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ON THE SPECIAL FORAMINA IN THE JAWS OF MANY
ORNITHISCHIAN DINOSAURS

By

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By A. GORDON EDMUND

CHARACTERISTIC of many ornithischian dinosaurs is a regular series of large foramina lying on the inner side of the jaws near the base of the teeth. These special foramina are best expressed in those forms with two or more teeth in each vertical series, i.e. the hadrosaurs and ceratopsians, but are present also in the ankylosaurs, pachycephalosaurids, and, to a lesser degree, in the stegosaurs. Apparently they are absent in the hypsilophodonts and iguanodonts.

The function of the special foramina has been the subject of much controversy for over sixty years. The purpose of this paper is to describe the special foramina in various groups, to review and discuss the pertinent literature, and to present what appears to be a reasonable and convincing explanation.

As was mentioned above, special foramina are best developed in those forms with several teeth in each vertical series. In these, the old tooth is pushed outward from beneath by its successor, the occlusal portion being worn away by use. There is no resorption from beneath, as in many other reptiles. This method of tooth replacement led ultimately to the development of the great dental batteries of the

FIG. 1. Lingual view of the upper and lower jaws of the hadrosaur *Corythosaurus casuarius*, R.O.M.Z.P. 1933. Crushing has distorted the nearly circular outlines of the foramina in the maxilla.

hadrosaurs and ceratopsians, in which each tooth on the triturating surface is backed by several (often 6 to 8) successors.

A typical example is seen in Fig. 1, the left upper and lower jaws of *Corythosaurus casuarius* (R.O.M.Z.P. 1933). Here the foramina in each jaw are arranged in a gentle curve, the foramina in the centre of the row being about 6 cm. from the alveolar margin. There are 43 vertical rows of teeth and foramina in the maxilla and 38 similar vertical rows and foramina in the dentary. While the foramina at the ends of the jaws are closer to the alveolar margin than are those at the centre, the teeth in the same areas are shorter, thus suggesting that the number of teeth in each vertical series is the same along the length of the jaw. Individual foramina measure about 5 mm. in diameter and are connected by a shallow groove on the surface of the dentary. The foramina in the maxilla appear identical with those in the dentary.

FIG. 2. Lingual view, lower right jaw of R.O.M.Z.P. 1944, an unidentified ceratopsian from the Oldman formation, Upper Cretaceous, of Alberta.

The foramina in the jaws of ceratopsians are arranged in a similar manner, as shown in Fig. 2. In this specimen, the right lower jaw of an unidentified ceratopsian from the Oldman formation of Alberta (R.O.M.Z.P. 1944), the greatest distance between the foramina and the alveolar margin is 6 cm. Each foramen is from 5 to 7 mm. in diameter, the larger ones accompanying the larger, central teeth. Special foramina are present in all of the well-known ceratopsians, including the more primitive genera *Leptoceratops* and *Protoceratops*. The latter is well represented by an excellent growth series, including the lower jaw of a very young individual (A.M.N.H. 6499) shown in Fig. 3. In this, the foramina are particularly obvious, being proportionately much larger than those of the adults of the same species. The arrangement of the foramina in adults of *Protoceratops* is the same as that of the advanced ceratopsian shown in Fig. 2.

Two well-preserved ankylosaur specimens in the Royal Ontario Museum show that definite special foramina were present in that group. In *Edmontonia rugosidens* (R.O.M.Z.P. 1212), for example, there is a row of foramina lying sub-parallel to the alveolar margin,

FIG. 3. Lingual view, right dentary of *Protoceratops andrewsi*, A.M.N.H. 6499, supposedly an unhatched individual.

although the row is not as regular as that seen in the hadrosaurs or ceratopsians. The individual foramina, shown in Fig. 4, are not uniform in size, and some are significantly closer to the alveolar margin than others.

Although specimens are rare, it appears that the arrangement of foramina in the pachycephalosaurids is similar to that in the ankylosaurs. A cast of the well-preserved skull and jaws of *Stegoceras validus* (Univ. of Alberta, No. 1) shows a fairly regular line of foramina in the lingual alveolar walls, similar to those seen in *Edmontonia* in Fig. 4.

FIG. 4. Lingual view, right maxillary dentition of *Edmontonia rugosidens*, R.O.M.Z.P. 1212.

Mention should also be made of the stegosaurs, since they apparently exhibit a tendency toward the development of special foramina, although these are probably of a temporary nature, coming into existence when required, then disappearing until subsequently needed.

This survey of the ornithischians thus reveals a considerable variation in the degree of development of the special foramina, ranging from large, regular permanent openings in the hadrosaurs and ceratopsians to the irregular and transient openings in the stegosaurs. Although this series does not have a direct lineal relationship, the variations in the special foramina may be considered as examples of stages in an evolutionary process, leading from a condition with no

foramina to one in which they are well developed. When we note that the better developed foraminal series are always found in forms with several teeth in each vertical series, which is also an advanced feature, this theory becomes more acceptable, and will be discussed at greater length below.

The earliest significant account of the special foramina in dinosaur jaws is that of Hatcher, Marsh, and Lull (1907). Similar foramina, however, were reported in teleost fish by Harlan (1824), Hays (1830), Cope (1875), and Loomis (1900). These workers were concerned with the same group of fish from the Niobrara Cretaceous, and particularly with the genus *Saurocephalus*. Cope (*op. cit.*) described the dentary of this fish as follows: “. . . a large foramen issues on the inner wall of the jaw, opposite each root. The fractured ends of the specimen exhibit the course of the canal which issues at this foramen. It turns abruptly downward between the inner wall of the jaw and the fang of the functional tooth, not far from the foramen. Its course is interrupted by the crown of the successional tooth. . . . The use of the foramina on the inner face of the jaw is thus made apparent, viz., the nutrition of the successional teeth from without. I cannot trace the canal below the crown of the young tooth to the base of the pulp cavity of the old tooth; and there are canals in the jaw below the latter, one of which probably carried the dental artery.”

Harlan (1824) and Hays (1830) were both of the opinion that the foramina were unquestionably for the passage of blood vessels and nerves into the jaw for the nourishment of the teeth.

Loomis (1900, p. 249), however, presented a different interpretation. “. . . bei *S. lanciformis* liegen diese Foramina volle 5 mm unter dem Zahnrand in einer ihm parallel gerichteten Rinne. . . . Die jungen Zähne stehen gerade unter dem inneren Ende der Foramina, aber die Oeffnungen sind viel zu gross, um als Blutgefäss-Foramina erklärt zu werden, abgesehen von der Schwierigkeit, die Herausbildung eines neuen Systems von Nerven und Blutgefässen zu begreifen. Im Gegentheil, der Gedanke liegt nehe, dass diese Foramina den Zutritt der Zahnleiste vermitteln, denn diese muss dahin kommen, wo der junge Zahn gebildet wird und bleibt bei Fischen immer mit dem Mundepithel verbunden. Ich zeigte die Exemplare Herrn Dr. Röse und er erklärte die Foramina ohne Zögern als Kanäle für die Zulassung der Zahnleiste an die Alveolen.”

Hatcher, Marsh, and Lull (*op. cit.*) described the jaws of numerous dinosaurs and considered Loomis' theory that the foramina are for the admission of dental germinal material. However, they considered it unlikely, and stated that the foramina “doubtless served for the transmission of nerves and nutrient blood vessels to the teeth.” This conclusion, however, was not supported by any evidence.

The other significant paper dealing with the foramina is that of Brown and Schlaikjer (1940). These authors consider the two theories previously advanced, and although they seem to reject them, they apparently do not arrive at any definite conclusions themselves. However, they assess the old evidence and present some new observations. Their analysis of the problem is concise and will be quoted directly. Referring to the blood vessel theory of Hatcher, Marsh, and Lull (*op. cit.*) they comment:

"This explanation seems extremely questionable, for such a condition would necessitate the presence of a nerve and blood vessel arrangement entirely foreign to any other known reptile. Furthermore, the Meckelian 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."

They also mention the theory of Loomis and Röse, (*in* Loomis 1900) "... 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." Brown and Schlaikjer (*op. cit.*) dismiss this theory as "... 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."

The theory that special foramina are for the transmission of blood vessels and nerves will now be considered in detail. In an attempt to find analogous or homologous structures in living reptiles, Brown and Schlaikjer (*op. cit.*) considered the lower jaws of the only living archosaurs, the crocodilians. In the crocodilian jaw, Fig. 5, there are a number of foramina in the dentary, lying lingual to the alveoli, occupying roughly the same position as the dinosaurian foramina. The number of foramina, however, is not the same as the number of teeth, and the foramina vary in size and are randomly distributed. Furthermore, they are not round or oval and cleanly punched out, as are the dinosaurian foramina, but appear to be identical with cranial foramina definitely known to be for the passage of blood vessels and nerves.

FIG. 5. Occlusal view, right dentary of *Caiman sclerops*, R.O.M.Z.P. R 172. Skull length, about 180 mm.

Brown and Schlaikjer (*op. cit.*, p. 9) mention a dissection of a lower jaw of a specimen of *Alligator mississippiensis* which "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 same function seems without question." The present writer is forced to disagree with the latter conclusion, and as will be seen, Brown and Schlaikjer do not present much evidence to support their statement. Indeed, they seem to feel that there is some doubt, since they continue, "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?" If we are to arrive at a

FIG. 6. (a) Lingual aspect of part of the maxillary dental battery of a hadrosaurian dinosaur, R.O.M.Z.P. 696. Part of the inner alveolar wall has been removed to show the vertical tooth series. (b) Transverse section of the above jaw, passing through two of the vertical tooth series. Members of one series are labelled 'A', those of the other are labelled 'B'. The edge of the foramen is about 1 mm. below the plane of the section.

plausible explanation of the problem, these questions must be satisfactorily answered.

While Brown and Schlaikjer indicate acceptance of the efferent vessel and nerve theory on page 12 of their paper, they continue, "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."

Not only does this explanation fail to contain any convincing arguments, but it presents several conflicting ideas. Blood vessels and nerves are laid down in vertebrate embryos before the deposition of osseous tissue, therefore foramina for their passage are not formed by the dissolving away of bone. Furthermore, tooth replacement in herbivorous dinosaurs such as the hadrosaurs and ceratopsians must necessarily have been a vigorous process continuing throughout life, thus requiring the same quantity of nutrients at all times. There is no reason to postulate, from a purely vascular argument, that the foramina were formed at one time (during rapid growth) for the admission of vessels to the odontogenic areas, and less reason to suggest that they later served to carry blood in the opposite direction. Whatever function the foramina had, it seems likely that they continued to perform it throughout life. The fact that the very young *Protoceratops* specimen had foramina almost identical with those of the adult bears this out.

It is extremely unlikely, as Brown and Schlaikjer (*op. cit.*) point out, that the foramina in question were used to supply blood to the teeth, even though they were intimately associated with the bases of the vertical tooth rows as in Fig. 6b. No known reptiles, and so far as the author is aware, no known vertebrate, possesses a vascular system

supplying the teeth through individual foramina in the lingual side of the jaws. A careful dissection by the author of the jaw of a small alligator showed branches of the mandibularis nerve and the accompanying arteries passing from the Meckelian canal through the depths of the alveoli and out to the lingual side of the jaws through the foramina shown in Fig. 5. There is no trace of vessels or nerves entering the jaw or alveoli through these foramina, and the blood supply to the teeth is quite adequately handled by the large vessels in the Meckelian canal.

As mentioned above, the vessels and nerves passing out of the foramina in the lingual side of the jaws in *Alligator* branch off the main trunks in the Meckelian canal and pass through the alveolar cavities. The arrangement of this branching is not regular, i.e. there is not one branch for each alveolus, but rather the vessels and nerves are randomly distributed and exhibit some anastomosing and re-branching. Before passing through the foramina to supply the lingual side of the jaw, the vessels give off branches to the soft structures within the alveoli, the relative sizes of the vessels suggesting that the alveoli may have received about as much blood as was transmitted to the lingual side of the jaw through the foramina. If the arrangement of vessels and nerves in the lower jaw of *Alligator* is typical of that in the advanced ornithischians, an increased blood supply to the teeth would not affect the size of the lingual foramina. An increase in the blood supply to the teeth would merely increase the size of the vessels flowing in and out of the Meckelian foramen. Another argument casting doubt on the purely vascular or neural function of the foramina in ornithischians is their serial arrangement. The foramina in *Alligator* are small and randomly distributed and are for the passage of vessels and nerves; those in the ornithischians are large and arranged so that one foramen lies at the base of each tooth row. This difference must indicate a basically different function.

It is conceivable that the special foramina in ornithischians may have served for the passage of efferent vessels and nerves, since there are few or no other foramina on the lingual side of the lower jaw in most ornithischians. As we have seen, in *Alligator* the great vessels and nerves within the jaws sent branches through the alveoli and out the foramina on the lingual side. There is no reason to expect that the serially arranged foramina in ornithischian jaws did not serve for the passage of vessels and nerves to the soft tissues on the lingual side of the jaw. Such a function, however, must have been a secondary one. The serially arranged foramina in ornithischians are very large, much larger than would possibly be needed for such a purpose alone, indicating that this was not their primary function.

Another significant observation by Brown and Schlaikjer (*op. cit.*) is that in ceratopsians those (posterior) foramina covered by the inter-

coronoid and splenial are as large as those that are not. If the purpose of the foramina was purely for the passage of nerves and vessels, the covered foramina would be smaller than the uncovered ones, since there would be no place for the vessels to go. True, there is a groove connecting the foramina, but the small space which it provides between the dentary and the overlying dermal bones is insignificant when compared to the sum of the cross-sectional areas of the covered foramina. Thus, it is very unlikely that the foramina are solely or mainly for the transmission of either afferent or efferent vessels and nerves.

Having examined the theories of Brown and Schlaikjer and of Hatcher, Marsh, and Lull, we shall consider that suggested by Loomis and Röse (*in* Loomis 1900). It is significant that most of the ornithischians are characterized by having the centre of dental development separated from the oral epithelium by a high alveolar wall, as in Fig. 6. In all animals, the tooth germs are produced by the dental lamina, an infolding of specialized oral epithelium which retains contact with the surface epithelium. Tooth germs elaborated by the dental lamina must be produced at or near the base of each vertical series, and yet in most ornithischians these bases are buried deep in the dental chamber. In such a situation the most efficient arrangement would be that in which the dental lamina lies alongside the bases of the teeth, with foramina through which its products might pass. Resorption of bone and tooth substance during the process of tooth replacement has been seen by the writer in most reptilian groups. This osteoclastic activity is responsible for the degradation of the old tooth prior to its replacement, and is seen in various forms in which the new tooth erupts through bony tissue. A similar osteoclastic effect is probably associated with the area in which replacement teeth are developing in ornithischian dinosaurs, thus accounting for the phylogenetic origin and continued presence of the special foramina at precisely the place where tooth replacement activity is most intense.

Brown and Schlaikjer have studied the relationship of the foramina to the teeth in ceratopsians and state: "That they are in such a position, one at the base of each vertical tooth series 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." Thus the foramina are in exactly the right place to permit passage of germ teeth from the dental lamina into the dental chamber. This is well shown in the illustrations of a hadrosaur maxilla (Figs. 6a and 6b).

There is a definite groove connecting all of the foramina in the jaw, almost certainly for the accommodation of the dental lamina. A similar groove for the same purpose has been seen by the writer in many reptiles, but would not be expected if the foramina were for the

passage of vessels and nerves. I know of no serially arranged nerve or vessel openings of this sort which are connected by a bony groove. The presence of the groove indicates the presence of some structure intimately associated only with the foramina, and this in my opinion was the dental lamina.

The second question asked by Brown and Schlaikjer, is, "Why are the openings so proportionately large . . . in the . . . extremely young individual?" The specimen referred to, *Protoceratops andrewsi* (A.M.N.H. 6499), bears six foramina and six tooth positions. The teeth seem relatively very large, as do the foramina. In a young reptile, especially a herbivore such as *Protoceratops* almost certainly was, an adequate, functioning dentition is essential right from the time of hatching. There can be no period of dental growth with provision of other nutrition such as is enjoyed by the mammals; the reptile must be hatched ready to fend for itself. Thus, it must have relatively large teeth, and also must have provision for their rapid replacement during growth. In actual fact, the foramina in the extremely young individual of *Protoceratops* (A.M.N.H. 6499) are one-half as large as in the adult specimens, while the dentary is only one-tenth as large. The teeth are in similar proportion.

The third question, "Why are they [the foramina] larger under the larger teeth in both young and old individuals," can be readily answered. A larger tooth requires a larger replacement, and this in turn requires a larger foramen for its passage.

In answer to Brown and Schlaikjer's fourth question, "Why are those foramina 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?" we can state, first of all, that the latter was almost certainly not their primary function. This has been discussed above. The teeth in the region of these covering bones are about as large and important as those elsewhere in the jaw, and are replaced just as frequently. They therefore need just as large foramina, and also need continuity with the dental lamina the same as do the other teeth. On page 9, Brown and Schlaikjer (*op. cit.*) state, ". . . the openings are connected by a shallow groove on the surface of the bone . . . which is especially well developed where the openings are covered by the intercoronoid and splenial." This groove is probably for the accommodation of the dental lamina. The lamina would easily fit the space provided, with the young teeth protruding into the foramina as they developed, and migrating labiad into the dental chamber exactly at the base of their respective dental series. The lamina probably lay partly in the groove where the foramina were not covered, but bulged slightly into the overlying soft tissues. Where covered, the groove has to be deeper to accommodate the entire thickness of the lamina.

The function of the foramina can be explained, as outlined above, so as to meet all known objections. As a confirmation, there are several fossil specimens which were preserved with the crowns of replacement teeth lying in their foramina. One of the best is an undescribed ceratopsian mandible (R.O.M.Z.P. 1944) (Fig. 2) in which a very young crown is seen to occupy the entire area behind the foramen at position 6. Parts of other small crowns can be seen in other foramina in the same jaw. *Leptoceratops gracilis* (N.M.C. 6888) though only in a fair state of preservation, has the crowns of replacement teeth showing in many of the foramina in both lower jaws. In *Edmontonia rugosidens* (R.O.M.Z.P. 1212) (Fig. 4) several foramina have crowns of replacement teeth lying in or behind them. The finding of such crowns seems to indicate strongly that the special foramina served for the passage of young teeth or tooth buds from the dental lamina into the dental chamber, although it could be argued that these small crowns merely drifted away from their original positions during the post-mortem maceration, and became lodged in the foramina.

An interesting observation is that in the ornithischians there is excellent correlation between the development of dental batteries and the development of the special foramina. The best dental batteries are seen in the hadrosaurs and ceratopsians, which also have the most completely developed special foramina. In the troodonts and ankylosaurs, where there are no more than two teeth in each vertical row, there are definite special foramina, but these may be of an irregular or transient nature. In the stegosaurs, with their relatively poor dentition, poorly developed, transient special foramina may have been present, but because of poor material we cannot be certain. In the hypsilophodonts and iguanodonts, no specimens known to the writer exhibit special foramina. A specimen of the hypsilophodont *Parkosaurus* (R.O.M.Z.P. 804) has recently been prepared to show the lingual aspect of the jaws, and no trace of special foramina can be seen. Thus, it appears that special foramina are associated with the development of a high alveolar wall on the lingual side. They are not seen in the primitive forms, are seen in some of the more advanced forms, and are best developed in the forms with very high alveolar walls. This definitely points to their function as orifices for the admission of dental germinal material.

Foramina similar to the special foramina in ornithischians have been described in nothosaurs and plesiosaurs. They were, like those of the ornithischians, originally considered to be for the transmission of blood vessels and nerves, but Edinger (1921) demonstrated their true function as sites of development of replacement teeth.

In summary, we can state the following: The serially arranged foramina lying sub-parallel to the tooth rows in many of the ornithischian dinosaurs are for the admission of parts of the dental lamina or for the

admission of young replacement teeth elaborated by the lamina. In the forms in which the special foramina are best developed, the base of the vertical tooth row is set deeply into the maxilla or dentary, separated from the normal position of the dental lamina by a thin but high wall. The foramina permit easy passage between the dental lamina and the base of the vertical tooth series.

The large size of the foramina, their serial arrangement, their numerical correspondence with the vertical tooth series, and the fact that the foramina covered by other bones are as large as those not covered, argue in favour of the above interpretation. No contradictory evidence has appeared to date. The theory that the foramina were solely for the admission of blood vessels and nerves supplying the teeth has been shown to be untenable, and in face of the arguments above it must be discarded.

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