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A NEW ELEMENT IN THE CERATOPSIAN JAW WITH ADDITIONAL NOTES ON THE MANDIBLE

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INTRODUCTION

During the preparation of the type skeleton of *Styracosaurus parksi*, our able laboratory assistant, Mr. Otto Falkenbach, discovered that the best preserved lower jaw possessed several weathered fragments in the region of the mandibular fossa that did not conform to any part or parts of the well-known elements in the ceratopsian mandible. A comparative study of these fragments has led to a reëxamination of all the ceratopsian material in the American Museum, and a number of the best preserved specimens in the National Museum, in the Peabody Museum of Natural History, Yale University, and in the Royal Ontario Museum of Paleontology. In addition, the mandibles of other dinosaurs in the American Museum, especially of *Plateosaurus* and *Tyrannosaurus*, have been restudied.

This investigation has resulted in the discovery of an intercoronoid—a primitive reptilian jaw element—not previously recognized in the Ceratopsia. Also, a clearer understanding of several of the other jaw elements is now possible, and a better interpretation of several dominant features of the whole ceratopsian mandible can now be given. These results are incorporated in this paper.

With the exception of the wonderful collection of *Protoceratops* from Mongolia, recently monographed by us (1940), most of the known ceratopsian material represents adult individuals, and few of the specimens have come down to us in perfect condition. Moreover, in most specimens the sutures are obscured by age, and it is extremely difficult to distinguish them from fractures. It is, therefore, only by careful and tedious preparation that certain elements of the jaw can be separated. Mr. Falkenbach has most skillfully disarticulated and re-prepared several specimens in the American Museum and National Museum collections, thus making it possible to study in detail, and to figure the intercoronoid and the other jaw elements, some of which have not been figured previously in their entirety.

Drawings shown in Figs. 4, 5, and 12 were made by Alastair Brown. All of the other illustrations were made by John C. Germann.

COMPARATIVE STUDY OF CERTAIN LOWER JAW ELEMENTS

In the Monograph on the Ceratopsia (Hatcher, Marsh, and Lull, 1907, p. 39), the ceratopsian lower jaws are said to be composed of eleven elements—dentary, splenial, angular, surangular, and articular which are paired, while the eleventh or predentary, is single and median in position, articulating with both rami. On page 137 of this same Monograph, an additional paired element, the coronoid, is just mentioned and is poorly figured. Also, the prearticular and articular are combined and designated as the articular. The prearticular, however, has subsequently been recognized in the Ceratopsia (von Huene, 1911, p. 161) but it has not been described, nor has it been adequately figured.

As a result of our study, the ceratopsian lower jaws are now known to be composed

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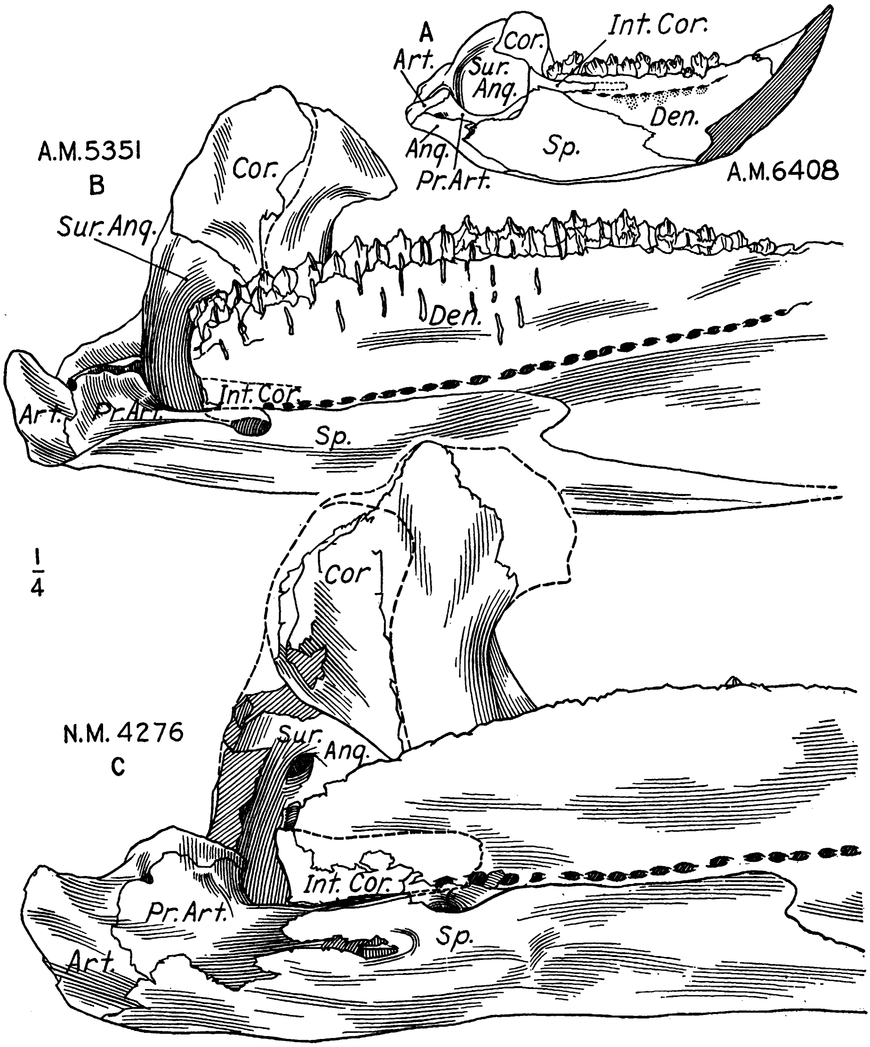

Fig. 1. Internal views of left mandibles. A, *Protoceratops andrewsi*. B, *Monoclonius nasicornus*. C, *Triceratops sulcatus*.
ang, angular; *art*, articular; *cor*, coronoid; *den*, dentary; *int cor*, intercoronoid; *pr art*, prearticular; *sp*, splenial; *sur ang*, surangular.

of seventeen elements. These are: the single predentary; and the dentary, angular, surangular, articular, prearticular, splenial, coronoid, and intercoronoid, all of which are paired.

In the later ceratopsians the articular, prearticular, and surangular are very intimately associated and tend to fuse at an early age. Likewise, the intercoronoid tends to fuse with the dentary and coronoid, but the splenials, angulars, and coronoids unite with other elements along squamose sutures with smooth surfaces that readily separate from each other. In *Protoceratops* there is very little fusing of the jaw elements, which are, therefore, perfectly distinct even in the very old individuals.

The salient changes which take place in the evolution of the ceratopsian mandi-

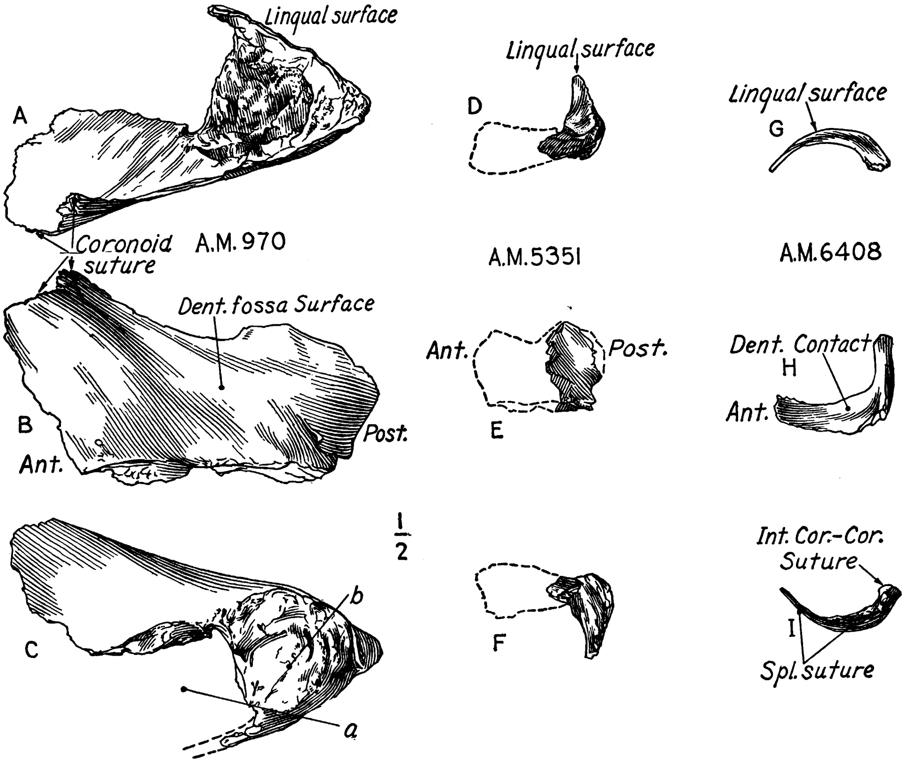

Fig. 2. Dorsal, lateral, and ventral views of the intercoronoids of *Triceratops serratus*, A–C; *Monoclonius nasicornus*, D–F; and *Protoceratops andrewsi*, G–I.

ble from the primitive *Protoceratops* stage to *Triceratops* of the late Cretaceous are given in the discussion which follows, and are for the most part illustrated by the three stages—*Protoceratops*, *Monoclonius*, and *Triceratops*—shown in Fig. 1.

Intercoronoid

This is the smallest element in the mandible and has not been recorded previously in any of the ceratopsians. It is well preserved in many of the *Protoceratops* specimens, and is also known in *Monoclonius*, *Styracosaurus*, and *Triceratops*. In *Protoceratops* it is a thin, narrow element that suturally unites with the ventral projection of the coronoid, extends around back of the alveolar portion of the dentary just behind the last alveolus, and continues forward along the inner alveolar border for one-half the length of the tooth row. Postero-internally it is in contact with the dorsal projection of the splenial, and a small ventral spur extends down behind this projection and nearly meets the prearticular.

In the later ceratopsians, the form and position of the intercoronoid have been altered somewhat. This change results mainly from the posterior extension of the alveolar portion of the dentary, which takes place as the vertical rows of teeth increase in number. In *Protoceratops* its posterior margin lies inward from and in front of the coronoid in the young, and opposite the middle of the coronoid in the fully adult, whereas in *Triceratops* the position of the posterior margin is behind or under the back of the coronoid. By this change in position the form of the intercoronoid has been quite altered. In *Protoceratops* it does not unite with the prearticular, whereas in *Triceratops* it not only unites with the prearticular, but overrides that

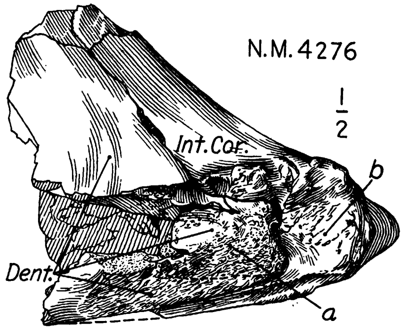

Fig. 3. *Triceratops sulcatus*. Ventral view of the posteriorly extended alveolar portion of the dentary in contact with the intercoronoid.
a, and *b*, sutural surfaces for articulation with the prearticular; *dent*, dentary; *int cor*, intercoronoid.

element half way back to the posterior margin. In accomplishing this change the ventral spur of the intercoronoid that projects down toward the prearticular in *Protoceratops* is undoubtedly the portion that later folds under the extended portion of dentary forming the floor which intervenes between that element and the prearticular. The whole posterior portion of the intercoronoid of *Triceratops*, therefore, has become cup-shaped enclosing the posterior end of the dentary while in *Protoceratops* the whole element is bar-shaped. (See Figs. 2, 3, 10, and 11.)

In *Styracosaurus* (A. M. No. 5372), only the anterior one-third of the intercoronoid is preserved. Its relationship to the exact number of vertical tooth rows cannot be determined because the posterior end of the dentary is broken away, but it extended forward below at least six. In *Monoclonius* (A. M. No. 5351), only that portion lying between the prearticular and the dentary is present. Enough is preserved, however, to show that it occupies relatively the same position as in *Triceratops*, although it is somewhat more primitive, being quite intermediate between the intercoronoid in that genus and in *Protoceratops*.

Previously, the intercoronoid was regarded as a jaw element which was present only in some of the early amphibians of the Carboniferous, and only in a very few of the earliest and most primitive reptiles.

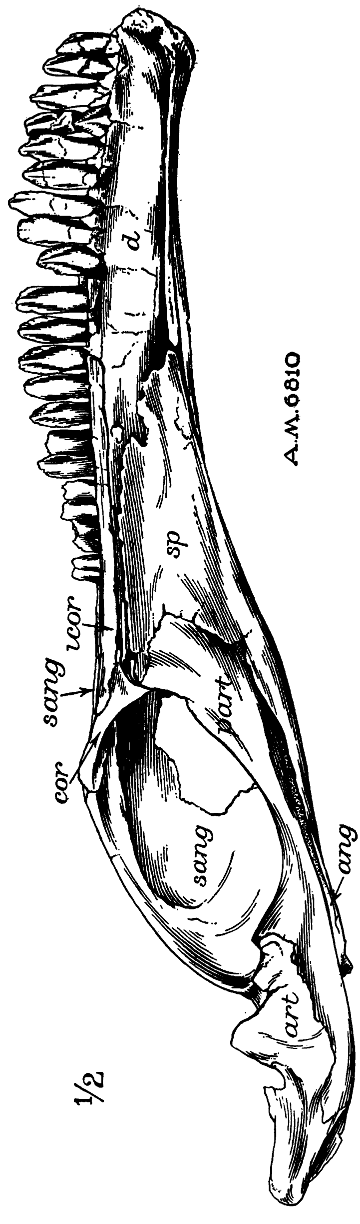

Fig. 4. Internal view of the left mandible of *Plateosaurus*.
ang, angular; *art*, articular; *cor*, coronoid; *d*, dentary; *icor*, intercoronoid; *part*, prearticular; *sang*, surangular; *sp*, splenial.

It might seem, therefore, somewhat of an innovation to regard this newly discovered element in the rather highly specialized ceratopsian lower jaw as the intercoronoid. At least, it would certainly seem so to those paleontologists who hold to the dictum that an intercoronoid cannot occur in a reptile later than Permian in age. The evidence now at hand, however, leaves no doubt as to the homology of this element. Not only does it have exactly the same relationship with other lower jaw elements in the ceratopsians as does the intercoronoid with the other lower jaw elements in the amphibians and early reptiles, but it is also present, and has that same relationship, in one of the earliest and most generalized of all the dinosaurs—*Plateosaurus*. This element is almost completely preserved in the unusually complete skeleton of that genus (No. 6810) in the American Museum collections. In this archaic form, the coronoid is quite small and is firmly in contact antero-inferiorly with the prearticular and the splenial. The intercoronoid is especially well developed. It overlaps the coronoid for nearly half the length of that element and extends forward along the inner alveolar border as a narrow thin bone for over half the length of the tooth row. The anterior end is broken, which indicates that it probably continued even farther forward than the preserved portion shows. A considerable portion of the inferior border is in contact with the splenial. (See Fig. 4.) This element was neither mentioned nor figured by von Huene in his Monograph on *Plateosaurus* (1926, p. 19, Pl. I) probably because the specimens which he studied were incompletely preserved.

An intercoronoid is also present in at least one of the described carnisaurians. In his description and figure of the lower jaw of *Tyrannosaurus*, Osborn (1912, p. 24, Fig. 18) regarded the element along the internal alveolar border, which suturally unites with the coronoid posteriorly, and with the splenial postero-inferiorly, as the "supradentary." This has a relationship with the other jaw elements that is typical of the intercoronoid in *Plateosaurus* and in the ceratopsians, and is undoubtedly homologous with that element. (See Fig. 5.)

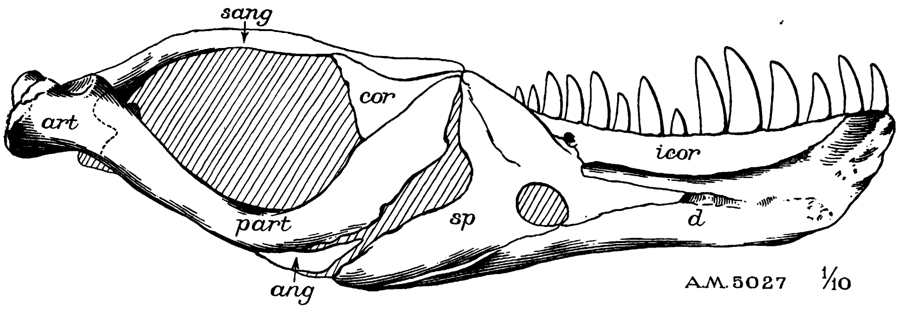

Fig. 5. Internal view of the left mandible of *Tyrannosaurus rex*. Modified from Osborn.

Coronoid

In *Protoceratops* the coronoid is relatively very large. The upper portion is very much expanded antero-posteriorly. Superiorly the anterior margin extends to, or nearly to, the front of the coronoid process of the dentary, and the posterior margin extends back behind that process and overlaps the inner surface of the surangular. The posterior portion of the coronoid and the coronoid process of the dentary, therefore, form a pocket into which the upper portion of the front of the surangular fits securely, as in all ceratopsians, although more extensively so than in the later forms. The superior margin projects slightly above the coronoid process of the dentary, and shows markings, as does the whole of the inner surface of the expanded portion, of the capiti-mandibularis muscle insertion. Ventrally the coronoid narrows abruptly where it curves inward to meet the intercoronoid behind, and just outside the last

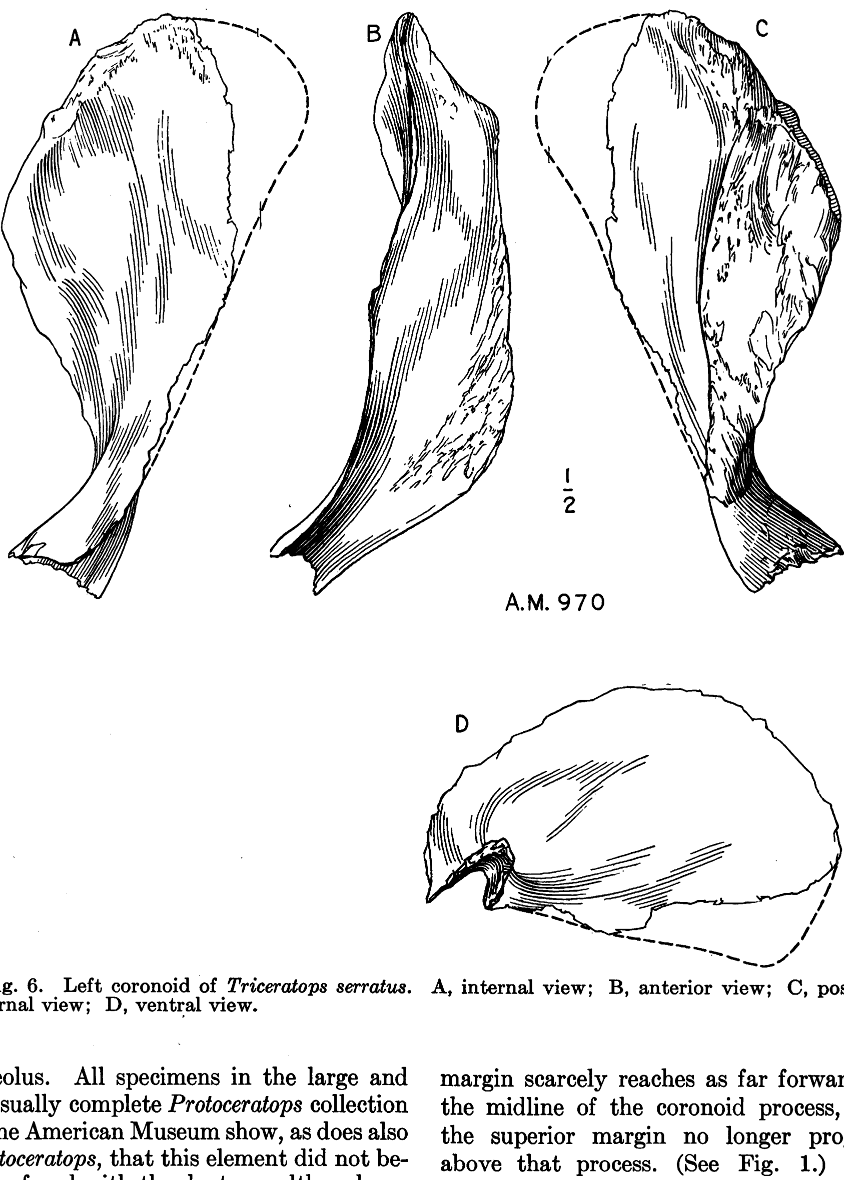

Fig. 6. Left coronoid of *Triceratops serratus*. A, internal view; B, anterior view; C, postero-external view; D, ventral view.

alveolus. All specimens in the large and unusually complete *Protoceratops* collection in the American Museum show, as does also *Leptoceratops*, that this element did not become fused with the dentary, although occasionally in a fully adult individual there is a tendency for it to become fused with the intercoronoid.

In the later ceratopsians, three main changes take place in the coronoid. There is a proportionate reduction in size; the ventral portion is deflected backward (see Fig. 6); and the whole element shifts posteriorly so that in *Triceratops* the anterior margin scarcely reaches as far forward as the midline of the coronoid process, and the superior margin no longer projects above that process. (See Fig. 1.) The coronoid of *Monoclonius* is quite intermediate in these features between that of *Protoceratops* and of *Triceratops*. (See Figs. 1 and 7.) These changes are interrelated with the posterior extension of the alveolar portion of the dentary and the clear demarcation of the coronoid process, the antero-posterior expansion of its summit, and of its erect position.

Splenial

The splenial of *Protoceratops* is proportionately short and very deep posteriorly. Throughout most of its length, it extends down to, or nearly to the ventral margin of the mandible. The postero-dorsal projection unites above for a short distance with the intercoronoid, and with the latter forms a covering over the last few foramina on the inner side of the dentary. On the back slope of this projection there is a shallow notch that forms the inferior margin of the internal mandibular foramen. Posteriorly it covers over only the anterior portions of the prearticular and the angular. These all seem to be primitive features, for

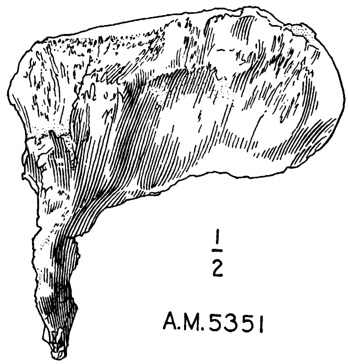

Fig. 7. External view of the right coronoid of *Monoclonius nasicornus*.

in the more progressive ceratopsians, *Monoclonius*, *Styracosaurus*, and *Triceratops* (see Figs. 1, 8, 9, and 10), the splenial becomes considerably modified, especially in the following features:

1.—As the alveolar portion of the dentary extends back and increases in depth, the splenial becomes shallow posteriorly.

2.—With the above-mentioned modification of the dentary, the postero-dorsal projection is carried downward and backward so that the internal mandibular foramen is almost entirely enclosed by the splenial.

3.—Posteriorly it extends back and unites with the articular, thus entirely eliminating the angular and the ventral portion of the prearticular from the lingual surface of the mandible. (See Figs. 10 and 11.) This change met the demand for greater strengthening in the region of the mandible when it assumed a more horizontal position instead of the upwardly curved form as in *Protoceratops* and *Leptoceratops*. Apparently this straightening of the posterior part of the mandible was controlled by the more vertical pull of the jaw muscles, as was also the high, clearly demarcated, erect coronoid process of the dentary.

Dentary, and the Supposed Nutrient Foramina for the Teeth

In *Protoceratops* the dentary is relatively shorter and deeper than in any other known ceratopsian. The ventral border is nearly straight in the young jaw, but with age it becomes sweepingly curved downward. This curving is reflected in the whole element and continues back onto the angular. It seems to be related to the relative increase in length of the predentary, the deepening of the skull, and the more upright position of the frill which changes the direction of pull on the mandible in the adult and old skulls.

The coronoid process is low and narrow, and is set only a short distance out from the tooth row. Down a short distance from the inner alveolar margin there are a series of foramina—one for each vertical series of teeth—which are connected by a shallow groove on the lingual surface of the dentary. The last few of these (usually three) are covered over by the postero-ventral portion of the intercoronoid and the dorsal projection of the splenial. Those that are covered over are just as well developed as those that are not; however, the foramina are largest under the largest teeth. These characteristics are also true of the later ceratopsians although usually more of the foramina are covered over by the intercoronoid.

The function of these foramina is somewhat questionable. Two theories have been presented concerning this point, the most popular of which is that they ". . . doubtless served for the transmission of nerves and nutrient blood vessels to the teeth" (Hatcher, Marsh, and Lull, 1907, p. 41). This explanation seems extremely questionable, for such a condition would necessitate the presence of a nerve and blood

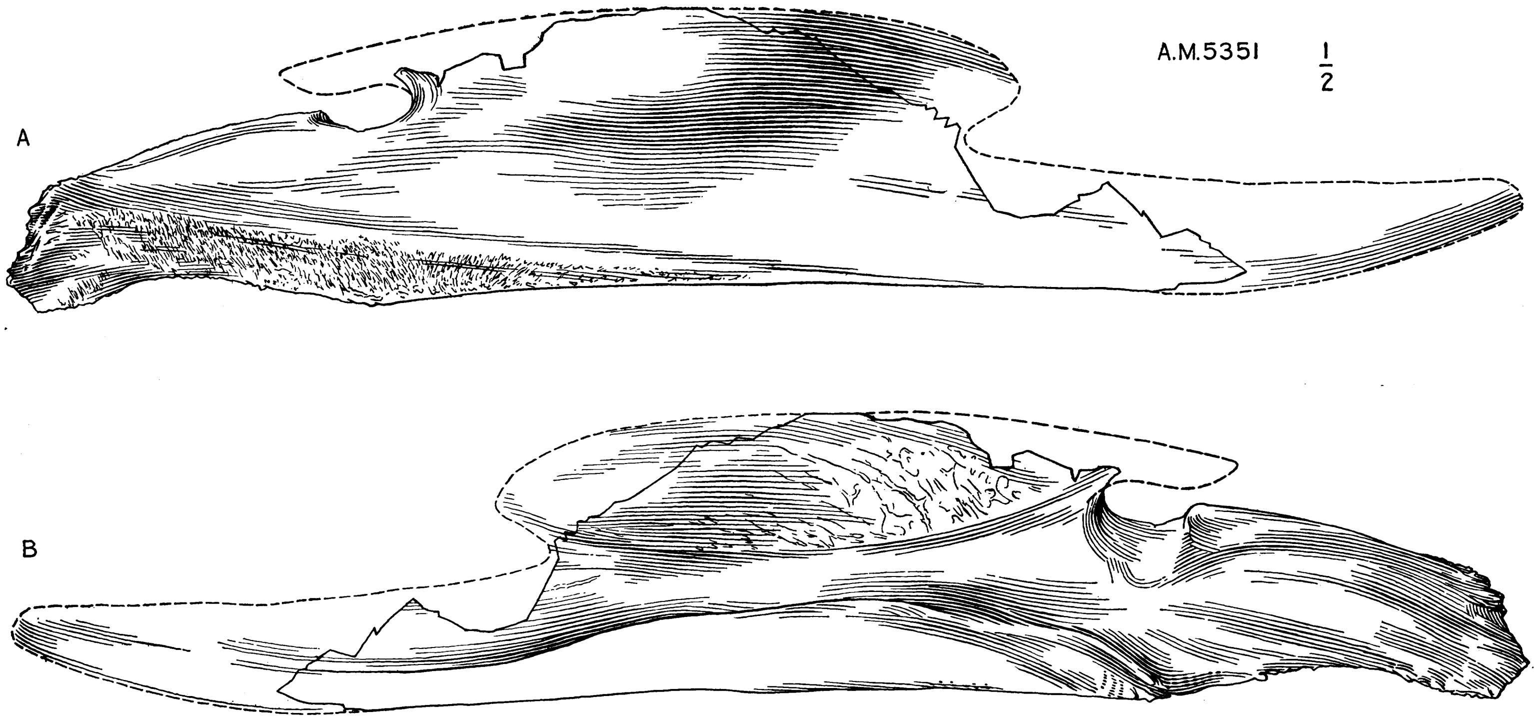

Fig. 8. Left splenial of *Monoclonius nasicornus*. A, internal view; B, external view.

vessel arrangement entirely foreign to any other known reptile. Furthermore, the Mechelian orifice is well developed and its boundary in no way suggests that this opening did not transmit the required supply of nerves and blood vessels in the customary manner. Another theory is: "... that the foramina were for the infolding of the mucous membrane from which the tooth papillae were formed and which could no longer fold in, in the ordinary manner, because of the great depth of the dental chamber which contains the magazine of teeth." (See footnote, Hatcher, Marsh, and Lull, 1907, p. 26.) This theory is highly improbable because such a condition is unknown in any recent form, and, as stated above, the posterior foramina are so completely covered over by the splenial and the intercoronoid that no such infolding could possibly have taken place. These two suggestions, therefore, seem entirely inadequate.

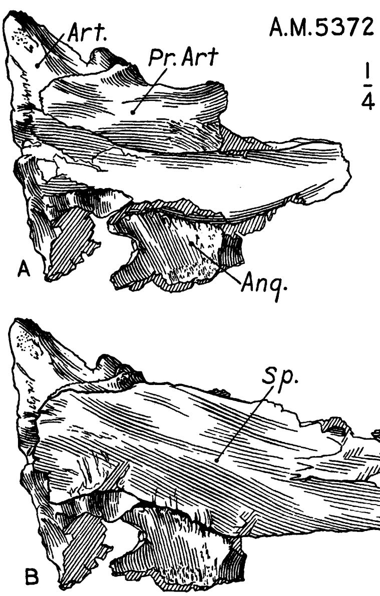

Fig. 9. Portions of the articular, prearticular, angular, and splenial of *Styracosaurus parksi*. A, internal view with the posterior part of the splenial removed; B, internal view with the posterior part of the splenial in place.

In considering the function of these openings, several facts should be kept in mind. First, the openings are proportionately very much larger in the young individual. For example, in one unique specimen, A. M. No. 6499—a right dentary of an unhatched individual[1]—the openings are one-half as large as they are in an almost fully adult specimen (as No. 6466), while the dentary is but one-tenth as large! Moreover, the groove on the surface connecting the openings is absent, and the openings are rounded instead of oval-shaped as in the older individuals. Second, the openings are serially arranged—one for each vertical series of teeth. Third, the openings seem to be larger under the larger teeth in both the young and older individuals. Fourth, openings are present, and are relatively just as large, under the postero-ventral portion of the intercoronoid and the dorsal projection of the splenial. Fifth, the openings are connected by a shallow groove on the surface of the bone (absent in the unhatched and extremely young individuals), which is especially well developed where the openings are covered by the intercoronoid and splenial.

Another important point is the search for analogous structures among living reptiles. In the Crocodilia, especially in the alligator, such openings do occur (see Fig. 12) and they are, we believe, analogous in function to those in the dentaries of the ceratopsians. They do not, however, correspond exactly in number to the number of teeth. A thorough dissection of the mandible of *Alligator mississippensis*, performed by Anatomist H. C. Raven, shows that these foramina are primarily for the emission of branches of the mandibularis which innervate the skin and membrane along the inner side of the jaw, and secondarily for a vascular system that supplies those structures. That the openings in the dentaries of the ceratopsians had the

[1] It is certain that this dentary is that of an unhatched individual. Five teeth, unworn, and each having the incipient form of a functional tooth, are deep set in their alveoli. There is a low thin ridge of bone, not present in any individual with functional teeth, along the outer alveolar border that overhangs the alveoli somewhat, and bears only slight alveolar markings on its upper surface. The teeth, therefore, were not erupted. The estimated size of this individual, based on the proportions of the beautifully preserved skull, jaws, and skeletal parts of a very young specimen, A. M. No. 6419, could not have been larger than one of the medium sized eggs found with *Protoceratops*.

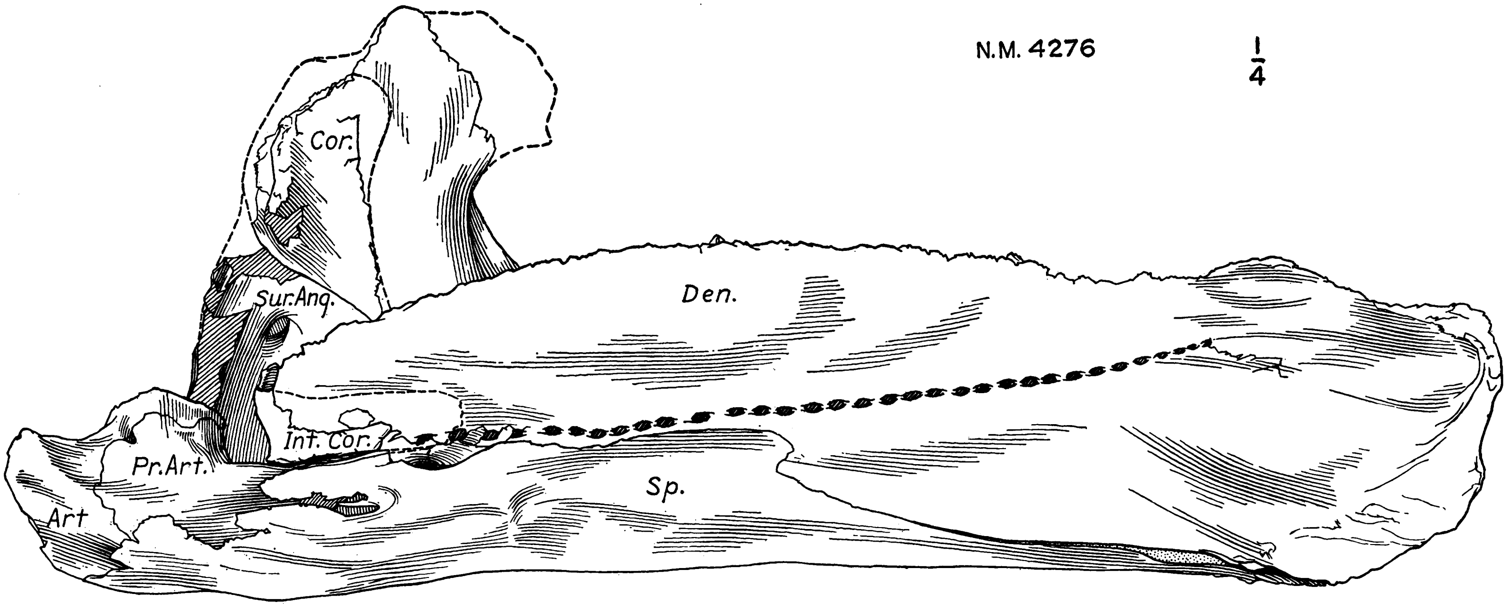

Fig. 10. Internal view of the left mandible of *Triceratops sulcatus*. *int cor*, intercoronoid.

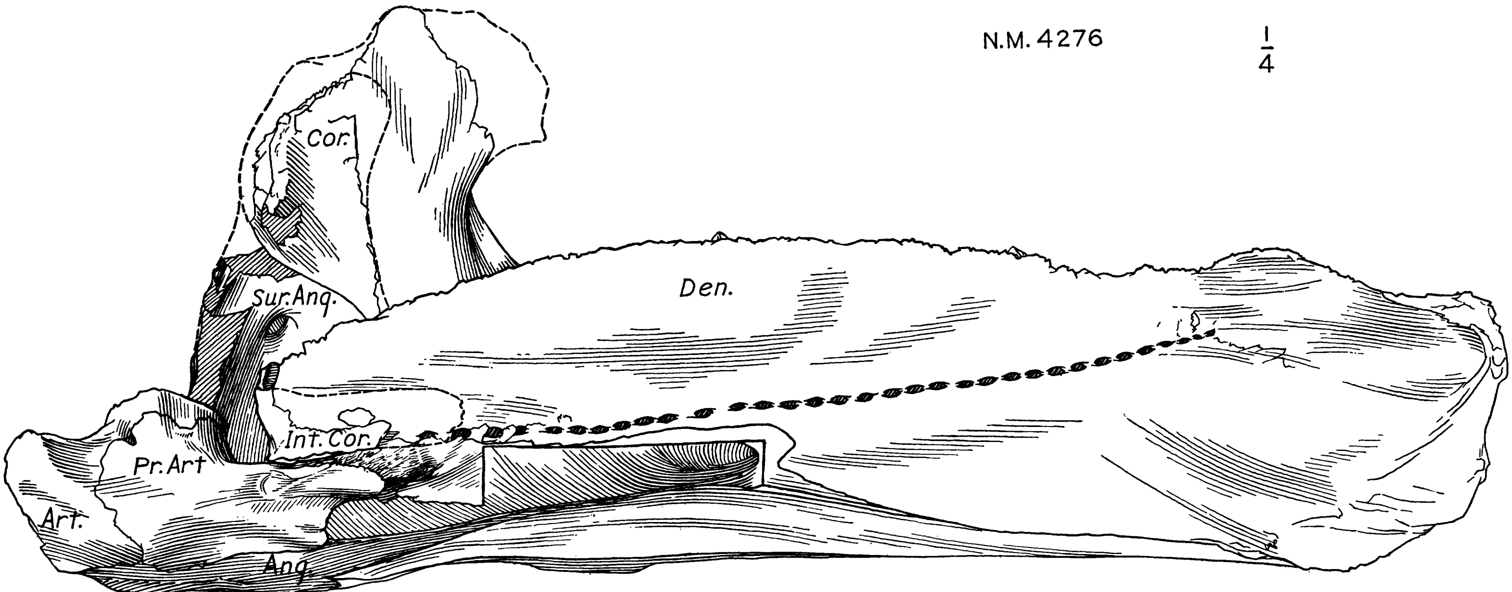

Fig. 11. Internal view of the left mandible of *Triceratops sulcatus*. The splenial is removed.

same function seems without question. Particularly suggestive of this is the presence of the connecting groove, which is especially well developed where the openings are covered by the intercoronoid and the splenial. To ascribe this function to these openings seems to be perfectly logical. It still leaves unanswered, however, the following questions: Why are these openings serially arranged with the teeth? The number of foramina in the alligator jaw does not correspond to the number of teeth. Why are the openings so proportionately large, and rounded instead of oval-shaped in the unhatched or extremely young individual? Why are they larger under the larger teeth in both young and old individuals? Why are those covered by the intercoronoid and splenial relatively as large as those that are not, if they were formed only as outlets for nerves and blood vessels? It would seem that the origin of these openings must be explained in some other way. The explanation which seems to us best to fit the case, is that these openings resulted from the dissolving of the bone at the base of each vertical series of teeth presumably at a very early stage when the animal's growth rate was most rapid. That they are in such a position is evident, for a cross section of the jaw shows that the inner surface of the dentary curves abruptly downward and outward, and that each opening is not only at the base of, but is actually almost under each vertical series of teeth. It is during this early growth stage of the animal that the openings are irregularly rounded and are proportionately the largest. In the older individuals, when the growth rate slowed down, or in the very old forms when growth may have ceased entirely, the regular supply of calcium, requisite for normal tooth-growth, was established and the openings then became oval-shaped and continued to function as outlets for nerves and vessels. This explanation of their origin certainly would account for their serial arrangement with the teeth, their proportionately large size and rounded form in the unhatched or extremely immature individuals, their larger size under larger teeth, and the relatively large size of those covered by the intercoronoid and the splenial.

As is to be expected, the dentary of *Protoceratops* most closely approximates that of *Leptoceratops*. This is particularly true in its shortness and deepness. The latter, however, is somewhat more advanced, especially in the tendency to become more elongated, and in the more clearly demarcated coronoid process.

Compared with the dentaries of the other ceratopsians, that of *Protoceratops* has the coronoid process set more closely to the tooth-row. That process is lower, and its dorsal end is neither clearly marked off nor antero-posteriorly expanded. Also, the alveolar area is proportionately shorter and has fewer alveoli. Posteriorly it extends back to a position nearly opposite the middle of the coronoid process, whereas in *Triceratops* it extends back under the posterior margin of, or behind the coronoid process. In this character *Brachyceratops* is intermediate between *Protoceratops* and *Monoclonius*, and *Monoclonius* is intermediate between *Brachyceratops* and *Triceratops*. In addition, as mentioned above, the dentary of *Protoceratops* is proportionately shorter and deeper than in any of the later forms. The tendency in the group is for the dentary to become much elongated. An extreme of this is demonstrated in *Triceratops*.

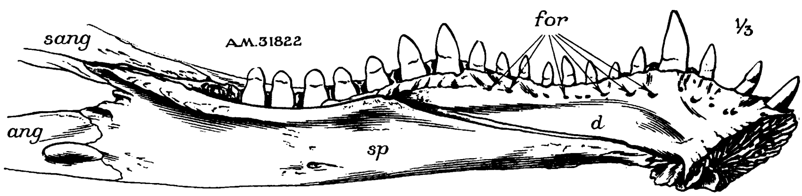

Fig. 12. Internal view of the left mandible of *Alligator mississippiensis*. *for*, foramina.

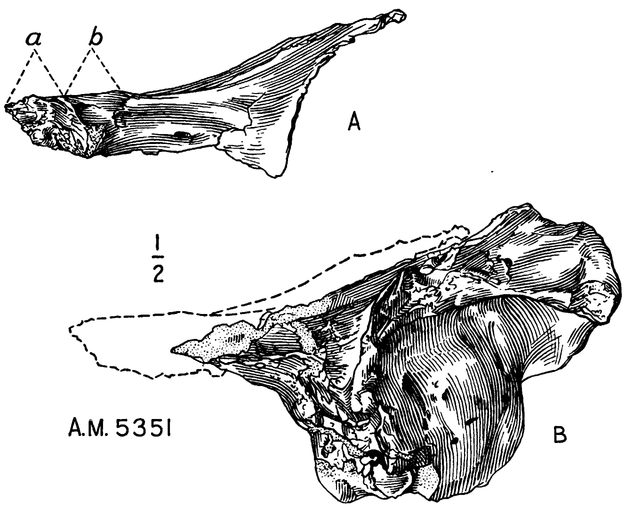

Fig. 13. Superior view of left articular and prearticular of *Monoclonius nasicornus*. A, prearticular. B, articular.
a, sutural surface for articulation with the dentary; *b*, sutural surface for articulation with the intercoronoid.

Prearticular

The prearticular was first recognized in the ceratopsian mandible by von Huene. He showed it as a distinct element in his figure of the inner side of the *Triceratops sulcatus* jaw, No. 4276, in the National Museum collection, and just mentioned its presence in the text of his paper (1911, pp. 161, 162). To our knowledge, this is the only previous mention of this element in any of the known ceratopsian material.

In *Protoceratops* the prearticular is relatively small, and remains at least partially non-fused with the articular even in the old individuals. Anteriorly it alone forms the dorsal border of the internal mandibular foramen. But in the later ceratopsians, as shown above, the splenial folds over that foramen and forms its lingual superior border. The anterior end is below, and definitely is not in contact with the intercoronoid, whereas in the later forms the contact between these two elements is extensive. Also, in all of the specimens in which the anterior margin of the prearticular seems to be completely preserved, it does not quite reach the dentary. In the later ceratopsians, however, when the alveolar portion of the dentary becomes extended posteriorly the prearticular is united extensively with the dentary. This is particularly well shown in *Monoclonius nasicornus* (A. M. No. 5351) and in the left mandible of *Triceratops sulcatus*, No. 4276, in the National Museum, when the splenial is removed. (See Figs. 11 and 13.)

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