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THE SKELETON OF *LEPTOCERATOPS* WITH THE DESCRIPTION OF A NEW SPECIES

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INTRODUCTION

The known material assignable to the genus *Leptoceratops* consists of one rather complete skeleton and fragmentary remains of four others. The type, described by the senior writer (1914) as *L. gracilis*, consists of parts of a skull and jaws, a series of articulated caudal vertebrae, a complete fore limb and parts of the hind limbs. Portions of another, but slightly larger, individual were found with this specimen. This material was collected from the Edmonton formation on the Red Deer River in southern Alberta, Canada. Recently Gilmore (1939: 1-11) described two very fragmentary specimens which he collected from the Two Medicine formation on the Blackfoot Indian Reservation in northern Montana. These specimens are smaller than the others, and they are geologically older. They undoubtedly represent a form specifically distinct from *L. gracilis*. Gilmore was fully aware of this but very wisely refrained from assigning them to a new species because of the inadequacy of the material.

The most complete *Leptoceratops* specimen is a fine skeleton with a fragmentary skull, Amer. Mus. No. 5464, which the senior writer collected in 1916 from the lower part of the St. Mary River formation near Buffalo Lake, Montana. This

specimen was prepared in 1918 by Peter C. Kaisen and skilfully mounted for exhibition by Charles J. Lang in 1935. Because of the fragmentary nature of the skull parts, the entire skull on the mounted skeleton was reconstructed in plaster. This reconstruction was based primarily on the skull of *Protoceratops*. Recently, in connection with our studies on the ceratopsians, the skull parts of this specimen were reassembled and prepared in the laboratory. During the course of this work it soon became evident that this specimen, with its large nasal and very pronounced nasal horn-core and with the straight ventral margin of its lower jaw, represents a new species of *Leptoceratops*. So different are the characters of the known skull parts from the restored skull that a completely new reconstruction of the skull was necessary. This new reconstruction was made by Charles J. Lang and Jeremiah Walsh under our scientific direction. In the following notes this new species is described, and a study of the skeleton is presented. We find it inadvisable, however, to reiterate here certain conclusions regarding the morphology of *Leptoceratops* which were fully treated in our recent paper on *Protoceratops* (1940b).

The drawings in this paper were made by Mr. Alastair Brown except where otherwise accredited.

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DESCRIPTION

CERATOPSIA

PROTOCERATOPSIDAE

Leptoceratops cerorhynchus, new species

TYPE.—Amer. Mus. No. 5464, portions of the skull and jaws and most of the post-cranial skeleton. Collected by Barnum Brown, 1916.

HORIZON AND LOCALITY.—St. Mary River formation, Upper Cretaceous, near Buffalo Lake, Blackfeet Indian Reservation, Montana.

DIAGNOSIS.—Nasal proportionately large, deep, heavy and with a very well-developed horn-core. Dentary long and with a straight ventral margin.

SKULL

Many fragments of the skull are present, but through lack of contact with adjacent parts they cannot be assembled. The preserved portions identified and placed in the restoration are as follows: nearly complete right nasal and a fragment from the posterior region of the left, a portion of the posterior end of the left maxillary, part of the right prefrontal, the posterior part of the right jugal, nearly complete right jugal, portions of the frontals, most of the right postorbital, the greater part of both squamosals, the upper part of the left quadrate and the distal end of the lateral extension of the left exoccipital.

The nasal presents the most unique features of any of the parts preserved. In all of its characters it is ideally intermediate between that of the adult *Protoceratops* and of *Brachyceratops*. This is especially true in its robustness and large size and in the very well-developed horn-core. The tip of the anterior process is lost, but the remaining portion shows that it was short, heavy and deep. The preserved part of the antero-ventral border shows that the narial opening was large and that its shape was more like that of *Brachyceratops* rather than like the narial opening of *Protoceratops*. On the inner surface of the anterior projection there is a deep and extensive surface for articulation with the posterior wing of the premaxillary which extends back to under the middle of the nasal horn-core. The dorso-posterior margin is missing, but postero-ventrally the sutures for the premaxillary and maxillary are preserved, and

portions of the sutures for contact with the lacrymal and the prefrontal are shown.

The presence of such a large nasal horn-core in *Leptoceratops* is surprising. Most of the nasal is known in the type species, *L. gracilis*, and a considerable part of the nasal was preserved in the referred specimen described by Gilmore (1939). Neither of these specimens shows any evidence of an actual upgrowth of the bone to form an incipient nasal horn-core. In both, however, the grain of the bone is directed toward the slightly convex area on the dorsal surface which probably would become more strongly arched in the adult stage. Also, in the type there is a shallow median groove on the dorsal surface of the nasals. From this evidence in the young individual we inferred (1940a:4) that as in *Protoceratops* an incipient nasal horn-core was present in the adult stage of *Leptoceratops*. This now seems to be proved by this adult specimen. What is surprising, however, is the large size of the horn-core. From a careful comparison with *Protoceratops*, the type *Leptoceratops gracilis* skeleton seems to be that of a young adult individual, and the skeleton which we describe here as a new species (Amer. Mus. No. 5464) is that of a fully adult or possibly an old individual. In size the latter is about the same as the largest known *Protoceratops* specimen (Amer. Mus. No. 6438), but the nasal horn-core is very much more developed. Correlated with this are several other marked differences in the general form of the entire nasal bone. It is relatively larger, deeper and heavier, and the border for the narial opening is more extensive and continues posteriorly under the horn-core. Because of these characters, together with characters shown in other parts of the skull and lower jaw, this specimen unquestionably represents a new species.

The nasal of *L. cerorhynchus* presents additional information concerning the origin of the nasal horn-core of the early ceratopsians. In two earlier papers (1940 a: 1-4, 1940b: 152) we pointed out that in *Protoceratops* the gradual upward arching of the nasals from the young to the adult

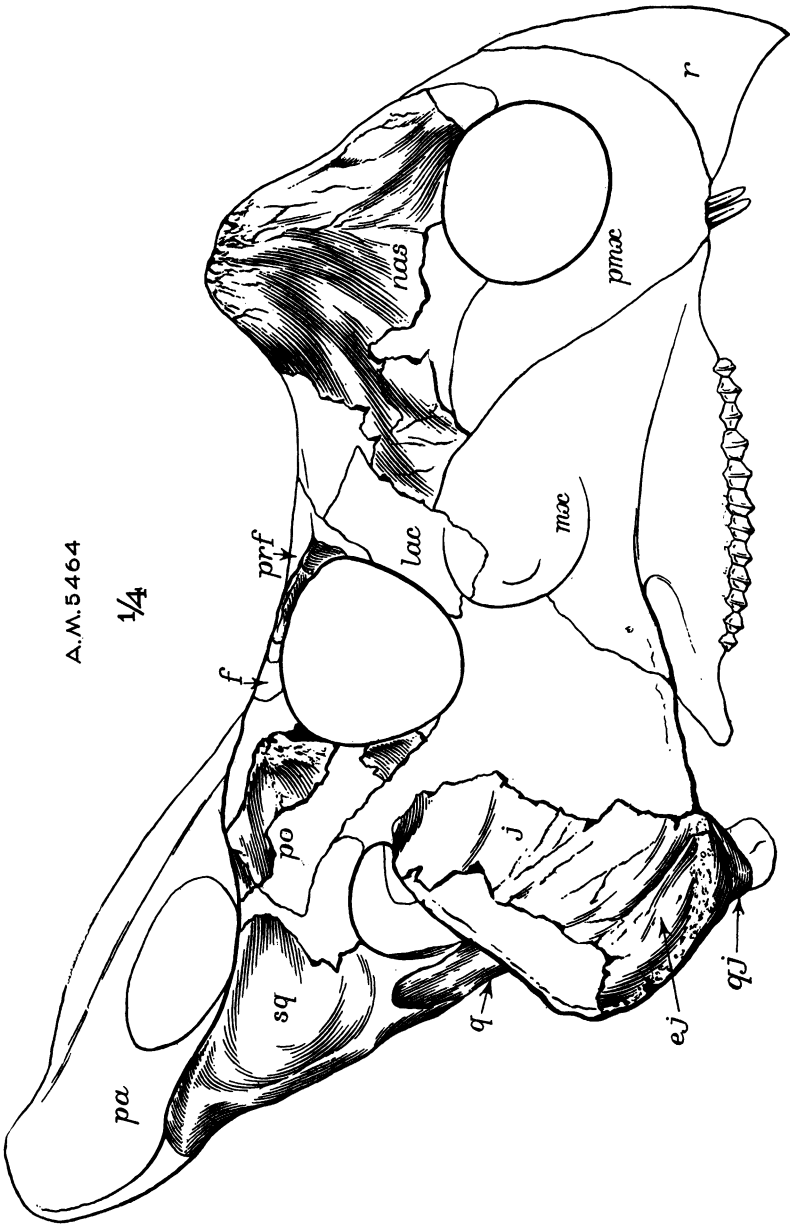


Fig. 1. Right lateral view of the restored skull of *Leptoceratops cerorhynchus*.

stage to form a pair of horn protuberances represents the beginning of the nasal horn-core in the ceratopsians. In this primitive form, however, these protuberances are separated by a fairly broad and shallow groove, and just how they merged along the median line to form the closely appressed halves of the *Brachyceratops* horn-core is not entirely clear. How this probably was accomplished is shown by *L. cerorhynchus*. The nasal has grown upward and inward, and on the mesial surface, extending down about a half-inch from the apex, there is a zone which shows the beginning of a union with the horn-core of the opposite side. Below this, the surface of the horn-core is concave, and there still remains a considerable space between the two halves at their bases. This space, however, was beginning to be filled by the deposition of porous bone at the base of the horn-core. Posteriorly this bone presents low pillar-like structures, for strengthening, along the floor. These are the features which make the nasal of *L. cerorhynchus* such an ideal intermediate structural stage between that of *Protoceratops* and *Brachyceratops*.

The only portion of the maxillaries preserved is a small piece from the posterior end of the left which contains the roots of the last seven teeth. On its postero-inner surface there is a large and elongated sutural surface for articulation with the ectopterygoid, showing that that bone was probably as well developed as in *Protoceratops*. The preserved tooth roots show that the teeth were somewhat larger than in the type of *L. gracilis*.

Most of the orbital border of the right prefrontal is preserved. It shows that the orbit was proportionately large, as in *Protoceratops*, and on its anterior outer margin there is a large facet for a freely articulating palpebral.

Both frontals are represented by badly broken fragments. The left is the most complete and has a portion of the post-orbital suture united with it. On the ventral surface of the right frontal the sutural surface for contact with the laterosphenoid is completely preserved and is only partially present on the left. The latter, however, has a considerable portion

of the sutural surface for articulation with the parietal. The extent of the development of the parieto-frontal depression cannot be accurately determined. Its anterior border is partially preserved and is but slightly developed. This seems to suggest that it was not as deep as in the specimen described by Gilmore (1939:3). In all of its known features the frontal of *Leptoceratops* is very similar to that of *Protoceratops*.

A large portion of the right postorbital is preserved. It is considerably heavier than in any of the known *Protoceratops* skulls. Some of the dorsal border is broken away, but the remaining portion is unusually rugose. Deeply set in a groove in its postero-dorsal margin is the very tip of the dorsal projection of the squamosal. On its ventral surface there is a deep pit for the end of the vertical projection of the laterosphenoid.

The left squamosal is nearly complete, and more than half of the right is preserved. In its general form it is like that of *Protoceratops*. In detail, however, there are some marked differences. Antero-posteriorly it is relatively much shorter, and the anterior projection is considerably deeper. On its antero-ventral margin there is a part of the suture for articulation with the ascending wing of the jugal. Since the squamosal forms most of the superior border of the lateral temporal opening, it is evident that that opening was relatively smaller than in *Protoceratops*. Another difference in the squamosal of the two genera is that in *L. cerorhynchus* there is no extension behind the point where the anterior projection originates, and the posterior margin is broad and heavy. The relationship with the quadrate, the superior portion of which is preserved, is the same in both genera. The distal part of the blunt spur that extends down in front of the quadrate is broken off, but its limits are clearly shown on the preserved portion of the quadrate. It is quite certain that it was not in contact with either the quadratojugal or the jugal. Behind the pocket which receives the upper end of the quadrate a considerable amount of bone is broken away. Enough is preserved, however, to show that the

position of the distal end of the exoccipital, a small portion of which is present, was the same as in *Protoceratops*. It probably was still not in contact with the quadrate.

The shortness, the proportionately great depth, especially of the posterior region, the heaviness of the posterior region and the lack of extension behind the point of origin of the anterior branch are all progressive characters of the squamosal, and they strongly suggest that the frill was short and narrow. This is also suggested by the preserved portion of the parietals of the type of *L. gracilis*.

The posterior portion of the right jugal, the entire right quadratojugal and the epijugal are preserved. The jugal, compared with that of *Protoceratops*, is considerably heavier, and it possesses a very prominent and heavy posterior margin which protrudes behind the line of contact with the quadratojugal. Superiorly, a portion of the margin of the lateral temporal opening is preserved. The form of this margin and the position of the preserved part of the ventral border show that the jugal occupied a more erect position than in *Protoceratops*.

There is no evidence that the quadratojugal was in contact with the squamosal. It is co-ossified with the jugal above and is fully co-ossified with the epijugal below. There is only a slight development of the antero-inferior projection. In this respect it is more like the quadratojugal of the later ceratopsians than like that of *Protoceratops*. Also, in contrast to the latter, it is proportionately deeper and narrower. The increase in depth is correlated with a smaller lateral temporal opening, and its relative narrowness indicates that the jugals did not flare outwardly as much as in *Protoceratops*.

The epijugal is relatively quite large. It is completely co-ossified with the quadratojugal and partially with the jugal. It is very rugose and occupies a more posterior position on the jugal and quadratojugal than in *Protoceratops*.

LOWER JAW

The lower jaws of this specimen are represented only by the antero-ventral portion of the left dentary and the upper part of the coronoid process, part of the left

coronoid, part of the left surangular and the anterior portions of the splenials.

The symphyseal region of the dentary is heavy and was not overlapped as extensively by the predentary as in *Protoceratops*, or as in *Leptoceratops gracilis*. The ventral border is straight, and the preserved portion shows that the whole dentary was relatively long. These features are in contrast to the short dentary, with its very curved ventral margin of *L. gracilis*. The coronoid process, the anterior portion of the surangular and the coronoid have the same relationship as in *Protoceratops* and present no characters that are outstandingly different from those elements in that genus.

The splenial is very much heavier, somewhat more elongated and its anterior end is decidedly more massive than in *L. gracilis* or in *Protoceratops*.

VERTEBRAL COLUMN

All of the cervicals are completely preserved. As in all the known ceratopsians, the centra of the first three are entirely fused. The hypocentrum (intercentrum) in front of the atlas is rather completely co-ossified with the centrum of the atlas. In its general form it is very much like that of *Protoceratops*. Its lateral wings, however, extend farther up the anterior margin of the atlas, which is a somewhat more advanced character. Except for their greater robustness, the first three cervicals are very similar to those of *Protoceratops*, and are, therefore, very primitive. Nevertheless, they are slightly more progressive in the following characters: the neural arches are lower; they are more completely co-ossified; and the neural spine of the axis, although it has the antero-posteriorly expanded, hatchet-shaped form of that of *Protoceratops*, extends farther backward. (See Figs. 2 and 3.¹)

¹ Lull (1933: 80, Fig. 35) erroneously illustrated the first three cervicals of this specimen. He shows them as representing four vertebrae. Apparently his drawing was made from a photograph in which fracturing might be confused with sutures. There is absolutely no justification for his conclusion, since the sutural areas are clearly defined in the specimen. In addition to this, if his sketch were correct there would be no intervertebral foramen between vertebrae three and four, and the capitular facet on three would be located in the middle of the side of the centrum. These conditions are impossible in the anterior cervicals of ceratopsians.

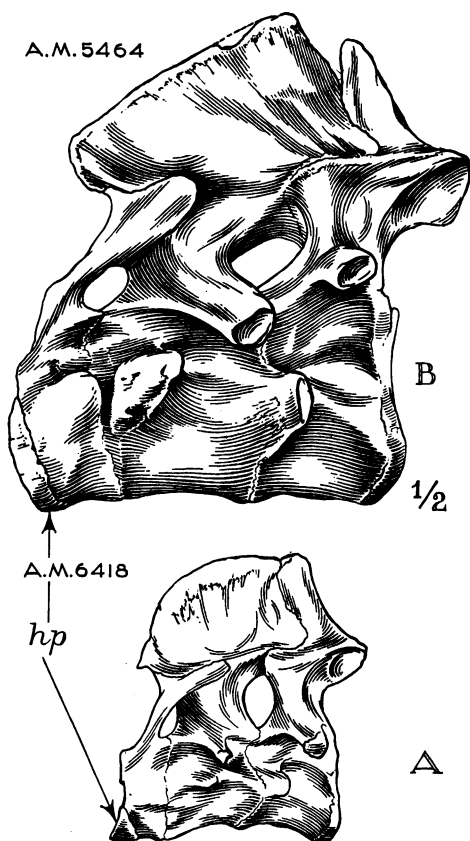
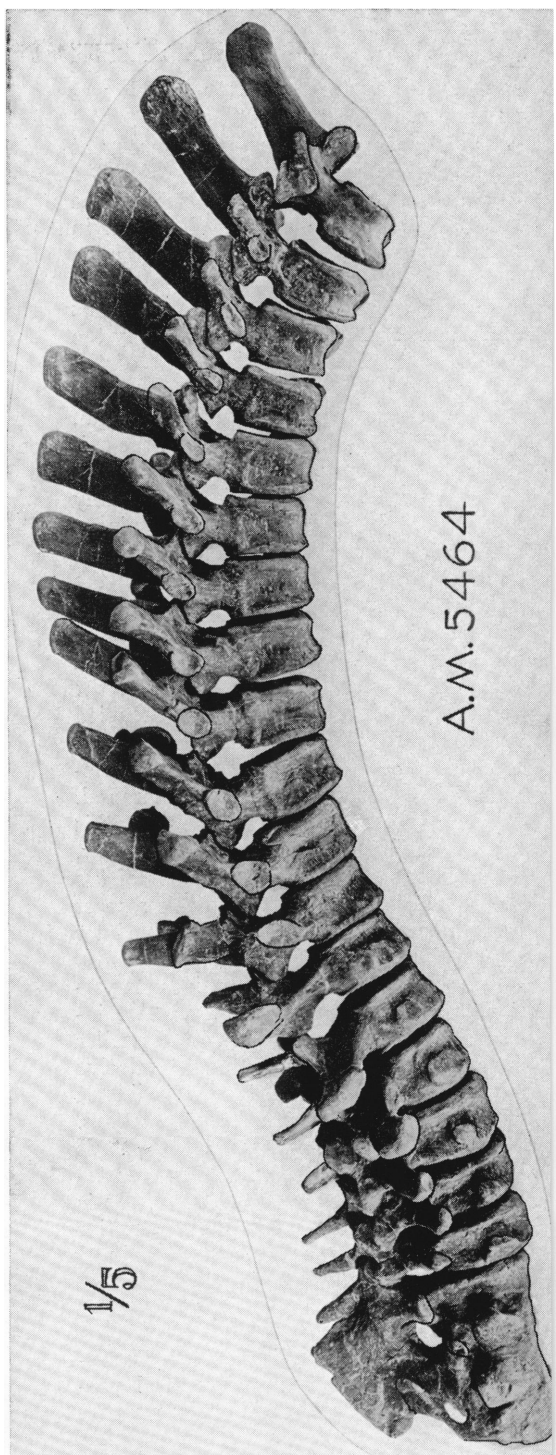


Fig. 2 (above). The first three cervical vertebrae of *Protoceratops andrewsi* (A) and *Leptoceratops cerorhynchus* (B); *hp* = hypocentrum (intercentrum).

Fig. 3 (right). The cervical and dorsal vertebrae of *Leptoceratops cerorhynchus*.



Cervicals four to nine are very similar to those of *Protoceratops* in their subequal size and in the lengths and directions of the transverse processes. In *Leptoceratops*, however, the ventral surfaces on all the centra are crest-like, whereas in *Protoceratops* this is the condition of cervicals four and five only.

The tenth vertebra in the column is con-

longer, and those of nine, ten and eleven have the greatest antero-posterior diameter instead of five, six and seven, as in *Protoceratops*.

2.—The neural spines and arches are more erect.

3.—The transverse processes are relatively longer, and on the posterior dorsals the capitular facets show a tendency to

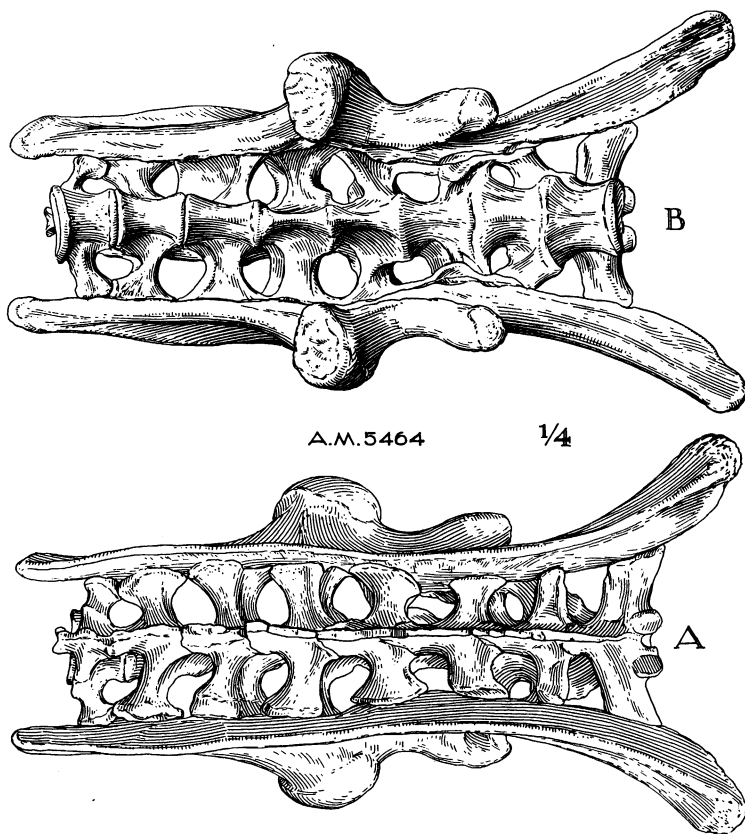


Fig. 4. *Leptoceratops cerorhynchus*. Dorsal (A) and ventral (B) views of the sacrum and ilia. Drawn by Erwin Christman.

sidered as the first dorsal since the capitular facet has shifted to the neural arch—a criterion for distinguishing the change from the cervical to the dorsals in all ceratopsians. Likewise, as in all known forms, the number of dorsals is twelve. They are very similar to those of *Protoceratops* except in the following features:

1.—The neural spines are relatively

migrate out on the ventral surfaces of those processes.

In characters 2 and 3 *Leptoceratops* is definitely more advanced.

The number of sacrals is eight. They are completely preserved except for the neural spines. Insofar as we can determine, this specimen is a fully adult individual. Therefore, eight sacrals probably

represent the maximum number for the genus. In most of its characters the sacrum of *Leptoceratops* most closely approximates that of *Protoceratops*. In several features, however, it is more progressive. The merged diapophysis and parapophysis on the sixth, seventh and eighth vertebrae are proportionately more robust. When seen from above, the greatest width is across the parapophysal ribs of the fourth "true" sacral vertebra (the 26th in the column, or the last of the four comprising the acetabular bar). This character is further emphasized in the later ceratopsians, giving the sacrum a definite oval outline in dorsal view, but in *Protoceratops* the greatest width is across the parapophysal ribs of the first "true" sacral vertebra (the 23rd in the column, or the first of the four comprising the acetabular bar). The prezygapophyses of the eighth sacral (sacrocaudal) are completely co-ossified with the postzygapophyses of the seventh sacral. In *Protoceratops* there is only a suggestion of this in the fully adult form.

Thirteen complete caudals and the centra of two others are preserved. The first of the series was found in articulation with the eighth sacral. On the basis of the development of the neural spines and transverse processes, and because of the size and proportions of the centra, the others are designated as the fourth, seventh, tenth and eleventh, fifteenth, sixteenth and seventeenth, twentieth, twenty-second, twenty-fourth, twenty-seventh and thirtieth in the restored series. The two centra, without arches and spines, are regarded as numbers thirty-eight and forty-one. The number comprising the entire series is considered as fifty-one. In arranging and restoring this series reference was also made to the partially complete caudal series of the type specimen of *Leptoceratops* (Amer. Mus. No. 5205) and to the several skeletons of *Protoceratops* in the American Museum collections. The caudal vertebrae in these two genera are very similar. This is shown especially by the tall and erect neural spines of the vertebrae in the mid-region of the series. In one important feature, however, the caudal vertebrae of *Leptoceratops* are more advanced than those of *Protoceratops*.

In the latter genus, in the anterior caudals the width, length and depth of each centrum are subequal, and from the twenty-fifth on, the centra are definitely longer than they are wide or deep. In *Leptoceratops* the centra of the last few caudals are still longer than they are wide or deep, but the others are wider and deeper than they are long—a character that is further emphasized in the later ceratopsians.

The neural spines of caudals eleven, fifteen, sixteen, seventeen, twenty and twenty-two show an ankylosis that is undoubtedly the result of an injury which is also reflected in the ischium described below.

RIBS

On the right side the first three and the eighth cervical ribs, and dorsals eight and twelve are missing. On the left side the first cervical, and the third, fourth, eighth, eleventh and twelfth dorsals were not preserved. All of the others are complete and are very much like those of *Protoceratops* except that the dorsal ribs are relatively longer—a feature even more pronounced in the later ceratopsians.

APPENDICULAR SKELETON

Unfortunately the pectoral girdle and both front limbs of this specimen are not preserved. Fortunately, however, the pectoral girdle and fore limb are almost completely preserved in the type specimen of *L. gracilis*, and enough of the hind limb of that specimen is preserved—supplemented by a complete tibia, fibula and hind foot of another specimen in the U. S. National Museum (Gillmore, 1939: 6-10)—to determine the characters of the pectoral girdle and the relative proportions of the fore and hind limbs. We have restored, therefore, the pectoral girdle with the same characteristics as shown in the type specimen of *L. gracilis* except for size. This specimen is considerably larger than the type of *L. gracilis*. As shown by the known material, the fore limb of *Leptoceratops* is almost three-fourths the length of the hind limb. In *Protoceratops* the fore limb is hardly more than one-half the length of the hind limb. *Leptoceratops*,

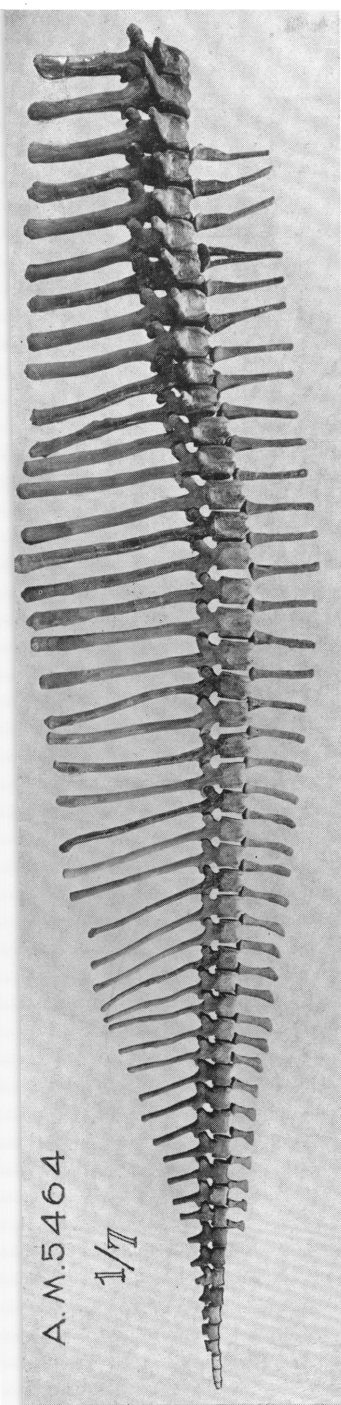


Fig. 5. Caudal vertebrae of *Leptoceratops cerorhynchus*.

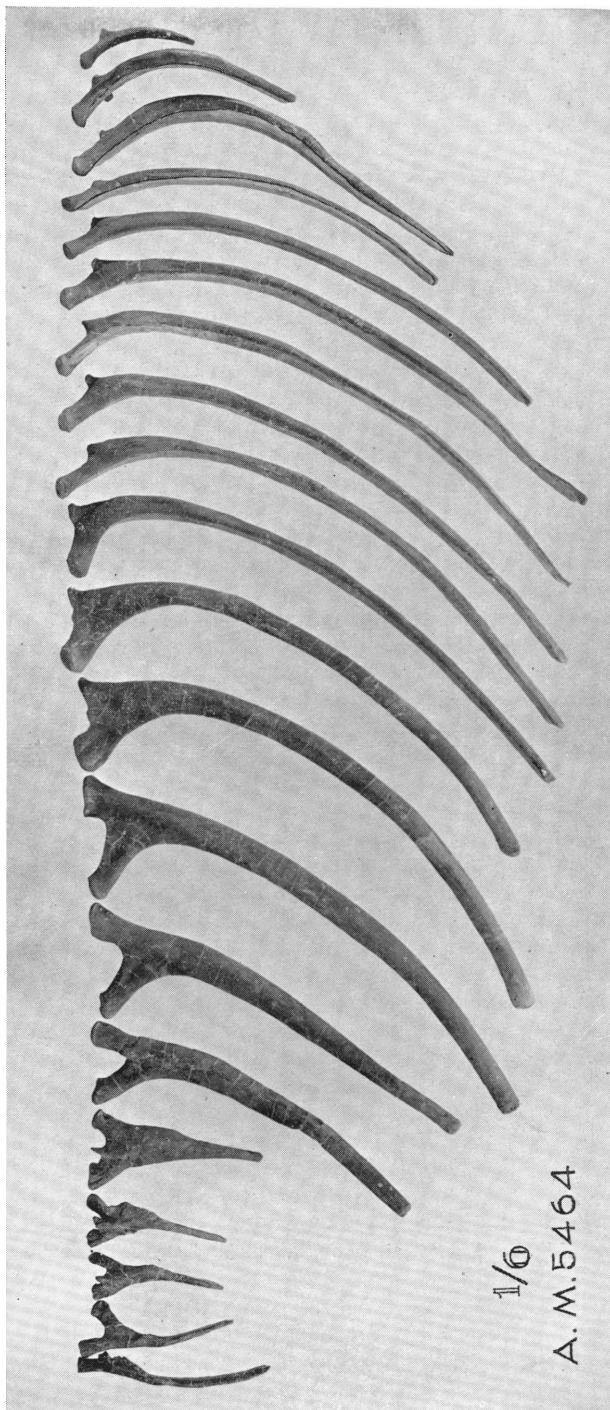


Fig. 6. *Leptoceratops cerorhynchus*. Cervical and dorsal ribs of the left side.

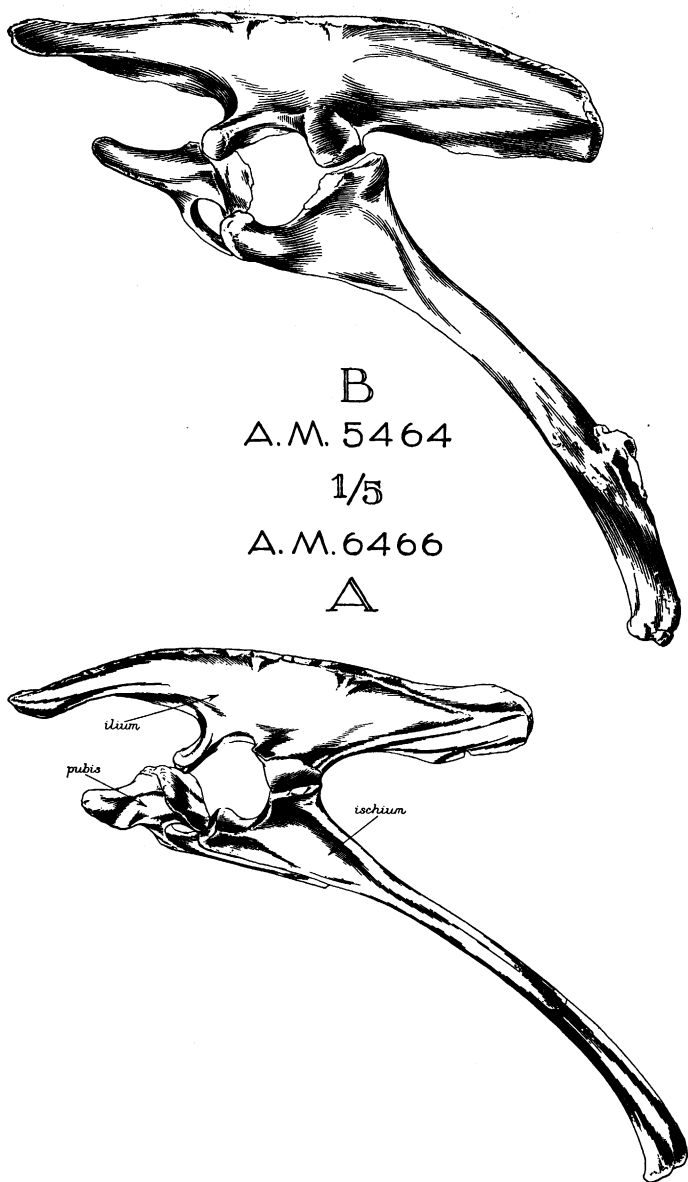


Fig. 7. Lateral views of the pelvic girdles of *Protoceratops andrewsi* (A) and *Leptoceratops cerorhynchus* (B).



Fig. 8. *Leptoceratops cerorhynchus*. Anterior views of the left femur and the left tibia and fibula with the astragalus and calcaneum attached.

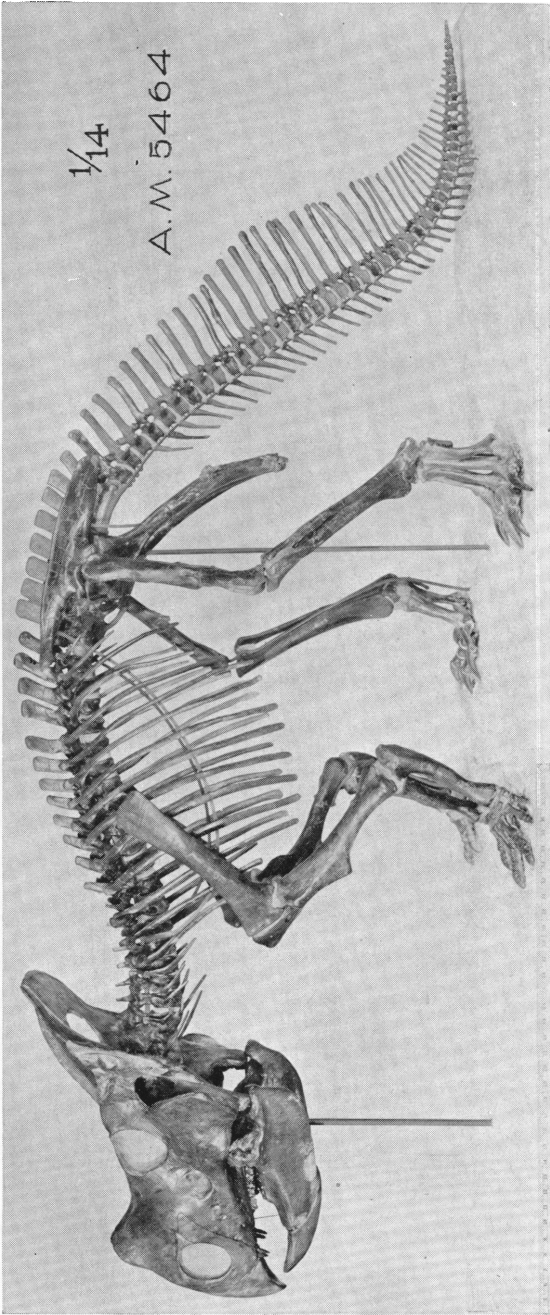


Fig. 9. *Leptoceratops cerorhynchus*. Left view of the mounted skeleton.

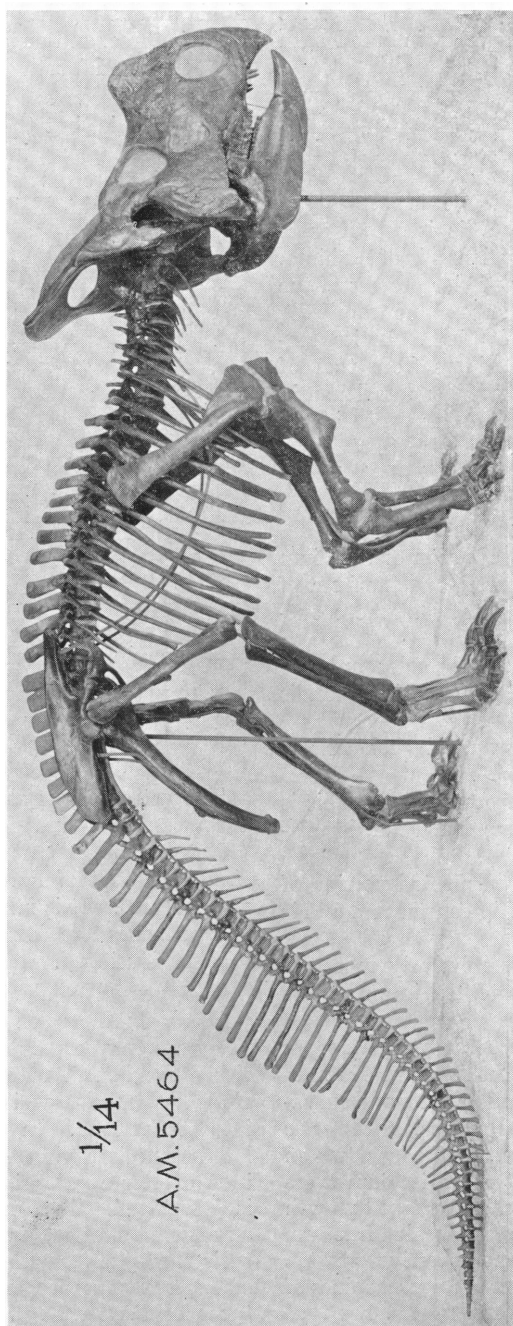


Fig. 10. *Leptoceratops cerorhynchus*. Right view of the mounted skeleton.

therefore, is definitely more advanced in this character, for in the more progressive ceratopsians the discrepancy in limb length is even less.

The pelvic girdle is completely preserved except for the right pubis and the distal part of the right ischium. Although it is more progressive than that of *Protoceratops* in a number of characters, it is decidedly of the primitive type. This is shown especially in the erect dorsal margin of the ilium, the relatively small anterior process of the pubis and the quite long and not markedly downwardly curved ischium. In its general form the ilium differs from that of *Protoceratops* in the straighter dorsal margin and in the relatively greater depth of the posterior projection. The main features in which the entire pelvic girdle is in advance over that of *Protoceratops* are as follows (see Figs. 4 and 7):

- 1.—The anterior projection of the ilium is more outwardly curved, and the front of its dorsal margin is somewhat more outwardly turned.

- 2.—The ilium has a broader anterior ventral shelf for the pubo-ischio-femoralis internus.

- 3.—The posterior ventral shelf of the ilium is better developed.

- 4.—The anterior process of the pubis is less dorso-ventrally expanded and is relatively longer.

- 5.—The posteriorly deflected portion of the pubis is more lightly constructed and is very much shorter.

- 6.—The ischium is relatively more robust, is somewhat shorter and is much more downwardly curved.

In spite of these progressive characters, the pelvic girdle is most like that of *Protoceratops* except in the robustness and curvature of the ischium, in which it is closer to that of *Brachyceratops*. Quite far down on the outer surface of the left ischium there is a rather large, irregularly shaped growth of bone which lies across a healed fracture. This, together with the excessive growths and healed fractures on the neural spines of some of the caudal vertebrae, shows that the animal suffered a severe injury.

The hind limbs of this specimen are represented by both femora; the left tibia,

fibula and astragalus; the second phalanx of digit three, and ungual phalanges of the first, third and fourth digits of the left foot.

As in *Protoceratops* the femur is shorter than the tibia, but the discrepancy is less than in that genus, indicating that *Leptoceratops* is more advanced in this character (see Brown and Schlaikjer, 1940b: 240).

As shown by us (1940b: 242), the femur of *Leptoceratops* is closest to that of *Protoceratops* but shows a definite tendency in the direction of the later ceratopsians in most of its characters. This is especially shown in its greater robustness and in its proportionate increase in length.

In general form the tibia is very similar to that of *Protoceratops*, but it is somewhat more advanced in most of its important features. Although it has been crushed, its proximal and distal extremities are more expanded, it is relatively somewhat shorter and it is decidedly more robust.

The fibula is of the long and slender type. It is, however, more robust, and its distal end is more expanded and less flattened than in *Protoceratops*. In these characters it is intermediate between the fibulae of that genus and *Brachyceratops*.

The astragalus is almost identical with that described and figured by Gilmore (1939: 7) except that it is larger. It is similar to that of *Protoceratops* except in two features. It is relatively smaller, and the median antero-dorsal projection is only slightly developed.

The ungual phalanges are elongated, pointed, and arched antero-posteriorly. They are transversely convex, and posteriorly the lateral margin of each has an elongated groove which leads anteriorly into a foramen. In *Protoceratops* each lateral margin is pierced by a foramen, and in the later ceratopsians an open notch is developed. The condition in *Leptoceratops*, therefore, is intermediate. In their claw-like form the ungual phalanges of *Leptoceratops* are more primitive than those of *Protoceratops*. This is the only important feature, however, in which *Leptoceratops* is the more primitive.

MEASUREMENTS

Length of ilium.....	407 mm.	trochanter to bottom of external condyle.....	331
Depth of ilium at ischiac peduncle....	107	Length of tibia.....	355
Length of posteriorly-deflected portion of pubis from anterior margin of obturator foramen.....	47	Greatest width of proximal end of tibia	120
Total length of pubis.....	118	Greatest width of distal end of tibia...	102
Length of ischium.....	422	Length of fibula.....	318
Maximum length of femur.....	346	Length of phalanx I ² left hind foot..	56
Length of femur from top of greater		Length of phalanx III ² left hind foot..	33
		Length of phalanx III ⁴ left hind foot..	68
		Length of phalanx IV ⁶ left hind foot..	61

CONCLUSION

From the available *Leptoceratops* material consisting of the type and the associated specimen from the Edmonton formation of Alberta, the two fragmentary specimens from the Two Medicine formation of Montana described by Gilmore, and the skeleton of *L. cerorhynchus* from the St. Mary River formation of Montana described above, we now know a considerable part of the skull and lower jaws and all of the post-cranial skeleton except some of the caudals. As shown by all of its known characters, *Leptoceratops* is unquestionably closer to *Protoceratops* than to any of the other known ceratopsians. This fact was first recorded by Gregory and Mook (1925) who placed the two genera in the family

Protoceratopsidae, extending the characters of this family first established by Granger and Gregory (1923). They have been followed in this by Lull (1933: 74), Gilmore (1939: 1) and others. As a result of our extensive study of *Protoceratops* it became necessary to modify and extend the Gregory-Mook definition of the family, and we listed twenty-six outstanding characters in our definition (1940b: 256-259), all of which are primitive for the ceratopsians. Insofar as the known material shows, *Leptoceratops* is also distinct from the Ceratopsidae in all of these characters, but in all of them this genus is slightly more progressive than *Protoceratops*.

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