A STUDY ON THE SKELETON OF DIADEMODON

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(Extracts from thesis presented for the degree of Doctor of Philosophy in the University of London, June, 1949, supplemented with additional information)

Abstract

In this work the genus *Gomphognathus* is declared synonymous with the genus *Diademodon*. The small skeleton of "*Microgomphodon*", described by Seely in 1895, is recognised as possibly that of a newly "born" *Diademodon*.

The structure of the skull is described in detail. Information was obtained from a wealth of fragmentary skull material belonging to many individuals of different ages. A special section is devoted to dentition and in another section new specimens are described, *D. laticeps* and *D. parringtoni* being introduced as new species.

In dealing with the skeleton certain aspects of interest are analysed. An answer is sought for the peculiar arrangement of the lumbar ribs. The girdles are dealt with separately and attention is given to the dimensions of the pelvic girdle, in particular with a view to the probability of viviparity. Attention is also given to features which could throw light on aspects such as blood temperature, breathing, and the characteristics of the skin.

Introduction

This account of the skeleton of *Diademodon* does not conform in all respects to my thesis as originally submitted. On the whole the work is much abridged. Large portions, such as a complete historical account, detailed lists of the material investigated, and detailed accounts of the skeleton of *Cynognathus* for comparison, are omitted. Other sections are abridged, certain sections more than others. It is impossible to indicate below exactly which sections appear as originally submitted. Where possible, additional information obtained after the thesis was submitted will be indicated.

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There has been for many years a controversy as to whether there are two distinct genera *Diademodon* and *Gomphognathus*. One of the results of this work is to show that the generic name *Gomphognathus* is redundant. The descriptions of the type specimens of the different *Diademodon* species were based on very fragmentary portions of skulls, whereas more complete specimens were later described as *Gomphognathus*. Seeley (1894 and 1895), who introduced the two generic names, did not at first notice a similarity between them. He did not demonstrate any particular difference, except a slight difference in the teeth. This was later found not to be of much importance. Still later it became difficult to say to which genus a newly described specimen should belong and species have been described as belonging to both *Diademodon* and *Gomphognathus*.

The consensus of modern opinion appears to be in favour of grouping all the species under the genus *Gomphognathus* and leaving only the badly known species

tetragonus under the genus *Diademodon*, together with the two isolated molars described as *D. brachytiara*. It will, however, be shown below that there is no reason why the specimen described as *D. tetragonus* should not be included in the same genus as the *Gomphognathus* species.

A good deal of well preserved *Diademodon* material, collected by Professor D. M. S. Watson in 1929, was placed at my disposal. Practically all the specimens have been developed, but not yet described. On these specimens, as well as on previously published work, the following detailed account of a generalised *Diademodon* is based. Most of the specimens were collected from a bone bed opposite the police station at Lady Frere. A few specimens come from Winnaarsbaken in the Burghersdorp district.

Acknowledgements

I wish to express my sincere thanks to Professor D. M. S. Watson, who placed this large amount of already developed material at my disposal and under whose guidance I prepared this work. I also extend my thanks to Dr. Swinton, of the British Museum of Natural History, for facilitating my access to the British Museum specimens, some of which had to be fetched from their war-time protected localities in the country.

My thanks also to Dr. A. C. Hoffman, Director of the National Museum, Bloemfontein, for permission to publish an account of a *Diademodon* skeleton in his care, and to Mr. J. W. Kitching of the Bernard Price Institute for his preparation work on this and other specimens in our own collection.

I would also like to record my sincere thanks to the University College of London for granting me the Margaret Brown Studentship, which enabled me to complete my two years as an internal student in the University of London.

The Structure of the Skull

The *basioccipital* forms the floor of the cerebellum and the bridge between the two occipital condyles. For *Cynidiognathus* Haughton (1922) demonstrated the suture between the basioccipital and basisphenoid shortly behind the dorsum sellae, on the floor of the brain cavity. The condition appears to be the same in *Diademodon*. Ventrally this suture is covered by the parasphenoid, which forms an intensively interdigitated suture with the basioccipital at the level of the seventh nerve foramen. This suture extends farther forward medially than laterally. Laterally it passes shortly in front of the anterior margin of the fenestra ovalis. The basioccipital does not form part of the margin of the jugular foramen, the suture between it and the exoccipital passing a millimeter or two medially to the foramen (see fig. 2).

The *exoccipitals* form the occipital condyles. They do not appear on the ventral margin of the foramen magnum, but form slightly more than half of the lateral margins. The exoccipital covers the opisthotic posteriorly and more medially it folds over the opisthotic ventrally (see figs. 1 and 2). Each exoccipital forms the posterior margin of the jugular foramen while the opisthotic forms the anterior margin. The former also forms the posterior margin of the floccular fossa.

The *supraoccipital* forms the roof of the cerebellum. It forms the whole of the dorsal margin of the foramen magnum, as well as small portions of the lateral

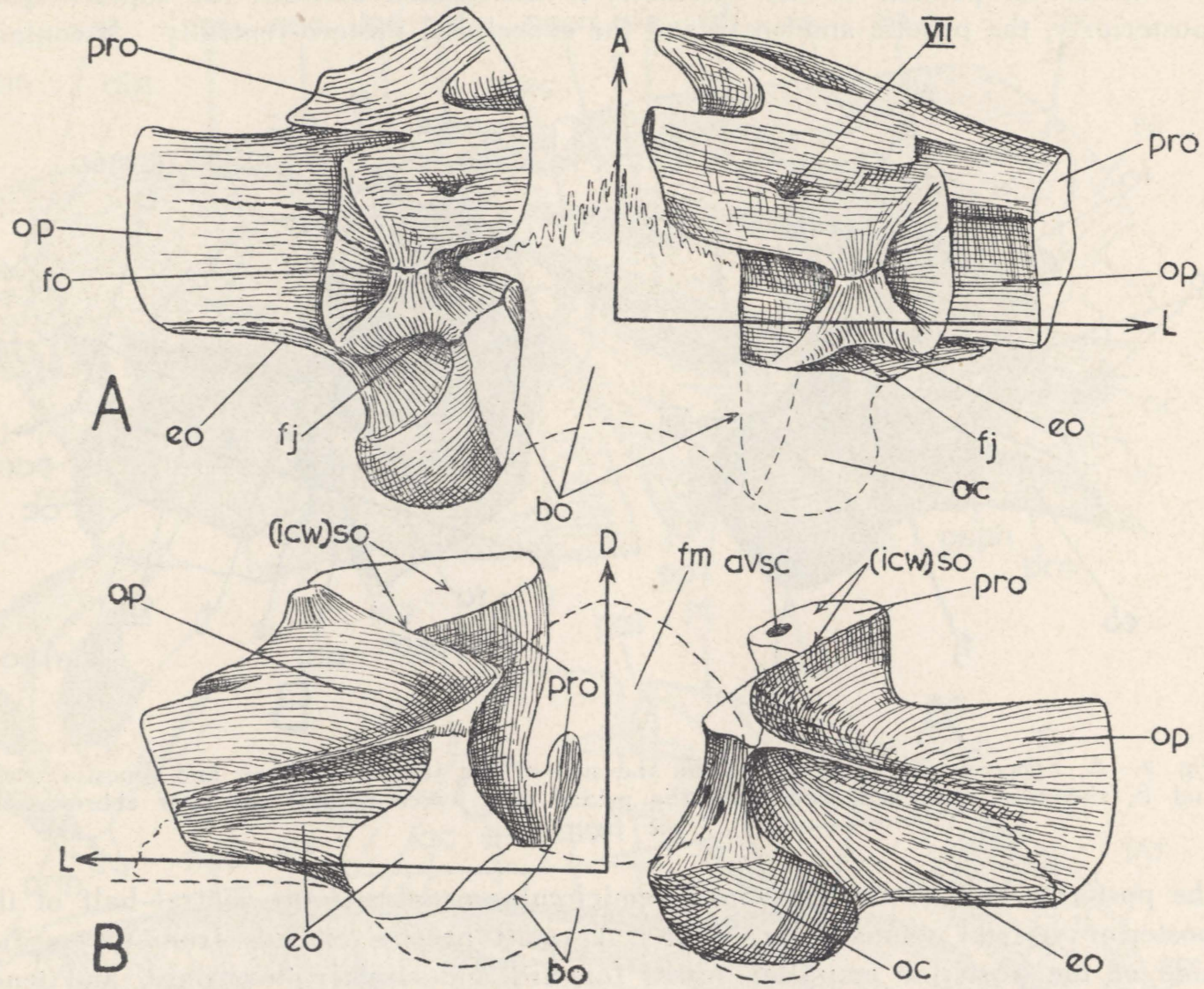


Fig. 1.—A, Ventral and B, Posterior view of the otic capsules of a young individual, R.152 and R.153 left, D.M.S.W. Collection, twice natural size. For abbreviations see figure 3.

walls. Its dorsal half is covered externally by the interparietal, and more laterally by the tabulars. Its dorsal extremity, which was cartilaginous during life, was enfolded by the parietals.

The supraoccipital forms the roof of the floccular fossa and contains in this region the dorsal halves of the two vertical semicircular canals of each side. It extends a good distance forward along the dorsal margin of the prootic. Immediately in front of the angle between the dorsal end of the supraoccipital and the prootic, the latter is not in contact with the parietal along the whole distance of their suture; a foramen is left for a vein.

The *opisthotic* is fairly long and massive, forming the paroccipital process. In the middle of its length it has a triangular cross section. The posterior face in this region is vertical, the antero-ventral face forms the roof of the middle ear and the antero-dorsal face is in contact with the prootic. Laterally the paroccipital process has a rounder vertical cross section, where the end is expanded. This end presses against the squamosal and is partly overlapped on its posterior face by the tabular. The opisthotic forms the ventral border of the post-temporal fossa

in certain species (*D. browni*), but in others it is separated from the fossa by a portion of the tabular (as in the new species described below as *D. laticeps*).

The medial portion of the opisthotic is interlocked between the supraoccipital posteriorly, the prootic anteriorly and the exoccipital postero-ventrally. It contains

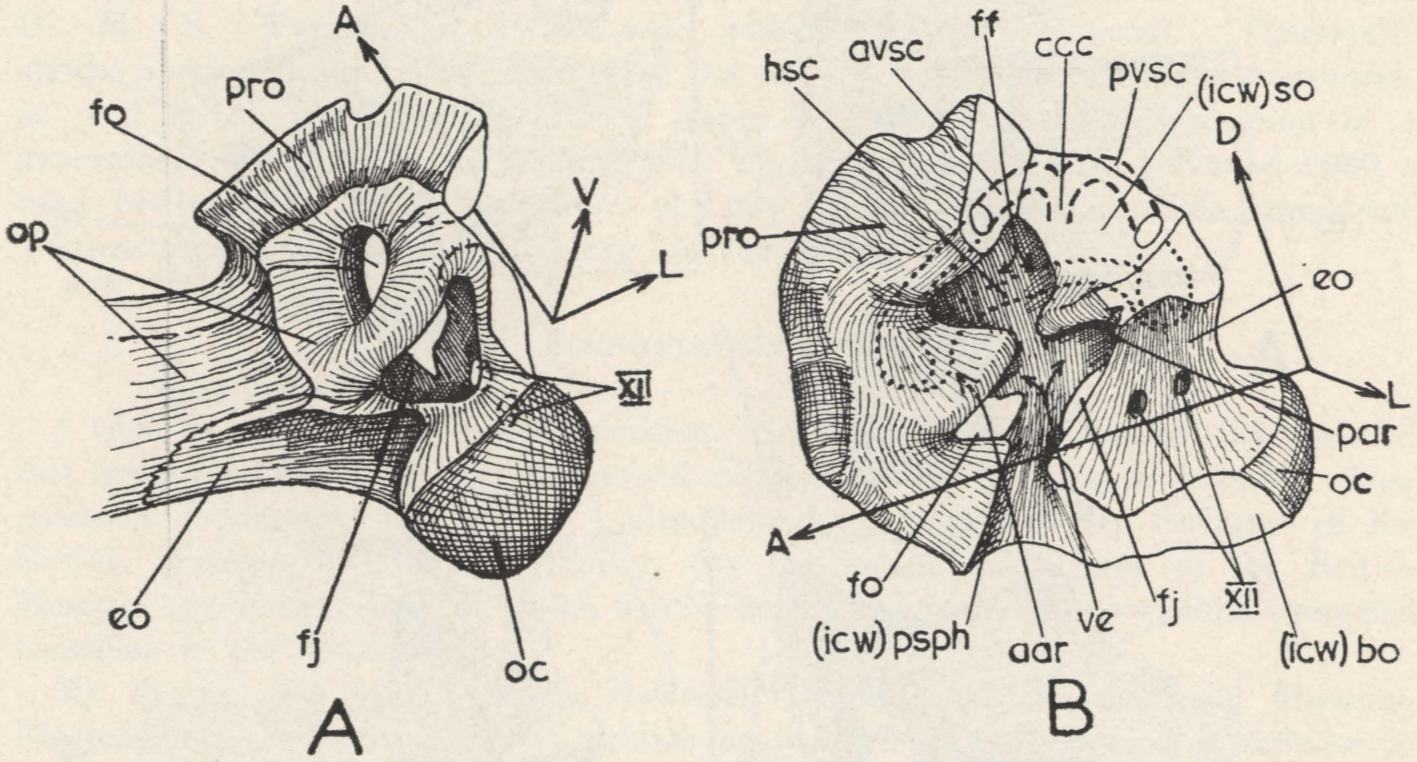


Fig. 2—A, Specimen R.152 as seen from the side of the jugular foramen and fenestra ovalis and B, the same specimen seen from the medial side, twice natural size. For abbreviations see figure 3.

the posterior half of the horizontal semicircular canal and the ventral half of the posterior vertical semicircular canal. A small process extends from the medial side of the posterior ampullar recess forward and slightly downward, and tends to separate the floccular fossa from the vestibule. The opisthotic forms the anterior half of the wall of the jugular foramen and the dorsal and posterior margins of the fenestra ovalis (see fig. 2a).

The foramen rotundum passes through the roof of the pit above the jugular foramen. It passes upward, outward and forward into the vestibule immediately above and, on the side of the latter, it lies below the ampullar recess. The opisthotic forms the lateral border of the foramen rotundum and the exoccipital forms the medial border.

The anterior foramen for the twelfth nerve passes through the medial wall of the pit above the jugular foramen, immediately behind the foramen rotundum, while the posterior foramen passes for a longer distance through the exoccipital and enters the pit through the posterior wall.

The *prootic* forms a good deal of the side wall of the brain cavity. Postero-ventrally it extends laterally and articulates with the antero-dorsal face of the opisthotic.

The whole of the dorsal margin of the prootic extends along the ventral margin of the parietal, but there is an opening between the two bones in front of the antero-dorsal end of the supraoccipital. The alisphenoid covers about half of the surface of the prootic externally. The dorsal half of the anterior margin of the prootic

articulates with a flap of the parietal, extending downward medially to the alisphenoid. Farther down, the anterior margin of the prootic presses against the

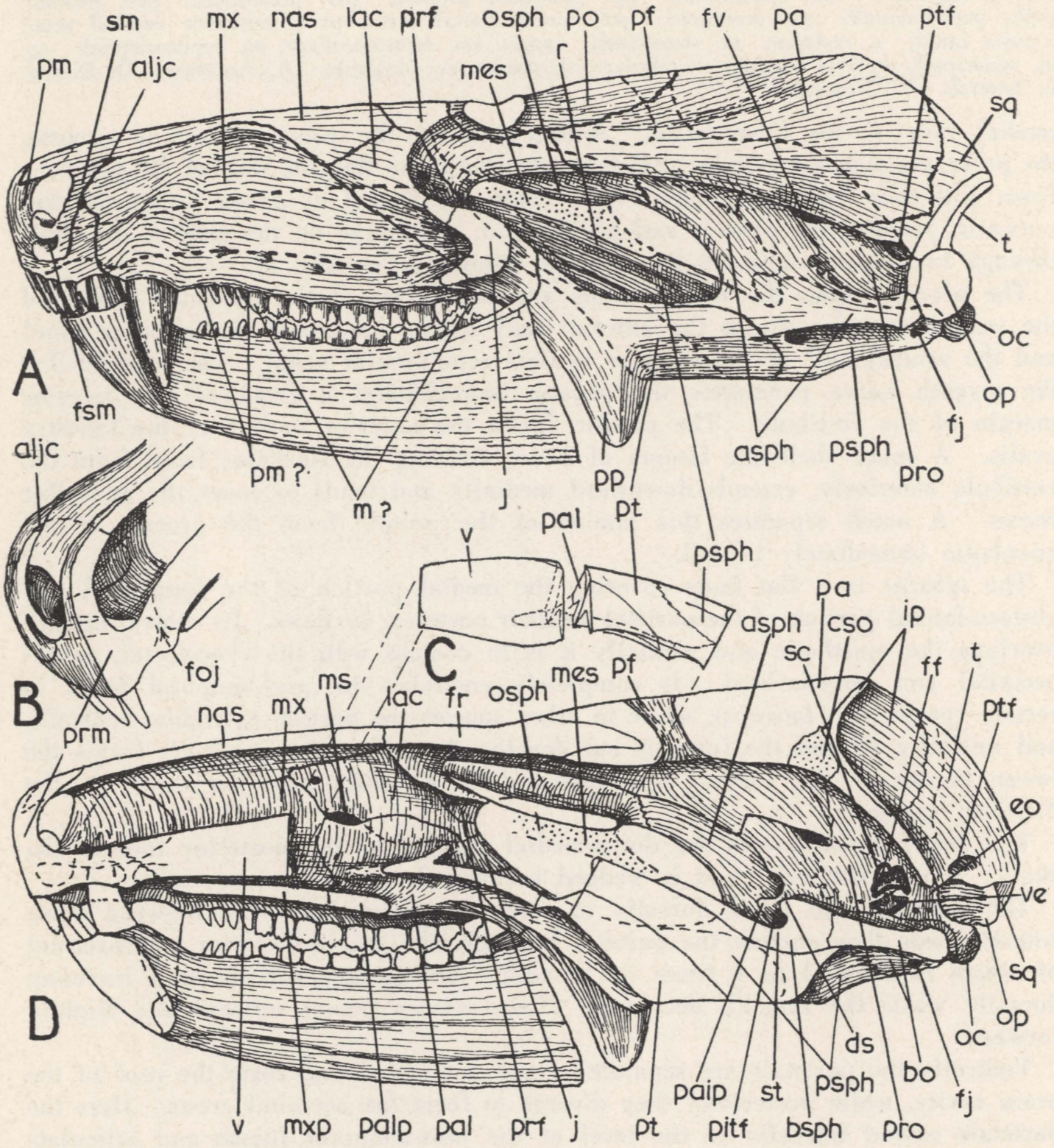


Fig. 3—A, Left view of reconstructed skull of *D. mastacus,* R.51, D.M.S.W. Collection, snout after *D. parringtoni,* R.159, D.M.S.W. Collection, zygomatic arch removed. B, Isometric view and medial section through the snout reconstructed after *D. parringtoni.* C, A portion of the vomer-pterygoid-rostrum removed to show structures behind. D, Medial section through the same reconstructed skull, based on evidences obtained from all material. ½ Natural size.

Abbreviations: aar, anterior ampullar recess; aljc, aperture formed by lower jaw canine; asph, alisphenoid; avsc, anterior vertical semicircular canal; bo, basioccipital; bsphs, basisphenoid; ccc, crus communis canalium; cso, cartilaginous supraoccipital; ds, dorsum sellae; eo, exoccipital; ff, floccular fossa; fj, jugular foramen; fm, foramen magnum; fo, fenestra ovalis; foj, foramen leading to organ of Jacobson; fsm, foramen below septomaxillary; fv, foramen for vein; hsc, horizontal semicircular canal; icw, in contact with; ip, interparietal; j, jugal; lac, lachrymal; mes, mesethmoid; ms, maxillary sinus; mx, maxillary; mxp, palatal plate

of the maxillary; nas, nasal; oc, occipital condyle; op, opisthotic; osph, orbitosphenoid; pa, parietal; paip, processus anterior inferior prootici; pal, palatine; palp, palatal plate of the palatine; par, posterior ampullar recess; pf, parietal foramen; pitf, pituitary fossa; pm, premaxillary; po, postorbital; pp, pterygoid process; prf, prefrontal; pro, prootic; psph, parasphenoid; pt, pterygoid; ptf, post-temporal fossa; pvsc, posterior vertical semicircular canal; r, rostrum; sc, semicircular canals; sm, septomaxillary; so, supraoccipital; sq, sq, squamosal; st, sella tursica; t, tabular; v, vomer; ve, vestibule. A, Anterior; D, Dorsal; L, Lateral; V, Ventral.

medial face of the alisphenoid. Antero-ventrally the prootic forms a process, the processus anterior inferior prootici, contributing to the side wall of the pituitary fossa and over which the fifth nerve (branches b and c) passes backward and outward, between the prootic and alisphenoid, to emerge on the side of the skull through two closely adjacent but separate foramina (see fig. 3).

The prootic forms the whole of the anterior halves of the floccular fossa and the vestibule, and contains the anterior half of the horizontal semicircular canal and the ventral half of the anterior vertical semicircular canal. The foramen for the seventh nerve penetrates the prootic immediately in front of the anterior margin of the vestibule. The prootic forms the anterior border of the fenestra ovalis. A small shelf-like lamina of bone, dividing the floccular fossa from the vestibule anteriorly, extends downward medially and tends to cover the ampullar recess. A notch separates this lamina of the prootic from the process of the opisthotic immediately behind.

The *tabular* is a flat bone covering the medial portion of the squamosal and postero-lateral portion of the parietal on their posterior surfaces. Its ventral margin overlaps the opisthotic and medially it is in contact with the exoccipital, supra-occipital and interparietal. It completely encircles the post-temporal fossa in certain species (*D. laticeps*), while in other species the portion extending ventrally and medially around the fossa is not developed, so that the opisthotic forms the lower border of the fossa. Any intermediate condition may be found in the different species.

The *interparietal* covers the dorso-medial portion of the posterior face of the skull. It is a flat bone and is wedged between the parietals posteriorly.

The *parietals* are fused dorsally to form the parietal crest. Between their anterior ends they enclose the parietal foramen, the antero-posterior measurement of which is about 3 to 4 times its breadth. The former measurement increases dorsally while the breadth decreases. The foramen passes upward and slightly forward.

Ventrally the parietals are separated from each other and form the roof of the brain cavity, while posteriorly they diverge to form the occipital crests. Here the parietals extend laterally to the level of the post-temporal fossae and articulate at this level with the squamosals. The prootics extend along the whole of the ventral margins of the parietals posteriorly and the alisphenoids overlap the ventral margins of the parietals anteriorly. The parietals send a lamina of bone down on each side along the medial face of the alisphenoid. This lamina is continuous with the prootic on the inside of the alisphenoid (see fig. 3). The posterior ends of the frontals are prolonged backwards as two tapering processes within the anterior ends of the parietals. The posterior ends of the postorbitals cover the anterior ends of the parietals laterally for about half the length of the parietal crest. The parietal foramen is situated half way between the anterior ends of the parietals

and the posterior ends of the postorbitals. Antero-ventrally the parietals are attached to the orbitosphenoid. Before diverging posteriorly the parietals enfold the cartilaginous dorsal portion of the supraoccipital.

The *postorbital* forms the medial half of the postorbital bar, practically the whole of the dorsal border of the orbit and the antero-medial border of the temporal fossa. Laterally it articulates with the jugal, anteriorly with the prefrontal and medially with the frontal and parietal. It has a posterior prolongation covering the anterior end of the parietal laterally.

The *frontals* are situated exactly in the middle of the roof of the skull and between the orbits. The orbitosphenoids lie immediately below the frontals but are not fused with them. Laterally to the orbitosphenoids each frontal sends down a lamina of bone, partly in contact with, but not fused to, the former. The lateral half of each lamina is formed by the prefrontal.

The *prefrontal* forms the dorsal border of the orbit and extends down behind the lachrymal on the inside of the orbit. It reaches the jugal on the floor of the orbit and articulates along the whole of its anterior length with the lachrymal. Antero-medially it is in contact with the nasal and medially with the frontal. The portion of the prefrontal extending down the inner wall of the orbit lies some distance lateral to the downward extending lamina of the frontal, to which the prefrontal contributes the lateral face.

The *lachrymal* forms the anterior border of the orbit and the anterior wall within the orbit. It forms a small portion of the lateral face of the snout. The maxillary overlaps the lachrymal from front to back. On the side of the nasal cavity the lachrymal overlaps the maxillary from back to front. Dorsally it lies flat against the medial side of the maxillary, but lower down it forms the roof of the maxillary antrum. At this level the medial margin of the lachrymal forms a ridge extending downward to the palatine. The portion of the lachrymal forming the roof of the antrum has a triangular cross section. Through the centre of this triangular portion passes the lachrymal duct, from back to front. The lachrymal also sends a lamina of bone down, covering the maxillary on the lateral wall of the antrum so that the latter only forms the floor of this cavity along the posterior half of its length. The medial wall is formed by the palatine.

The lachrymal duct opens shortly above the opening leading to the maxillary antrum. The latter opening is formed where the palatine does not quite reach the medially extending ridge in the lachrymal, at the level of the roof of the antrum. This opening is a long, narrow slit extending horizontally.

The *nasals* are comparatively large and form practically the whole of the dorsal surface of the snout. The nasals are much broader posteriorly than anteriorly. The lateral margin of the nasal is very much thicker than the medial and the lateral face of this margin is flat and vertical, where it is in contact with the maxillary.

The ventral surfaces of the nasals and frontals are grooved, possibly signifying that these animals possessed a series of ethmoturbinals, not unlike the mammalian plan (Watson, 1913), the function of which was to increase the surface within the nasal cavity over which the air passed when inhaled. This development could be explained in terms of a possible increase in the breathing tempo with a view to

a finer smelling sense, seeing that the ordinary reptilian communication between mouth and nasal cavities is lost, but otherwise, more likely, the arrangement developed with a view either to moistening the air before it was inhaled, to prevent a too great amount of evaporation directly through the lung epithelium, or to warm the air before it was inhaled. The arrangement therefore reflects almost certainly upon an increase in the breathing tempo, but also quite likely upon the probability that these animals were to some extent homoeotherm, which, due to an increased metabolism, is the natural result of an increase in breathing tempo. Actually, as will be shown below, there are quite a number of other features also reflecting upon the probability that they were homoeotherm.

The *septomaxillary* forms the posterior and ventral borders of each external naris. A good deal of the septomaxillary is visible on the outside surface of the snout. On the inside, within the nasal cavity, it extends back in a thin lamina flat against the maxillary. A lamina of the premaxillary extends for a good distance backward between this lamina of the septomaxillary and the maxillary. Dorsally the septomaxillary is clasped between the nasal and maxillary, and below this the septomaxillary curves over the lateral margin of the external naris. A little more than half way down the side of the external naris the septomaxillary forms a prolongation passing ventro-medially to the floor of the external naris, so that a foramen is formed underneath. This extension of the septomaxillary is carried farther medially along the floor of the external naris and finally reaches its fellow of the opposite side behind the dorsally extending prolongations of the premaxillaries and in front of the openings passing between the latter bones to the mouth cavity. The lateral half of the floor of the foramen underneath this bridge of the septomaxillary is formed by another portion of the same bone, but more medially the floor is formed by the premaxillary. This foramen is possibly associated with glands on the floor of the nasal cavity secreting a fluid to keep the skin around the nostrils wet, for the same purpose as referred to in the previous paragraph. This region appears to have been richly supplied with blood and innervated by nerves, judging from the size of the foramina for the maxillary branches of the fifth nerve, especially the one enclosed by the maxillary, premaxillary and septomaxillary.

The *premaxillaries* form the anterior end of the snout. Together they form a prolongation extending upward between the external nares and finally backward between the anterior ends of the nasals. Laterally they extend upward and backward as a lamina between the septomaxillary and the maxillary. The premaxillary forms the anterior wall of the excavation for the lower jaw canine. It also extends backward on each side of the excavation, but the maxillary covers it on the lateral and medial walls. Between the two excavations the premaxillaries pass upward through the palatal plates of the maxillaries and clasp between them, on the side of the nasal cavities, the anterior end of the vomer. Before the premaxillaries pass upward into the nasal cavity, they form together a very small process, extending downward. On each side of this process is a small opening leading upward into the nasal cavity.

The *maxillary* forms practically the whole of the lateral face of the snout and most of the secondary palate. In the middle of its length it extends farther upward and turns over on to the dorsal surface of the snout. This portion of the maxillary

is depressed and in some specimens investigated there are traces of grooves running from this depression in the direction of the external nares. It appears that this depression lodged a gland secreting a fluid, released around the external naris, for the purpose of moistening the air before it is inhaled.

From the level of the posterior borders of the canines to the level of the sixth postcanine teeth, the maxillary forms a palatal plate, articulating medially with the palatal plate of the maxillary of the opposite side.

Posteriory the maxillary overlaps the lachrymal externally and is itself gripped in a notch by the jugal. The whole of the posterior half of its medial side is covered by the palatine below and the lachrymal above.

The maxillary is traversed by a vacuity, extending longitudinally practically the full length of the bone. The anterior half of this vacuity is entirely enclosed by the maxillary, but the posterior half is enclosed by the lachrymal above and laterally, by the palatine medially and by the maxillary ventrally.

The *transverse bone* is a small relic situated between the palatine, pterygoid and jugal. It is only visible from below; it is covered on the side of the orbit by the jugal and lachrymal. In some species it is small and does not extend over the ridge running from the pterygoid process to the posterior border of the secondary palate. In others it is L-shaped and the foot of the L extends over this ridge. The palatine extends within the angle of the L, but leaves the tiny suborbital foramen in the corner. The pterygoid articulates along the ventral margin of the foot of the L and the jugal along the lateral margin of the upright portion.

The *jugal* forms the lateral half of the postorbital bar and the whole of the lateral and ventral borders of the orbit. It also forms part of the floor of the orbit. In this area it is in contact with the pterygoid and, more anteriorly, with the palatine.

Immediately behind the orbit the jugal forms a very characteristic process extending equally outward, backward and downward. There can be no doubt that it served for the attachment of the superficial masseter muscle and was likely a development to facilitate antero-posterior movement of the lower jaw.

The jugal forms the bulk of the zygomatic arch. The anterior end of the squamosal is clasped between two folds in the jugal, while the posterior end of the latter is firmly gripped by the squamosal.

The *squamosal* contributes largely to the zygomatic arch, although not nearly as much as the jugal, but a flat plate of bone also extends medially over the auditory region. It does not contribute to the wall of the brain cavity.

Medially the squamosal joins the parietal in forming the crest on each side of the occipital region. Here it is covered posteriorly by the tabular. It forms the dorsal margin of the post-temporal fossa anteriorly.

Between this extension of the squamosal and the main body is a V-shaped notch leading backward and downward to a crest on the ventral side of the skull. The crest terminates in the region where the reptilian tympanum was situated.

Laterally to this crest is the external auditory meatus groove leading upward over the posterior face of the zygomatic arch. The lateral border of this groove is massive and round, but the inner border extends as far laterally as the lateral border and between the two borders the external ear opening was situated. The

tube leading down the groove rapidly decreases in diameter and is twisted in a horn-shape, a construction which is suitable for amplifying the sound.

The squamosal extends forward and inward around the distal end of the opisthotic, where it forms a groove lodging the canal leading to the tympanum. The latter appears to have been situated in the position where this portion of the squamosal articulates with the posterior end of the alisphenoid prolongation to the quadrate. Medially to this articulation the posterior prolongation of the alisphenoid is not in contact with the opisthotic but the pterygo-paroccipital foramen is formed between the two. The posterior process of the alisphenoid articulates with the squamosal over an anteriorly projecting angle of the paroccipital process. It also articulates with the quadrate in this region.

The *quadrate*, and *quadratojugal*, form the condyle for the articulation of the lower jaw. They are either indistinguishably fused, or the quadratojugal is absent. The lateral portion, probably representing the quadratojugal, develops an upwardly directed plate which passes through a notch cutting antero-posteriorly across a prominent transverse ridge in the squamosal. The rest of the plate covers the anterior face of the ridge in such a way that the quadrate is capable of a certain amount of antero-posterior movement. The dorsal edge of the plate is strongly concave. The quadrate portion of the condyle develops another smaller plate also fitting in an excavation in the anterior face of the ridge, immediately on the inside of the quadratojugal's wedge.

The *stapes*. Only the medial portion of a stapes is included in the material obtained by Professor Watson in 1929. The proximal end of the stapes is oblong and rounded. Less than half of the area covers the fenestra ovalis. The foramen passing through the stapes is relatively large and the bone in front and behind very slender. The distal portion of the stapes, according to the badly preserved specimen adhering to the skull of *D. polyphagus* (British Museum of Natural History, R.2578) is elongated and does not expand. The foramen is nearer the proximal end.

The *vomer* forms a fairly long plate-like bone within the nasal cavity. It rests in front in a groove formed by the premaxillaries, above the palatal plates of the maxillaries. It reaches backward to a level shortly in front of the pterygoid processes, where it separates the anterior ends of the pterygoids, which here form a crest between the orbits. Slightly farther forward the vomer passes upward and builds a similar crest continuous with that of the pterygoids. At this level the vomer separates the palatines completely from each other.

Posteriorly the vomer has an inverted trough-shape, with a median partition extending longitudinally. The whole structure is situated within a deep median longitudinal depression in the palate, posterior to the secondary palate, and passing anteriorly into the choanae. The median partition increases in height forward and nearly reaches the palatal plates of the palatines at the posterior border of the secondary palate. At this level the vomer only forms a median septum, continuous with the median septum in the inverted trough farther back; the lateral walls of the inverted trough-shaped structure, lying flat against the palatines and pterygoids, are resorbed farther forward. As these lateral portions are gradually resorbed anteriorly, the median partition is continued on the dorsal side of the inverted trough and grows higher anteriorly. The partition separates the anterior ends of

the pterygoids and the two palatines, but not the palatal plates of the palatines.

More anteriorly the vomer forms a thin partition in the lower third of the height of the nasal cavity. The ventral margin of this plate is thickened and round, while the upper margin has a distinct groove, extending along the whole of the length of the vomer and carried backward over the pterygoids and parasphenoid rostrum to the basisphenoid. In this groove the cartilaginous mesethmoid rested.

The median partition within the inverted trough decreases in height posteriorly but before it disappears it is formed for merely a millimeter or two by the pterygoids. The posterior ends of the left and right halves of the vomer terminate in tapering points on each side of this pterygoidal portion of the partition.

The *palatines* cover the medial sides of the posterior halves of the maxillaries. Antero-ventrally they form palatal plates continuous with each other and with those of the maxillaries. The dorsal portion of each palatine forms the medial wall of the maxillary antrum. It is very high in this region. The opening to the maxillary antrum passes over the dorsal margin of the palatine near its anterior end. At the level of the floor of the antrum the palatine sends a shelf-like plate of bone medially, covering the lateral portion of the inverted trough-shaped vomer dorsally. Above this shelf is a broad trough, separated from its fellow of the opposite side by the median septum, formed in this region by the vomer in front, the pterygoids in the middle, and the parasphenoid at the back. This trough leads backward on to the floor of the orbit. Anteriorly it terminates in a depression in a vertical transverse wall formed by the palatine. This depression is evidently the area of insertion of the anterior oblique muscles of the eye.

The *pterygoid* is a fairly massive bone with a long ventrally directed process. The upper surface forms part of the floor of the orbit. The lateral surface of the pterygoid process guides the lower jaw.

The pterygoids extend backward to the level of the pituitary fossa. The parasphenoid extends upward and forward between their posterior ends. Anteriorly each pterygoid is continuous with the horizontal shelf-like portion of the palatine, dorsally to the internal nares.

Within the depression antero-medially of each pterygoid process there is a small foramen for the palatine branch of the seventh nerve.

The *orbitosphenoid* forms the side walls and floor of the olfactory lobes portion of the brain case. It lies between the two descending folds formed by the frontals and prefrontals. Farther back it appears to have closer contact with the parietals. Posteriorly it is continuous with the anterior end of the alisphenoid. It is not in sutural contact with the frontals and anteriorly it allows an opening through which the brain cavity communicates with the nasal cavity.

The *alisphenoid* extends from the ventral margin of the parietal behind the orbitosphenoid down to the posterior end of the pterygoid and from there outward and backward to the quadrate. Its anterior margin is free. In front of this margin nerves II, III, IV, Va and VI pass out from the brain cavity. The alisphenoid sends a very thin tapering process forward along the dorsal margin of the posterior portion of the pterygoid. Between this margin and the parasphenoid there is a fairly deep groove leading backward to a canal which passes through the parasphenoid and basisphenoid into the brain cavity, apparently shortly in front of the pituitary fossa.

The alisphenoid covers the anterior half of the prootic externally. Shortly above and behind the pituitary fossa the posterior margin of the alisphenoid allows a foramen, in some species incompletely divided into two, between itself and the prootic, for the second and third branches of the fifth nerve. This nerve passes over the processus anterior inferior prootici, then back and upward between the alisphenoid and prootic. Deep depressions in the ventral side of the skull, on each side of the midline, medially to the posterior prolongations of the alispenoids, and leading from the tympanic cavity upward and forward, reach the pituitary fossa medially to the processus anterior inferior prootici. Laterally to this depression the alisphenoid extends backward and outward to the quadrate. Originally the posterior prolongation was formed by the pterygoid, but it was gradually replaced by a similar prolongation of the alisphenoid.

The *parasphenoid* covers the basisphenoid ventrally. Posteriorly it overlaps the basioccipital-basisphenoid suture and forms an intensively interdigitated suture with the former. Laterally the parasphenoid extends backward to the margin of the fenestra ovalis and is fused with the prootic very near to this margin. The suture extends forward ventrally to the foramen for the seventh nerve and in the direction of the pituitary fossa.

The parasphenoid forms the crested margin of the central triangular area at the base of the skull, anterior to the level of the fenestrae ovales. Immediately in front of the apex of this triangular area the parasphenoid is flanked by the pterygoids. The parasphenoid is visible between the pterygoids for half the distance of the crest in front of the apex. More anteriorly it turns upward and forward and appears on the dorsal side of the pterygoids where it forms a median crest. The dorsal margin of this crest is thicker than the lamella below and it forms the parasphenoid rostrum. It extends forward to about the middle of the orbits.

The *basisphenoid*. It is difficult to ascertain the extent of the basisphenoid in the material investigated. It must be continuous with the basioccipital behind the dorsum sellae. It forms the dorsum sellae and sella tursica. Farther forward it extends over the parasphenoid rostrum. Laterally it joins the alisphenoid in front and the prootic behind. Its anterior end is as high as the vertical thickness of the rostrum and lies immediately dorsal to it. This end is continuous with the posterior end of the cartilaginous mesethmoid.

The *mesethmoid*, having been cartilaginous, has been destroyed before fossilization, but the following is evident. It extended from the anterior end of the basisphenoid forward to the anterior end of the vomer and rested for the whole distance in a groove running along the dorsal margin of the septum formed by the parasphenoid, pterygoids and vomer. It also extended upward to the posteroventral angle of the orbitosphenoid and from there farther forward as a septum, completely dividing the orbits from each other and the nasal cavity in two halves.

The Lower Jaw

The *dentaries* form almost the whole of the lower jaw. They reach backward almost to the quadrates and the coronoid processes pass upward through the temporal fossae, reaching almost to the level of the dorsal surface of the skull.

The ventral margin of the dentary is thick and round, and projects slightly

backward at the postero-ventral angle. Above this thick edge is a groove on the medial side, in which the splenial is situated. Each dentary increases slightly in thickness dorsally to this groove, the portion lodging the roots of the postcanine teeth.

The *splenials* are long rod-like bones lodged within grooves on the medial sides of the dentaries. They extend from the region of the symphysis, where they are in contact with each other, backward to a short distance in front of the postero-ventral angles of the dentaries. Their posterior ends project a short distance away from the angulars in a postero-ventral direction. These portions lie closely above the postero-ventral projections of the ventral margins of the dentaries, but they do not reach as far back. Each splenial tapers backward, is thickest in the middle of its length, and expands again slightly before fusing with its fellow of the opposite side.

The *coronoid* is a fairly large, flat, diamond-shaped bone. It covers the dentary medially, above the posterior half of the splenial, and reaches nearly to the dorsal margin of the dentary. It lies exactly between the dentary and the pterygoid process.

The *prearticular* lies directly in front of the articular and within the angle between the posterior portions of the coronoid and splenial.

The *angular* lies ventrally to the prearticular and articular and its anterior end lies dorsally to the posterior end of the splenial. It extends nearly to the region of articulation. An angular process extends from the anterior end of the angular in a postero-ventral direction, but a good distance above the postero-ventral projection of the lower margin of the dentary, and much farther back. It extends a few millimeters beyond the margin of the dentary. The angular appears well elevated from the dentary and the angular process seems to render additional strength to the construction in the suspensory region. The process is somewhat flat and expands towards its end.

The angular passes upward between the prearticular-articular and the dentary and even separates a good deal of the surangular from the dentary.

The *surangular* is a long bone lying closely against and dorsally to the prearticular and articular. It extends practically along the whole length of these two bones. Above the posterior part of the prearticular, the surangular divides in two, a dorsal portion extending forward well elevated from the prearticular, and a ventral portion, much shorter and smaller, extending forward in a groove formed by the prearticular medially and the angular laterally. The two portions taper forward. Between the two there is a fenestra which, farther forward, lies between the dorsal portion and the prearticular-angular. The surangular reaches backward to the region of articulation and appears to have formed part of the articulating facet.

The *articular* forms the facet for articulation with the quadrate. It is not clear where the suture is between the prearticular and articular.

The articular facet is about twice as broad as high and is concave vertically, but straight transversely. The total breadth of the articular exceeds any breadth measurement of the dentary. The facet is oval, but its long axis does not extend straight transversely, rather upward medially.

Below the facet is a condyle on which the anterior pterygoid muscle was inserted.

According to Gregory and Camp (1918) a depressor mandibulae muscle was present in *Cynognathus*, but if such a muscle was present in *Diademodon* it could only have assisted in the antero-posterior movement of the lower jaw, as an effective antagonist to the superficial masseter and the anterior pterygoid muscles.

The Dentition

The dental formula of *Diademodon* was decided upon in the original work as 4:1:4:9 for the upper jaw and 3:1:4:9 for the lower jaw. Authors have been very uncertain about the dental formula of *Diademodon* in the past, even with the then existing evidence and, in the light of the material investigated in London, it was not possible to state with certainty that this formula held true for all species.

The first account of the dental formula of *Diademodon* was given by Seeley in 1895 in his description of the lower jaw of *D. kannemeyeri* (*Gomphognathus kannemeyeri*). He showed that there are three incisors, one canine and thirteen postcanine teeth, of which the first four may be regarded as premolars. At that time the formula of the upper jaw was still unknown.

In 1905 Broom described a dentary of *D. mastacus* from which he deduced the dental formula ?:?:4:7 for the lower jaw. According to his diagram, however, the seventh molar cannot be an ultimate, nor even a penultimate tooth. I was quite confident in assuming that this specimen had at least two additional unerupted molars.

In his description of *D. browni*, Watson (1911) recognised nine postcanine teeth and objected to a subdivision into molars and premolars. In 1913 Broom pointed out that there is a single dental succession in all the teeth in front of the large flat crowned molars, so that a subdivision into premolars and molars is permissible. For the specimen he described as *D. platyrhinus* he deduced the dental formula 4:1:4:8 for both the upper and the lower jaws. Four incisors in the lower jaw is obviously a mistake. Furthermore, as the rows of postcanine teeth are not continuous on either side, it is not safe to say with certainty that there were only eight molars.

In 1919 Broom investigated the dental formula of this genus again and for *D. kannemeyeri* he recognised five premolars and nine molars. He stated that the first premolar on the left side appears to correspond with the second premolar on the right side, so that the eighth molar on the left side corresponds with the ninth on the right. The ninth on the left side had no corresponding tooth at first, but after additional development the tooth was discovered on the right side. If the first tooth on the left is taken as a second premolar, there is a total of fourteen teeth on each side, of which Broom recognised the first five as premolars. I expressed the opinion that Broom counted a "milk and a permanent" premolar in the same socket as two separate premolars on the right side.

Broom (op. cit.) grouped all the species under the genus *Gomphognathus*, characterised (wrongly?) by possessing five premolars, and left only one species in the genus *Diademodon* (*D. tetragonus*) with an unknown dental formula. He made a third genus *Cyclogomphodon* for his original *D. platyrhinus* on account of its different dental formula, and also introduced *Octogomphus woodi*. In the

original of this work doubt was expressed over the validity of these two genera, but two specimens in the Bernard Price Institute supported the validity of the genus *Cyclogomphodon* (Brink and Kitching, 1953).

Broili and Schröder (1935) gave the dental formula for their *D. browni* as 4:1:5:7:, but it is possible that a "premolar" was lost in the diasteme behind the canine and that this together with the three behind are the "premolars," leaving nine "molars." These "molars" have transversely ovate flat crowns, and the "premolars" conical crowns. There are nine transversely ovate flat-crowned "molars" in the British Museum specimen of *D. browni.* Specimen No. 225 in the Bernard Price Institute for Palaentological Research is a beautiful skull of *D. browni,* showing four conical "premolars" and nine transversely ovate flat crowned "molars" (Brink and Kitching, 1951).

In their second specimen of *D. mastacus* Broili and Schröder (op. cit.) encountered eight molars (although their figure appears to illustrate nine). They found eleven postcanine teeth in the lower jaw, but it appears as though, judging from the material investigated, the "premolars" of the lower jaw were inclined to fall out with advancing age. This phenomenon supplies additional evidence that there was a *single* dental succession in the "premolars."

Broili and Schröder's *"Gomphognathus" grossarthi* (op. cit.) has an additional tenth "molar" on each side. For their specimen of *"G" haughtoni* the same authors give eight "molars," as counted on the right side, but the left side shows nine, and in a specimen in the Watson Collection, which is most decidely a *D. haughtoni,* I found nine "molars." Their dental formula for *D. broomi* shows nine "molars," as does a specimen of the same species in the collection of the Bernard Price Institute (Brink and Kitching, 1953). Incidentally, the three new species introduced by Broili and Schröder are now represented by a second specimen each, two of which are in the Watson collection and one in the collection of the Bernard Price Institute.

All the specimens investigated in London demonstrated four conical "premolars" and nine flat-crowned "molars."

On my return from London I noticed a *Diademodon* specimen in the South African Museum, Cape Town, with eleven "molars" in addition to four "premolars." Some time later, Mr. J. W. Kitching collected a similar specimen on the farm Luiperdskop in the Burghersdorp district. The skull is larger than that of *Cynidiognathus* and almost as long as the type skull of *Cynognathus crateronotus.* This specimen has four "premolars" and twelve "molars". It is described below as *D. mastacus,* with an explanation for its peculiar dentition.

* * *

I was recently informed by Dr. A. W. Crompton of the National Museum, Bloemfontein, that in his research on the dentitions of higher Cynodonts from Tanganyika Territory he investigated certain *Diademodon* specimens (from South Africa) and discovered evidence of tooth replacement even in the seventh "molar". He found in a maxillary of a young individual (sp. indet.) a small longitudinal "socket" in the position of the seventh "molar", from which a longitudinally flattened postcanine tooth had apparently been shed. Underneath was the large flat

crowned seventh "molar" still unerupted. I interpreted a similar "foramen" as a gubernacular canal. Crompton is of the opinion that each large transversely ovate flat-crowned "molar" in *Diademodon* was preceeded by a small longitudinally flattened predecessor. With additional evidence in Crompton's support, I am prepared to agree that *Diademodon* does not yet represent the stage where premolars can be distinguished from molars in the mammalian sense, in spite of structure and the fact that there is strong evidence of a *single* succession. I do, however, wish to express my doubt regarding replacement of the triangular eighth "molar" and the subsequent longitudinally flattened teeth. These do not oppose their fellows in the lower jaw directly, but pass laterally to them so as to fulfil a cutting, rather than a grinding, function. There would be no purpose in their replacement by transversely ovate flat-crowned teeth. In addition, as will be shown below, the postcanine series of teeth can increase to a third longitudinally flattened tooth behind the characteristic triangular eighth, without any attempt being made to replace the latter. It appears, therefore, that *Diademodon* presents at least the stage where the single dental succession is limited to a certain number of postcanine teeth, less than the full complement that can develop, but the arrangement is still too different from the typically mammalian condition, so that, to avoid misinterpretation, "postcanine teeth" should still be used in the case of *Diademodon*, rather than to try and distinguish premolars and molars. Where "molars" are subsequently used, they signify postcanine teeth behind the four anterior conical "premolars".

* * *

There are species of *Diademodon* in which it was not yet possible to establish the "molar" tooth structure. The structure of the crown is not similar in all the "molars" in the series in one particular specimen, the most conspicuous differences occurring in the seventh, eigth and ninth "molars." From the largest tooth forward the only outstanding change that occurs from tooth to tooth is a decrease in the number of tubercles on the posterior crenulate margin. There are rather appreciable differences in the structure of the "molar" crowns between different species.

The largest tooth in the "molar" series of the upper jaw is the fifth, sixth or seventh, depending on the species. This tooth is much broader than it is long.

The crown is transversely ovate, except in the eighth, which is often triangular, and the ninth and subsequent, which are laterally compressed. The "premolars" are always conical and round or slightly longitudinally ovate. They often tend to bend over backward and inward. They are sometimes slightly spaced, irregular, and often do not correspond with their fellows of the opposite side. There is a short diasteme between the first "premolar" and the canine.

The canines are large and strong. There are several loose canines in the Watson collection, some showing impressions of the succeeding teeth. These teeth are slender, with a sharp crenulate posterior edge, and are no doubt "milk" canines. The larger canines have strong roots with no impressions of succeeding teeth, and the crowns are ovate in cross section, with no crenulate edges.

There is a large diasteme between the canine and the fourth incisor. The diasteme is bridged by a thin wall, the antero-lateral wall of the excavation for the lower

jaw canine. There is no diasteme between the third incisor and the canine in the lower jaw, but a long diasteme behind the canine. This diasteme is often enlarged by the loss of the anterior "premolars" at older age.

The lower jaw "premolars" increase considerably in size backward, but in the "molars" the increase is rather gradual. The lower jaw "molars" are as broad as they are long. The anterior two-thirds of the row of lower jaw "molars" bite centrally on the row of upper jaw "molars" and the individual teeth bite in between those of the upper jaw. The eighth lower jaw "molar" bites on the medial half of the upper eighth, while the subsequent teeth miss each other completely. The dorsal margin of the dentary rises upward between these ultimate teeth.

The lower jaw "premolars" generally hardly reach the level of the tips of the upper jaw "premolars" and pass a certain distance medially to them.

The lower jaw "molars" wear over the whole of their surfaces, while the upper jaw "molars" wear only over the middle of the crowns. This shows that there could have been very little lateral movement of the lower jaw when the jaw was closed. With the jaw half open lateral movement was possible to a certain extent, because some of the canines show wear over their tips. The pterygoid processes have little effect in guiding the lower jaw when the latter is lowered to the level where the canine tips can oppose each other. The quadrates were evidently streptostylic to allow for antero-posterior movement while the lower jaw is closed.

There is a great variation in the amount of wear on the "molars" in different specimens of *Diademodon*. The most obvious explanation is difference in age. Actually specimens are found with much worn teeth, but the posterior molars are newly erupted, while others with nearly a full complement of fully erupted teeth show less wear. This phenomenon can only be explained in terms of diet. It appears that *Diademodon* was an omnivorous animal with scavenger habits as far as its meat diet was concerned. Certain individuals managed to obtain a larger meat diet; they show less wear on the molars and much wear on the canines. Others were forced to a largely vegetable diet, showing much wear on the molars and less wear on the canines.

Diademodon appears to have been a rather slow animal, judging from the size of its skull compared with its somewhat weak legs and especially considering the cumbersome lumbar region, which will be discussed below. As such this animal apparently gradually turned from an active hunting carnivore to a lazy omnivorous scavenger. Its inactivity and its partly vegetable diet is further reflected on by the fact that it evidently fell prey to other Cynognathid carnivores only slightly larger in size. Much of the Diademodont material investigated comes from a bone bed indicating the spot where they were captured and devoured by Cynognathids while scavenging for remains of previous kills. Most of the skeletal bones of *Diademodon* were broken and gnawed before fossilization.

* * *

In the original work tables of measurements, actual and proportional, covering the whole skull are given. Here an extract from one table is given, covering only the "molar" teeth. From the table it will be observed that the lengths of the rows of molar teeth differ considerably between species, but agree within a millimeter

TABLE I

Measurements taken from the posterior margin of the canine, on the alveolar border, to the individual teeth inclusive. Incomplete snouts reconstructed.

	4th "pm."	1st "m."	2nd "m."	3rd "m."	4th "m."	5th "m."	6th "m."	7th "m."	8th "m."	9th "m."	Length of 9 "molars" inclusive.	Length of largest "molar."	Breadth of largest "molar."	Reference
D. broomi ..	14	17	12	25	28·5	35·5	14·5	47	—	—	**48**	7	10	Type specimen.
,, ..	18	23	27·5	32·2	37·5	43	49·5	54	59·5	64·5	**48**	7	10	B.P.I. 313
D. browni ..	13·5	16	18	21·5	27	31·5	36	40	45	50	**40**	5	8·5	Broili and Schröder
,, ..	—	20	23	27	32·5	39	44	48	53	58	**41**	5	9	B.M.N.H. R3587
D. entomophonus	—	—	—	—	—	—	—	—	—	—	**45**	6	10	Type specimen.
D. grossarthi ..	22	26	31·5	36·5	44	50	57	64·5	71	78·5	**60**	7	10	Type specimen.
,, ..	—	31	37	45	52	60	69	76	—	—	**60**	7	10	D.M.S.W. R180
D. haughtoni ..	20	25	31	38	43	52·5	61·5	73	82	90	**72**	7	11	Type specimen.
,, ..	20	25·5	31·5	38	43	52·5	60·5	72	81	89	**72**	7	11	D.M.S.W.
D. laticeps ..	23·5	29	34·5	41	48	55·5	62	69	77	81	**61**	7·5	12·5	Type specimen.
D. mastacus ..	—	—	—	36·6	42·2	46	52	59	65	—	**55**	6·5	11·5	Type specimen.
,, ..	—	28·5	34	40	46	51·5	58	64	71	77·5	**55**	6·5	11·5	D.M.S.W. R51.
,, ..	25	28·5	34·5	40	46	51·5	58	65	71	78	**55**(9)	6·5	10·5	B.P.I. 314.
D. parringtoni ..	20	23	27	32	36	42	47	52	57	—	**48**	6	8·5	Type specimen.
D. polyphagus ..	21	26	30	35	40·5	46·5	53·5	59·5	65	70	**51**	6·5	9	Type specimen.
,, ..	20	24	28	32	37	43	50	56	61	66	**50**	6·5	9	B.M.N.H. R2578.
D. tetragonus ..	13	16	19·5	23	28	33	37	—	—	—	—	5	6	Type specimen.

B.P.I.—Bernard Price Institute.
B.M.N.H.—British Museum of Natural History.
D.M.S.W.—In Professor D.M.S. Watson's Collection.

or two within a single species, notwithstanding considerable differences in the size of the skulls. This phenomenon immediately provides a means of distinguishing between species.

The length and breadth measurements of the largest molar of each specimen also shows a marked similarity within species, irrespective of age or the size of the skull, and characteristic differences between species.

Considering the lengths of the rows of molars, it appears rather unlikely that *D. entomophonus* could be a *D. browni*. *D. kannemeyeri* and *D. mastacus* differ in the build of their lower jaws.

There is absolutely no reason why *D. tetragonus* should stand in a separate genus. As far as breadth of the molars is concerned, there is a great variation amongst the species, but there is a gradual transition in the length: breadth ratio of the largest molars from *D. tetragonus* (6:5) to *D. laticeps* (2:1) so that no definite line can be drawn between two separate genera on this ground.

The Skeleton

While working on a reconstruction of the skeleton of *Diademodon*, based on fragmentary material in the private collection of Professor D. M. S. Watson, I was informed that the National Museum in Bloemfontein had a very beautiful nearly complete skeleton, without skull, a specimen certainly worth describing. Recently I had the opportunity to investigate this specimen and with the kind permission of the Director, Dr. A. C. Hoffman, I was allowed to incorporate observations based on it into this work.

There was no means of establishing the number of vertebrae in the trunk of *Diademodon* from the material investigated in London. An estimate was made, using the vertebral column of *Cynognathus crateronotus* as a guide. The Bloemfontein specimen shows two vertebrae more than my original estimation. There were also no good thoracic ribs among the material investigated in London; the thoracic ribs were, therefore, also provisionally restored in accordance with those of *Cynognathus*. The new specimen shows some differences. In *Diademodon* rib processes occur throughout the thoracic region as in *Thrinaxodon*, but they are much more vestigial. In the characteristics of the ribs, therefore, *Diademodon* is more primitive than *Cynognathus*, but in the dentition it is much more advanced.

It must be stressed that the Bloemfontein specimen is without skull so that there is no absolute proof that the specimen actually belongs to the genus *Diademodon*, but the individual skeletal bones show such a close resemblance to those of *Diademodon* that there can be little doubt. On the other hand the arrangement of the overlapping processes in the lumbar ribs is not as far advanced as in *D. kannemeyeri*, which may be due to a difference in age. In addition, the specimen comes from Thaba 'Nchu and not unlikely from *Lystrosaurus* zone beds, but in this area *Cynognathus* zone beds follow immediately on the *Lystrosaurus* zone. This specimen may therefore represent an early *Diademodon*, or actually an ancestral form, but in the absence of distinguishing characteristics it is best referred to as a *Diademodon*.

This specimen was collected by Dr. E. C. N. van Hoepen in 1929, west of Thaba 'Nchu mountain in a donga running in the direction of Victoria Nek, and

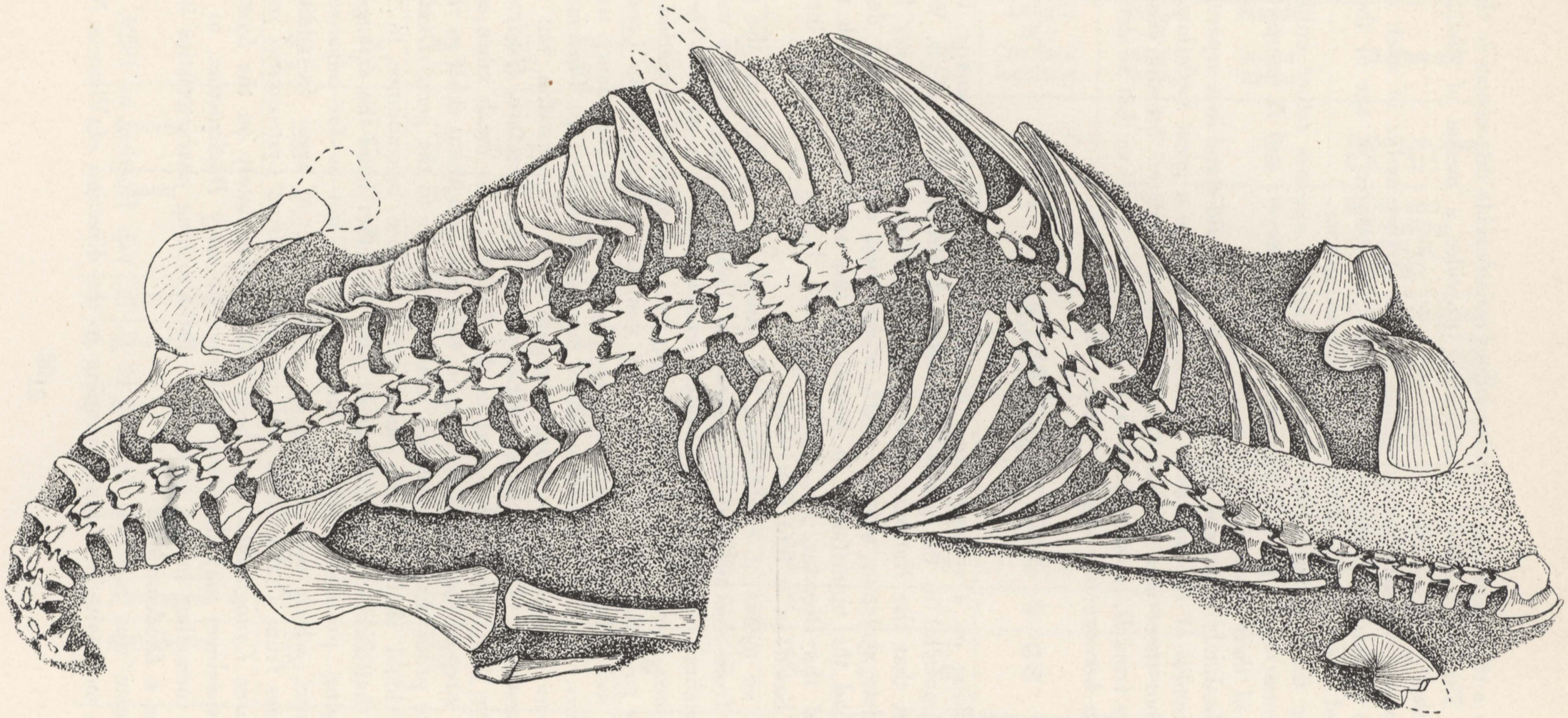


Fig. 4.—Dorsal view of the skeleton of an immature *Diademodon*, No. 531, National Museum, Bloemfontein, $\frac{1}{3}$ natural size.

north of the northern boundary of the farm Victoria. It is numbered 531 in the collection of the National Museum, Bloemfontein (see fig. 4). It should be added that this locality could possibly have been wrongly registered in the catalogue of the National Museum.

The Vertebral Column.

It appears as if the proatlas partly overlaps the atlas. It articulates with the atlas ventrally, the articular surface of the atlas facing upward. A slight depression extends from the articular surface in the form of a shallow groove medially along the antero-dorsal margin of the neural arch of the atlas. It is evident that the proatlas fits in this groove so that it actually overlaps the arch of the atlas.

The atlas consists of three parts, two lateral and one ventral. The lateral portion has an articular facet, facing medially and backward, and articulating with the lateral face of the odontoid process. Another articular facet faces antero-medially and articulates with the postero-lateral side of the occipital condyle. Lateral to these facets the bone decreases in horizontal width fairly rapidly and then increases in vertical thickness farther outward. This portion is the transverse process. On the border between the main body of the bone and the transverse process is the facet on which the pro-atlas articulates. The facet is actually formed by the dorsal surface of a shelf-like ridge resting medially on the large facet articulating with the occipital condyle. Underneath this shelf is a deep depression leading to a foramen passing medially into the neural canal. Dorsally the main bone passes upward and inward in the form of a lamella, to form the neural arch. This arch is broad and thin and is horizontal longitudinally. It grows slightly broader medially. The posterior margin of the neural arch is prolonged backward and

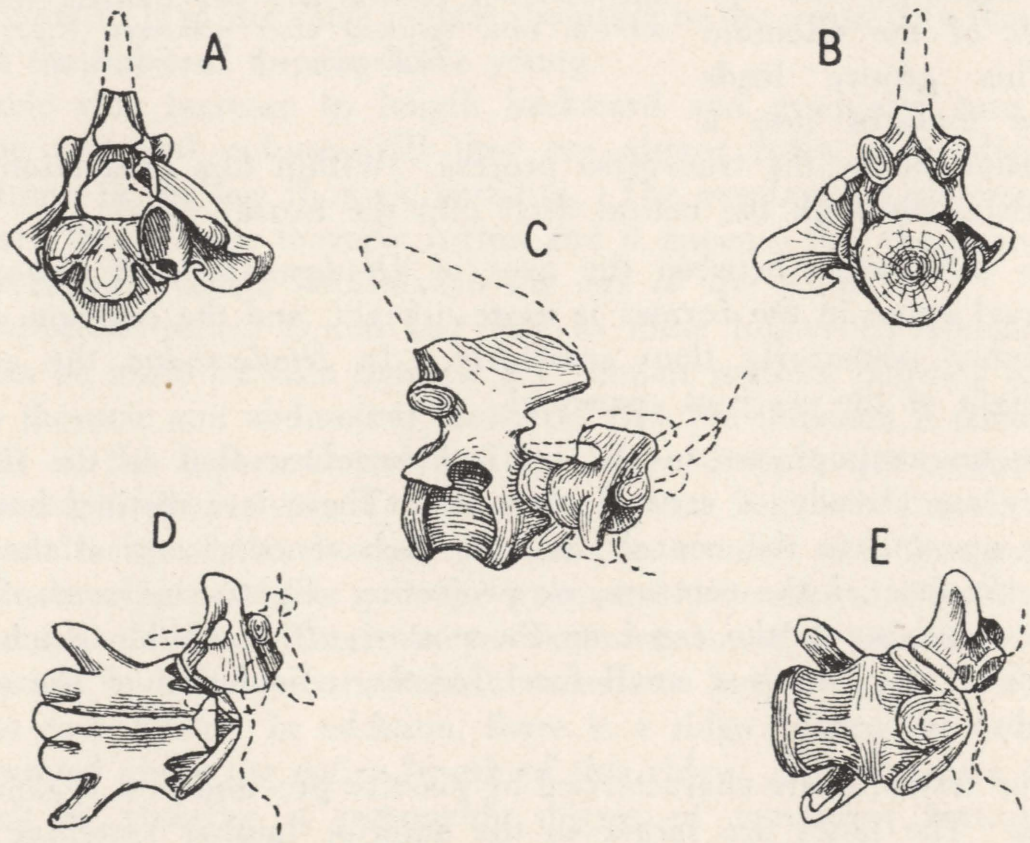


Fig. 5.—A, Anterior, B, Posterior, C, Lateral, D, Dorsal and E, Ventral view of axis and portion of atlas, R.205 and R.202, D.M.S.W. Collection, ½ natural size.

upward to form a process, immediately before it joins the main body of the bone. The atlas intercentrum was attached at each end to a surface situated ventrally, between the two main facets of each of the two lateral atlas bones. The intercentrum is thicker in the middle of its breadth and has a facet articulating with the ventral facet of the odontoid process.

The three facets on the axis are of the same size and it is clear that the ventral facet fulfilled as important a function as the lateral ones. This may suggest that the up and down movement of the skull was rendered possible rather by the articulation between the atlas and axis than between the atlas and skull. Actually little movement seems to have been possible between the atlas and skull, due to the intervention of the proatlas. Furthermore, the atlas intercentrum is in direct articulation with the basioccipital.

The axis is essentially similar to that of *Cynognathus*. The transverse process has a deeply concave articular surface or facet at its end. This facet faces mainly inward, but also downward and slightly backward. It is the articulation facet for the tuberculum of the axis rib. The facet becomes narrower anteriorly and is continued on to a small projection of bone in an anterior, medial and ventral direction. A small fenestra was enclosed between the rib below, the transverse process behind, and the neural arch in front. A fairly well definable groove passes between the tubercle and the lateral facet of the odontoid process. This groove leads through the fenestra into a deep excavation below the transverse process. Within this excavation is a small foramen passing through the neural arch into the neural canal.

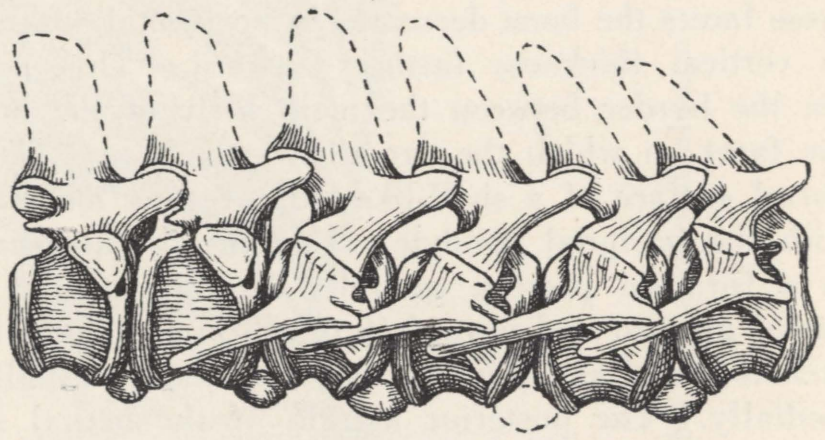


Fig. 6.—Four cervical and two thoracic vertebrae, with cervical ribs, restored after specimen R.227, D.M.S.W. Collection, ½ natural size.

The main differences between the axes of *Diademodon* and *Cynognathus* are that the dorsal spine in the former is more upright, and the centrum of the latter is much higher posteriorly than anteriorly. In *Diademodon* the anterior and posterior height of the centrum are equal.

There are no anapophyses in the cervical vertebrae, but in the first thoracic vertebra they are already of considerable size. There is a distinct border around the anterior opening to the neural canal of each centrum and at the same level as the anterior face of the centrum, or projecting slightly in front of it. It fits into the wide opening to the canal on the posterior side of the vertebra in front. On each side of the rim is a small facet for the articulation of the anapophyses of the vertebra in front.

The lumbar vertebrae are characterised by massive pre- and post zygapophyses and anapophyses. The latter are larger in the anterior lumbar vertebrae and larger than in the thoracic vertebrae. They project into recesses below the prezygapophyses

of the vertebra behind. The border around the anterior opening to the neural canal is much smaller than in the thoracic vertebrae.

The posterior two of the four sacral vertebrae are fused, but the anterior two, although firmly held by the ala of the ilia, are not fused with each other or with the vertebrae in front or behind, apparently not even at old age.

The London material includes four caudal vertebrae following on the sacrals and it was at first deduced that *Diademodon* had a fairly long tail. The Bloemfontein specimen shows nine caudal vertebrae in what appears to be the complete tail.

Besides the proatlas, atlas and axis, there are four cervical vertebrae. The number of thoracic vertebrae could not be established from the London material, but in the Bloemfontein specimen there are seventeen. There are seven lumbar vertebrae. The boundary between thoracic and lumbar regions can be recognised where the shafts of the ribs continue beyond the overlapping processes, where these processes cease to overlap effectively, and where the ribs become fused to the vertebrae.

The Ribs.

The Bloemfontein specimen demonstrates an axis rib.

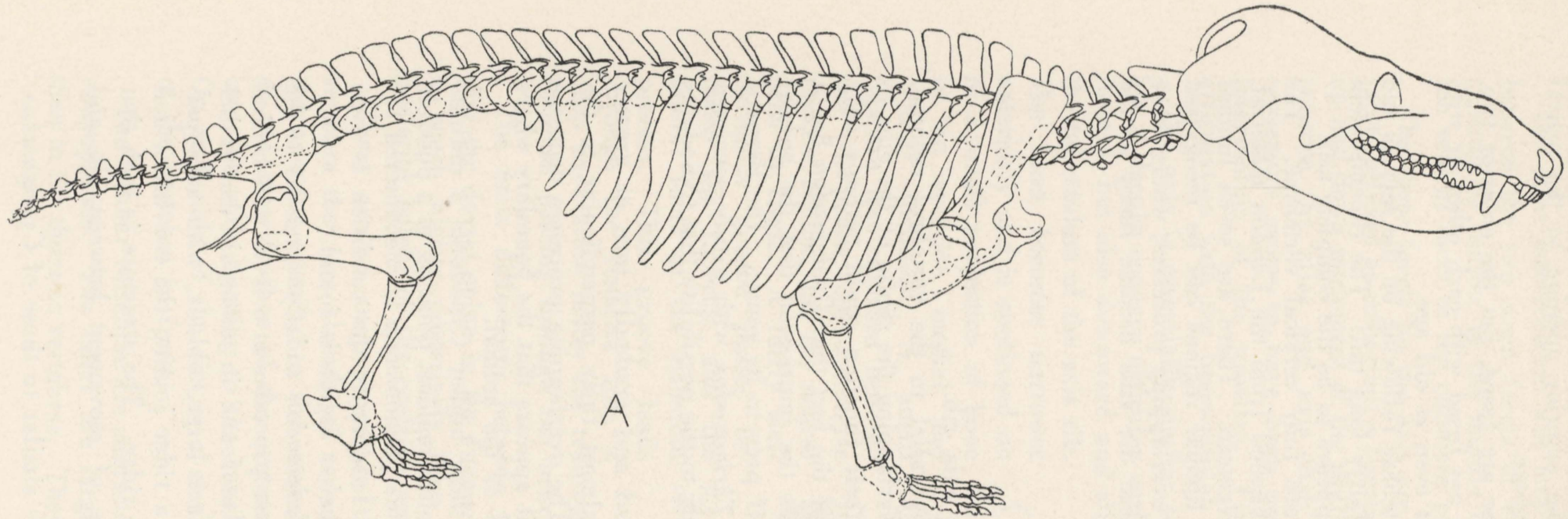
The cervical ribs normally extended nearly parallel to the vertebral column. It is evident, due to the conspicuous processes overlapping the shafts of the ribs in front, that their movement was restricted and their function could perhaps only have been to give support to the neck, in view of the fact that *Diademodon* has a comparatively large head. This structure creates the impression that the animal had the habit of lifting its head high, to carry off prey to its young. The Bernard Price Institute recently acquired a specimen of *Thrinaxodon* with a tiny specimen immediately next to it in the same nodule, pointing to the possibility that Cynodonts actually had the habit of nursing their young.

The thoracic ribs increase in length backward and gradually turn at greater angles to the vertebral column, till they are almost fully perpendicular to the vertebral column in the last thoracic vertebra. The overlapping processes decrease in size forward through the thoracic region and it appears that the boundary where effective overlapping ceases depends on the age of the animal.

A very important aspect is the fact that in these higher Cynodonts a definite distinction can be made between thoracic and lumbar regions, pointing to a possible division into thoracic and abdominal cavities. This phenomenon is encountered for the first time in the higher Cynodonts; in the Ictidosaurs the condition is even further advanced, where a typical mammalian lumbar region is found.

Another peculiarity of the thoracic ribs of *Diademodon* and *Cynognathus* is the fact that the tubercula articulate with the transverse processes at a level well behind the capitular articulations. There are no facets as found in mammals, but rather areas of contact, and the two respective areas are large, oblong, with axes perpendicular to each other. In addition, there is a ridge joining the two areas and the rib articulated along the entire length of this ridge. The structure is such that it is difficult to visualise a reasonable degree of movement between rib and vertebra.

The lumbar ribs of *Diademodon* are essentially similar to those of *Cynognathus*.



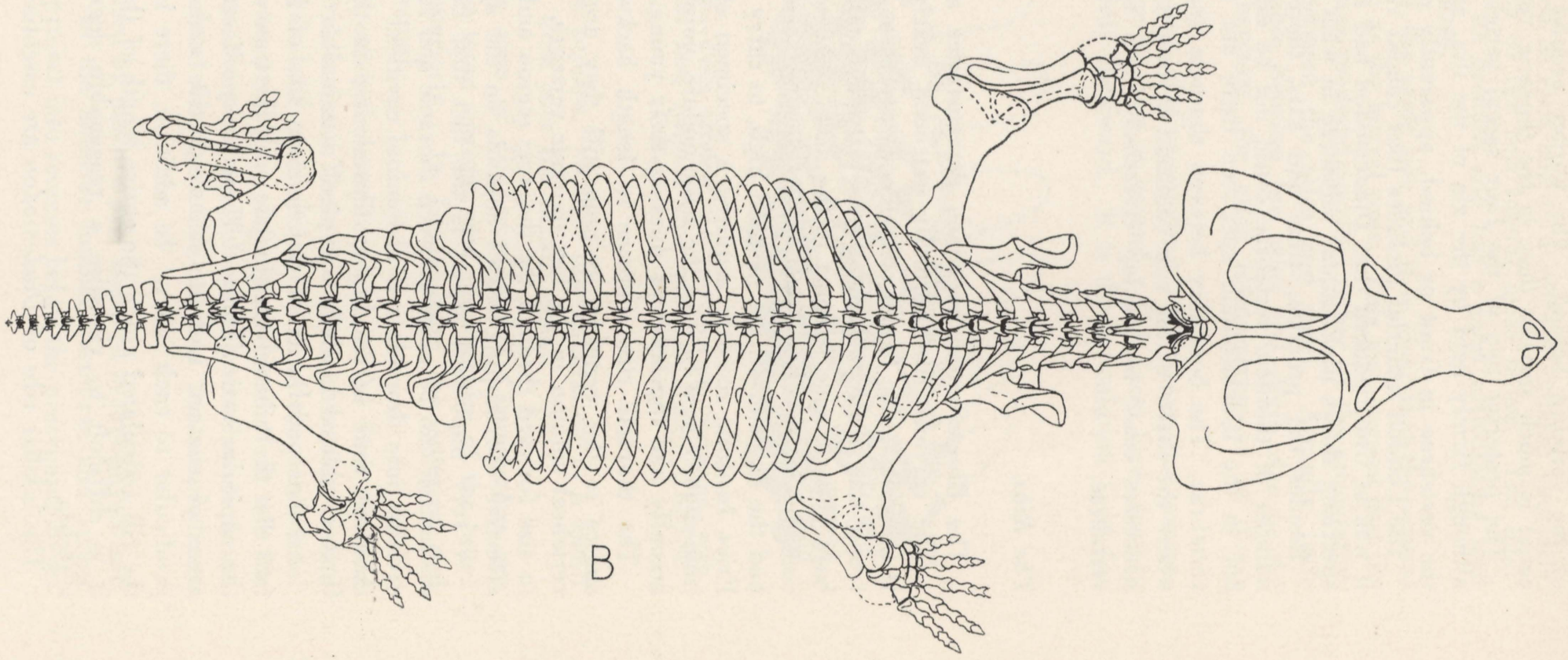


Fig. 7.—A, Lateral and B, Dorsal view of the reconstructed skeleton of *Diademodon*.

The peculiar development of overlapping and clasping processes in these ribs must have a significance and after careful experimenting and consideration the following appears to be the most likely explanation.

In the anterior region of the thorax the ribs are inclined to the vertebral column, so that antero-posterior movement can result in an increase or decrease in the volume of the thorax, but the nature of the articulations is such that it is difficult to visualise any appreciable movement. In the posterior region of the thorax, the most important as far as breathing is concerned, the ribs are perpendicular to the vertebral column so that any movement can have little effect on the volume of the thorax. It thus appears that the thoracic ribs had little to do with breathing. The only alternative is a diaphragm, and as in these animals for the first time a definite distinction can be made between thoracic and lumbar ribs, it is perhaps worth considering.

It appears as though a gradually developing diaphragm came into operation in the higher Cynodonts. With the going into action of the diaphragm, the function of the ribs became neglected at a stage before a co-operation between diaphragm and intercostal muscles could be established. At this stage the intercostal muscles apparently failed to act as effective antagonists to the diaphragm, and to prevent the latter from drawing the ribs together instead of straightening itself, thus losing all effect, the ribs turned perpendicular to the vertebral column. This view is supported by the fact that only those ribs in the region of the diaphragm are perpendicular to the vertebral column.

It appears, however, that even before a tendency developed for the ribs to turn perpendicular to the vertebral column, a series of overlapping processes developed, which enabled the ribs to find support against those behind, to counteract atmospheric pressure in the process of breathing with the aid of a diaphragm alone. This condition is illustrated by *Thrinaxodon*, where simple overlapping processes extend throughout the trunk region.

In *Diademodon* the overlapping processes decreased in size in the anterior thoracic region after the posterior thoracic ribs have turned perpendicular to the vertebral column and established firmer contact with the vertebrae themselves, but in the lumbar region the structure became more complicated. In addition to the original processes, folds of the anterior processes now also overlap the posterior processes of the ribs in front so that the latter are actually clasped between two folds. This condition is reached only in old individuals. This phenomenon must obviously also have some purpose and the only explanation is that it was developed to ensure that no rotation of the torso could take place on the vertebral column in the lumbar region. The decrease in size of the processes in the thoracic region now points to the probability that rotation in the torso became restricted to this region alone. Experiments and mathematical analyses were carried out to establish whether a reasonable amount of increase and decrease in the volume of the thorax could be effected by twisting of the torso and results were favourable, but it was found that even with exaggerated twisting in the process of running, by the ordinary alternate movement of the legs in the typical reptilian fashion, the increase and decrease in volume was insufficient to account for the required volume of air. By no means does it account for any air supply when the animal is at rest. The possibility of the presence of a diaphragm must still be considered.

A diaphragm could have served under normal conditions, while twisting of the torso could have supplemented the air supply, provided the rhythmic movements of the legs corresponded with the rhythmic movement of the diaphragm. Judging from the size of the head, the rather small limbs, and the structure of the vertebral column and ribs, there may be a tendency to believe that *Diademodon* was a rather slow animal, but the tempo of breathing could still have been much faster than in other earlier forms, so that the significance of ethmo-turbinals and glands in the region of the etxernal nares, supported by reasonable evidence (see pages 9-10), now come into consideration.

It would be well worth considering to what extent a possible retaining of normal costal breathing in addition to the taking into commission of a diaphragm was responsible for the differentiation of the Ictidosaurs.

The Limbs and Girdles.

The inner surface of the scapula is moderately concave longitudinally, but strongly convex transversely. The outer surface is the opposite. Immediately above the glenoid facet the trough turns sharply forward to form quite a considerable depression dorsally to the suture between the scapula and precoracoid. This depression is carried forward to the anterior margin of the scapula, less than a centimeter below the fairly prominent acromion process on the same margin. Viewed from the front the anterior margin has a very marked S-shaped curve below this process. On the medial side of the scapula there is a slight depression between the anterior margin and the large convex middle portion. It starts about 25 mm. dorsally to the acromion process and extends down to the S-shaped curve, where it is suddenly terminated by a strongly elevated area, corresponding to the depressed area on the outer side. Immediately below the elevated area on the ineer side is another depressed area leading across

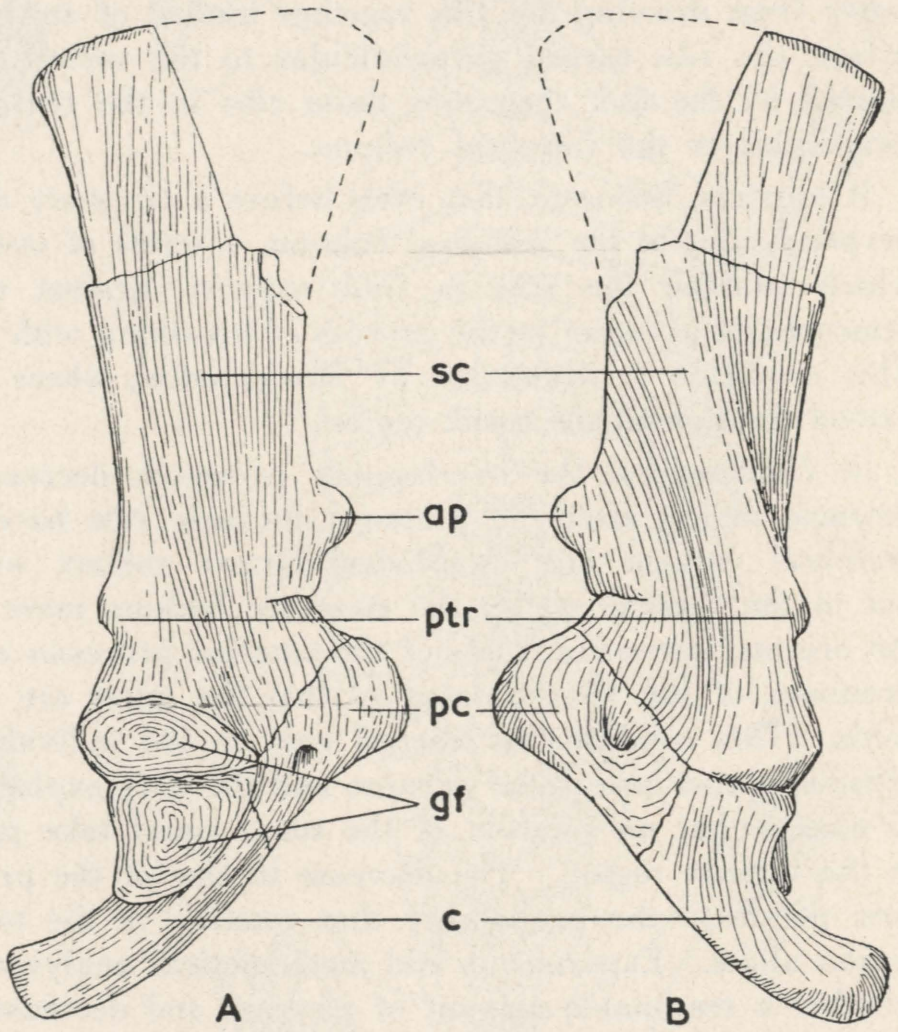


Fig. 8.—A, Lateral and B, Medial view of the right scapula of *Diademodon laticeps*, R.224, D.M.S.W. Collection, ½ natural size.

Abbreviations: ap, acromion process; c, coracoid; gf, glenoid facets; pc, precoracoid; ptr, process for trigeminus muscle; sc, scapula.

the region where the scapula, precoracoid and coracoid meet, to the foramen in the precoracoid. The posterior margin of the scapula is sharp in the dorsal half; lower down it becomes broad and massive. A short distance above the glenoid region is a fairly prominent process on which the triceps muscle was inserted.

The precoracoid does not contribute to the glenoid region. The coracoid is projected backward in a strong three-sided process.

The scapula is directed upward and forward. The interclavicle is very broad short and stout. The clavicle is also much shorter and more robust than in other Cynodonts.

The upper margin of the ilium is perfectly straight. The anterior margin is well rounded and semicircular. From the posterior end of the ilium the ventral margin proceeds forward in a straight line and then turns sharply backward to contribute to the margin of the acetabulum. Anteriorly the ventral margin runs for a very short distance horizontally backward and then turns downward and forward with a wide curve to contribute to the anterior margin of the acetabulum. The sutures between the ilium, ischium and pubis run through the acetabulum and divide it into three equal parts. On the dorsal border of the acetabulum and on the narrowest part of the ilium is a strongly elevated area with a large concave facet on its ventral slope. Antero-ventrally this facet is continuous with the rest of the acetabulum, but postero-ventrally it is separated by a groove.

The symphysial portion of the pubis is straight and horizontal. The anterior margin is sharply bent outward and downward so that it is also horizontal, but at right angles to the symphysial margin. On the margin of the acetabulum the pubis forms an elevated area similar to that of the ilium. The anterior margin of the acetabulum, where the ilium and pubis meet, is extended a short distance forward.

The ventral margin of the ischium is continuous with the ventral margin of the pubis and lies in the same straight line. The ischium was fused with its fellow of the opposite side along the whole of this ventral margin.

The postero-ventral portion of the ischium is thickened very similar to that of animals which have the habit of sitting on their ischia. A very prominent ridge extends from the postero-dorsal angle of the ischium across the outer face to the acetabulum.

The ischium develops a very large elevation on the border of the acetabulum. The three elevated areas on the border of the acetabulum are roughly equidistant; that of the ilium is the largest.

Judging from the structure of the pubis, it is quite impossible for a cartilaginous prepubis to have been present, because the anterior margin is bent downward.

The "birth" canal formed by the pelvis of *D. laticeps* measures 50 mm. in diameter. This is the maximum breadth that the skull of a newly "born" individual could have had. The transverse measurement of the skull of *D. laticeps* is 230 mm., so that the transverse measurement of the skull of a newly "born" individual is practically 1/5 of that of its mother. Perhaps the specimen is a male; the "birth" canal could then be bigger in the female and the head narrower, so that the ratio is smaller, and in addition the skull of a newly "born" individual could have been proportionally still narrower. The skull will have to increase from four to five times before it is an adult and it is difficult to harmonise this considerable increase

in size with the characteristics of the dentition. Where as great an increase in the size of the skull is found in the Monotremata, it is important to note that the dentition is not as complete.

The increase in the size of the skull would be much greater if the mother laid eggs. The diameter of an egg measures considerably more than the diameter of the skull when newly hatched. It is, however, possible that the egg may have had a soft skin (which is rather unlikely), and that the egg could then have been so large that even the skull within the egg could have exceeded 50 mm. in breadth. The characteristics of the dentition show clearly that the latter is so well adapted to a considerable increase in size of the skull and, as the breadth of the skull may have been considerably narrow, proportionally, at "birth", it is useless to try and base conclusions on these circumstances. An aspect worth considering in this respect is the fact that egg-laying amniot vertebrates usually have small skulls in proportion to their bodies. Giving birth to young appears to be an adaptation to the increase in the size of the skull. Where the higher Cynodonts have very large skulls it would still be well worth considering whether they actually gave birth to their young.

When born or hatched, *Diademodon* evidently had only a few "milk" teeth. The permanent molars were originated within their sockets as the individual increased in size. In some of the smaller lower jaws of *D. laticeps* the eighth molar sockets have not yet been formed. A very distinct backward extending fold of the dentary forms them as it grows farther back with advancing age.

From the material investigated it was established with some certainty that only a single succession occurred in the incisors, canines, and first four postcanine teeth; evidence of replacement in the so-called "molars" has been demonstrated since by Crompton (by kind information). However, the fact that the postcanine series does increase at older age with teeth showing no signs of replacement (see page 18) indicates that the typically mammalian arrangement is nearly achieved. This arrangement, combined with the consideration that the set of delicate teeth with which *Diademodon* started life was quite unsuitable for the type of diet of the adult, now points to a possibility that newly "born" individuals obtained food from their mothers perhaps in much the same way as modern mammals. However primitive it may have been it may be accepted that, if it were the case, the nature of the food was similar to the milk of modern mammals and that this "milk" was obtained from glands related to modern mammary glands. As milk glands are modified hair glands, the possibility that *Diademodon* had a hairy covering over its skin must then also come into consideration. This line of thought can be carried still further by considering to what extent *Diademodon* was homoeotherm, because both hair and sweat glands, which are inseparable, are adaptations to an increase in blood temperature. The importance of the possible presence of a diaphragm now comes into account again. It may be accepted that a diaphragm also developed as an adaptation to the increase in the temperature of the blood, or rather that the temperature of the blood was raised on account of the increase in the rate of breathing with the aid of a diaphragm. The presence of glands in the skin is affirmed by the depressions in the maxillaries dorsally, with traces of grooves running to the external nares, and the evidence pointing to the fact that the skin around the external nares was itself rich in glands (see page 10).

A graphical comparison between the lengths and other measurements of humeri and femora of different sized individuals of *Diademodon* proved to be of considerable interest. Not only could fragmentary bones be reconstructed with the aid of these graphs, they could also be brought to a particular size. The graphs were invaluable for the reconstruction of the complete skeleton shown in figure 7. From the graphs it could be established that the skeleton of "*Microgomphodon*", described by Seeley in 1895, is possibly that of a very tiny *Diademodon*. From this tiny skeleton interesting observations could be made in respect to the increase in size from "birth" to maturity in this genus.

In the original work descriptions are given of some other limb bones such as a beautiful tibia and fibula, an ulna, and some carpal and tarsal bones. These descriptions are not included here, because the author would like to wait till a wealth of *Diademodon* against a list of reptile-like characteristics, omitting the irrelevant or Museum, Bloemfontein, is described in the near future. This collection includes some hundreds of isolated teeth of both genera.

Summary

This account of the skull and skeleton of *Diademodon* has brought out some interesting new facts and the importance of many other facts is stressed. On the whole attention is drawn to the relatively far advanced mammalian characteristics of the higher Cynodonts, as far as certain definite skeletal features are concerned, but some indefinite suggestions are also made regarding the morphology of certain other features pertaining to soft anatomy. Before summing up the latter, it seems advisable to balance a list of the definite mammal-like anatomical characteristics of *Diademodon* against a list of reptile-like characteristics, ommitting the irrelevant or the otherwise rather obvious features. The mammal-like characteristics of *Diademodon* are the following:

(1) The presence of a typical mammal-like zygomatic arch.
(2) The mammal-like dentition, considering its thecodont nature, dental differentiation into incisors, canines and postcanine teeth, the flat-crowned cusped postcanine teeth showing abrasion, the single dental succession and the further, rather vague, probability of distinguishing premolars and molars.
(3) The typical mammal-like secondary palate, developed in association with the complex dentition as a result of the habit of masticating food.
(4) The further related development of a strong coronoid process, also related to the development of the strong zygomatic arch.
(5) The additionally related development of an angular process in an endeavour to establish a stronger articulation between skull and lower jaw.
(6) The epipterygoid is a typical mammal-like alisphenoid, forming part of the wall of the brain case.
(7) The pterygoids do not extend to the quadrates and are completely fused medially.
(8) There are two occipital condyles.
(9) Maxillary sinusses are present.
(10) Certain skull bones like the postfrontal, preparietal, etc. have disappeared while others like the transverse bone are on the point of disappearing.

(11) The carpus, tarsus and digital formula are mammal-like.
(12) There is a definite distinction between thoracic and abdominal regions as far as ribs are concerned.
(13) The pelvis and scapula are mammal-like.
(14) There appear to have been glands in the skin, judging from depressions and grooves on the maxillaries, the innervation of the region of the external nares and the characteristics of the external nares.

The reptile-like characteristics of *Diademodon* are the following:

(1) The characteristics of the region of articulation between the lower jaw and skull.
(2) The size of the brain, which does not yet allow for the incorporation of the squamosal into the wall of the brain case.
(3) Certain skull bones, like the interparietal, tabulars, prefrontals and septo-maxillaries, as well as some lower jaw bones, are still present.
(4) The pectoral girdle as a whole is in many respects still reptilian.
(5) There are still cervical ribs, intercentra and chevron bones, while discs have not yet developed between the centra, and the proatlas is still present.
(6) The skeletal bones have not yet developed typical mammal-like bony epiphyses.

Indications that ethmo-turbinals of mammalian pattern have developed in higher Cynodonts, considered in relation with the structure of the palate and dentition and the nature of the thoracic and lumbar ribs, reflect upon some further extremely mammal-like characteristics, which, although very indefinite, are still well worth considering.

Whatever the extent of the development of mammal-like ethmo-turbinals may have been in *Diademodon*, it is nevertheless certain that they developed for one, or all, of the following reasons: (1) To increase the surface over which the air passed when inhaled, for smelling purposes, because with the development of the secondary palate communication between the mouth cavity and the organs of Jacobsen was limited to an extreme. (2) To increase the surface so as to moisten the air sufficiently before it was inhaled, to prevent too great an amount of evaporation of water vapour taking place through the lung epithelium, directly from the blood. (3) To increase the surface to warm the air adequately before it was inhaled. (4) To clean the air.

If the first was the stimulating factor, it can be said that mammal-like ethmo-turbinals developed as an adaptation to a finer smelling sense. In the second case it could be an adaptation to a dry climate. In the third case it could be an adaptation to a rise in the blood temperature. Whatever the case may have been, it is rather obvious that on the whole mammal-like ethmo-turbinals developed as a result of, or associated with, an increase in the breathing tempo.

This consideration may now reflect upon the question whether the increase in breathing tempo is a result of the animal's agility and activity. Taking the structure and proportions of the skeleton of *Diademodon* into consideration one feels inclined to believe the opposite. Considering the arrangement of the ribs, it appears rather likely that a diaphragm, either partly or fully developed, could explain the increase in breathing tempo.

Whether or not *Diademodon* had a partly or fully developed diaphragm, an increase in breathing tempo must have involved an acceleration of the animal's metabolism and consequently a rise in the temperature of the blood, resulting in the development of mammal-like ethmo-turbinals for the purpose of warming the air before it was inhaled. The question then arises whether any attempt was made to preserve and regulate the temperature, that is, whether *Diademodon* had already developed hair and sweat glands. The presence of depressions and grooves on the maxillaries suggest that glands were present, and as such rather specialised glands, so that ordinary more primitive sweat glands could have been present in advance, together with their associated hairs. Only a skin impression of a *Diademodon* can settle this question.

Assuming in the mean time that *Diademodon* could have had sweat glands with hair on its skin and that apparently it had already specialised certain of these glands on the snout into more intricate organs, could it not also have specialised other sebaceous glands into milk glands? This question cannot be solved with palaeontological data, but it is interesting to note that *Diademodon* had almost achieved the mammalian arrangement of one "milk" set of teeth prior to its complex permanent set, and comparing this complex permanent set with the delicate "milk" teeth, it is difficult to visualise that both adult and newly "born" lived on the same type of food.

These rather indefinite considerations may be carried even further to the question whether *Diademodon* laid eggs or gave birth to its young. This question can be solved by the discovery of a female specimen which died immediately prior to "giving birth", although even then it would still be impossible to establish with certainty whether *Diademodon* was viviparous or ovoviviparous. But in the absence of such a specimen one can still consider the relative increase in size from newly "born" to adult, using measurements obtained from the pelvis of an adult individual of which we know the size of the skull. If such an increase in size is considered in relation with the complex dentition it is difficult to think otherwise than in terms of "birth". It appears furthermore that giving birth is an adaptation to an increase in the size of the skull, relative to the size of the body and as these proportions in *Diademodon* compare favourably with those of mammals and not with those of reptiles and birds, it could serve as a consideration that *Diademodon* actually did give "birth" to its young.

Description of New Specimens

Diademodon parringtoni sp. nov. (fig. 9)

Type: The anterior portion of a snout, No. R.159, in the D.M.S. Watson Collection, University College, London.

Locality: Lady Frere Commonage, in *Cynognathus* zone beds.

The palate is relatively narrow, but this may largely be due to lateral compression. There is evidence of eight "molars" and four "premolars" on the right side, and two "molars" and four "premolars" on the left side. The "premolars"

pass evenly over to the "molars" without a sudden change in size, judging from the sockets alone. The canines appear to have been relatively small.

There is a considerable diasteme (12.5 mm.) between the canine and the fourth incisor. There is evidence of only the third and fourth incisors on both sides, the first and second being lost through damage of the anterior margin of the snout. The excavations for the reception of the lower jaw canines are large and deep.

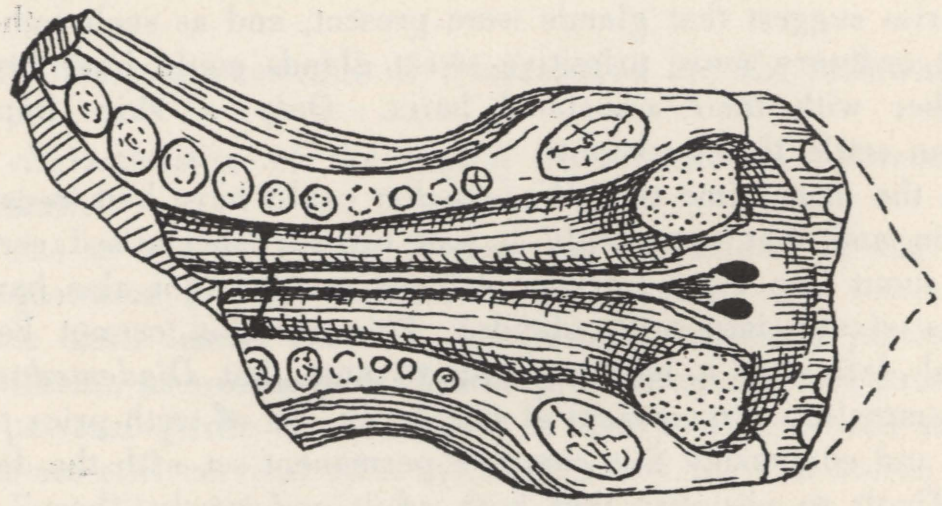


Fig. 9.—Ventral view of the snout of *D. parringtoni*, R.159, D.M.S.W. Collection, natural size.

The side of the maxillary bone is not vertical, the snout being considerably broader in the lower half of its height. About 12 mm. above the teeth the maxillary turns sharply inward, forming a prominent ridge on which the three foramina for the maxillary branch of the trigeminus nerve are situated. This very prominent ridge may be taken as one of the characteristics of this species.

Another very conspicuous characteristic of this species is the fact that the anterior portion of the snout has a very marked quadrate shape, in contrast with the longitudinally ovate or rounded shape in other species. The sides of this anterior portion, extending from the level of the posterior margins of the canines to the fourth incisors, are straight and parallel to each other.

A portion of the palatine of the one side is present. Enough is preserved to reveal the characteristics of the posterior margin of the secondary palate. This margin forms an angle with the portion of the palatine flanking the posterior molar teeth, at a level of the posterior margin of the fifth "molar" tooth from the front. For a short distance it extends straight across, but sharply upward. Towards the midline it turns forward, but still upward.

The depressions on the latero-dorsal side of the snout, over the dorsal portions of the maxillaries, are fairly deep.

The following are some useful measurements.

Minimum breadth of snout	40	mm.
Maximum breadth of anterior portion of snout	45	mm.
Breadth of canine socket	6.5	mm.
Length of canine socket	12.5	mm.
Breadth of largest molar socket	8	mm.
Length of largest molar socket	6	mm.

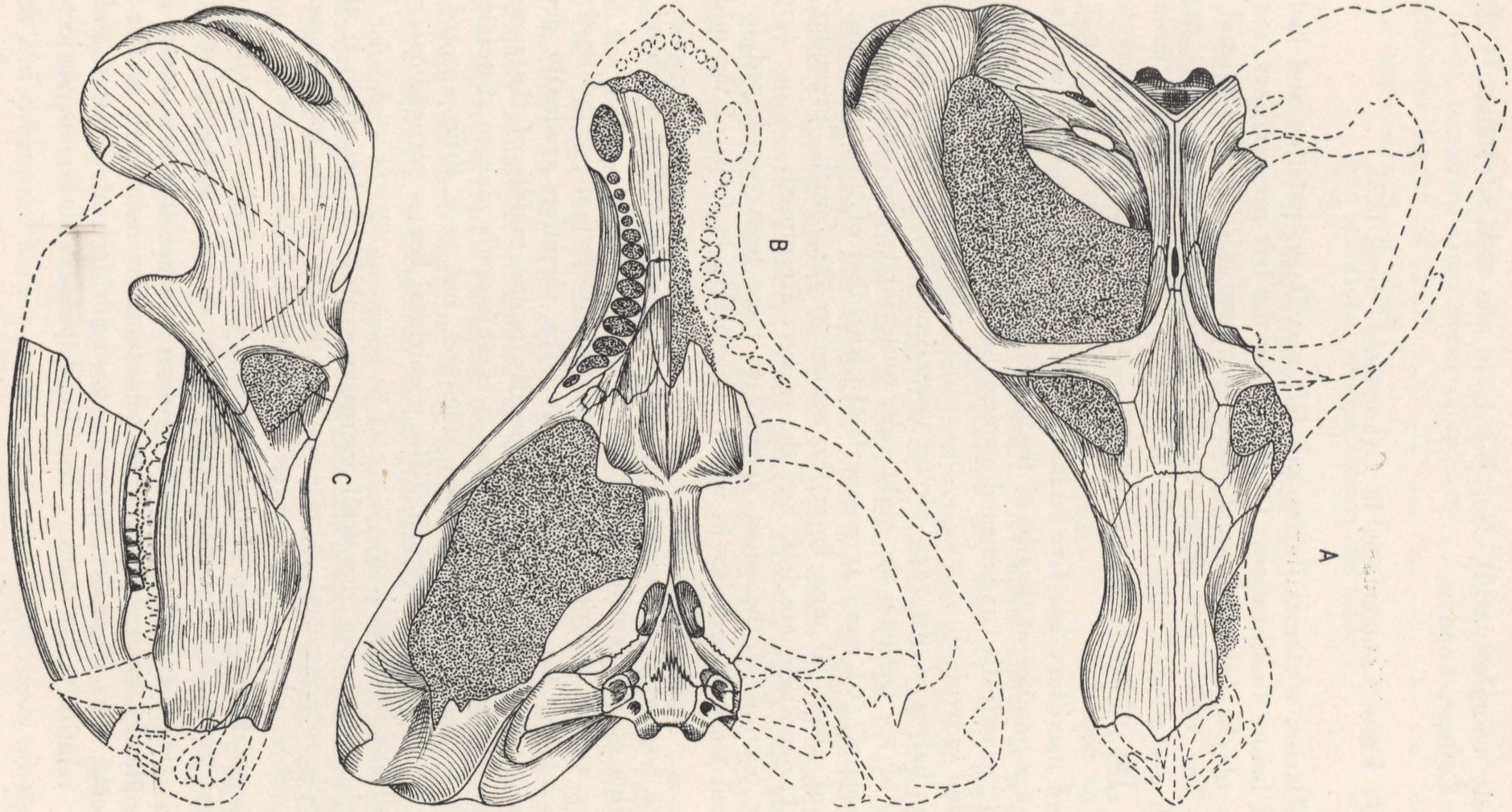


Fig. 10.—A, Dorsal, B, Ventral and C, Side view of the skull of *Diademodon laticeps*, R.131, D.M.S.W. Collection, $\frac{1}{3}$ natural size.

Diademodon laticeps sp. nov. (fig 10)

Type: A fairly complete skull, No. R.131, in the D.M.S. Watson Collection, University College, London.

Locality: Lady Frere Commonage, in *Cynognathus* zone beds.

The premaxillaries, septomaxillaries and left maxillary, palatine and lachrymal were dislocated before fossilization. Of these only the left premaxillary, maxillary and a portion of the left lachrymal were recovered (R.155, R.132 and R.149 respectively). The whole left zygomatic arch was broken away after exposure.

All the teeth are missing, except the ultimate and the fifth upper "molars" on the left side. The ultimate tooth is slightly damaged, while the other tooth is broken off at its neck.

The dislocated maxillary has five teeth, but they are unfortunately all damaged. The bone shows a number of details of the maxillary antrum.

A dislocated, practically undamaged canine has been found (R.158) possibly belonging to this individual.

The posterior halves of the rami of the lower jaw (R.134) are broken away. It shows evidence of ten teeth on the right side, posterior to the canine. The length of the nine "molars" (61 mm.) agrees perfectly with that of the upper jaw. There is a diasteme of about 20 mm. from the canine to the fourth "premolar"; the anterior three "premolars" are lost, and the sockets are closed.

The anterior portion of the snout appears to have been egg-shaped in dorsal view. The snout starts decreasing in width immediately in front of the middle of the canines.

The posterior border of the secondary palate is straight and at the level of the posterior margins of the fourth "molar" teeth.

The posterior end of the parietal crest does not project above the level of the most dorsal points on the zygomatic arches. The elevation gradually decreases forward. There is a peculiar elevation dorsally in the middle of the snout, also found in *D. parringtoni*, but in the latter it is apparently due to distortion.

The orbits face equally forward and sideward, but very little upward. The lateral margin of the orbit is vertical. The postorbital bar is perpendicular to the axis of the skull and horizontal.

From the orbits backward the skull increases rapidly in breadth. If the left zygomatic arch is reconstructed, it appears that the two arches form an angle of 45^0 with each other, which is the largest angle found in this genus.

Another distinguishing feature of the zygomatic arches is that they slope inward ventrally, so that the skull is broader dorsally than ventrally across the squamosals.

The species is also characterised by a very deep external auditory meatus groove, practically completely covered by a prominent lamellar outgrowth of the medial edge. The groove runs vertically down the posterior face of the arch and starts very suddenly relatively far back. The jugal process does not project much outward.

The following are some useful measurements:

Length of canine socket	23 mm.
Breadth of canine socket	13 mm.
Total height of zygomatic arch	97 mm.
Height of snout, measured from necks of molars	53 mm.
Approximate total length of skull	280 mm.
Approximate total breadth of skull	230 mm.

For additional measurements see table 1.

Diademodon mastacus Seeley

Specimen: Slightly more than half (longitudinally) of a large skull, No. 314 in the collection of the Bernard Price Institute.

Locality: The farm Luiperdskop near Burghersdorp, in *Cynognathus* zone beds, collected by J. W. Kitching in January, 1952.

This specimen is an unusually large skull. As stated above, it is larger than the average *Cynidiognathus* and approximates in size to the type skull of *Cynognathus crateronotus*. Nevertheless in structure and proportions it is a typical *Diademodon* and cannot be distinguished from *D. mastacus* in any structural feature. It has the characteristic vertical face of the maxillary as found in all other known specimens of this species. The zygomatic arch is very high posteriorly and the external auditory meatus groove descends vertically down to the quadrate region. The lamellar outgrowth medially to the groove turns slightly laterally, but not nearly as much as in *D. laticeps*. The skull is very robust in appearance and could be that of a very old male.

This specimen is most peculiar in that it has twelve "molars" in addition to four "premolars". The "premolars" are typically cone-shaped and similar in size to those of the average *Diademodon*. The first "molar" has a transversely ovate crown. All the "molars" up to the eighth are considerably worn, the anterior ones practically to their necks. The eighth tooth is easily recognisable as the tooth which is usually somewhat triangular in all species, and the ninth is laterally compressed. Up to the ninth tooth the dentition cannot be disinguished from that of *D. mastacus*, but then there are three additional teeth exactly similar to the ninth, hitherto not yet encountered in a *Diademodon mastacus* specimen. In Broili and Schröder's (1935) specimen of *D. grossarthi* a tenth tooth is encountered, and an undescribed specimen in the South African Museum, Cape Town, shows the tenth and eleventh molars. It appears that *Diademodon* rarely reached the age where additional "molars" to the usual nine started erupting.

The discovery of this specimen makes it difficult to decide upon a definite dental formula for *Diademodon*. It would be safer to rely upon the characteristics of the eighth, ninth and subsequent "molars" than upon the actual number. The seventh is always transversely ovate and usually the largest tooth. The eighth is often somewhat triangular, and the ninth laterally compressed. All subsequent teeth agree in shape and size with the ninth.

The ninth and subsequent molars in the present specimen shows no sign of wear, as they miss their opponents of the lower jaw.

According to Crompton (by kind information) there is evidence of replacement of the eleventh postcanine tooth in *Diademodon*, but according to this specimen it is highly doubtful whether replacement occurred in the characteristic triangular twelfth, while in the subsequent longitudinally flattened teeth there is certanly no sign of replacement. This is rather important, because, although *Diademodon* does not illustrate a mammalian arrangement in its dental sucession, it nevertheless presents that stage where the series of postcanine teeth is increased by additional "permanent" teeth, a significant progression towards the mammalian condition.

The posterior border of the secondary palate is at the level of the posterior borders of the fifth "molars" in an average *D. mastacus*. In the present specimen it is at the level of the posterior borders of the seventh molars. It appears that the posterior border of the secondary palate tends to grow farther posteriorly with advancing age. It naturally could not have been at the level of the fifth "molars" at "birth".

The following are some useful measurements: (in millimeters)

Greatest length of largest molar	6.5
Greatest breadth of largest molar	10
Length of row of *nine* "molars"	55
Distance from posterior margin of canine	
to 1st "premolar" exclusive	11
to 4th "premolar" inclusive	25
to 1st "molar" inclusive	28.5
to 2nd "molar" inclusive	34.5
to 3rd "molar" inclusive	40
to 4th "molar" inclusive	46
to 5th "molar" inclusive	51.5
to 6th "molar" inclusive	58
to 7th "molar" inclusive	65
to 8th "molar" inclusive	71
to 9th "molar" inclusive	78
to 12th "molar" inclusive	100
Maximum breadth of snout (reconstructed)	63
Minimum breadth of snout (reconstructed)	42
Interorbital breadth (reconstructed)	60
Total length of skull (to squamosals)	324
Breadth across squamosals (reconstructed)	220

If the above measurements, based on the "molars", are compared with table I, it will be noticed that there is a remarkable similarity between the present specimen and the much smaller specimen of *D. mastacus* (R.51) in the Watson Collection.

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A NOTE ON THE LOCALITY OF *WALTERIA SKINNERI* BRINK AND KITCHING

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Brink and Kitching state in "Annals and Magazine of Natural History", Series 12, Volume IV, 1951, page 1218, that the anterior half of this Therocephalian skull (Bernard Price Institute, No. 220) was collected on the farm Vleifontein, 20 miles east of Laingsburg, C.P., by Mr. A. J. Walter Skinner.

As a result of geological reconnaissance work in the Laingsburg District in June, 1952, I am able to tender the following information as regards the locality where this skull was found:

Vleifontein is not a farm but a railway siding, 12 miles east-northeast of Laingsburg and situated on Ecca shales. It was further ascertained that the skull was originally in the possession of Mr. le Roes residing on the farm Ruiterskop, about 3 miles south-east of Vleifontein siding. As Mr. le Roes is interested in rocks, he has quite a collection of sundry samples, amongst others the skull in question and a fragment of fossil bone, obtained from his son's farm Elandsfontein, which lies in the Beaufort West District and is situated about 14 miles by road to the north-northwest of Merweville.

Elandsfontein, the true locality from which specimen B.P.I. 220 comes, is underlain by lower Beaufort beds of the *Tapinocephalus* zone, some 2,100 feet above the contact between the Ecca and the Beaufort series.

A SABRE-TOOTH CAT FROM THE MAKAPANSGAT VALLEY

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Abstract

Three cranial fragments from the Limeworks dumps in the Makapansgat valley, Potgietersrust, Central Transvaal, represent a new sabretooth cat — *Machaerodus darti*. It differs from *M. transvaalensis* Broom in having a more rounded canine.

Three fragments from the Lime-Works dump at Makapansgat, Potgietersrust, Central Transvaal, represent a new fossil sabre-toothed cat. They comprise a beautifully preserved lower jaw with the canine broken, the anterior portion of the snout and mandible of another individual and an isolated ? milk molar. The specimens were collected during 1948 by Messrs B. J., J. W. and S. C. Kitching of the Bernard Price Institute for Palaeontological Research and developed under the supervision of Mr. J. W. Kitching.

Machaerodus darti sp. nov.

The mandible, No. 607 in the Bernard Price Institute, collected by Mr. J. W. Kitching in 1948, is taken as the type (fig. 11). It is complete except for the crown of the canine, incisors, retro-articular process and the tip of the coronoid process. In size it is similar to that of a very large leopard (condylo-symphysial length = 154 mm.) but in its other features it is very different.

Thus the third lower premolar is greatly reduced in size, having no anterior cusp, but still being two-rooted. The accessory cusps of P_4 are moderately developed, but much smaller than the protoconid. The talonid is well-developed. A vestigial heel is present on M_1. All the cusps have a slight backward pitch.

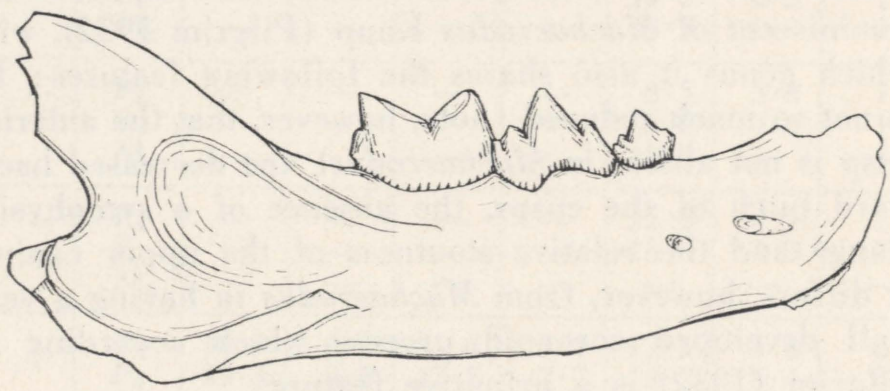


Fig. 11.—Lateral view of the jaw of *Machaerodus darti*, No. M.607, B.P.I., ½ natural size.

The masseteric fossa is deep and well-defined and the coronoid is directed posteriorly as in typical felids. The diastema is large (21 mm.) and a mental process is very small. In cross-section the canine is oval and measures at its neck 16.5 by 10 mm.

Unfortunately the snout portion is very severely damaged, but the upper and lower incisors and the right upper and lower canines are reasonably well-preserved (figs. 12 a and b). The lower canine has a cross-section similar to that described

for the type lower jaw. The symphysial fragment is so similar to that seen in the type, that the two specimens can scarcely belong to different species. The lower canine is not conical as in the Felinae, but is compressed and had a total length of circa 35 mm. The upper canine is much larger than the lower and the total length was probably about 65 to 70 mm. It measures at the neck 24 by 15 mm. The posterior edge is sharp and crenulations were absent, unless they have disappeared through damage. The width between the lateral sides of the canines is 70 mm.

In lateral view the isolated tooth is very similar to P_3 of *Acinonyx*, but it is much narrower and the central cusp is more slender. These two features are also characteristic of the milk molars of the large cats and it is therefore possible that this tooth is an anterior milk molar of the same species as that represented by the type jaw and snout fragment.

The reduction in size of P_3 is reminiscent of *Megantereon* Croizet & Jobert (Matthew 1929), but the tooth is not as vestigal as in the latter genus (table II). In the absence of the anterior cusp it resembles *Paramachaerodus* Pilgrim (1932). The other cheek teeth are very similar to that of *Megantereon falconeri* (Pomel), according to Matthew's figure (1929), except that the cusps are not pitched backward so strongly. On the other hand the structure of the jaw is very different from that of *M. falconeri*. The Makapansgat specimen is relatively shallow. At the level of the post-canine diastema it is 28.5 mm. high whereas the corresponding measurement is 34.5 in *M. falconeri*. The large mental process found in *Meganteron* is vestigial in the present specimen.

The lower canine of the new species appears to be much better developed than in the Plio-Pleistocene sabre-toothed cats hitherto described. The compressed nature and oval cross-section at the neck is, however, reminiscent of *Machaerodus* Kaup (Pilgrim 1932), with which genus it also shares the following features: P_3 is not so much reduced (note, however, that the anterior cusp is not absent in *Machaerodus*), the decreased backward pitch of the cusps, the absence of a symphysial flange and the relative stoutness of the upper canine. It differs, however, from *Machaerodus* in having a very well developed coronoid process which according to Pilgrim (1932) is a primitive feature.

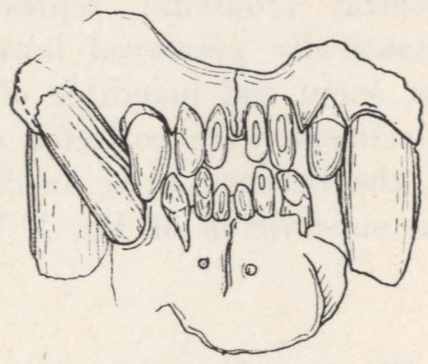


Fig. 12.—A, Front and B, Side view of portion of snout of *Machaerodus darti*, No. M.209, B.P.I., ½ natural size.

The Makapansgat specimen therefore differs from all the known Old World Plio-Pleistocene sabre-toothed cats and probably represents a new genus, but until this form is better known and it can be ascertained beyond doubt that all these fragments belong to the same species, it is preferable to refer the specimens to an existing genus, of which *Machaerodus* appears to be the most suitable.

From other South African limestone caves, Broom has described a number of sabre-toothed forms. Three species (*barlowi*, *gracilis* and *whitei*) were referred

TABLE II

		Maximum Length	Maximum Width	Minimum Length	Minimum Width	Average Length	Average Width	Number of Specimens
Panthera leo	P_3	19·4	10·0	17·3	9·5	17·9	9·9	6
	P_4	28·2	14·9	25·4	12·2	26·6	13·6	6
	M_1	30·5	15·4	26·0	13·5	27·5	14·4	6
Panthera tigris	P_3	—	—	—	—	—	—	—
living	P_4	22·8	—	20·8	—	—	—	—
After Bongersma	M_1	27·0	—	23·0	—	—	—	—
Panthera tigris	P_3	—	—	—	—	15·2	7·3	1
fossil	P_4	22·9	11·0	20·0	10·8	—	—	—
After Bongersma	M_1	—	12·5	—	12·1	23·8	—	1
Acinonyx	P_3	13·4	5·8	12·3	5·6	12·8	5·7	3
	P_4	17·3	7·1	15·5	6·8	16·5	7·0	3
	M_1	18·6	8·1	17·3	7·7	17·9	7·8	3
Machaerodus darti	P_3	—	—	—	—	12·2	7·1	1
	P_4	—	—	—	—	21·4	10·0	1
	M_1	—	—	—	—	25·9	11·6	1
Megantereon falconeri No. 6557 B.M.	P_3	—	—	—	—	10·3	4·8	1
After Matthews (drawing)	P_4	—	—	—	—	22·8	9·9	1
After Pilgrim	M_1	—	—	—	—	24·5	11·0	1
Megantereon falconeri G.S.I., D.100.	P_3	—	—	—	—	8·0	6·3	1
After Pilgrim	P_4	—	—	—	—	21·0	10·5	1
	M_1	—	—	—	—	26·0	13·0	1
Megantereon megantereon	P_3	—	—	—	—	—	—	—
	P_4	—	—	—	—	—	—	—
	M_1	—	—	—	—	20·0	10·0	1
Megantereon gracilis	P_3	—	—	—	—	—	—	—
	P_4	—	—	—	—	14·0	6·5	1
	M_1	—	—	—	—	19·7	—	1
Megantereon whitei	P_3	—	—	—	—	6·5	3·8	1
	P_4	—	—	—	—	15·0	7·0	1
	M_1	—	—	—	—	18·0	—	1
Felis crassidens	P_3	—	—	—	—	15·0	8·5	1
	P_4	—	—	—	—	18·6	9·0	1
	M_1	—	—	—	—	—	—	—
Panthera pardalis	P_3	14·3	6·2	11·4	5·4	12·3	5·8	6
	P_4	19·3	9·6	17·3	7·7	18·2	8·4	6
	M_1	19·6	9·1	17·1	7·8	18·5	8·3	6

to the genus "*Meganthereon*" and a fourth (*transvaalensis*) to *Machaerodus*. *Megantereon whitei* from Skurweberg and *M. gracilis* from Sterkfontein both differ from the Makapansgat specimen in having a single-rooted and an even more vestigal P_3 as well as much smaller cheek teeth generally (table II). On the other hand P_4 and M_1 are not very different structurally from that of the Makapansgat

specimen, as appears from Broom's drawings and descriptions (1937, 1939, 1946 and 1948). The lower jaw and teeth of *M. barlowi* from Sterkfontein are unfortunately unknown but the upper canine is very similar in size to that of the Makapansgat specimen (25 by 16 mm. and 60 to 65 mm. in length, Broom, 1937). In *Machaerodus transvaalensis* Broom (1939) from Bolt's Workings, Sterkfontein, which also is without lower teeth, the upper canine measures at the neck 24.5 by 12 mm. and is therefore considerably flatter than that of the new species.

The new form is named after Professor R. A. Dart, who has done so much for the palaeontological development of the Makapansgat Valley.

I wish to thank Prof. R. A. Dart, head of the Department of Anatomy, and Dr. H. B. S. Cooke of the Geology Department very cordially for their help in the preparation of this paper.

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