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THE OSTEOLOGY OF THE SKULL OF THE PELYCOSAURIAN GENUS, DIMETRODON.

DURING the summer of 1904 the author collected in the Permian beds of Texas two skulls of the genus *Dimetrodon* belonging in the suborder *Pelycosauria*. These skulls were in an excellent state of perfection, which permits the completion of previous descriptions and the correction of some errors.

Especially valuable is the fact of the preservation of the temporal arches, permitting a description of this region, which has been hitherto only partially known and falsely interpreted. The two skulls are numbered 1001, *Dimetrodon incisivus* (?), and 1002, *Dimetrodon gigas*, of the University of Chicago collection of fossil vertebrates. The specimen of *Dimetrodon gigas* was almost perfectly preserved, only a portion of the temporal arches of the left side and the middle portion of the epipterygoid being lost. The larger part of the following description is taken from it; some details, and the description of the lower jaws, are added from specimen 1001.

As shown in Fig. 1, the skull has proportions much like those of the modern lizards or the carnivorous Dinosaurs. The eyes are not located so far back in the head, and the facial region, while elevated, does not bear the great disproportion to the skull shown in previous restorations.[1]

The quadrate of *Naosaurus* was correctly interpreted by Cope as an elevated element similar to the same bone in the modern *Sphenodon*. This was later denied by Baur and Case,[2] and the statement was made that the quadrate was a depressed bone completely surrounded by the bones of the temporal region, and in this regard similar to the African Theriodonts.

[1] E. D. COPE, "On the Homologies of the Posterior Cranial Arches of the Reptilia," *Transactions of the American Philosophical Society*, Vol. XVII (1892); G. BAUR AND E. C. CASE, "On the Morphology of the Skull of the *Pelycosauria* and the Origin of the Mammals," *Anatomische Anzeiger*, Vol. XIII (1897), pp. 109–20; *idem.*, "The History of the *Pelycosauria*, with a Description of the Genus *Dimetrodon*," *Transactions of the American Philosophical Society* (2), Vol. XX (1899), pp. 1–58.

[2] *Op. cit.*

The determination was made on a partially preserved skull of *Dimetrodon incisivus*, and a series of unfortunate conclusions have been drawn from this erroneous determination. The present specimens show that Cope was correct in his determination of the quadrate as an elevated bone, and also demonstrates its remarkable similarity in position and relations to the quadrate of *Sphenodon*.

Figs. 1, 2, and 4 show the general form and relation of the quadrate. It is an elevated, thin plate of bone ending freely above, articu-

FIG. 1.—Left side of the skull of *Dimetrodon gigas*. About one-fourth natural size. Full length of skull, 46 cm.

lating with the pterygoid anteriorly, and the quadrato-jugal, squamosal and paroccipital posteriorly. The lower end is terminated by two elongate articular condyles, which run almost parallel antero-posteriorly, but are slightly convergent anteriorly. The inner condyle stands out from the side of the bone, and its inner side articulates with the posterior end of the pterygoid. The outer condyle projects beyond the posterior edge of the bone, and its upper surface is flat, forming a sort of shelf, to the upper side of which is articulated the lower end of the quadrato-jugal.

The quadrato-jugal is a very slender plate of bone that articulates with the posterior edge of the quadrate for its full length. Above, the quadrato-jugal passes between the squamosal and prosquamosal, and articulates with the parietal; below, it is separated from the quadrate by a fair-sized quadrate foramen.

Anterior to the quadrato-jugal is another element in the position usually assigned to the quadrato-jugal; *i. e.*, it articulates with the jugal anteriorly and passes back to articulate with the quadrate region. It is separated from the quadrato-jugal posteriorly (which is identified beyond doubt by the presence of the quadrate foramen) by a distinct suture, and occupies the exact position of the anterior portion of the squamosal of the living *Sphenodon*. It is separated from

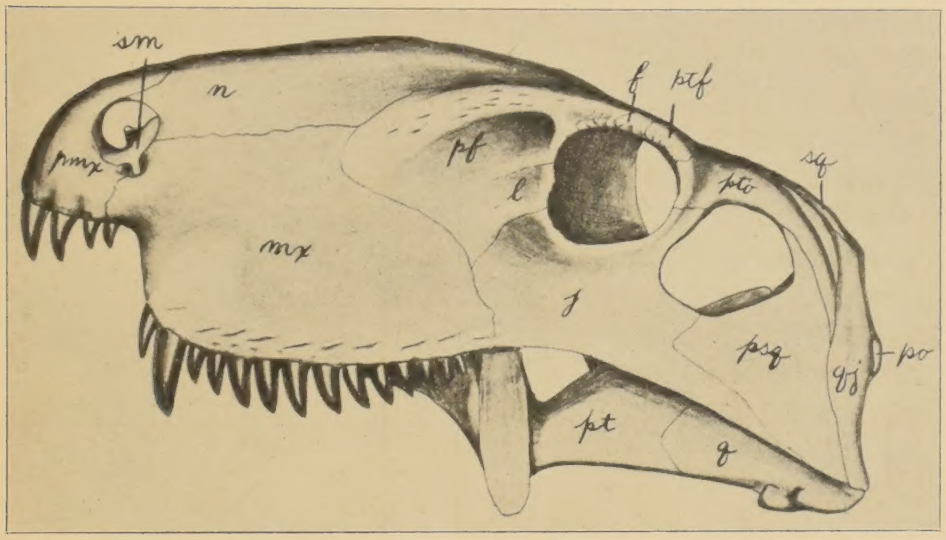

FIG. 2.—Restoration of the left side of the skull of *D. gigas*. *bo*, basi-occipital; *bs*, basi-sphenoid; *f*, frontal; *j*, jugal; *l*, lachrymal; *mx*, maxillary; *n*, nasal; *pmx*, premaxillary; *pv*, prevomer; *pt'*, ascending plate of pterygoid; *pt*, pterygoid; *pf*, prefrontal; *ptf*, postfrontal; *pto*, postorbital; *pa*, parasphenoid; *psq*, prosquamosal; *ps*, ethmoid; *po*, paroccipital (opisthotic); *q*, quadrate; *sq*, squamosal; *st*, stapes.

the squamosal above by the meeting of the quadrato-jugal and parietal; but if these were to separate, and the squamosal and this element came in contact or fuse, we should have the exact condition of the primitive *Rhyncocephalia* (*Saphaeosaurus*), or *Sphenodon*. For this reason I have determined the bone as the prosquamosal. This bone articulates posteriorly with the postorbital, quadrato-jugal, and the lower extermity of the parietal.

The inferior temporal vacuity is formed by the jugal, prosquamosal and postorbital. It is nearly as large as the orbit. The superior temporal vacuity is formed by the postorbital, prosquamosal, quadrato-jugal, and parietal. It is very small, amounting to a small

slit in the *Dimetrodon gigas* No. 1002, and is even doubtfully open in the *Dimetrodon incisivus* (?) No. 1001. The edges of the bones adjacent to the opening are thinned,and in case where the opening is uncertain there is clear evidence of the thinness of the roof of the skull. If this superior temporal opening is just appearing, as seems certain, we have confirmatory proof of the origin of the temporal arches by a process of natural trephining of the completely roofed skull, as proposed by Baur. It is important to notice that the bones

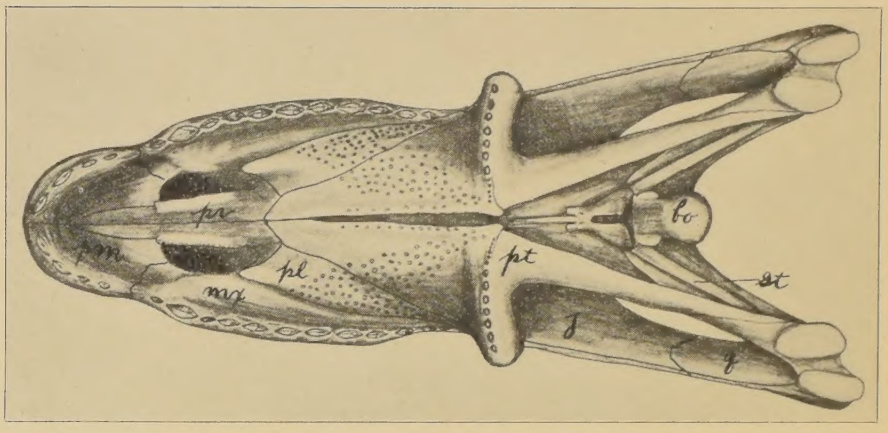

FIG. 3.—Palatal view of the same skull. Letters as in Fig. 2.

have arranged themselves in the position of the perfect arches before the openings appear.

On the posterior face of the skull the remnants of fairly strong stapes was found in position. Unfortunately, neither end was preserved, so that it is impossible to confirm Cope's description of the anterior end of the Pelycosaurian stapes.

On the inferior face of the skull the position of the pterygoids and other bones is confirmed, but the external processes of the pterygoids are shown to have been located farther forward than supposed—at the posterior end of the maxillaries. It is determined that there were no posterior palatine openings between the palatine and maxillary. Anteriorly the nares are separated by the paired prevomers; the sides of the prevomers are marked by rugosities at the inferior opening of the nasal canal.

The ectopterygoid (transverse) is made out for the first time. It is a short bone, articulating with a strong, curved ridge on the inner

side of jugal, which at its lower end becomes sessile, and anteriorly with the maxillary. It covers the anterior and the upper portion of the outer process of the pterygoid.

The bones of the facial region are very similar in position to those of previously described specimens, but there is shown a separate bone at the anterior end of the nasal, forming the posterior wall and a portion of the floor of the external nares. This occupies the same position as the bone called the septo-maxillary in *Sphenodon* by Howes and Swinnerton.[1] The bone has a very peculiar form, being bent at right angles so that the anterior portion forms the posterior half of the floor of the nares, and the posterior half forms the posterior wall. The two bones of the opposite sides meet in the median line, so that they would close the nares; but the inner part of the posterior half is only one-half as high as the outer, so that the inner opening of the nares is elevated. The air entering the nares could not pass directly backward or downward, but first rose over the half partition, and then down into the mouth. The lower edge of the septo-maxillary joins the maxillary and premaxillary. The suture between maxillary and septo-maxillary is marked by two foramina.

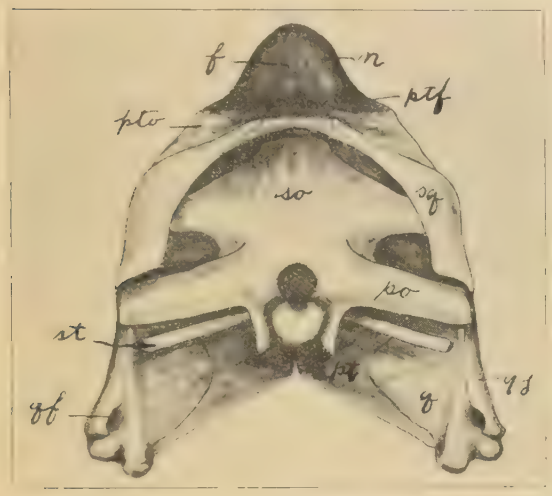

FIG. 4.—Posterior view of same skull. Letters as in Fig. 2.

The section of the skull shows several peculiar conditions. There are paired prevomers which are anteriorly united with the premaxillaries. Passing backward, they are convex upward, so that the anterior portion of the mouth is vaulted. Opposite the maxillary-

[1] G. B. HOWES AND H. H. SWINNERTON, "On the Development of the Skeleton of the Tuatera *Sphenodon* (*Hatteria*) *punctatus*," *Transactions of the Zoölogical Society of London*, Vol. XVI (1903), Part I, No. 1, pp. 1–87, Plates I–VI, Figs. 18.

premaxillary suture the prevomers are free from the side walls of the skull, leaving the elongate openings of the posterior nares. The sides of the posterior nares are marked on the prevomers by rugose ridges. The prevomers are united on the lower surface, but the upper portion is divergent, and receives anteriorly the lower edges of two vertical plates that seemingly originate from the inner edges

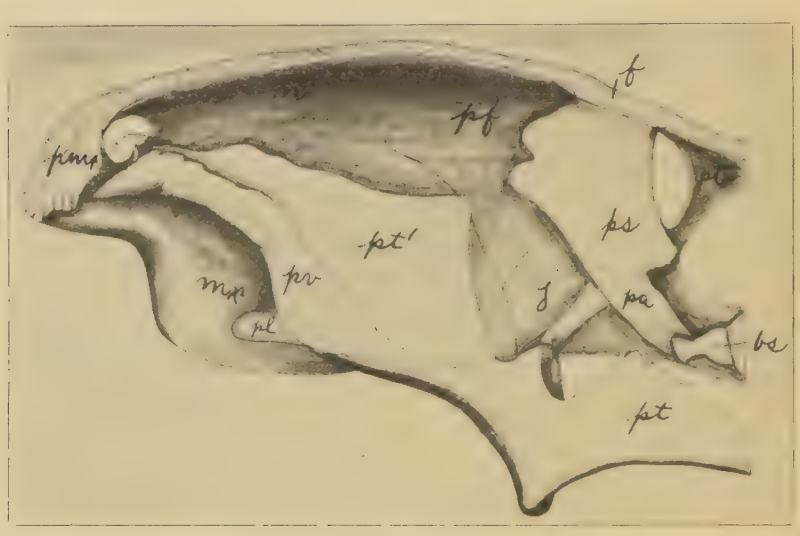

FIG. 5.—Section of the same skull showing septal bones. Letters as in Fig. 2.

of the pterygoids and extend directly upward in the skull. Owing to the somewhat crushed condition of these very slender plates, it is impossible to tell exactly the point of their connection with the prevomers below, but apparently they lie between them, and there was either a squamous contact, or the bones were free in life and have been crushed together in fossilization. The origin of the two vertical plates is somewhat obscure. They occupy the position of vomers behind the prevomers, but the true vomer is a single median bone, and, moreover, is accounted for. Broom[1] has described in *Proterosuchus* two slender vertical plates rising from the inner edges of the pterygoids, with a single median vomer between. It seems that these plates must be the same sort of a structure. They occupy

[1] R. BROOM, "On a New Reptile (*Proterosuchus fergusi*) from the Karoo Beds of Tarkastad, South Africa," *Annals of South African Museum*, Vol. IV (1903), Art. 7.

exactly the same position, but are relatively much larger than figured by Broom.

Posteriorly the parasphenoid is much reduced, and is attached as a slender vertical plate of bone to the anterior end of the basisphenoid between the basiptergoid processes. Above, the parasphenoid articulates directly with a thin vertical plate of bone which expands antero-

FIG. 6.—Lower jaws of *Dimetrodon incisivus* (?), showing the inner and outer surfaces. Full length of jaws, 33 cm.

posteriorly as it rises in the skull, and finally articulates in the median line with the under side of the frontals. This bone can only be the ossified ethmoid portion of the median cartilaginous septum. The anterior edge of the ethmoid is somewhat irregular and thin, and represents the true vomer; the posterior inferior angle is rounded and thickened, and there is an excavation which evidently marks the exit of the 11 nerve from the skull. The presence of a median septum of this character is very peculiar in view of the fact that there are well-developed epipterygoid bones indicated by the preserved lower ends in contact with the posterior portion of the pterygoids.

There was no sign of the lower jaws with the skull of *Dimetrodon gigas*, but with the other skull, No. 1001, the jaws were preserved nearly perfectly. They show that the portion identified by Baur and Case as the articular region of the skull is in reality the articular region of the lower jaw. The articular is small and nearly inclosed by other bones. Its upper face is marked by two deep cotyli, and the posterior edge in specimen No. 1001 has a small hook-shaped projection. The quadrate is supported by the angular, surangular, and splenial (Baur), prearticular (Williston). The posterior ends of these bones stand out from the thin expanded posterior end of the bone, supporting the articular bone on a sort of pedicel instead of on the upper edge of the jaw. This explains why the articular region is so often found isolated in the fossil beds. The posterior portion of the jaw is very thin, but expanded vertically. In both jaws the coronoid bone is lost, but it was a small, thin plate, as shown by the sutures for its attachment. Anteriorly the angular passes far forward, forming the posterior half of the outer side of the jaw. The splenial or prearticular reaches nearly to the middle of the jaw, where it disappears under the splenial (presplenial of Baur). The spenial reaches to the symphasis, but does not take part in it.

As previously described, there are enlarged incisor and canine usks in the upper jaw, and enlarged incisors in the lower jaw. In *Dimetrodon gigas* the edges of the teeth are crenate, but this and the number of the teeth in the jaws seem to be somewhat variable in the different species of the genus.

In general, the whole skull may be said to bear a remarkable resemblance to the skull of *Sphenodon*, in most parts being directly comparable to it, and varying only in the temporal arches—the ossified interorbital septum, and the vertical plates of the upper side of the pterygoids.

E. C. Case.

State Normal School,
Milwaukee, Wis.

ON THE STRUCTURE OF THE FORE FOOT OF DIMETRODON.

During the summer of 1903, while in charge of the University of Chicago expedition in the Permian fossil fields of Texas, the author collected the right fore leg and foot of a Pelycosaurian reptile of the genus *Dimetrodon*. The species is not determinable at present, but is very close to *Dimetrodon incisivus*, if not that species exactly. When found the bones were badly softened by decay, but after cleaning and hardening I find that those of the carpus, with one exception, are perfectly preserved and in their natural positions. This is particularly fortunate, as it is the exception to find any considerable portion of a skeleton together in the Texas fields.

The author has previously described[1] an imperfect front foot of *Dimetrodon*, No. 114 of the University of Chicago collection, and attempted to place the bones in their natural relations. The present specimen shows that the position of the bones in the figure was erroneous and must be corrected.

Fig. 1 shows the right front foot from the lower surface. The bones added from another specimen are in line only. The specimen has received the number 1003 in the University of Chicago collection of vertebrate fossils.

A study of the specimen brings out first of all the striking resemblance of the foot to the foot of *Sphenodon* (Fig. 2), not only in the number of the bones, but in the arrangement and to some extent the form. This emphasizes the Ryhnchocephalian nature of the Pelycosaurs already demonstrated from the structure of the skull.

The carpus consists of eleven elements. The ulnare is a stout bone with wide proximal end, and resembles the same bone in *Sphenodon* very closely. The radiale is larger than the ulnare, but is not so stout; it is very thin, but elongate and articulates with the distal row of carpals. The intermedium reaches well up between the radius and ulna. There are two centrale. Centrale 1 occupies a central

[1] Journal of Geology, Vol. XI, No. 1 (1903), p. 11.

position in the carpus and is much larger than the second. Centrale 2 lies between the ulnare and the third, fourth, and fifth carpals, but is surrounded by bones, as its outer side articulates with the sesamoid. The form and articulation of the five carpals of the distal row are best

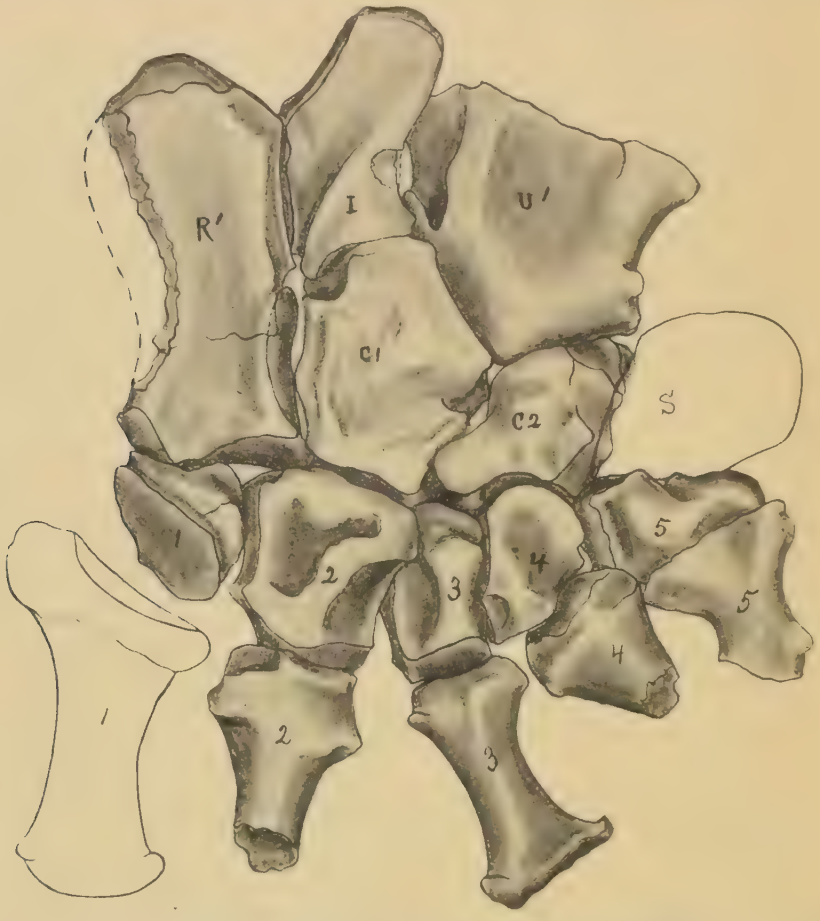

FIG. 1.—Lower side of the manus of the right foot of *Dimetrodon* sp. *r'*, radiale; *u'*, ulnare; *i*, intermedium; *c* 1, centrale one; *c* 2, centrale two; *s*, sesamoid; 1, 2, 3, 4, 5, carpals and metacarpals. Natural size.

seen from the figure. The fifth carpal is peculiar in its prominent position at the side of the carpus, standing well away from the rest of the bones.

A second specimen of *Dimetrodon* discovered the same summer afforded a nearly complete anterior portion of the skeleton. It has received the number 1001 in the Chicago collection. The bones of

this specimen were somewhat scattered, so that, although the bones of the fore legs and feet were preserved, they were not in position. From the specimen 1003 the bones of the carpus of both sides in specimen 1001 have been placed in position, and both show the presence of an extra element which, from the position of articular surfaces and from comparison with *Sphenodon*, evidently occupies the position of the pisiform bone on the ulnar side of the mammalian carpus. It is a sesamoid bone of considerable size.

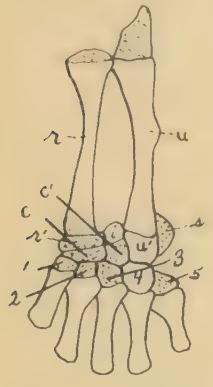

FIG. 2.—Upper side left manus of *Sphenodon* after Bayer and Howse, from Osborn. Lettering as in Fig. 1. Natural size.

The bones of the carpus fit snugly together, with well-developed articular surfaces, making a strong foot. This is also shown by the possession of well-developed phalanges and powerful claws.

The first digit was shorter and stouter than the second. The broad proximal end is characteristic of the first metacarpal. The second digit was probably the largest of the foot, judging from the length of the metacarpal and the imperfect foot of specimen 114. The third and fourth metacarpals are more slender than the second. The fifth metacarpal is a very broad and thin bone articulated to the prominent fifth carpal, so that it stood out from the others at a considerable angle. The articular surface between the fifth carpal and metacarpal is twisted in a peculiar manner, so that it permits of a considerable range of motion. This perhaps explains the fact that the fifth metacarpal and digit were found in the specimen 114 lying at right angles to the fourth. In the description and figure of 114 they were called first and second.

FIG. 3.—Manus of *Procolophon*. From Osborn after Broom. Lettering as in Fig. 1. Natural size.

It is interesting to compare the carpus of *Dimetrodon* with the carpus of *Procolophon* in the light of Broom's determination of the *Rhynchocephalian* nature of *Procolophon*.[1] Fig. 3 is an outline

[1] BROOM, *Records of the Albany Museum*, Vol. I, No. 1 (1903). See also OSBORN, *Memoirs of the American Museum of Natural History*, Vol. I, No. 8 (1903), p. 480.

drawing of Broom's restoration, slightly modified according to Osborn; *i. e.*, the bone marked centrale 2 was called by Broom radiale. It will be seen that the carpus is essentially the same if the radiale is restored. The fifth carpal is missing, but that may well be left open for future evidence, as there is so commonly a fifth carpal in the primitive reptiles.

E. C. Case.

State Normal School,
Milwaukee, Wis.