

Additional evidence as to the dentition and structure of the skull in the South African fossil reptile genus Diademodon / by H.G. Seeley.

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ADDITIONAL EVIDENCE AS TO THE DENTITION
AND STRUCTURE OF THE SKULL IN THE
SOUTH AFRICAN FOSSIL REPTILE GENUS
DIADEMODON. BY H. G. SEELEY, F.R.S.,
F.Z.S., King's College, London.

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Additional Evidence as to the Dentition and Structure of
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(Text-figure 130.)

The genus *Diademodon* was founded on the molar teeth and imperfect middle portions of small skulls. Four species were figured in Phil. Trans. Royal Society, 1894, B, pl. 89, referred to *D. tetragonus*, *D. brachytiara*, *D. mastacus*, and *D. browni*. They were the most remarkable evidences of dentition of mammalian type in extinct reptiles which have been found in South Africa. There would have been grounds, had the remains been mammalian, for referring them to three genera; and in the description of plate 89, figure 11 is described as the left maxillary region of *Diademodon* (or *Gomphognathus*) *mastacus*. And in the original description of *D. browni* (*l. c.* p. 1039) it is observed, "it is probably the type of a distinct genus." Later in the same year the group Gomphodontia was defined as comprising animals with a Theriodont type of dentition, in which the molar teeth are expanded transversely, and as having more or less tuberculate crowns, of the type shown in *Diademodon*. In that group the genus *Diademodon* was included (*l. c.* 1895, B, p. 3). The types of *Gomphognathus* had the crowns of the molar teeth well worn, but the elevation of the external cusps or ridge in *G. polyphagus* made a suggestive resemblance to *Diademodon mastacus*; while the condition of the single well-preserved crown in *Diademodon browni* makes an equally suggestive approximation to *Diademodon brachytiara*. In 1896, in a short communication to the British Association at Liverpool, I briefly noticed another skull discovered by Dr. D. R. Kannemeyer. I have removed the matrix in the laboratory of King's College, so as to demonstrate the sutures in the middle part of the skull and to expose the palate. The specimen is slightly squeezed so as to have a lateral obliquity towards the right side, from which the similar example of *Diademodon browni* is not free. There is a coincidence in the anterior and posterior fractures being in identical positions in both specimens, favouring comparison. They are closely related species, but the snout in the new example is narrower and rather smaller, and the dentition being unworn favours the idea of specific difference, though the forms of the transversely ovate sections of the molar and premolar teeth are almost identical.

As preserved the specimen is $2\frac{1}{2}$ inches long. It extends between an anterior transverse fracture through the two concave pits on the snout, which lie at the junction of the maxillary and nasal bones, which in *Gomphognathus* are situated midway between the orbits of the eyes and anterior nares, and a posterior fracture

behind the orbits, just behind the post-frontal bones, which are imperfectly preserved. The lateral margins converge forward in a wedge-like outline similar to the corresponding part of the skull of *Gomphognathus*. Owing to the lateral compression the anterior transverse measurement is narrowed by one or two tenths of an inch. As preserved it is one inch wide, and the vertical height from the median longitudinal ridge on the palate to the nasal bones is the same. The corresponding measurements in *Diademodon browni* are: vertical $1\frac{1}{10}$, transverse $1\frac{4}{10}$ inch. The pre-orbital lateral areas of this, formed chiefly by the maxillary bones, are inclined towards each other, are gently convex from the alveolar border to the nasal region, longitudinally furrowed by two shallow concavities on each side, and then round with a gentle convexity into the upper surface formed by the nasal bones.

Diademodon browni distinctly suggests an angle between the sides of the face, which are more vertical, and the roof of the snout; but the difference between the specimens is one of degree. In both there is some lateral concavity of the pre-orbital region from front to back.

The head widens backward to the posterior fracture, which passes through the back of the frontal bone, the post-frontal bones, and the pterygoid bones. The specimen is about $2\frac{3}{10}$ inches wide behind the dentary tract, which is in a line with the middle of the orbits, and $1\frac{4}{10}$ inch high at the back of the frontal bones.

The bones seen on the superior aspect of the skull are the frontal, post-frontal, pre-frontal, nasal, lachrymal, and maxillary. The naso-maxillary region is convex from side to side, but as the nasal bones extend between the orbits their flattened upper surface merges in the flattened frontal region. The orbits are inclined so to look outward, and to a less extent upward and forward. The vertical measurement of the rounded cavity is one inch, and the transverse measurement between them over the pre-frontal bones is $1\frac{2}{10}$ inch. In *D. browni* it appears to have been $1\frac{11}{20}$ inch.

Only the part of the post-frontal bone which is above the back of the orbit is preserved. It is rather less than half an inch wide between the temporal vacuity and the suture with the pre-frontal bone. It is transversely channelled owing to elevation of its front and back borders. These bones are slightly raised above the frontal bones, which extend longitudinally between them. As preserved the frontal bones are oblong, $\frac{8}{10}$ inch long, and more than half an inch wide towards the middle at the suture between the post-frontal and pre-frontal bones, and narrow anteriorly to the transverse suture with the nasal bones. Both bones are longitudinally concave with the median sutural line raised. This feature is absent in *Diademodon browni*. The lateral sutures with the post-frontal and pre-frontal bones are similarly raised as slight ridges, but there is no ridge between the frontal and nasal bones.

The pre-frontal bone forms much of the superior border of the

orbit where the margin is compressed posteriorly and rounded in front. The bone is in front of the post-frontal, external to the frontal, makes an oblique suture with the nasal, and a narrow junction with the lachrymal bone, as its sutural junctions diverge outward and forward. It is $\frac{3}{4}$ inch long from the post-frontal to the lachrymal and $\frac{9}{20}$ inch wide at the fronto-nasal suture, where it is widest in about its middle length. The inner short border next the frontal is parallel to the longer external border above the orbit and lachrymal. The pre-frontal bone forms a large part of the internal anterior wall of the orbit.

The nasal bones, somewhat lanceolate in form, are imperfect anteriorly. They extend from the frontal bones forward as preserved to between the pair of pits on the front of the snout, which are not seen in *Diademodon browni*, with a length of $1\frac{4}{10}$ inch, and in this length they are not in contact with the pre-maxillary bones. They are separated from each other by a fine straight suture, and widen from the frontal suture anteriorly, with the lateral divergence of the sutures dividing them from the pre-frontal and lachrymal bones, to $1\frac{1}{4}$ inch at the front of the lachrymal bones; and anteriorly the sutures between them and the maxillary bones converge forward, to a transverse width over the nasal bones of half an inch, at the anterior fracture through the lateral-nasal pits. The bones are smooth, convex from side to side, and slightly raised posteriorly, with a partial prolongation forward of the median frontal sutural ridge.

The lachrymal bone is best exposed on the left side, where I have partially removed the matrix from the orbit. It is at the front of the orbit between the maxillary bone below and the nasal and pre-frontal bones above. Externally it is of irregular sub-quadrate form, half an inch in each measurement. It has a considerable extension in the front of the orbit internally, below the pre-frontal bone. On the lower part of the inner front border the bone is pierced by two circular canals placed one below the other.

The maxillary bones form the sides of the face from the hinder fracture at the back of the alveolar tract below the orbit, where the bone is $\frac{4}{10}$ inch deep, forward to the anterior fracture, where the depth is $1\frac{1}{10}$ inch. The ascending orbital border below the orbit is compressed, rounded, and slightly reflected outward. Below the lachrymal canal the depth to the alveolar border is $\frac{17}{20}$ inch. A slight wide shallow concavity extends longitudinally forward, from the orbital junction between the lachrymal and maxillary bones; but on the right side the bone appears to be accidentally impressed in this region. The lower part of the maxillary bone is moderately concave in length, and markedly convex downward owing to the compression of the bone immediately above the molar teeth. On the convex ridge above are two ovate foramina above the teeth, such as occur in many fossil reptiles.

The palate has shared in the side to side compression and

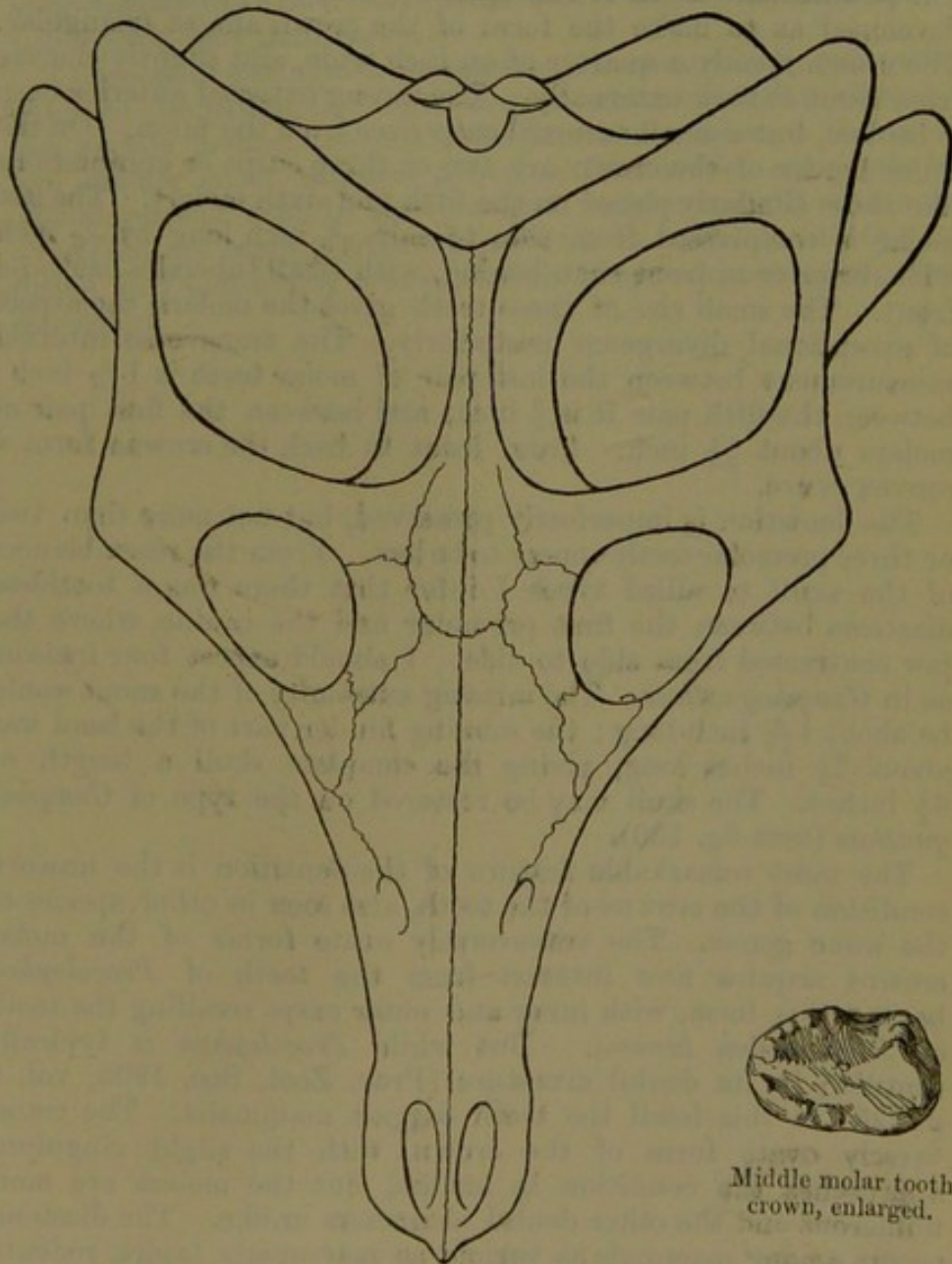
distortion of the specimen and is probably narrowed by a tenth of an inch. The teeth extend in diverging curves as they range backward and outward. The transverse width over the premolars in front is $\frac{17}{20}$ inch; over the last molars it is about $2\frac{2}{10}$ inches. These measurements are less than in *Diademodon browni*. Ten teeth are indicated or preserved, of which the two in front, with small circular fractured bases to the crowns, are classed as premolars, and the eight succeeding teeth are molars. They have the crowns transversely ovate, each with its axis at right angles with the concave external alveolar border, except the last tooth, which is parallel to the alveolar border. The crowns increase in width to the fifth molar and then become smaller, the seventh and eighth rapidly narrowing acquire a triangular or comma shape. The length occupied by the eight molars is $1\frac{13}{20}$ inch.

The anterior teeth are separated by the hard palate between them. They rise with a vertical inner alveolar border corresponding to the compressed external border. As preserved the hard palate is $\frac{11}{20}$ inch wide between the last premolar teeth, and $\frac{3}{4}$ inch wide where it terminates between the fifth pair of molars. It is narrower than in *D. browni*, in which the fourth molar appears to be the largest. The hard palate as preserved is made by the maxillary bones, which extend behind the second molar teeth, and unite by a transverse suture with the palatine bones, so that the suture is in about the same position as in *Gomphognathus polyphagus* (Phil. Trans. 1895, B, p. 16, fig. 7). Its distinctive feature is a strong elevated median ridge dividing the palate into two concave channels. This ridge is continued backward by what I regard as the vomerine bone, dividing the posterior nares, extending upon the median union of the posterior palatine bones. This ridge on the hard palate is absent from *D. browni*; its presence makes the transverse hinder border of each half of the hard palate concave, instead of both bones combining to form one concave posterior surface. The back of the palate behind the posterior nares has a close general resemblance to the corresponding region of *Gomphognathus*. There are the same pair of convex rounded tumid areas behind the hard palate converging backward from the hinder cheek-teeth to terminate in a pair of hemispherical convexities which were just in front of the median post-palatal ridge in that genus, flanked externally by the broken bases of the pair of transverse processes which descended between the rami of the mandible (compare *l. c.* p. 24, fig. 11). The transverse width over these processes in this specimen is $1\frac{7}{10}$ inch. Those processes are regarded as being made chiefly by the transverse bones and as defined by sutures which converge inward from behind the maxillary bones backward to the hemispherical tubercles at the posterior fracture.

The teeth have been more or less broken, possibly by strain or compression. Small parts of the enamelled surfaces of the tuberculate crowns remain in the first and second molars of the right side. The first shows a marginal external rim behind the crown

and laterally, and a small central tubercle in front. The second indicates two lateral external tubercles. None of the crowns show the slightest trace of wear by the apposition of the mandibular teeth, in this respect being in striking contrast to *Gomphognathus*, in which the crowns of all the molar teeth are always worn so that nothing remains of tuberculate structure except the external cusp. The fifth, sixth, seventh, and eighth crowns are preserved on both sides.

Text-fig. 130.



Middle molar tooth
crown, enlarged.

Restoration of the skull of *Diademodon entomophonus*. About $\frac{2}{3}$.

The fifth and sixth crowns are transversely ovate, less than $\frac{4}{10}$ inch wide and $\frac{1}{4}$ inch from front to back. They have a strong

external crenulate border and a median crenulate transverse ridge, dividing the concave posterior half of the crown, which has a crenulate external margin, into larger external and smaller internal concave spaces (see text-fig. 130). In front there is a sharp or crenulate marginal border, with transverse crenulations or cusps; on the middle of the crown two small anterior cusps and two posterior cusps. These crowns are essentially of the type of the described species of *Diademodon*. The last tooth of *D. mastacus* shows a tendency to develop a posterior talon (*l. c.* 1894, B, pl. 89, figs. 11, 12). The penultimate tooth of this specimen has the posterior talon so developed as to make the form of the crown almost triangular. The crown is only a quarter of an inch wide, and slightly shorter from front to back externally. The strong external anterior cusp is broken, but a small external cusp rises from the talon. On the inner border of the crown are two or three cusps or crenulations like those similarly placed on the fifth and sixth molars. The last molar is compressed from side to side, $\frac{2}{10}$ inch long by $\frac{1}{10}$ inch wide, broader in front than behind, with small tubercles back and front. The small size of these teeth gives the molars the aspect of exceptional divergence posteriorly. The transverse internal measurement between the last pair of molar teeth is $1\frac{8}{10}$ inch; between the fifth pair it is $\frac{3}{4}$ inch, and between the first pair of molars about $\frac{1}{2}$ inch. From front to back the crowns form a convex curve.

The dentition is imperfectly preserved, but not more than two or three premolar teeth appear to be lost. From the resemblances of the skull to allied types I infer that there was a toothless diastema between the first premolar and the canine, where the jaw contracted from side to side. I should expect four incisors as in *Gomphognathus*. The missing extremity of the snout would be about $1\frac{8}{10}$ inch long; the missing hinder part of the head was about $2\frac{1}{2}$ inches long, giving the complete skull a length of $6\frac{1}{2}$ inches. The skull may be restored on the type of *Gomphognathus* (text-fig. 130).

The most remarkable feature of the dentition is the unworn condition of the crowns of the teeth, also seen in other species of the same genus. The transversely ovate forms of the molar crowns acquire new interest from the teeth of *Procolophon* having this form, with inner and outer cusps recalling the tooth of *Diademodon browni*. But while *Procolophon* is typically reptilian in its dental armature (*Proc. Zool. Soc.* 1905, vol. i. p. 225), in this fossil the teeth suggest mammalia. The transversely ovate form of the crown, with the slight cingulum, approaches the condition in lemurs, but the molars are more numerous and the other dental characters unlike. The diastema occurs among mammals as various as marsupials, tapirs, rodents, but is never associated with a transversely ovate molar, and full series of incisor and strong canine teeth as in these fossil reptilian types. Mammals of various groups have the molar teeth progressively increasing and afterwards decreasing in size, as

among lemurs, insectivora, carnivora. But the feature of this reptilian type is its generalised mammalian resemblances in dental characteristics, which are highly specialised distinctions among mammals, so that the teeth have undergone an evolution of mammalian type. It is not to be anticipated that a complete skeleton of *Diademodon* will make a closer approximation to that of a mammal than is already evidenced by other Theriodont reptiles; but the dental characters emphasise the mammalian approximations which have been found in the shoulder-girdle, pelvic arch, and limb-bones.

I propose to distinguish this species, characterised by the median ridge on the palate, the ovate unworn multituberculate crowns of the middle molars, the moderate interspace between the orbits, and slender snout rounded above, as *Diademodon entomophonus*. The absence of wear to the crowns is only consistent with a diet which did not involve trituration. It is in contrast with the condition in *Diademodon browni*, which it approximates in general characters.

