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SPECULATIONS ON SOME ADVANCED MAMMALIAN CHARACTERISTICS IN THE HIGHER MAMMAL-LIKE REPTILES

By A. S. Brink

Abstract

This paper deals with a number of skeletal characters of the higher mammal-like reptiles from which inferences may be drawn regarding soft anatomical and physiological features. Although these characters, when evaluated individually, do not indicate conclusively the exact proximity of these animals to truly mammalian conditions, the collective evidence and mutual support which they afford suggest that enlightening progress can be made towards establishing the following: the significance of the mammalian single dental succession, secondary palate, ethmoturbinals, as related to a high constant blood temperature; the latter's relationship, in turn, to hair and sweat glands; the origin of milk glands; and the mode and significance of mammalian birth. These considerations throw some instructive light on the origin of mammals.

Introduction

In dealing with "the origin of mammals" the palaeontologist is interested in a group of animals which lived during the late Triassic and early Jurassic — advanced Therapsids which are classified under the Class Reptilia, or fragmentary specimens which may resort under the Class Mammalia. At this level in the evolution of the Vertebrates the palaeontologist is naturally anxious to know exactly *when* he is handling a specimen which is "still a reptile" or one that is "already a mammal". He must be able to define a "stage" where reptiles actually became mammals, in such a way that he can consider forms just earlier than this "stage" as definite reptiles, and forms subsequent to this "stage" as true mammals.

Not only our popular conception but, indeed, our zoological definition of a mammal is that of an animal where milk glands occur, functional in females only, and where females (with Monotremes as an exception) give birth to viable young. This definition can be elaborated by qualifying the mode of birth as placental, with Marsupials as an exception. Although there are two types of exceptions to the rule of placental birth, it is to be noted that ovovivipary does not occur in any mammal, while in other vertebrates which produce living young they are always products of ovovivipary. A common characteristic of mammals, contrary to all other vertebrates, is the fact that females nurse their young for a particular period with the aid of milk glands.

This definition is naturally of no avail to the palaeontologist. Instead, the palaeontologist relies on a definition based on the jaw suspension. He would consider an animal in which the jaw articulation is "still" between the articular and quadrate as a reptile and one where it is "already" between the dentary and squamosal as a mammal. This definition is artificial. It must be borne in mind that the comparative

anatomist invented it in his own interest and not in the interest of the reptiles and mammals concerned.

In the first instance, according to this "palaeontogical" definition, *"Ictidosaurus"* (Crompton, in preparation), with its double articulation, is neither reptile nor mammal, but in fact both.

Secondly, it is difficult to believe that the more advanced typically mammalian characteristics such as blood temperature, mode of birth, and milk glands were suddenly acquired simultaneously with the dentary-squamosal articulation. It is more likely that these characteristics were acquired gradually and at different levels, as were many other mammalian skeletal features within the Therapsids. As far as milk glands are concerned, if these were acquired simultaneously with the dentary-squamosal articulation, the "palaeontological" definition of the difference between a reptile and a mammal will not be artificial; but palaeontology has no room for idealism. It is as likely — in fact more likely — that milk glands appeared on the scene either earlier or later than the dentary-squamosal articulation. If milk glands were acquired subsequently to an established dentary-squamosal articlation then, for a certain length of time, animals lived which were, according to the "palaeontological" definition, true mammals, but according to our zoological conception, not yet true mammals. On the contrary, if milk glands were acquired earlier than the dentary-squamosal articulation then, for a time, animals existed which were mammals in the general sense of the term, but structurally, as far as the jaw suspension is concerned, not yet true mammals.

On the strength of some unfortunately rather vague points of evidence at present at our disposal, it appears fairly likely that these advanced mammalian characteristics, warm constant blood temperature, birth and nursing with the aid of milk glands, were acquired earlier than the dentary-squamosal articulation. These points of evidence are to be found among advanced members of the Cynodontia which, according to our present knowledge, appear not to have given rise to mammals. According to Crompton (1955) the line of evolution to mammals passed along the primitive Therocephalia, through the Scaloposaurids, close to the Bauriidae on to the Ictidosaurs, here turning into true mammals. The Cynodontia originated from the Therocephalia during early *Cistecephalus* zone times and closely parallels the Scaloposaur — Ictidosaur — Mammal line, so that it is not a great risk to consider certain peculiarities of the Cynodonts as vaguely reflecting some occurrences along the true mammalian line (see figure 29).

The Diaphragm and Supporting Evidence

In previous thoughts on blood temperature etc. in higher mammal-like reptiles arguments are based on the masticatory nature of the dentitions of these animals, but the author considers that the diaphragm presents itself as a better subject on which to base such speculations.

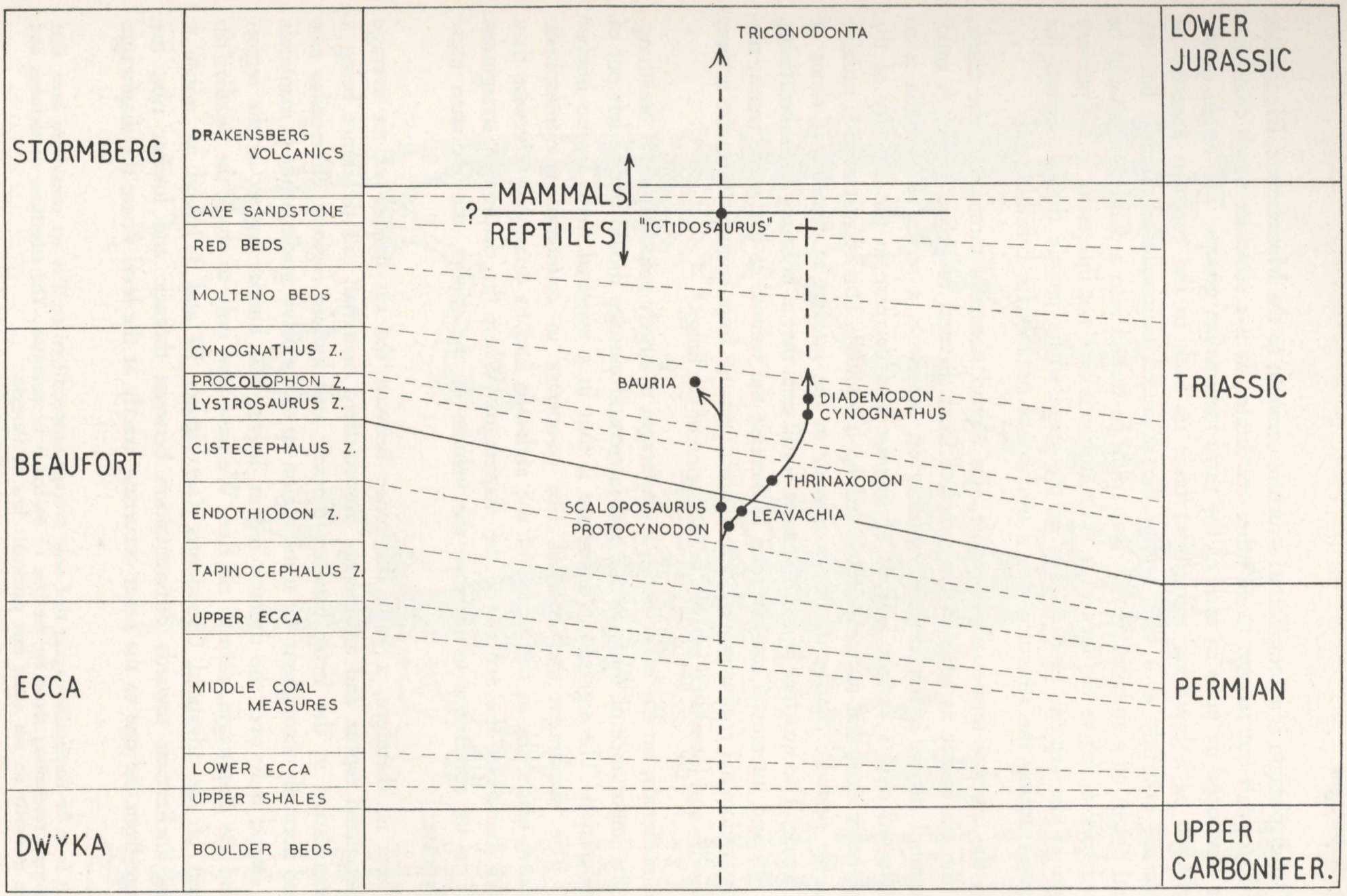


Fig. 29—Diagrammatic representation of the genera discussed, related to geological time (to scale) and the Karroo strata (to scale for maximum thickness across the Permia and Triassoc).

The diaphragm

The diaphragm is a complicated structure common to the Monotremes, Marsupials and Placentals but foreign to all other vertebrates. It is a structure which could not have developed *de novo* in each of the three mammalian groups. The origin of the diaphragm as a breathing mechanism takes us back to the common ancestry of mammals, evidently at a level within the advanced mammal-like reptiles; but the actual origin of a suitable septum that could be turned into a diaphragm should be traced back as far as the fish stage. The author is here not interested in the primary origin of the septum as such, but in the stage where muscle tissues entered the septum, turning the structure into a mechanism suitable for breathing.

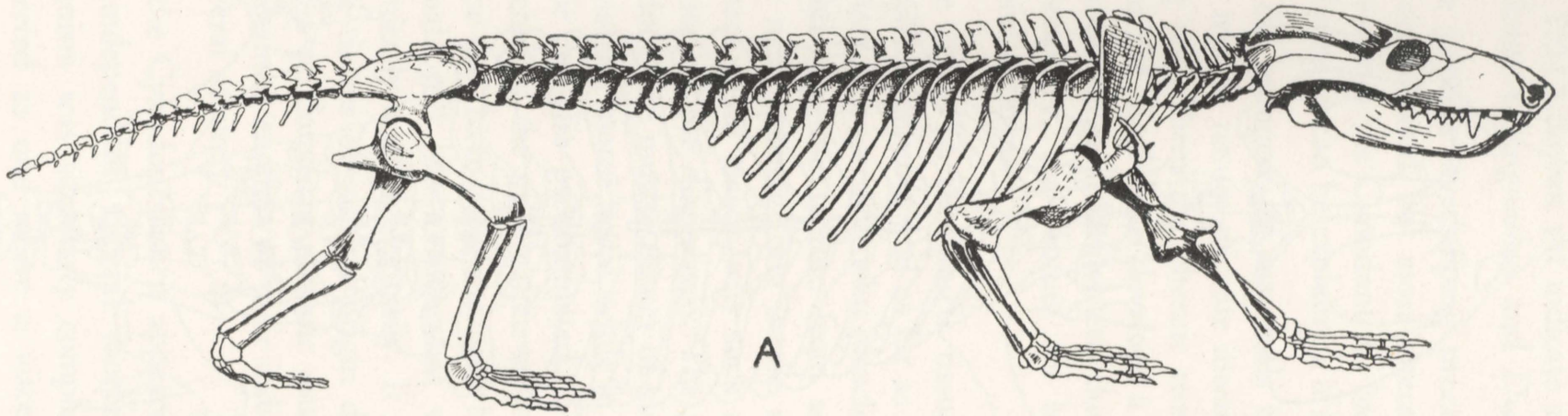
In the average unspecialized reptile, ribs extend normally throughout the trunk, but the rib basket as such is not complete from pectoral to pelvic girdle. A small abdominal region is left rib-free ventrally or, otherwise, a series of gastralia is so constructed that a certain amount of increase and decrease in the capacity of the trunk other than that necessary for breathing is allowed. This construction is suitable only for periodic change in trunk capacity in the interest of females at times of egg laying. The structure of the rib basket is still such that in ordinary costal breathing, the ribs and intercostal muscles tend to increase the volume of the whole trunk; ribs in the abdominal region prevent atmospheric pressure from counteracting the actions of the ribs and intercostal muscles in the region of the lungs.*

In mammals, on the other hand, a diaphragm is largely responsible for breathing, but the importance of thoracic ribs and intercostal muscles should not be left out of consideration. The significant difference is that in a mammal there are no lumbar ribs. The diaphragm and thoracic ribs co-operate in counteracting atmospheric pressure, while ribs in the region of the abdomen had to disappear otherwise they would counteract the actions of the diaphragm. When the diaphragm straightens itself in its endeavour to increase the volume of the thorax, the abdomen must reciprocate.

There is, therefore, a basic difference between the rib baskets of an average unspecialized reptile and an average unspecialized mammal, this difference being a differentiation in the latter between thoracic and lumber regions. In reptiles ribs extend normally throughout the trunk region up to the pelvic girdle, while in mammals ribs extend only over the thoracic region, leaving the lumbar region, or the region behind the diaphragm, entirely rib free. We have now only to study the peculiar rib baskets of the advanced Cynodontia (see figures 30 and 31) and we notice a strong inclination towards differentiation between thoracic and lumbar ribs, the change from the one to the other occurring exactly at the level where the diaphragm

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* It is to be emphasized again that only average unspecialized reptiles are considered here, that is, animals resembling those on the line of evolution to mammals. The structures of tortoises and turtles naturally do not assist this particular line of thought.



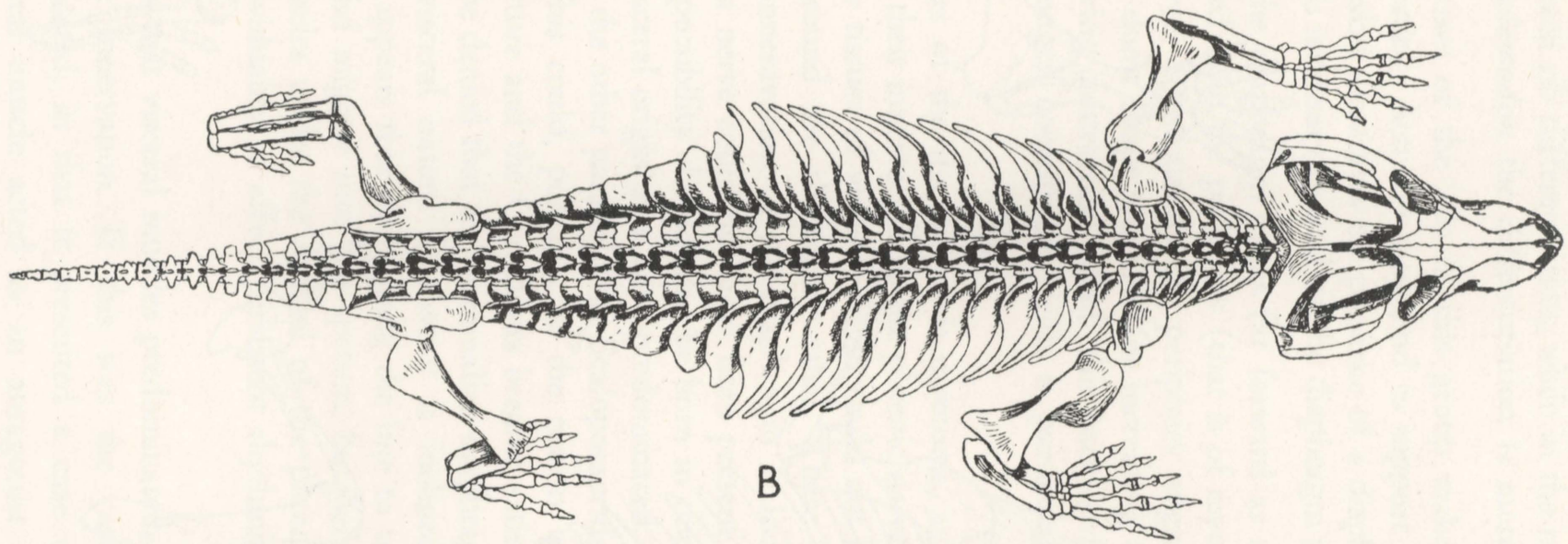


Fig. 30—Thrinaxodon liorhinus. Side and dorsal views of a reconstructed skeleton based on specimen No. C.392 in the National Museum Bloemfontein (see also Brink 1954, Res. Nat. Mus., i, 5, p. 115). This figure is used again by kind permission from the National Museum.

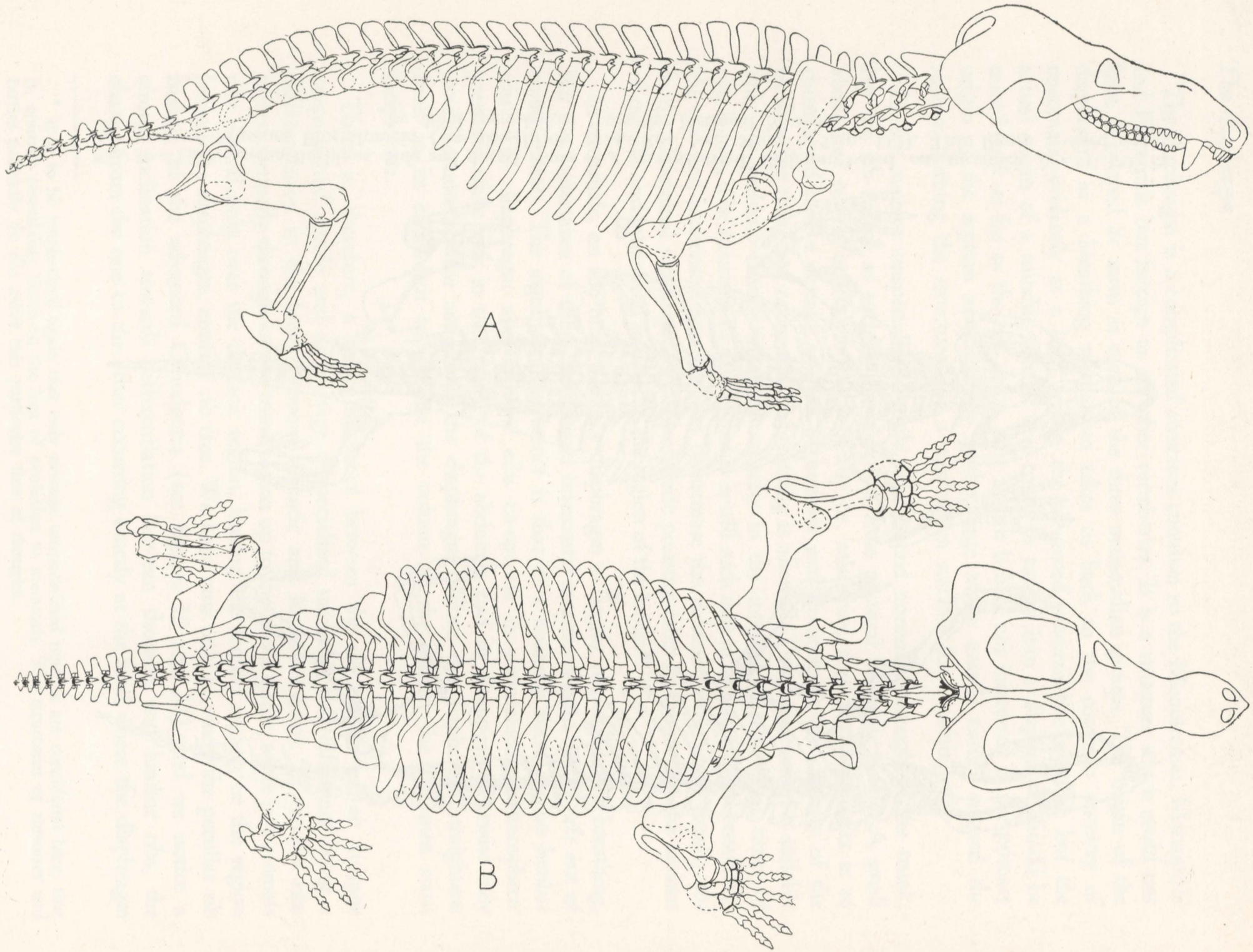


Fig. 31—Diademodon cf. laticeps. Side and dorsal view of a reconstructed skeleton based on numerous specimens. The skull is after D. laticeps, R. 131 in the D. M. S. Watson Collection, University College, London, and the skeleton after specimen No. 531 in the National Museum, Bloemfontein.

is found in mammals. As such we have some vague evidence in favour of a diaphragm-like structure already operating in the interest of breathing as early as in *Thrinaxodon* of the *Lystrosaurus* zone. The *Cistecephalus* zone Cynodonts (*Leavachia,* for example, Brink 1951) do not yet indicate such rib differentiation, while in the more advanced Cynodonts *Cynognathus* and *Diademodon* the differentiation is more pronounced.

The peculiar overlapping processes of the ribs in this group make the problem more complicated, but more interesting. Actually they tend to support more strongly the view that the Cynodont rib basket illustrates the presence of a diaphragm. Before their function can be explained, it is necessary to analyse the diaphragm in more detail.

In the ontogeny of mammals the diaphragm arises far forward as a septum into which muscle tissues migrate inward from the periphery (that is of myotome origin), taking with them the phrenic nerve. Subsequently the periphery migrates backward so that the diaphragm develops a dome shape, suitable for increasing the volume of the thorax when it straightens during contraction. With this backward migration of the periphery, the septum no longer corresponds with a particular rib pair or vertebral segment.

The origin of the muscle tissues of the diaphragm is myotome, as illustrated in mammalian embroys and as far as their innervation by the phrenic nerve is concerned. But there is no reason why muscle tissues of visceral origin could not have migrated outward into the septum from around the alimentary canal. There is no visceral motor nerve participating in the inneravation of the diaphragm in living mammals, but there is no reason why such a nerve could not have been present earlier in the evolution of the diaphragm. The possibility should also be born in mind that in the Cynodont line muscle tissues of visceral origin may have predominated, even supplied by a visceral motor nerve, while in the other parallel line, Scaloposaurids to mammals, somatic muscles predominated. This could, perhaps, be the reason why the latter line achieved the mammalian structure and the Cynodonts became extinct. Whatever the case may have been, it cannot be denied that the mammalian diaphragm in modern mammals still has a somewhat visceral nature in that it is inclined to contract rhythmically and involuntarily. It appears that even along the line to true mammals, muscle tissues of visceral origin did migrate into the spetum, but became absorbed into the predominant somatic muscles under the control of the phrenic nerve. But they retained enough of their individuality to effect persistent rhythmic contractions of visceral nature.

In the Cynodont line it appears that visceral muscles predominated, perhaps even with independant visceral motor innervation. If this was the case, the whole mechanism was singularly complicated, in that it presented a case which can be interpreted as one where a visceral muscle acted as an antagonist to a somatic muscle. On contraction the somatic intercostal muscles tend to pull the ribs forward; the ribs, being inclined to the vertebral column, swing outward and effect an increase in the volume of the thorax. In addition to straightening itself, the contracting

diaphragm tends, on the contrary, to pull the ribs of the left and right sides closer together, exactly opposite to the effect of the intercostal muscles and fully antagonistic to them. In modern mammals, where the diaphragm is largely somatic and innervated by a somatic motor nerve, there is no problem, because the intercostal muscles can conveniently co-operate with it, but where the diaphragm appears to have been more visceral in nature, as was probably the case in the Cynodontia, the problem is rather complicated. Mention should be made of the comparably antagonistic mammalian jaw muscles of visceral origin (masseter and temporal) and somatic origin (platysma), but in this case the visceral muscles had adopted all the characteristics of voluntary muscles (except their innervation by dorsal roots of cranial nerves) and also lost the visceral nature of their function.

It appears that the antagonistic actions between largely involuntary diaphragm and fully voluntary intercostal muscles in the Cynodontia could not effectively be brought to well timed co-operation. As an adaptation, overlapping rib processes developed so as to prevent the diaphragm from decreasing the size of the rib basket beyond a particular minimum. At this minimum the diaphragm could continue its rhythmic contractions with no risk of further decrease in the volume of the thorax. Nothing, however, prevented the intercostal muscles from co-operating at will at times when the animal felt a demand for more oxygen. It is evident from the structure of the Cynodont rib basket (see figure 30) that the overlapping processes had little effect on the general agility of the animal, the only effect being the prevention of an abnormal decrease in the volume of the trunk.

In the higher Cynodont, *Cynognathus* and *Diademodon,* the processes in the region of the thorax decreased in size so that overlapping was no longer effective (see fig. 31). But the posterior thoracic ribs in the region of the diaphragm are held more strongly in position by more complicated processes, more of interlocking than of simple overlapping nature. On the whole the ribs tend to articulate more perpendicularly on the vertebrae, thus making it more difficult for atmospheric pressure to compress the thorax, or for the diaphragm to contract the rib basket; but in addition it was observed (Brink, 1955) that the articulations between the capitula and tubercula and the vertebrae in the posterior region of the thorax of *Diademodon* are such that little antero-posterior movement was possible. If an animal like *Diademodon* had no diaphragm it is difficult to visualise how it breathed at all.

Dentition

Judging from the dentitions of the higher Cynodonts, their metabolism was considerably increased and demanded an improved supply of oxygen. Their general structures and peculiarities are better compared with those of mammals than with odd specializations far removed from the line of evolution of present interest, such as tortoises and turtles where there is no diaphragm and ribs cannot contribute to the breathing process either.

The Gomphodont dentition especially is very suitable for intricate mastication of food. Animals masticate food for the obvious reason of extracting the maximum benefit from it. Such food is more rapidly digested and the animal is required to search for more food more frequently. In general, the animal's metabolism is accelerated. An increase in metabolism requires an increased supply of oxygen. It would appear rather inconsistant that a complicated dentition should develop for the purpose of accelerating the animal's metabolism while no provision is made for proper digestion with an increased supply of oxygen. This cannot be regarded as a point of evidence acutally reflecting on the presence of a diaphragm, because mastication occurs in a great variety of specialized reptiles, but it is important that in this respect the dentition supports rather than contradicts the view that a diaphragm was present.

Secondary palate

Another supporting, rather than contradictory, point of evidence, is the mammal-like secondary palate. The function of the mammalian secondary palate can be interpreted as one or all of the following: (a) To serve as a solid platform for the tongue to operate against in turning masticated food over or passing it from one side of the mouth to the other; (b) To prevent masticated food from passing up into the nasal cavity; (c) To allow the animal to breathe while it is masticating its food. It is in this last function that we find encouraging support.

Ethmoturbinals

Even if the nasal cavity is taken into consideration, supporting rather than contradictory evidence can be obtained. With the development of the secondary palate, the nasal cavity is considarbly elongated, to which no weight can be attached as such, but it appears from internal nasal casts that ethmoturbinals were apparently developed on a mammalian pattern in animals like *Thrinaxodon* and *Diademodon* (Watson 1913 and Brink 1955). The complicated mammalian pattern of ethmoturbinals can be interpreted as having developed to increase the surface of the mucous tissues within the nasal cavity for one or all of the following reasons: (a) To clean dusty air before it is inhaled into the lungs; (b) To moisten the air adequately so as to prevent an unnecessary loss of water through evaporation directly from the blood through the lung epithelium; (c) For better smelling purposes; (d) To warm the air before it is inhaled. Whichever one of these is taken as the predominant function of ethmoturbinals, they all equally reflect an increase in breathing tempo.

Although much stronger evidence is required than that analysed above before it can be concluded that a diaphragm was present without any doubt in the higher Cynodontia, there is no reason why the possible repercussions of this implication should not be investigated.

In the first instance the diaphragm reflects directly on an increase in blood temperature. The diaphragm would be responsible for an increased supply of oxygen, accelerating the animal's metabolism and effecting a rise in blood temperature. Whether a diaphragm assisted or not, the dentitions as such are well suited for intricate mastication, reflecting an increase in metabolism and a consequent rise in blood temperature. It is also worth recalling that one of the functions of complicated ethmoturbinals is the warming of air before it is inhaled. While this does not in itself demand warm blood, the presence of such ethmoturbinals is consistent with this condition, whereas the presence merely of elementary ethmoturbinals would oppose it.

More interesting than the mere rise in blood temperature is the question whether this condition was of the mammalian homoeotherm nature, that is, to what extent body temperature was controlled and kept constant.

Hair

Fossilized skin impressions have been found, but unfortunately not yet one showing the presence of hair in an advanced mammal-like reptile. Should such a specimen be found — and it is not unlikely that even a footprint could indicate the presence of hair — then the question of homœotherm blood temperature could be considered as solved, as well, perhaps, as that of the diaphragm.

Although there is no direct evidence supporting or contradicting the view that hair could have been present in the higher Cynodontia, it is interesting to note here the mention made by Watson (1931) of the probable presence of "vibrissae" in these animals, considering the peculiar pitted nature of the maxillaries anteriorly in the region above the canines and the rich nervous innervation and blood supply of these areas evidenced by the size and number of foramina for branches of the maxillary nerves. Vibrissae are obviously specialized hair to that ordinary hair must have been present even in earlier forms.

The question now arises, was hair developed as an adaptation to a rise in blood temperature, protecting the animal against unnecessary loss of self-generated heat, or did it develop as a barrier against environmental heat changes? Cowles (1946) favours the view that hair developed as a protection against a too rapid absorption of heat from the sun and at the same time guarded the animal against the rapid loss of such absorbed heat on passing into cooler surroundings. He suggests that only after this adaptation was there opportunity for the animal to generate its own heat with little danger of losing it too rapidly. This latter view is certainly worth keeping in mind, especially while there is no certainty regarding the alternative view; but it should be observed that a great variety of reptiles have survived to the present day and still live in areas where extreme temperatures prevail. Furthermore, too rapid absorption of heat from the sun would be a danger only to very small animals, so small that the amount of diffused heat absorbed through the fur cover would not

last long after the animal reached shade again, or after sunset. This heat retention would not last significantly longer than in an ordinary reptile of larger size or, at least, not to such an extent that the value of this retention of heat was actually exploited to promote an increased metabolism involving intricate dentitions and a diaphragm. Actually two different types of heat insulating coverings developed over the skins of two different classes of vertebrates, birds and mammals, and both are homoeotherm, a circumstance favouring the view that hair and feathers developed as an adaptation to loss of self-generated warmth and not as a protection against excess absorption of the sun's heat.

Sweat glands

In mammals, however, hair is not the only feature indicative of homoeotherm blood temperature. In general, sweat glands are intimately associated with hair, both structurally and functionally. While hair serves to insulate the animal against unnecessary loss of temperature, sweat glands serve to regulate temperature more effectively and to prevent it from rising too high. If evidence could be obtained supporting the view that sweat glands were present in certain higher Cynodonts, it would reflect directly on hair and body temperature and indirectly on the diaphragm. But, whereas a skin impression may still indicate the presence of hair, the chance of finding direct evidence for sweat glands in a skin impression is hopeless, and hair is not sufficient evidence for sweat glands.

It is, however, a common characteristic of mammals that they develop specialized glands, such as milk glands from sebaceous skin glands. If it could be demonstrated that an advanced mammal-like reptile possessed specialized skin glands of sweat gland nature, it would almost logically follow that simpler sweat glands had been present previously. Such evidence is available in the peculiar depressions situated dorsally on the maxillaries in the middle of the length of the snout in *Diademodon* and *Cynognathus*. In certain *Diademodon* specimens grooves extend forward to the external nares from these depressions (see figure 32). These grooves cannot be interpreted as impressions of veins or arteries, because they diverge from the depressions. Arteries would branch and spread towards the depression and veins similarly would converge away from it. The only interpretation that can be given to this depression is that it lodged a specialized skin gland, of sweat gland nature, the grooves being the impressions of ducts leading forward to the external nares where a fluid was released, evidently to supplement the function of the ethmoturbinals in moistening the air before it was inhaled (Brink 1955). This is additional support for the view that the breathing tempo was increased, adding evidence in favour of the diaphragm. Furthermore, animals like *Diademodon* and *Cynognathus* apparently had wet nostrils, a characteristic of mammals and quite unlike the true reptiles. The fact is that the higher Cynodontia show evidence of specialized skin glands of sweat gland nature, so that ordinary more simple sweat glands must have been present at an earlier stage. This circumstance reflects in itself upon a constant body temperature, hair and, indirectly, the diaphragm.

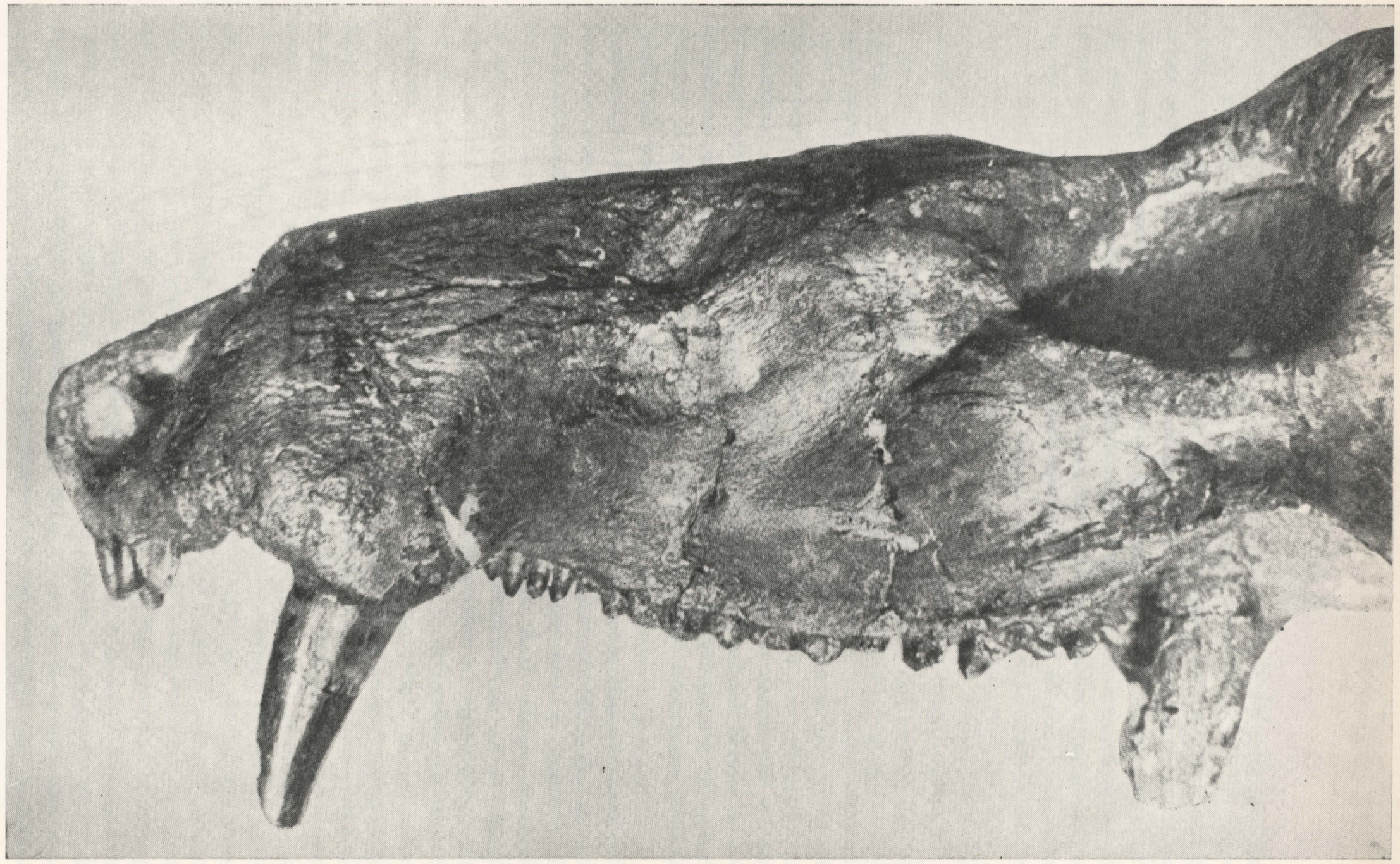


Fig. 32—Diademodon mastacus. Side view of skull No. 314 in the Bernard Price Institute collection, showing the peculiar depression dorsally on the maxillary and the grooves extending from it to the external nares.

The question now arises (if the depressions on the snouts of the advanced Cynodontia are correctly interpreted as evidence supporting specialization of skin glands), to what extent could other sebaceous skin glands have been specialized to a level where nourishing secretions were made available to young? The two forms of specialization can, unfortunately, not be related to one another, but the fact that there is evidence of specialization of skin glands in one region of the body shows that it is not entirely unlikely that a specialization of a related kind may have occurred in another part of the body. This question can never be solved directly with palaeontological evidence, but the dentitions of these animals give some encouraging indirect support to the view that milk glands could actually have been present.

It appears as though a young *Diademodon* was launched in life with a dentition extending not farther than about the fourth postcanine tooth. The whole dentition of the young individual at this stage consisted of simple conodont teeth, differentiated into incisors (four for the upper and three for the lower jaws), one canine, and four post-canine teeth. Apparently only subsequently to "birth" did the series of post-canine teeth start extending backwards with the eruption of a longitudinally ovate cusped tooth behind the fourth conical tooth, later replaced by a transversely ovate, flat-crowned grinding "molar". This process was continued evenly by the eruption of subsequent longitudinally ovate cusped teeth, replaced by transversely ovate flat-crowned grinding "molars", each of the latter being slightly larger than the one in front. By the time the sixth or seventh of these flat-crowned teeth had erupted, the incisors, canines, and first four post-canine teeth had already been replaced by similar, slightly larger teeth — almost certainly only once in the incisors and first four post-canine teeth, but not as certainly in the case of the canines.

The evidence in support of only one replacement in all the teeth up to the eleventh post-canine (perhaps excluding the canine) are the following:

(1) It appears as though replacement of the original dentition present at "birth" occurred only when the animal reached a particular age. Evidence of replacement of these teeth is found mostly in specimens of a particular size, smaller than the fully adult size. There is little evidence of replacement of these teeth in animals smaller or larger. This could be a misinterpretation because of an insufficient number of specimens forming part of the growth series.

(2) The incisors and first four post-canine teeth in the largest adult *Diademodon* are not much bigger than they could have been at "birth". More than one replacement could provide the adult with larger and stronger teeth in this section of the series. The difference in size between the adult canine and its apparent size at "birth" does, however, call for more than one replacement; but direct evidence supporting more than one replacement of the canines has not yet been found in *Diademodon* material.

(3) There is evidence that when any of the first four post-canine teeth are lost in old individuals, especially in the lower jaws, no further replacement is provided. The sockets close as in a mammal.

(4) There is certainly not more than one replacement in the seven following "molars", because they increase evenly in size backward. Additional replacement would tend to cause an irregular series of differently sized teeth. It should be mentioned that there is no certainty that replacement occurred at all in the teeth behind the first four post-canine teeth. A longitudinally ovate cusped predecessor has not yet been found in an actual *Diademodon* specimen. Their presence is deduced from the longitudinally ovate openings above the crowns of unerupted flat-crowned molars in the case of two or three specimens, but these openings could equally well be interpreted as ordinary gubernacular canals.

Whatever the case may have been as far as dental replacement is concerned in *Diademodon,* it is practically certain that the subsequent eighth tooth in the flat-crowned series, or the twelfth post-canine, had no predecessor, or else is not replaced by a subsequent tooth. This tooth is generally somewhat triangular in most species in the upper jaws. It is usually followed by another tooth in the series, longitudinally ovate and cusped, and in very old individuals the series may be extended to four similar teeth behind the triangular twelfth.

The dentition of *Diademodon* can now be divided into three sections. A line drawn across from left to right (see figure 33) passing between the fourth and fifth post-canine teeth of each side, divides the dentition into what appears to be the complement of teeth at "birth" anteriorly (Section A) and those developing subsequently to "birth" posteriorly (sections B and C). Another line passing between the eleventh and twelfth post-canine teeth of each side divides the dentition into those that appear to have been replaced once anteriorly (sections A and B) and posteriorly those that are permanent molars in the mammalian sense (section C). While there is no certainty about the actual replacement of teeth in section B, it is best not to differentiate yet between premolars and molars in the case of *Diademodon.*

Although we are not yet as certain about dental replacement in *Diademodon* as we would like to be, it seems nevertheless quite clear that a newly "born" *Diademodon* could not have had a dentition much more elaborate than that represented by section A in figure 33. This is the dentition with which the small individual "dealt with" its food, while its mother had the elaborate section B at her disposal for mastication. Could it be that they ate the same type of food? The mother could have masticated the material first and then passed it on to her young by mouth, more or less as in birds, but, considering that we are dealing with animals virtually on the threshold to mammals, we might as well regard milk glands as a possibility.

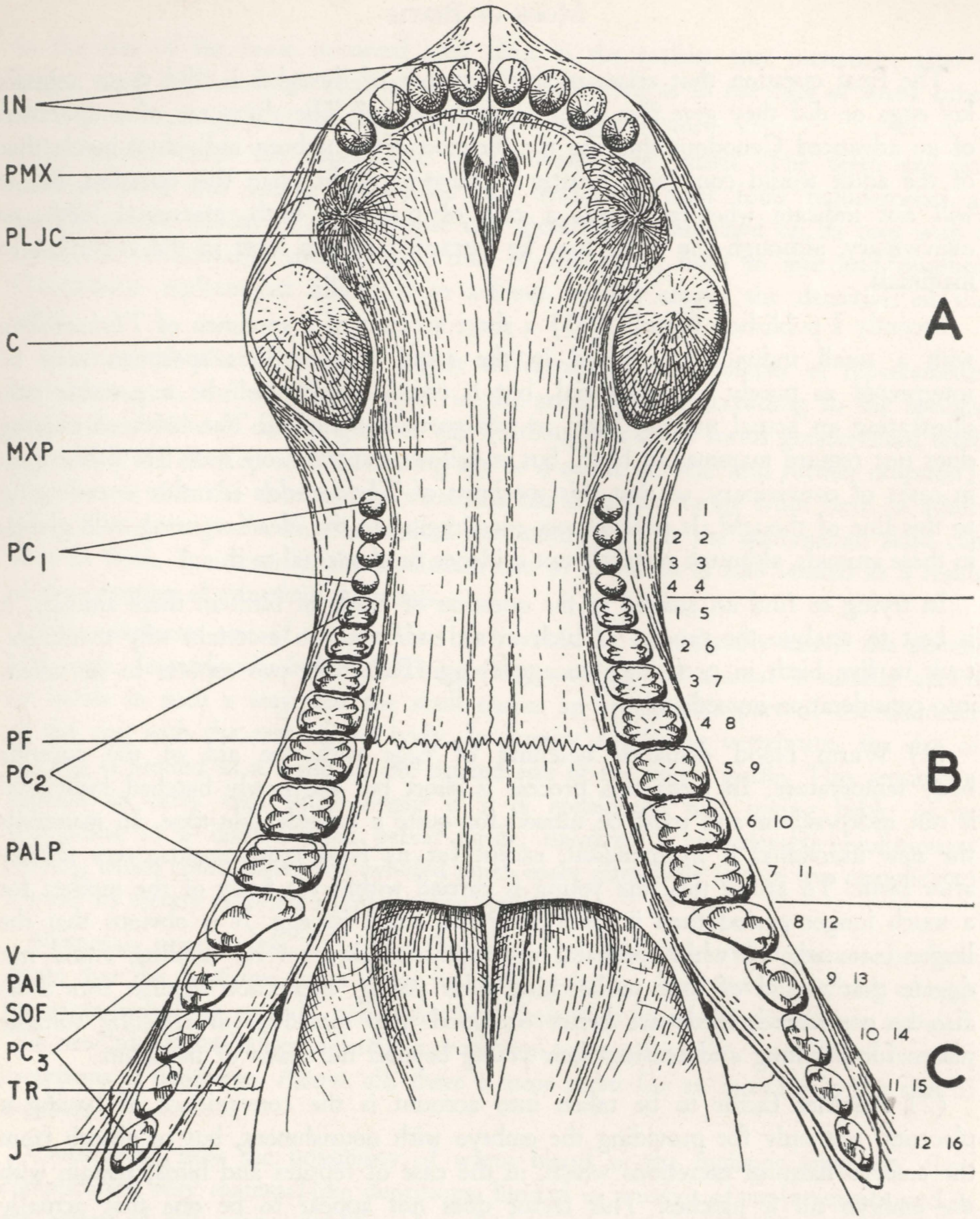


Fig. 33—Diademodon mastacus. **Palatal view based on specimen No. 314, right side reconstructed after left, distortion corrected, and the teeth indicated as not worn, with crown characteristics average and diagrammatic. Natural size.**

Abbreviations: C, canine; In, incisor; J, jugal; MXP, palatal plate of the maxillary; PAL, palatine; PALP, palatal plate of the palatine; PC_1, first four post-canine teeth, referred to as "premolars"; PC_2, subsequent seven grinding "molars" with a probable single predecessor to each; PC_3, five "permanent molars" with no predecessors, the anterior usually somewhat triangular in shape; PF, palatal foramen; PLJC, pit for lower jaw canine; PMX, premaxillary; SOF, sub-orbital foramen; TR, transverse bone.

The final question that arises in this sequence of thoughts is, did these animals lay eggs or did they give live birth to their young? The discovery of a specimen of an advanced Cynodont showing the skeleton of an unborn individual inside that of the adult would contribute greatly to throwing light upon this question, but it will not indicate whether it was a case of placental birth, marsupial birth, or ovovivipary, although the latter may be discarded at this level in the evolution to mammals.

Recently I published (Brink 1955) a short account of a specimen of *Thrinaxodon* with a small individual included in the same nodule. This specimen may be interpreted as purely circumstantial, but it could equally well be a genuine case illustrating an actual nursing habit in this particular animal. The habit of nursing does not require mammalian birth, but it follows naturally on such live birth, even in cases of ovovivipary, so that this specimen of *Thrinaxodon* is rather encouraging to this line of thought. It is also most encouraging to the idea favouring milk glands in these animals, although certainly not evidence fundamental to it.

In trying to find an answer to the question of mode of birth in these animals, it is best to analyse the process as such in an endeavour to ascertain why mammals took to live birth in preference to egg-laying. There are two aspects to be taken into consideration immediately:

(1) Warm blood demands hatching of eggs with the aid of the parent's body temperature. In birds this process is short but the newly hatched individual is not independant and must be nursed for quite a considerable time. In mammals the new individual is independant, except for its food requirements, very shortly after birth. To attain this, the young is carried within the body of the mother for a much longer period than it takes a bird to hatch its egg. It is obvious that the larger mammals, in which prenatal development takes several months, could not devote that period of time to hatching their young. Protection against foes must also be considered. Birds are better equipped than mammals in selecting suitable places for hatching and rearing their young beyond the reach of predators.

(2) Another factor to be taken into account is the convenience of having a placenta, not only for providing the embryo with nourishment, but to absorb from the embryo harmful excretions which, in the case of reptiles and birds, remain with the embryo till it hatches. This factor does not appear to be one that actually instigated the habit of giving birth in preference to egg-laying; it is merely a convenient result of placental birth.

The actual answer to this question of mode of birth lies in the fact that mammals have a large skull relative to the size of their body, especially at birth, and the factor that influences the size of the skull at birth in mammals is the complicated dentition, not the size of the brain. According to the geological record, a substantial increase

in the size of the brain occurred later than in the earliest true mammels, after a larger sized skull at birth facilitated it. The dentition, as in the case of many other developments, is again at the root of this interesting problem.

In reptiles teeth are expendable to a considerable extent. The teeth are not differentiated and young individuals can deal with their food requirements as readily as the adults. A small reptile can therefore be launched on its own with a dentition considerably smaller than that of the adult, both in size and number. Continuous replacement allows it to achieve in due course the dentition of the adult.

In mammals the dentition is highly differentiated, the number of replacements limited to one, the number of teeth in the series limited according to the species, and individual teeth do not grow in size (although in some forms greater sized teeth apparently do develop with advancing age as a result of wear and further eruption). The fact is that the dentition in mammals has a limited range from birth to adult. This limited range decides the limited minimum size that the mammalian skull can have at birth. Incidentally, the maximum size in the adult is also limited as a result of the arresting af growth in mammals.

This minimum size of the skull at birth would be considerably less if the animal laid eggs. Immediately before hatching from an egg, the animal is usually curled up inside in such a way that the skull shares an appreciable part of the diameter of the egg with the rest of the body. In amniot egg-laying vertebrates the size of the egg is limited as a result of the limited size of the pelvic girdle. This argument appears to carry very little weight if it is considered that giving birth, as an adaptation to a limited sized pelvic girdle, involved a considerable evolutionary process, which could have been avoided much more effectively and in less complicated manner by merely evolving a larger pelvic girdle.

Mammals nevertheless did adapt themselves to live birth and there can be little doubt that the dentition was a major influencing factor. As a result, hatching of eggs for excessively long periods, necessitated by their high blood temperature, is avoided. The new adaptation is best suited for protection against foes. The problem of harmful excretions is overcome. Above all, there is now room for an increase in the size of the brain.

Considering now the possibility of warm blood in the higher Cynodonts, their complicated, very mammal-like dentitions, limited in number of replacements and in the extent of the series, and the relatively large size of their skulls compared with their bodies (see figures 30 and 31), one cannot avoid strongly favouring the mammalian type of birth in these animals.

Origin of Mammals

This question of mode of birth now leads to a further consideration, that is, the differentiation between Monotremes, Marsupials and Placentals. It appears that

the Monotremes represent a line of evolution in which no attempt was made at giving birth. Instead, at the expense of their dentitions, their skulls remained relatively small compared with the size of their bodies. They are small animals with not too lengthy hatching periods.

The Marsupials overcame the difficulty of giving birth to young with a limited sized skull, by producing embryos and allowing them to develop further in marsupiums to the required size.

The placentals managed to adapt themselves fully to the main disadvantage of giving birth, i.e. labour, which proved to be more successful, considering their wider adaptive radiation.

Unfortunately nothing of what has been said above contributes in throwing light upon the origin of these three branches of mammals. If the later Cynodonts actually did give birth to their young they are certainly unlikely ancestors to the Monotremes. The earlier Cynodonts are too early to be taken into consideration. The later Cynodonts do not appear to have given rise to mammals.

In the actual line of evolution to mammals via the Ictidosauria, birth could have occurred before the established dentary-squamosal articulation, but for this there is not even indirect palaeontological evidence. If it were the case, there should already be a differentiation between the Monotremes and the balance of the mammals earlier than the Ictidosauria. The differentiation between Marsupials and Placentals could have occurred later.

Summary

Although the evidence in support of the views advanced in this paper is not substantial enough to justify any definite conclusions, the field presents invaluable material for most enlightening speculation of the utmost importance on questions hitherto rarely exploited. The strongest evidence is that afforded by the differentiation into thoracic and abdominal regions in the rib baskets of higher Cynodonts and their peculiar lumbar arrangement, indicating the probable presence of a diaphragm. Subsequent exploitation is effected on the assumption that the diaphragm was actually present, merely to investigate all the related significant repercussions. It is assumed that the diaphragm would be responsible for an increased rate of breathing for which support is found in the secondary palate and mammal-like ethmoturbinals, as well as some apparently significant qualities of the nostrils and a further tentative conclusion is reached that the temperature of the blood in these animals must have been high as a result of increased metabolism. This tentative conclusion is in turn substantially supported by the masticatory nature of the dentitions and indirectly also by the nostrils and ethmoturbinals. In the absence of contradictory evidence, thoughts on high blood temperature are extended to the question of constant blood temperature. Some evidence in support of hair and sweat glands is again afforded by the apparent nature of the skin around the external nares, judging by the rich nervous innervation

and blood supply of this region and, as such, these glands and hair appear to have been rather specialized, especially a conspicuous pair lodged in depressions dorsally in the middle of the length of the snout in all higher Cynodonts. With the line of thought extending to specialized glands, milk glands are considered, with fairly substantial support derived from the nature of the dentition of *Diademodon* and with nursing of young in mind, thoughts are given to the question of mode of birth as opposed to egg-laying which, however vague, leads directly to the roots of the question of the origin of mammals.

The general line of thought exposed in this paper can be substantially supported by further palaeontological discoveries such as skin impressions, footprints, more occurrences of female specimens in close association with newly born young and prenatal specimens appropriately in situ within skeletons of adult females.

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