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A POSSIBLE EXPLANATION OF FENESTRATION IN THE PRIMITIVE REPTILIAN SKULL, WITH NOTES ON THE TEMPORAL REGION OF THE GENUS *DIMETRODON*

BY
E. C. CASE

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ANN ARBOR

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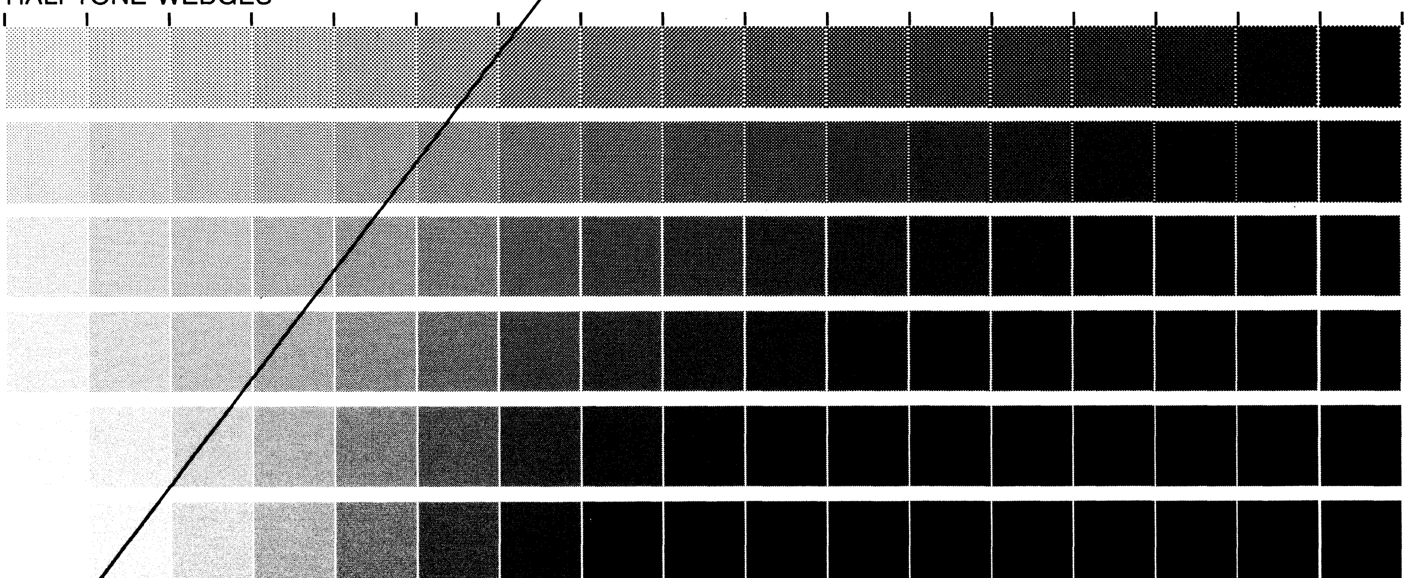

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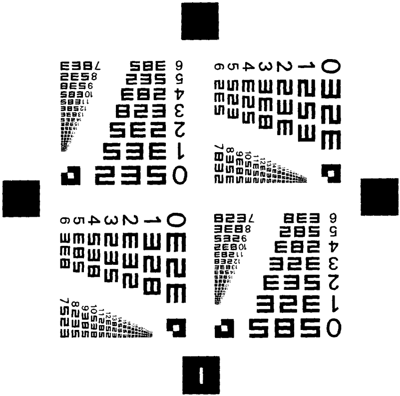

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CONTRIBUTIONS FROM THE MUSEUM OF GEOLOGY

UNIVERSITY OF MICHIGAN

Editor: EUGENE S. McCARTNEY

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VOLUME I

The Stratigraphy and Fauna of the Hackberry Stage of the Devonian, by Carroll Lane Fenton and Mildred Adams Fenton. (*In Press.*)

VOLUME II

1. A Possible Explanation of Fenestration in the Primitive Reptilian Skull, with Notes on the Temporal Region of the Genus *Dimetrodon*, by E. C. Case. Pages 1–12, with 5 illustrations. Price, \$.30.
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A POSSIBLE EXPLANATION OF FENESTRATION IN THE PRIMITIVE REPTILIAN SKULL, WITH NOTES ON THE TEMPORAL REGION OF THE GENUS *DIMETRODON*

E. C. CASE

THE successive failures of proposed phylogenetic series based entirely, or in large part, upon morphological characters has proved very conclusively how unsatisfactory such a method of procedure must be. Even those morphological characters which have proved the most stable are being repeatedly challenged and the interpretation of their meaning questioned. Each worker with new facts at hand or with new ideas has shifted the known specimens into new arrangements, much as the blocks of a mosaic might be shifted to meet the fancy of the worker. The possible number of new combinations is rapidly reaching its limit and we are still unsatisfied with the results. Gregory has recently voiced the need for a new line of work which shall take into account the causative element in changes upon which we must depend for our final and satisfactory taxonomic and phylogenetic arrangements.

This idea is not entirely new; Cope, Ryder, Dollo, Abel and others have all made tentative and constructive suggestions along this line, but the time has now come when the causative element must assume a dominant position over the purely morphological. This means that the paleontologist can no longer be a pure morphologist, nor continue to trace relationships through characters which may or may not be of fundamental value. He must become a biologist and a paleogeographer in the broadest sense of those words. Paleogeography, like modern geography, is a description of "the response of the individual to the environment." The paleontologist must, therefore, restore the environment and trace its effect upon the organism. This implies a depth and breadth of knowledge of so many branches of science that the task is seemingly impossible. The only answer is that it is absolutely necessary. Probably the solution will be found in groups of specialists working upon the same problem.

The author has been attempting to apply these principles in his own work, so far as his ability permitted, and one result has been the recognition of a possible explanation of the origin of fenestration in the primitive reptilian skull. Various suggestions have been made in tentative explanation of the origin of the temporal fenestrae, but they have all been confessedly vague. Such expressions as "natural trephining," absorption, and the like, mean nothing and are meant to mean little more. Gregory and Adams (*Science*, Vol. XLI, p. 763, 1915), while recognizing the effect of muscular stress upon bone, speak no more clearly of the process than in the use of the word "perforation" of the skull by certain muscles, and of the bones disappearing or decreasing in size "to make more room" for the play of enlarged muscles.

In efforts extending over some years, as opportunity offered, the author has sought for a physiological explanation of the process of normal changes in bones. He has been struck, as was Gregory, by the lack of publications which could be used in this connection. Much has been done upon the structure of bone, much upon the relation of the form and structure of the long bones to imposed stresses, and, of course, much upon the effect of pathological process, but there has been singularly little done that can be used to explain the normal changes which occur through long intervals of time in the cranial and axial bones.

One entirely normal process has repeatedly attracted the attention of the author. It is a commonly observed fact that such bones as the scapula and the blade of the ilium in the human subject, to which are attached powerful muscles by broad insertion on either side, are thinned in the central portion and thickened on the edges; in the less muscular subjects this may continue, especially in the case of the scapula, to complete perforation of the bone. The same condition is occasionally observed in the lower mammals.

To the upper surface of the mammalian scapula are attached two large muscles, the *supra-* and *infra-spinatus;* to the lower surface the *subscapularis*. These have a broad insertion through the periosteum. On the lower surface accessory tendinous attachment of the *subscapularis* is marked by the presence of two oblique ridges. The main tendinous attachment, and hence the points of the main application of muscular stresses, are upon the edges of the bone and upon the spine. Similar conditions appear on the blade of the ilium. On the outer side are the *gluteus medius* and *gluteus minimus* separated by the gluteal line; on the inner side is the *iliacus*. The conditions of attachment are very similar to those obtaining in the scapula. In both cases there are broad and strong muscles with a wide attachment to a flat surface of the bone and tendinous attachment to the edges. The result of the stronger attachment of the muscles by tendon to the edge of the bone is an enlargement and strengthening of the periphery; this is increased by the tendinous attachment of the smaller muscles in the same peripheral position.

The result of the stronger tendinous attachment in stimulating the growth of trabecular tissue is easily seen in the scapula; if this bone is held up to the light, the two oblique lines stand out upon the thin translucent bone as darker areas because of the presence of an increased amount of *spongiosum*. The same thickening can not be observed in the middle gluteal line upon the ilium, however. In both bones the middle portion, where the insertion of the muscle is through the periosteum, is thin and there is no indication of the presence of *spongiosum*.

These observations suggest a line of search for the origin of the perforations in the temporal region in the primitive reptilian skull. As mentioned above, there is very little in the literature that can be used in examining this suggested explanation. Gebhardt (*Roux's Archiv.*, Vol. II, 1901) in an elaborate work comes to the conclusion that there is little relation between the position of the trabeculae and the direction of imposed stresses. Others, notably Culmann (reported by Von Meyer in *Reichert and Dubois-Raymond's Archiv.*, 1867, and quoted by Koch in the article cited below), investigating the femur on purely mechanical lines, have found the trabeculae to be arranged in the direction of the imposed stresses during the process of carrying weight, or the imposed shocks resulting from walking, running and jumping.

An article by Dr. J. H. Koch (*Am. Journ. Anat.*, Vol. 21, 1917) dealing with the architecture of bones contains much valuable matter. This paper discusses the femur in particular but draws conclusions applicable to the other bones. Certain of his conclusions available for the present argument are quoted below from his summary of the laws of bone structure:

(*p. 273*) 1. The inner structure and the external form of human bone are closely adapted to the mechanical conditions existing at every point in the bone.

2. The inner architecture of normal human bone is determined by the definite and exact requirements of mathematics and mechanical laws to produce a maximum of strength with a minimum of material. Further, the observations here recorded for the femur, the largest and heaviest bone of the body, must in a general way hold true for all the bones of the body; else we must assume the absurd conclusion that the structure of the femur is in conformity with mechanical laws and the other bones are based upon unknown laws. The numerous experiments by Rauber and Messerer in testing human bone to destruction have shown that the physical properties of all the larger bones of the body are substantially the same. Hence, the laws promulgated above for the femur must hold in a general way for all the bones of the human body.

(*p. 284*) The doctrine of the functional form of bone, with its corollary of the functional pathogenesis of deformity, advanced by Wolff, and maintained by him with rare courage and persistence for so many years, is confirmed mathematically for the first time by the studies presented in this paper, for the structure of normal bone.

(*p. 285*) Koch shows that Gebhardt's contention that the *spongiosum* is not homogeneous with the compact bone is erroneous and that the two "act together as a homogeneous structure."

(*p. 288*) The evidence presented in this paper is believed to warrant the following conclusions:

1. The normal form and internal architecture of the human femur results from an adaptation of form to normal static demands.

2. The proportions of the femur are everywhere such as to show a definite mathematical relationship between the body weight and the internal structure of the bone; there is a definite relationship between the structure and the stress at every point.

3. Spongy bone is homogeneous with compact bone as a structural material and differs from it mechanically in possessing smaller strength approximately in proportion to its density as compared with compact bone.

4. (Concerns the femur only.)

5. (Concerns the femur only.)

6. The general law of bone, the adaptation of form to function holds true mathematically and mechanically in the normal human femur and therefore for all other normal human bones.

Special conclusions:

1. A foundation is laid for the study and mechanical analysis of the spongy bone entering into the structure of other parts of the skeleton, by the application of the principle that spongy bone and compact bone are homogeneous materials and differ in strength approximately in proportion to their densities.

2. The thickness and closeness of spacing of the trabeculae vary directly with the intensity of the stresses imparted to them.

(*p. 289*) . . . The close adaptation of the structure of normal bone to its function leads logically to the conclusion that continued deviation from the normal static conditions to which a bone is subjected must be followed by a structural adaptation to meet the changed conditions (altered function).

Whether the persistent altered static (mechanical) conditions in the bone be due to fracture, bone disease, paralysis followed by postural changes, or other causes [phylogenetic, Case] the fundamental mechanical principles apply with equal force; transformation of the inner structure of the bone takes place, and the inner structure is altered to conform to the new mechanical conditions usually with a high degree of economy.

Dr. Koch does not consider muscular stresses in particular, but indicates that they would have the same effect as external imposed stresses, yet in a lesser degree. This idea he reiterates in a letter to the author. From the conclusions of Dr. Koch, quoted, and from other valuable material in the paper, unquoted, we may safely infer that thickening of the bone by the growth of *spongiosum* occurs at points of greatest stress and that there is a lack of such tissue in places of less stress. In the case of long bones which must resist stresses other than muscular, the compact portion of the bone remains, but in the flat cranial or axial bones where only minor, muscular, stresses are to be resisted, the compact bone would at least cease to develop and in places even waste away.

In applying this idea to the fenestration of the skull we note that the *temporalis* and *masseter* muscles, or their equivalents, the *capiti mandibularis*, were broadly attached to the lower surfaces of the bones forming the temporal roof of the Stegocephali and the stegocrotaphus reptiles. Adams (*Anns. New York Acad. Sc.*, Vol. XXVII, 1919) has given us a most useful account of the jaw muscles in the various forms of vertebrates and has attempted a restoration of these muscles in certain extinct forms. His restorations of the myology of *Eryops* and *Labidosaurus* show the broad attachment of the *capiti mandibularis superficialis* and *medius* to the under side of the bones of the temporal roof. In these cases the broad muscles are attached to only one side of the bone or bones involved, but there seems no reason to doubt that the effect would be the same as if both sides were covered. The location of the main muscular stresses would then be concentrated by tendinous attachment to the edges, and the inner portion, where the attachment was broadly through the periosteum, would tend to thin and even waste away. Such wastage of the temporal bones would very possibly be restrained by the action of natural selection preserving the thick roof bones in the ground-clinging forms, but as soon as the reptiles felt the effect of the new spatial relation attained by even partial and temporary assumption of the quadrupedal habit, or even by the assumption of the habit of frequently raising the head from the ground, the mechanical factor of the localized muscular stresses would begin to have its effect.

In the paper in *Science*, mentioned above, Gregory and Adams give certain conclusions reached by the senior author which are of especial interest in this connection: "In comparing the skull patterns of the Osteoicthyian fishes (Dipnoi, *Rhipidistia*, etc.) sutures came to be regarded as loci of movement or progressive overgrowth, conditioned in part by muscular action, while centers of ossification were considered as centers of relative stability." There can be little doubt that this observed fact is as applicable to the Amphibia and Reptilia as to the fishes.

Williston (*Journ. Geol.*, Vol. XXV, p. 415, 1907) says of the formation of the opening in the skull of the Synapsida: "This opening, I believe, arose by the separation of the squamosal and jugal, and not by a perforation of the bone."

In the process of the imposition of stresses upon the lower side of the roof in the Stegocephali and the stegocrotaphus reptiles, the broad insertion of the muscles would extend across the sutures and the tendency would be to a wasting of the bones, which would be especially active at the sutures. This would result in a fenestration, and as soon as this occurred there would be a readjustment of the muscular attachment. The muscles would develop tendinous attachment to the free edges of the bones, there would be a local thickening by the growth of *spongiosum*, and the bones would contract into narrow arches and the zygocrotaphus skull would be established.

The ideas suggested here may, by the increase of detailed information and the application of refined methods, lead to the solution of some other problems in the development of the early reptiles. Koch has shown that muscular stress will influence the architecture of bone in the same way, but to a less degree than the stronger external stresses; further, he has shown that there is a very definite relation between the direction of the trabeculae and the direction of imposed stresses. When we have worked out the position of the equivalents of the *temporalis* and *masseter* muscles in the Synapsida and Parapsida and the method of mastication, it is very possible that the attachment and insertion of the muscles will reveal the direction of the applied stresses and lead to the solution of the question whether the upper or lower arch appeared first, or whether the two were synchronous in origin.

NOTES ON THE TEMPORAL REGION OF THE GENUS *DIMETRODON*

There are, at present, three skulls of the genus *Dimetrodon* known in literature; a skull of *D. incisivus*, No. 1001, University of Chicago, a well-preserved skull of *D. gigas*, No. 1002, University of Chicago, and a well-preserved skull of *D. incisivus*, No. 4636, American Museum of Natural History. To these must be added a well-preserved skull of *D. gigas* in the possession of the author at the University of Michigan. This last specimen has only recently been studied with care. It reveals much concerning the temporal region which has long been in doubt, since the condition of preservation in the other specimens and the fragility of the bones have rendered the interpretation difficult.

The author has published figures and interpretations of the first three skulls mentioned, but his interpretation of the temporal region has not been accepted without question by other workers.

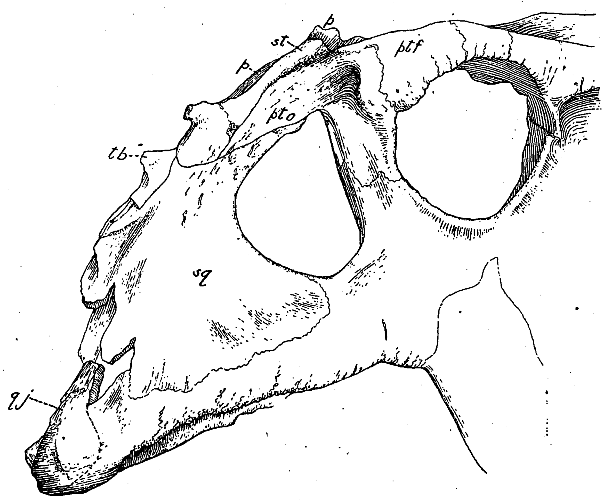
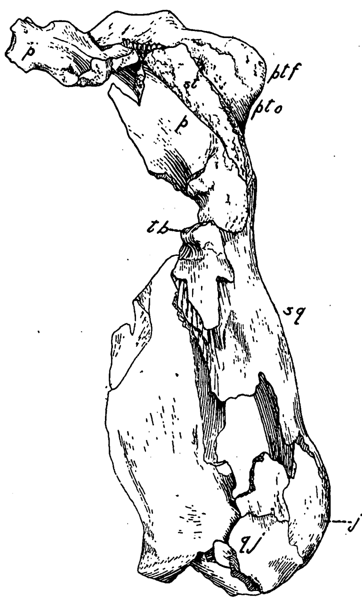


FIG. 1. Temporal region, right side, of a specimen of *D. gigas* in the author's possession.

The specimen here described is naturally cleaned by weathering and shows the sutures and separate bones with exceptional clearness. In Figures 1 and 2 are shown the details of the temporal region. In previous papers, summarized and completed in Publication 55 of the Carnegie Institution of Washington, the author suggested that there were two bones in the supratemporal region, which he considered the postorbital and the parietal. Between these two bones an opening is apparently present in the two skulls preserved in the University of Chicago. This opening the author considered as a natural one and interpreted it as the superior temporal opening of the rhyncocephalian skull. The character of the openings has been questioned and as the opening does not appear in the specimens in the American Museum, nor in the skull in the author's possession, and as the accumulating evidence has shown that the Pelycosauria has a very primitive skull and can no longer be considered as belonging in the order Rhyncocephalia, the author is compelled to believe



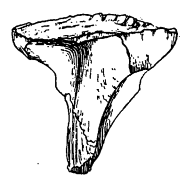


FIG. 2. Posterior view of the temporal region of the same specimen shown in Figure 1.

FIG. 3. The postorbital bone of the left side of the same specimen showing the articular face for the supratemporal bone.

that he was wrong, and that the opening in the two Chicago specimens is accidental, formed by the separation of two weakly attached bones in the process of maceration or fossilization.

In the author's specimen, as shown by Figures 1 and 2, there are not two but three bones in the supratemporal arch. They are the postorbital; a bone lying parallel to the postorbital, which can only be the supratemporal (a possibility suggested by Broom some time ago); an extension of the parietal downward for some distance. The distinctness of the first two bones has been in doubt as the line between them can be interpreted as either a crack or a suture in most specimens, but the sutural separation can be clearly seen in the skull in the author's possession, and is further proved by the fact that the separate postorbital of the opposite side of the skull shows a sutural surface for the missing supratemporal (Figure 3).

It was the slight displacement of these two bones, only weakly attached, which formed the accidental openings interpreted by the author as a supratemporal fenestra in the Chicago specimens. These two bones extend downward for a nearly equal distance, overlapping the squamosal. The lower end of the parietal, in the author's specimen, extends below the supratemporal and bears on its lower end a protuberance which, in combination with a similar protuberance on the bone lying below it, forms a notch for the reception of the distal end of the paroccipital. The squamosal, long called the prosquamosal by the author, is well known in its general form, but the specimen shows that the posterior end is reflected around and covers the posterior edge of the quadrate, much as is described by Watson for the same bones in the Deinocephalia of South Africa. Lying on the reflected portion of the squamosal and just below the distal end of the parietal is a small and incomplete bone with a protuberance, mentioned above, which forms the lower edge of the notch for the reception of the distal end of the paroccipital process. The distinctness of this element is confirmed by the loss of its lower end, which reveals the strong articulating ridges on the edge of the squamosal; this bone is in the position of, and has the relations of, the tabulare. Below this bone and slightly anterior to it is another bone, which the author has consistently called the quadratojugal, and which he is now convinced has been rightly determined. This bone lies upon the posterior edge of the quadrate with a small foramen separating it from the quadrate below, and runs upward upon the reflected edge of the squamosal. The upper end is lost, but there is a deep articular groove on the squamosal just anterior to the lower end of the tabulare, marked with articular grooves and ridges, which can have received only the lower surface of the upper end of the quadratojugal.

In such primitive forms as the Pelycosauria one other element, the dermsupraoccipital, should be present or represented by vestiges. No trace of this element has been found in any skull of *Dimetrodon* except that of *D. incisivus*, preserved in the American Museum. As is shown in Figure 4 and on Plate XVIII of Article XIX, in the *Bulletin of the American Museum of Natural History*, Vol. XXVIII, 1910, there is a broad thin plate of bone which lies between the upper edge of the occipital plate and the

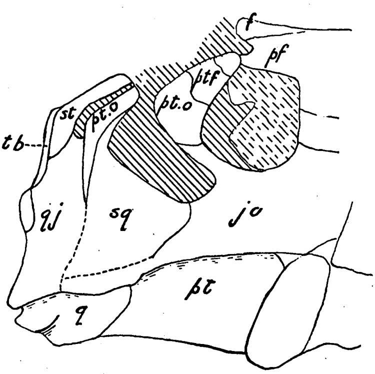


FIG. 4. Redrawing of a portion of the outline figure of the skull of *D. gigas* previously published.

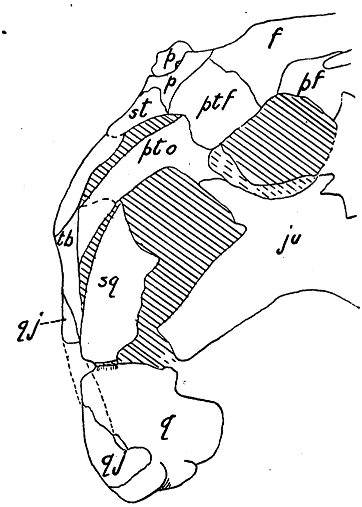


FIG. 5. Redrawing of a portion of the outline figure of the skull of *D. incisivus* previously published.

parietals; this can only be the remnants of the dermsupraoccipital. Its fragile nature easily explains its absence in other specimens.

Because of the various interpretations which have been put upon this region by Williston, Broom, Huene, the author and others, the author has compared his former interpretations with that made of the specimen here described and finds that they can all be brought into harmony and into harmony with most of the interpretations by others. Figure 4 is a re-drawing of a portion of the outline published in Publication 55 of the Carnegie Institution, Plate 8, *D. gigas*, and Figure 5 is a re-drawing of the figure of *D. incisivus*, Plate 17 of the same Publication. A comparison of these drawings with those previously published shows very slight changes in the outline, where the imperfection of the specimen has caused an error in the tracing of sutures or the confusion of sutures with cracks. This and a re-identification of the bones make the interpretation of the various specimens mutually confirmatory. But one point of difference remains between the author's ideas and those of others; the bone lying on the posterior side of the quadrate and separated from it by a small foramen seems now to be without doubt the quadratojugal. Broom had always contended that this bone lay on the side of the skull approximately in the same position that it occupies in *Sphenodon*. Of this the author, and Dr. Williston in confirmation, could find no evidence. In the author's specimen the jugal comes in contact with the quadrate with no evidence of any quadratojugal taking part in the formation of the lower arch.[1]

One other point is worthy of notice; as shown by the several drawings, there is a notable difference in the posterior portion of the lower arch between *D. gigas* and *D. incisivus*. In the latter the squamosal does not extend anywhere near so far down upon the quadrate as in the former; *D. incisivus* therefore has a free dependent quadrate region which is strikingly similar to the condition shown by the single arched primitive reptiles of South Africa.

[1] The conclusions here stated are quite in consonance with the description of the same region in *D. gigas* published by Gilmore, *Proceedings U.S. National Museum*, No. 2300, Vol. 56, pp. 529–39, 1919.