Their upper surface is convex, both transversely and longitudinally, and is marked by two deep grooves, which lead backward to the supra-orbital foramina in the parietals, as shown in Plate IV.

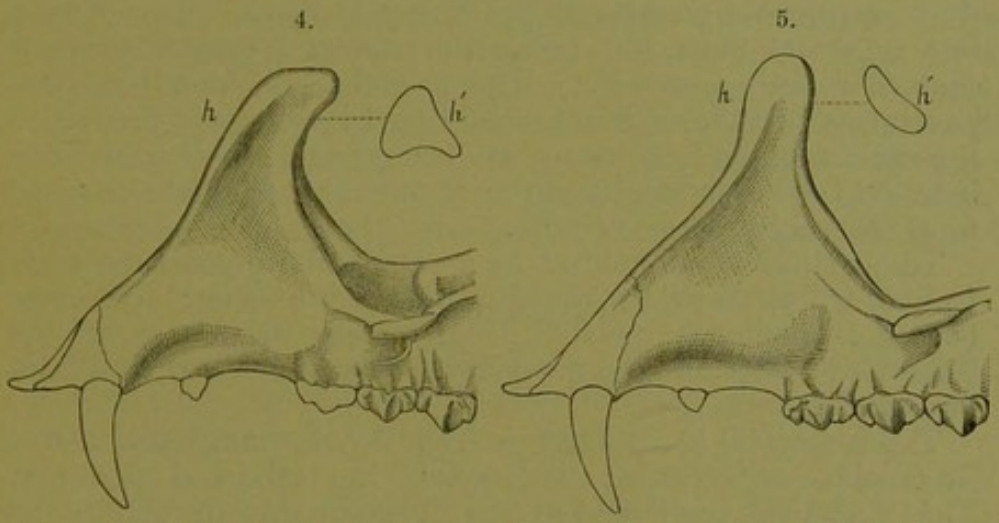


FIGURE 4.—Front of skull of *Protoceras celer*, Marsh; seen from the left side.
FIGURE 5.—Front of skull of *Protoceras nasutus*, Marsh; seen from the left.
Both are male skulls, and drawn one-half natural size. Miocene.
h, maxillary horn-core; *h'*, section of same.

The frontals, which bound the nasals behind, are large massive bones, much wider than long. The suture which unites the two frontals is distinct, and cuts the naso-frontal suture nearly at right angles. At the lateral junction of the frontal and nasal, there is on each side a low tuberosity, resembling a diminutive horn-core, and these form the third pair of elevations on the skull. At the postero-external angle of the frontals, above the orbits, another pair of much larger protuberances is seen, and the summits of these are widely expanded transversely, as shown in Plate IV. The upper surface of the frontals is rugose, and the deep grooves already mentioned are characteristic features.

The parietal bones are much smaller than the frontals, and are separated from them by a distinct sigmoid suture. These bones support the posterior pair of horn-cores, as shown in Plate IV. The general form and position of these elevations on the male *Protoceras* skull are represented in the accompanying plates, but they differ in each species. Behind these horn-cores, there is a low sagittal crest separating the deep temporal fossæ. Back of the parietals is the short supra-occipital, which forms a weak lambdoidal crest bounding the temporal fossæ behind.

The inferior portion of each fossa is formed by the squamosal, which covers the lower half of the brain case, and joins the parietal above by a distinct suture, as shown in Plate III. The squamosal sends forward a short zygomatic branch, which fits into a notch in the posterior part of the malar. There is a distinct postglenoid process. The tympanic bone is not dilated into a definite bulla, but below the auditory meatus forms a short descending process. The periotic is behind the tympanic, separated from it above by the post-tympanic process of the squamosal, and below by an open suture. It is wedged in between the latter bone and the strong and elongate parocciptal process of the exoccipital.

The orbit is closed behind by a descending process from the frontal, which meets the upper branch of the malar. Its lower border is bounded by the malar, which in front joins the lachrymal above and the maxillary below, as shown in Plates II and III.

The lachrymal is bounded in front by the maxillary, above by the nasal and frontal, and below by the malar and maxillary. The lachrymal foramina are two in number, well within the orbital border. The orbits are large, suboval in outline, and widely separated from each other. Their posterior position is a characteristic feature of the genus *Protoceras*.

The Base of the Skull.

The lower surface of the male *Protoceras* skull is represented in Plate V. The narrow occiput, surmounted by the supra-occipital, is a noteworthy character. The widely expanding orbits greatly increase the width of the skull in this region, and from here forward, its wedge-like shape is a striking feature. The large foramen magnum and the narrow diverging occipital condyles are well seen in this view. The basi-occipital and the basisphenoid bones are firmly coössified, the suture between them being indistinct. In front of the latter bone is the parasphenoid, separated from it by a well-marked suture, and passing forward above the vomers, which are here distinct. The pterygoids are attached to the posterior border of the palatines, and above to the alisphenoids. There is no distinct alisphenoid canal.

The palatine bones are narrow, and bound in front the posterior nares, which extend forward to near the middle of the penultimate molars. The maxillary plates form the roof of the palate forward to the premaxillaries. At their narrowest portion, they are deeply grooved for the approaches of the palato-maxillary foramina, which are situated somewhat in advance of the second premolars. The maxillary plates are separated in front along the median line, to receive the posterior branches of the premaxillaries, and on the suture between the two elements, the anterior palatine foramina are in their usual position. The turbinal bones were apparently quite small.

The Lower Jaw.

The lower jaw is well represented in Plate II. It is long and slender, especially in front, thus corresponding to the skull. The condyle is broad and strongly convex above. The coronoid process is very short, and its summit is but little higher than the condyle. The angle is rounded and well developed. The ramus expands downward and is thickened beneath the molar teeth, and has a sharp upper edge along the diastema between the first and second premolars. It again extends downward at the symphysis, becoming more robust to support the front teeth.

The Dentition.

The dentition of *Protoceras* is of the early ruminant type, as shown by the short-crowned, selenodont molar series. The dental formula is as follows:

$$\text{Incisors } \frac{0}{3},\ \text{Canines } \frac{1}{1},\ \text{Premolars } \frac{4}{4},\ \text{Molars } \frac{3}{3}.$$

In the male skull, the upper canines are well developed, as shown in Plate II. They are compressed and somewhat trihedral in transverse section, and in life formed efficient weapons of warfare. The first upper premolars, a short distance behind, are small compressed teeth, each with two roots; and after a still longer diastema, the second premolars begin the continuous series. The second and third upper premolars each have a large outer cusp and an inner cingulum, while the fourth has a distinct inner crescent, as shown in Plate V, which also represents faithfully the superior molars. These have all short crowns and the double crescents of true selenodont dentition, with a well-developed inner basal ridge on each. The accurate drawings of the accompanying plates render unnecessary a detailed description of these teeth and most of the others here figured. This is true, also, of various minor points in the structure of the skull.

The teeth of the lower jaw of *Protoceras* are indicated in Plate II, and the full series is shown. The three incisors are directed well forward, and diminish in size from the first to the third. The still smaller canine is situated close to the last incisor, and is similar in form. A long diastema follows, and gives the upper canine freedom of motion. The first premolar is somewhat similar to the corresponding one above, but is larger and directed more forward. A still longer interval separates the first and second lower premolars, the latter beginning the continuous molar series. The second premolar has the crown much compressed, while the third and fourth are triangular in form. The three true molars have the usual crescents corresponding to those above, but no inner cingulum.

The upper molar teeth of the female skull are shown in figure 7, below, which represents the type of the genus. On Plate VI, figure 2, the upper dentition of *Protoceras comptus* is represented, the type specimen figured being the skull of a female not yet adult.* The last three deciduous teeth are here still in use, the first and second true molars are in position, while the last had not yet come into place.

The Brain.

The brain in *Protoceras* was of good size, not diminutive as in the early ungulates. It was, moreover, well convoluted for a Miocene mammal, and forms an interesting addition to our knowledge of the brain development in Tertiary *Mammalia*.

The natural brain cast figured in Plate VII, figures 3 and 4, is from an adult female skull, and represents accurately the brain cavity of this individual, except the small space occupied by the olfactory lobes. The latter were well developed.

The Female Skull.

The type species of the genus *Protoceras*, as already stated, was the skull of a female, and it may be well to repeat here its essential features as given in the original description already cited. In figures 6 and 7 below, most of the main characters of this type specimen are represented.

"In general form and proportions, this skull is of the ruminant type. Its most striking feature is a pair of small horn-cores, situated, not on the frontals, but on the parietals, immediately behind the frontal suture. These prominences were thus placed directly over the cerebral hemispheres of the brain.

* This Journal, vol. xlviii, p. 93, July, 1894.

"The frontal bones are very rugose on their upper surface, and this rugosity extends backward on the parietals, and to the summit of the horn-cores, as well as between the latter, and along the wide sagittal crest. The horn-cores are well separated from each other, and point upward, outward, and backward, overhanging somewhat the temporal fossæ. They are conical in form, with obtuse summits.

"Between the orbits, the frontals are depressed, and marked by two deep grooves leading backward to the supra-orbital foramina. Behind these, halfway to the horn-cores, is a median prominence resembling in shape the corresponding elevation on the skull of the male giraffe. The brain cavity is unusually large for a Miocene mammal. The occiput is very narrow, indicating a small cerebellum, and the occipital crest is weak. The occipital surface slopes backward.

6. 7.

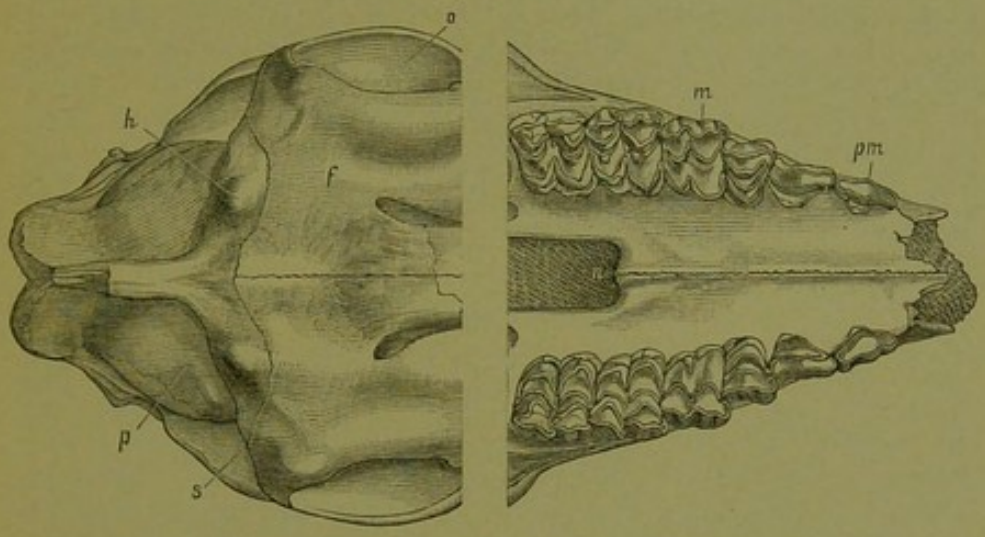


FIGURE 6.—Back of female skull of *Protoceras celer*; type; seen from above.
FIGURE 7.—Front of same skull; seen from below.

Both figures are one-half natural size. Miocene.

f, frontal; *h*, horn-core; *m*, first molar; *n*, posterior nares; *o*, orbit; *p*, parietal; *pm*, second premolar; *s*, suture between frontal and parietal.

"The facial region of the skull is narrow and elongate. On the outer surface of the maxillary, just above the antorbital foramen, there is a deep depression, which probably contained a gland. The usual ruminant fossa in front of the orbit appears to be wanting. The orbit is large, and completely closed behind by a strong bar of bone.

"The dentition preserved is selenodont and brachyodont, with only three premolars and three molars.* The first premolar is much compressed transversely, and has but a slight inner lobe. The second premolar is triangular in outline, the inner lobe being much more developed. The last premolar has this lobe expanded into a strong cusp, and the crown thus becomes broader than long. The true molars have two inner cusps, each with a basal ridge. The outer crescents have a median vertical ridge. The enamel of the molar series is more or less rugose. There was a wide diastema in front of the premolars.

"The posterior nares are situated far forward, the anterior border being opposite to the posterior cusp of the second true molar. The glenoid facet is large and convex, but the post-glenoid process is quite small. The paroccipital processes were well developed, but there were apparently no auditory bullæ."

A number of other female skulls, some of them in excellent preservation, have since been obtained from the same region in which the type was found, and a study of these makes clear the main points of their structure. It is not quite certain to which of the three species of *Protoceras* now known some of these skulls should be referred, but further investigation will doubtless determine this point, as the present material in the Yale Museum is apparently sufficient for this purpose.

The Skull of Calops.

The small artiodactyle described by the writer in 1894, under the name *Calops cristatus*, is from essentially the same geological horizon in South Dakota in which *Protoceras* was found. As stated in the first description, *Calops* possesses characters indicating a near ally of *Protoceras*, and as the resemblance has proved even closer in more perfect specimens since discovered, denoting that the two genera belong to the same family, it may be well to quote here the main points of the original description.†

"The type specimen is a skull in fair preservation, indicating a fully adult animal, which when alive was about half as large as a goat. In its general form and in most of its characters, this skull agrees so closely with the type of *Protoceras* as to suggest at once some affinity between the two. The dentition preserved in the premolar and molar series is essentially the same. The high maxillary plates joining the short, pointed nasals; the deep lachrymal fossa; and the posterior orbit

*More perfect specimens since discovered prove that there were four premolars, the first being absent in the type.

†This Journal, vol. xlviii, p. 94, July, 1894.

strongly closed behind, all suggest an ally of *Protoceras*, but the parietal ridges are here elevated into distinct crests, and are without horns.

"This skull when complete was about six inches in length. The distance from the front of the nasals to the junction of the parietal crests is about four inches and a half. The space occupied by the last three premolars and the true molars is about two and one-half inches."

In a later notice, a second more perfect specimen from the same horizon was described,* the main points stated being as follows:

"The brain was comparatively well developed, and an unusually large part of the cerebral lobes was covered by the parietals. The frontal region of the skull between the orbits was more or less concave. The antorbital depressions extend well forward. There is a diastema between the upper canine and the first premolar, and between the first and second premolars. The canines above and below are small. The first lower premolar appears to be wanting. The second and third premolars have secant crowns, much elongated fore and aft. The postglenoid process is quite small, but the paroccipital is large and robust. The lower jaw has a very short coronoid process, and the condyle is sessile. The angle of the jaw is well rounded and somewhat dependent."

This second specimen proves to be distinct from the type, and is here recorded as a new species, *Calops consors*. The skull, which is in good preservation, is represented on Plate VII, figures 1 and 2. These two views exhibit the main features of the skull in the genus *Calops*. The most striking difference between this specimen and the type is the position of the orbit, which in the latter is entirely behind the molar series, as in *Protoceras*, while in the specimen here figured, as shown in Plate VII, nearly half the orbit is in front of the posterior end of this series.

The Dentition of Calops.

The teeth of *Calops* correspond essentially with those of *Protoceras*, being of the same early ruminant type, with the characteristic, short-crowned, selenodont molar series, and apparently the same dental formula. In the female skull represented on Plate VII, figure 1, most of the teeth are seen in position. There were no upper incisors. The canine was of moderate size, and placed well back of the premaxillary suture. The first premolar is small, with a compressed crown and two roots, and is situated somewhat behind the middle of the

* This Journal, vol. xlviii, p. 273, September, 1894.

interval between the canine and second premolar, as shown in the figure cited. The remaining upper premolars correspond closely with those of *Protoceras* in form, and this is true, also, of the molars. The lower incisors of *Calops* are small and procumbent. The canine also was small, and probably similar in form to the incisors. The first lower premolar is caniniform in shape, with a single root, and a sharp compressed crown, which came nearly in apposition to the superior canine. The remaining lower premolars and molars agree closely except in size with those of *Protoceras*.

The remains of *Calops* now known all appear to have pertained to females, and this naturally suggests the question—what the male skull was like, and especially whether it was provided with horns. The probabilities at present are in favor of the latter view, but it must be left to future discoveries to settle that point.

All the known remains of *Protoceras* and *Calops* are from the upper Miocene of South Dakota. The horizon, which is a definite one, has been appropriately called by Dr. Wortman the Protoceras beds. They appear to be identical with the series in Oregon which the writer had previously named the Miohippus beds, as that genus and several others are common to both regions.

Yale University, New Haven, Conn., July 24, 1897.

EXPLANATION OF PLATES.

PLATE II.

Male skull, with lower jaw, of *Protoceras celer*, Marsh; oblique side view. Three-fourths natural size.

PLATE III.

The same skull; seen from the left side. Three-fourths natural size.

PLATE IV.

The same skull; seen from above. Three-fourths natural size.

PLATE V.

The same skull; seen from below. Three-fourths natural size.

PLATE VI.

FIGURE 1.—The same skull; seen from in front.
FIGURE 2.—Front of skull of *Protoceras comptus*, Marsh; seen from below; young female, showing deciduous dentition.

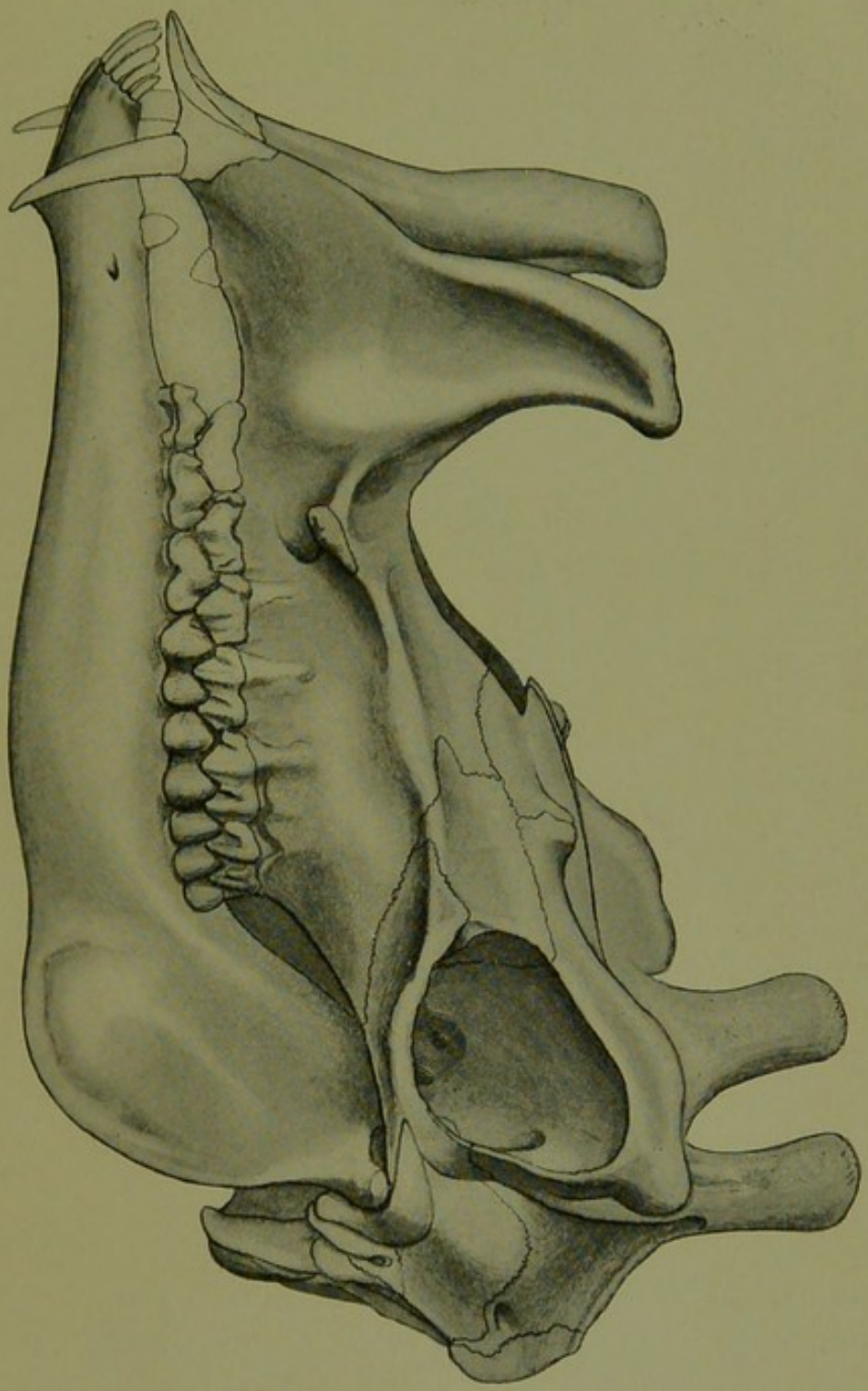
Both figures are three-fourths natural size.

PLATE VII.

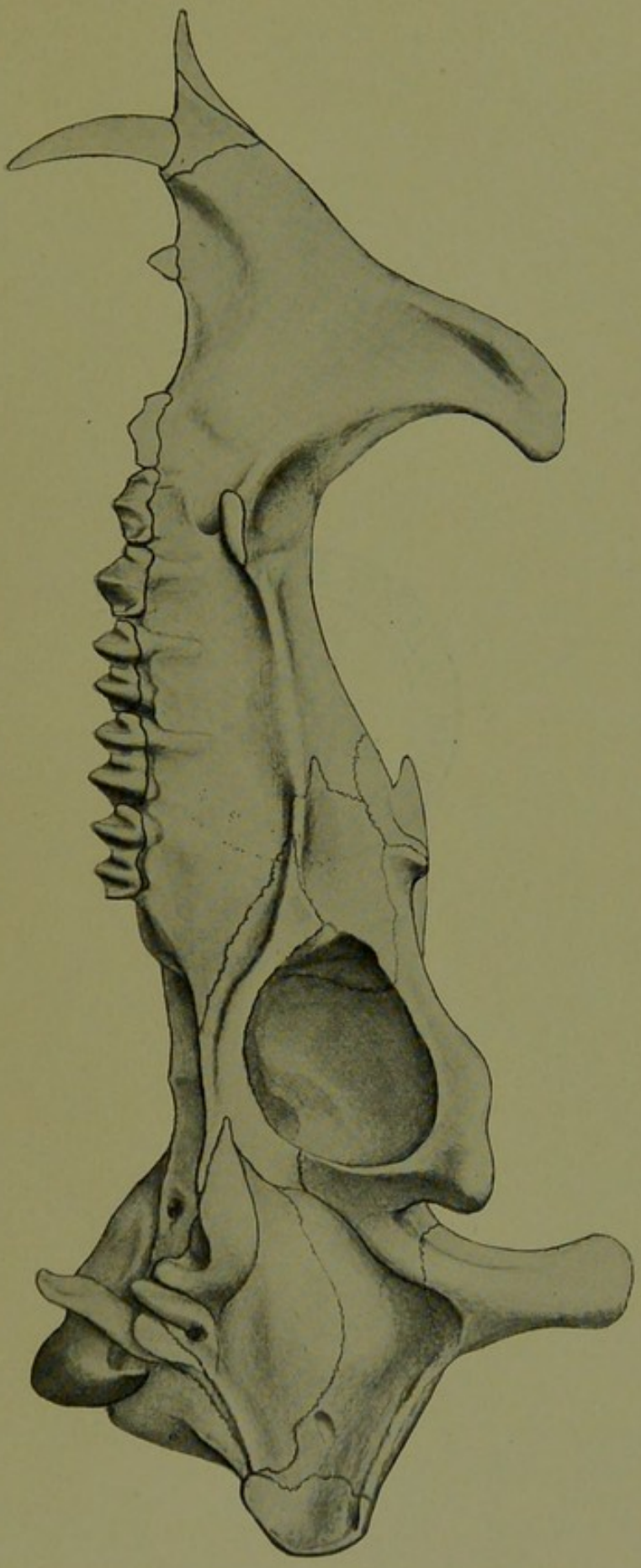
FIGURE 1.—Skull, with lower jaw, of *Calops consors*, Marsh; seen from the left.
FIGURE 2.—The same skull; seen from above.
FIGURE 3.—Natural brain cast of *Protoceras celer*; female; side view.
FIGURE 4.—The same; seen from above.

The figures are all one-half natural size.

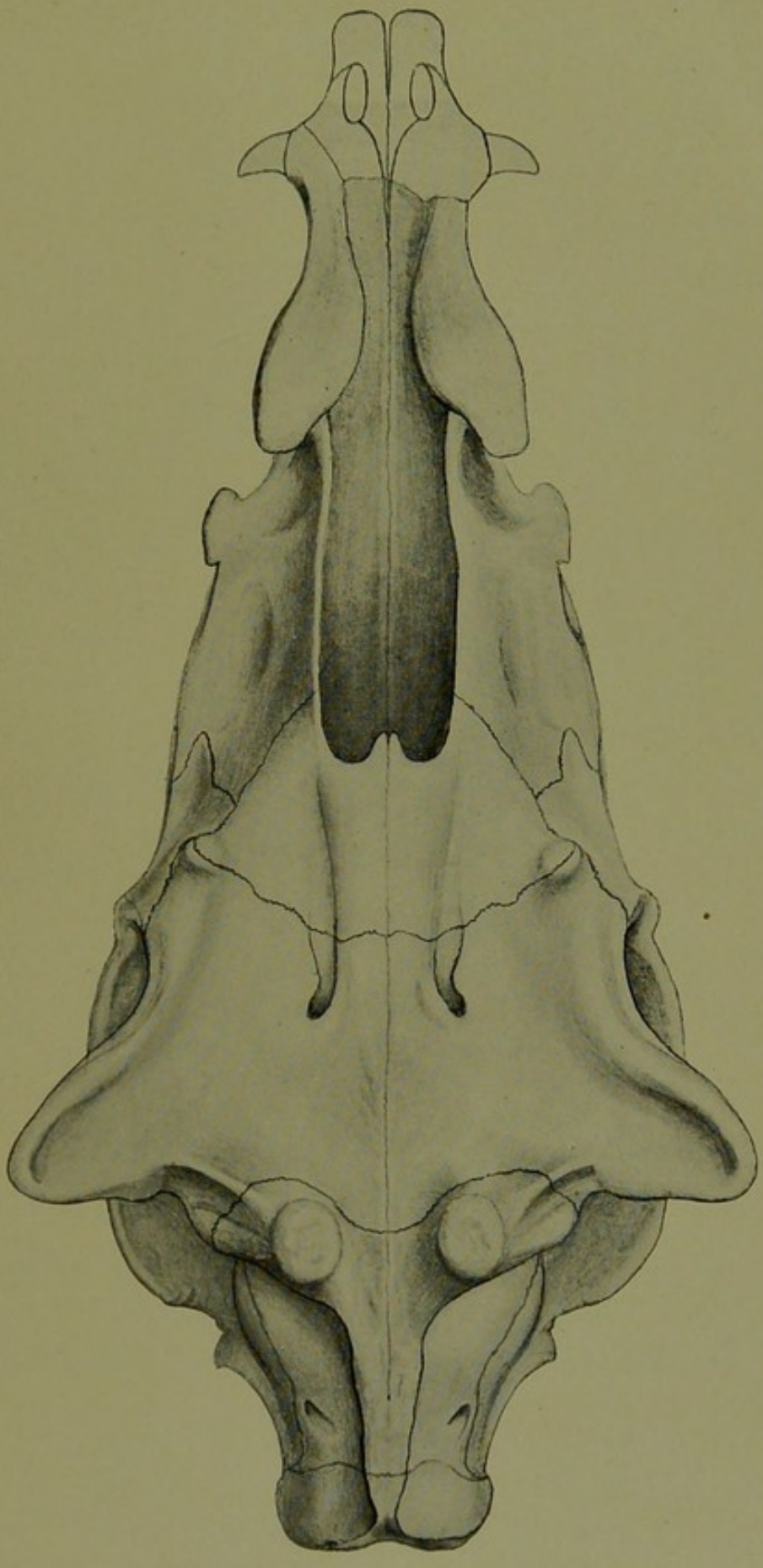
[To be continued.]



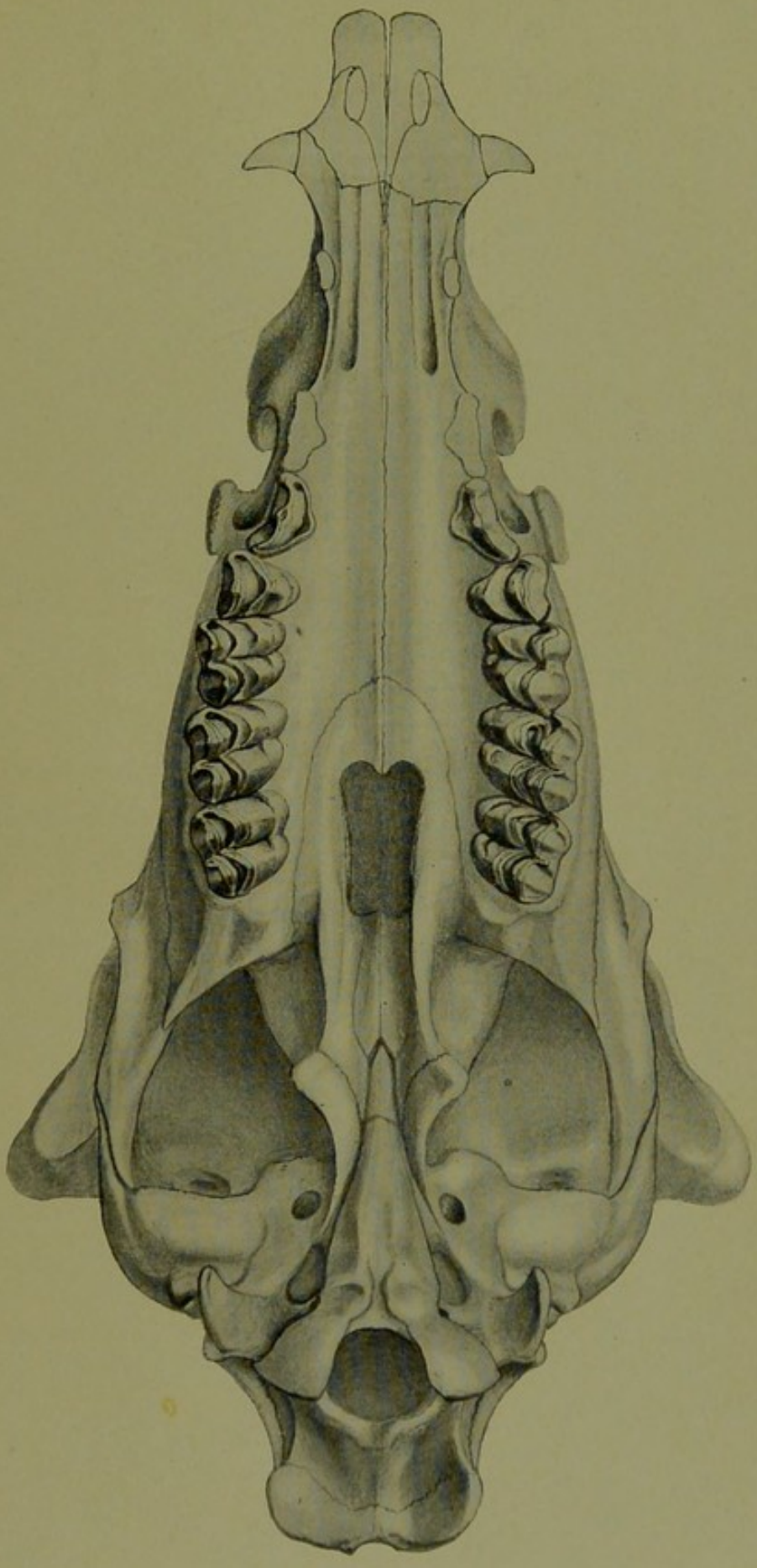
Male skull of Protoceras celer, Marsh. Miocene.
Three-fourths natural size.



Male skull of PROTOCERAS CELER. Miocene.
Three-fourths natural size.

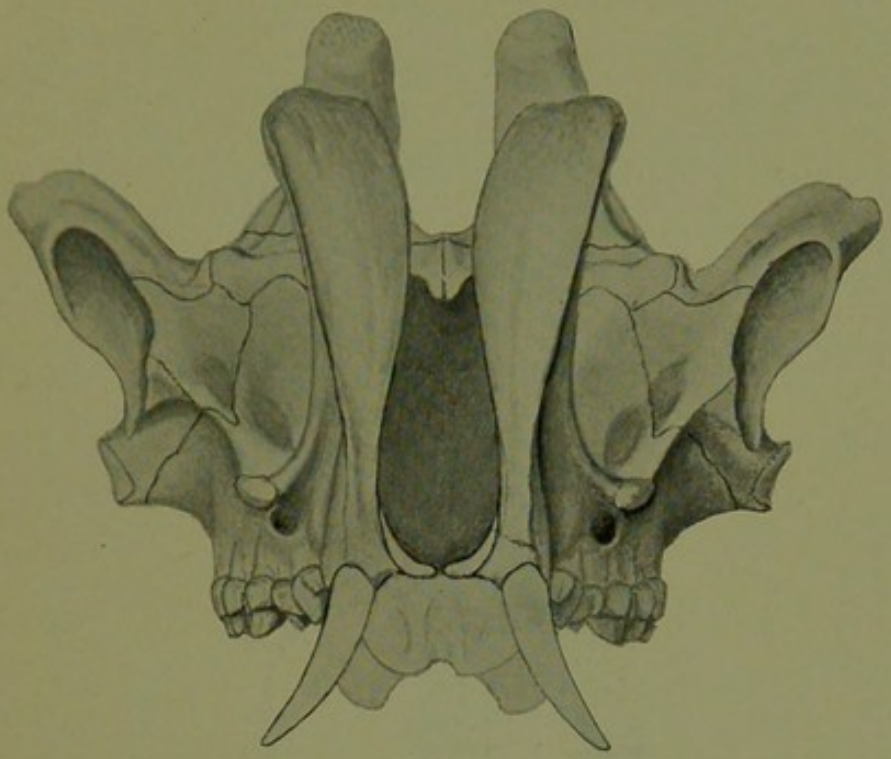


Male skull of PROTOCERAS CELER. Miocene.
Three-fourths natural size.

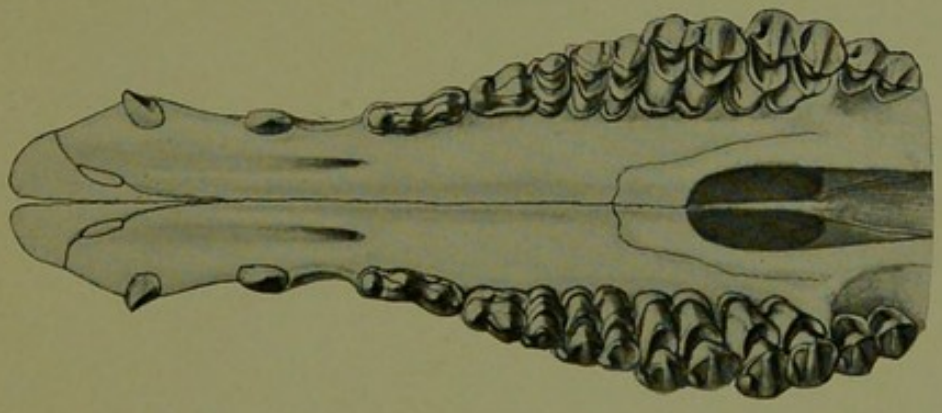


Male skull of PROTOCERAS CELER. Miocene.
Three-fourths natural size.

1.



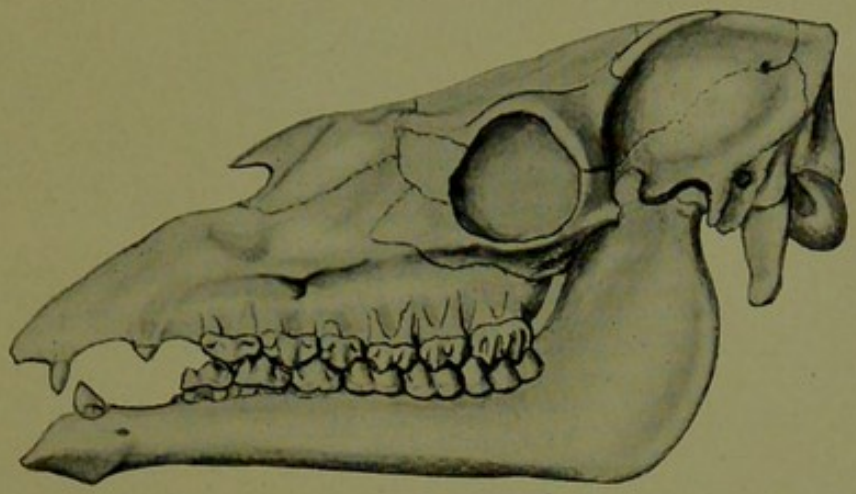
2.



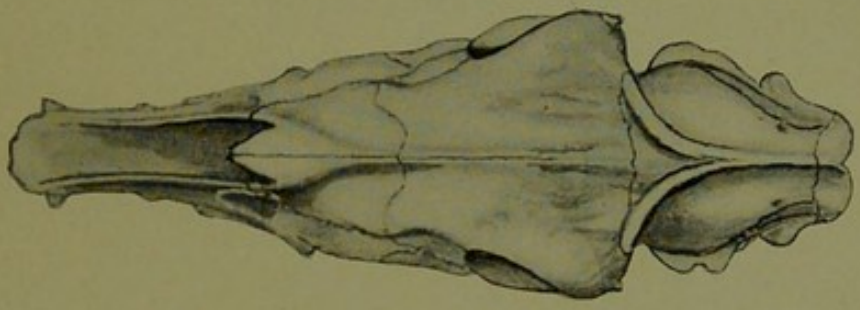
1.—Male skull of PROTOCERAS CELER. Miocene.
2.—Female skull of PROTOCERAS COMPTUS, Marsh. Miocene.

Three-fourths natural size.

1.



2.



3.

4.

1 and 2.—Female skull of CALOPS CONSORS, Marsh. Miocene.
3 and 4.—Brain cast of PROTOCERAS CELER. Miocene.

One-half natural size.