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THE IMPORTANCE OF KAROO FOSSILS IN THE SEARCH FOR MAMMAL ORIGINS.

by

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ABSTRACT

It has long been known that mammals belong to the group Synapsida (more familiar to most in South Africa by the now discredited term Mammal-like Reptiles), a group with a long fossil history, much of which was first established from the Karoo. In palaeontology mammals are traditionally defined by the possession of a squamosal/dentary jaw joint, as opposed to the quadrate/articular jaw joint of non-mammalian tetrapods. This paper recounts some of the advances in our knowledge of the therapsids (advanced synapsids) over the past 50 years, including the discovery of a sequence of forms leading to those which possess both premammalian and mammalian jaw hinges, transitional forms which thus by definition qualify as mammals. Brief mention is made of some historical aspects of phylogenetic interpretation, pointing out that some early workers following Darwin, were as aware of the central role of species in phylogenetics as are the disciples of Hennig and Eldredge and Gould. Brief reference is made to the crown group definition of mammals proposed by Rowe (1988), as it contrasts with the traditional character-based definition. Finally, it is encouraging that modern workers are not only as aware of the problems of distinguishing homology and homoplasy as were earlier workers, but are starting to acknowledge the importance of missing information. In this way, just as the double jaw joint was first predicted and then found, we can actively seek to fill some of the many remaining gaps in our knowledge.

KEYWORDS: Synapsids, Mammal Origins.

> "The animals which are dealt with in this story are not in fact members of a single line of descent leading up to mammals. Nonetheless, our now very extensive knowledge of these reptiles makes it evident that the phenomenon of parallel evolution is so widely displayed among them that so long as we pick the members of our series from not too remote groups, and of the right time, we shall not be seriously in error."
>
> D. M. S. Watson 1953.

THERAPSIDS

It has been known since the late 19th century that some of the fossils of the Karoo are extraordinarily mammal-like, primarily through the efforts of Broom, but also Olson, Owen, Seeley and Watson. Broom was able to show that the therapsids became increasingly mammal-like with time, and were unquestionably ancestral to mammals.

There was disagreement as to which of the theriodont groups was the most probable source of the mammals. Broom (1932, 1938) always favoured derivation from bauriamorph therocephalians. Others favoured cynodonts, and this unsettled situation was still evident in the 1950s. Romer (1956) stated guardedly "...the phyletic relationship of cynodonts to mammals is debatable."

Also in 1956, A. S. Brink, a student of Watson's and the first scientific officer of the Bernard Price Institute, published a much cited paper, entitled "Speculations on some advanced mammalian characteristics in the higher mammal-like reptiles." Brink accepted Crompton's (1955) opinion that mammals were derived from therocephalians, but went on to consider only cynodonts, this approach being validated by the extraordinary number of advanced characters shared by therocephalians and cynodonts.

It is instructive at this time to examine some of Brink's (1956) speculations and to see how they have been scientifically tested in the intervening years.

Brink's speculations.

1. In his paper Brink was preoccupied with the possibility that cynodont therapsids may have possessed a diaphragm. Jenkins (1971) in a major study of the cynodont skeleton concluded that there is no evidence for the presence of a diaphragm, and that is the position as it remains today.

2. Brink suggested that the improved dentition of cynodonts (the postcanine teeth have several additional cusps which would have enabled them to break up food into smaller pieces before swallowing) indicated improved mastication and hence more rapid digestion. No-one would dispute that, and a considerable literature on tooth morphology and replacement has built up since that time.

3. The secondary palate was also involved with improved mastication. By separating nasal and oral passages the animal could chew and breathe at the same time, a necessary "preadaptation" for the

suckling behaviour of mammals. It is also involved in the next point.

4. It raises the possibility that mammal-like scroll bones (turbinals) could have been present in the nasal passages of therapsids. Watson as early as 1913 had suggested that attachment ridges for these delicate structures (themselves never preserved) were present in therapsids. This question has recently been investigated by Hillenius (1992, 1994). By careful experimental work with living animals, he has shown that of the three types of turbinals (nasal, ethmoidal and maxillary) it is only the maxilloturbinals of mammals that are exclusively respiratory – they reduce desiccation associated with rapid, continuous breathing, which is a characteristic of endothermic animals. The other turbinal bones are related to the more primitive olfactory function. Hillenius (1992, 1994) thus claims that attachment ridges for maxilloturbinals would be the first reliable indication of endothermy in this lineage that can be used in the fossil record. Like several other advanced mammalian characters, ridges for attachment of maxilloturbinals are present in therocephalians and cynodonts.

   Starting in the Late Permian, "full endothermy" may, according to Hillenius, have taken 50Ma to develop: whether this was a gradual or punctuated progression we would still like to know. Hillenius' use of the term endothermy is significant: an endotherm is an animal which, because it generates metabolic heat, is "warm blooded". Thus sharks, tuna and sea turtles for example are all endothermic. Most birds and mammals are homeotherms, that is endotherms capable of maintaining constant body temperature. Crompton, Taylor and Jagger (1978) presented an elegant argument as to why homeothermy should be linked to the appearance of the first mammals – in effect it opened up the niche of nocturnal insectivore for the first time.

5. Not mentioned by Brink, but not unrelated to the diaphragm question, is the matter of gait. Primitive amniotes deploy their limbs out sideways – they are termed sprawlers. Most extant mammals bring the limbs in under the body to give themselves an erect stance and parasaggital gait. Lizards can run just as fast as mammals of the same size, with no difference in the energy cost of running, but, in the process, lizards incur an oxygen debt so cannot *sustain* these speeds. This difference was investigated by Carrier (1987), whose work can be summarised as follows. Ectothermic tetrapods have a sprawling gait and short-burst anaerobic exercise metabolism. Endothermic tetrapods have erect posture and parasaggital gait and sustained aerobic metabolism. Sprawlers flex the body laterally during rapid locomotion, thus compressing the lungs alternately and effectively preventing breathing. (Carrier has done the experiments necessary to demonstrate this with live lizards and dogs.) In upright tetrapods body flexure is in the vertical plane and rapid movement actually enhances ventilation of the lungs.

   Of living animals a muscular diaphragm is present only in mammals, birds, crocodiles and turtles (these latter of course being a special case). In this context it is noteworthy that early (terrestrial) crocodiles had a fully erect posture and were thus in all likelihood endothermic (bone histological studies are needed to confirm this).

THE SEARCH FOR THE DOUBLE JAW HINGE

One of the great triumphs of 19th century anatomists was the establishment, from embryological studies, of the homology between the non-mammalian articular and quadrate and the mammalian malleus and incus; this became known as Reichert's Theory. The therapsids exhibit a steady increase in the size of the dentary and reduction of the post-dentary bones. As Parrington (1949) pointed out, Reichert's theory implied that at some stage the original tetrapod quadrate/articular and the mammalian squamosal/dentary jaw articulations must have existed together, as it is hardly conceivable that there could be a stage with no bony jaw hinge. Thereafter the hunt was on to find a fossil that would bear out this prediction.

Some pertinent fossils had already been found. The very mammal-like South African cynodont *Diarthrognathus* was first mentioned by Broom (1925); the British putative mammal *Morganucodon* was first described (as *Eozostrodon*) by Parrington (1941), but it was some time before the skull was pieced together.

Kermack and Mussett (1958) demonstrated the presence of both articulations in *Morganucodon*, and in the same year Crompton claimed the same for *Diarthrognathus*, but later (1972) retracted, stating that although *Diarthrognathus* had a dentary "condyle", there was no squamosal glenoid. However, one may visualise this part of the dentary being restrained and guided by aponeuroses and fasciae, and it was eventually possible to show (Gow 1981) that Crompton had misidentified the quadrate and articular.

Romer (1956) described two very exciting advanced cynodonts from South America, *Probelesodon* and *Probainognathus* (Romer 1969 a, b). In the former there seemed to be a facet on the squamosal with which the surangular of the lower jaw made contact, while in the latter a more convincing squamosal facet could have articulated with both the surangular and the dentary. Here are two animals achieving a similar result to *Diarthrognathus* but doing it rather differently – yet another instance of parallelism in cynodonts. What all three seem to be doing, is bracing the articular region of the lower jaw from the *side*, presumably against muscle forces tending to splay the jaw rami. The quadrate/articular joint was still functional in *Probelesodon* and *Probainognathus*, as indeed it still was in *Morganucodon*. It is easy to conceive of a

Probainognathus-like condition leading to a form with a more transverse squamosal glenoid to accommodate a true dentary condyle which would, in time, free the quadrate and articular from their traditional role.

THE FATE OF THE POST-DENTARY BONES

The quadrate=incus, articular=malleus homologies have been secure since the 19th century. The position of the eardrum (tympanum) is very different in reptiles and mammals, and for a long time the position of the tympanum in non-mammalian synapsids was unsure. This problem was resolved by Allin (1975). Non-synapsid reptiles have the tympanum behind the quadrate, whereas Allin showed that in synapsids the tympanum lay in front of the quadrate, supported by the reflected lamina of the articular bone, which is thus the homologue of the mammalian tympanic bone.

THE SEARCH FOR THE FIRST TRUE MAMMALS

Several groups of mammals are known from the Late Triassic/ Early Jurassic, but I will consider here only morganucodonts as they are the only adequately known group. Others are too poorly known (for a review see Lucas and Luo 1993), though their presence suggests that mammals must have appeared even earlier.

Walter G. Kuhne moved to England from Germany just before the outbreak of World War II, knowing from previous fossil finds that there was a good possibility of finding early mammal fossils in fissure fills in the Triassic palaeokarst of Wales. He found the tritylodontid *Oligokyphus* in 1939, and penned its description during internment on the Isle of Man. Also in 1939, Kuhne found two tiny mammalian molar teeth which he sold to Cambridge University and which Parrington (1941) described as *Eozostrodon* (*E. parvus* and *E. problematicus*). Kuhne discovered in 1947 what he was to call *Morganucodon*. He published his description in 1949 on the basis of a single molar tooth, explicitly recognising that *Eozostrodon* could be part of the same dentition. *Morganucodon* was clearly a mammal and at the time the earliest known, with an age of 190-200 Ma.

By this time it was known that another tritylodont, *Bienotherium* (Young 1947), occurred in the Lufeng Beds in China, and in 1948 a Catholic priest, Father Oehler, found the skull of a mammal in these beds. This specimen was to be described by Father Rigney who had instigated the search, but he only received it in 1956, after a series of misfortunes which included being imprisoned by the Chinese for four years. Rigney (1963) finally described the specimen as *Morganucodon oehleri*. Subsequently the work on *Morganucodon* became the preserve of K.A. Kermack at University College, London. He and co-workers have published superb, detailed accounts of the skull and jaws of *Morganucodon* based mainly on fissure fill material of Early Jurassic age (Kermack, Mussett & Rigney 1973, 1981).

Both *Tritylodon* (Owen 1884) and of course *Diarthrognathus* were already known from the Stormberg (Elliot and Clarens Formations) of southern Africa, and it was not long before Crompton initiated a field programme with one of its primary objectives the search for Triassic mammals. The first (*Erythrotherium*, Crompton 1964) was found by pure chance in the laboratory in the matrix surrounding a small fabrosaurid dinosaur skeleton. Not long afterward, *Megazostrodon* (Crompton and Jenkins 1968) was found. Incredibly, both these tiny specimens turned out to be almost complete articulated skeletons. Kitching subsequently found a second skull of *Megazostrodon* that was described by Gow (1986).

At present the oldest known mammal is *Adelobasileus* (Lucas & Hunt 1990) from the Dockum beds of Texas, dated at 225Ma. This little skull is remarkable as it shows unmistakable signs of having passed through the gut of a predator (Lucas & Hunt 1990).

This brief historical overview has been necessarily selective: enormous strides have also been made in our knowledge of early mammal dentitions, muscle systems, jaw mechanics and braincase structure, to list just a few aspects. These things have been made possible through increasing technical sophistication in the study of living as well as fossil animals.

PHYLETIC EVOLUTION

As evolutionary biologists we are interested in the relationships of the animals we study. The basic premise is that the more similar two animals are the more likely they are to be closely related. But of course this is not necessarily true, and also their characters may be similar for different reasons, not all phylogenetically useful. The closer two evolving groups are to each other, the more likely they are to evolve similar (homoplasic) characters in parallel. Despite considerable progress in the theory of phylogenetic interpretation during the past thirty years these problems have not gone away, nor are they likely to. There has been speculation particularly about the origin of major new groups: was it poly- or monophyletic? That is, were there several crossings of the grade boundary, or just one? Some of the early workers were quite clearly concerned about this question. Haeckel (1897) said, "We are compelled if we in any way acknowledge the Theory of Evolution, to assume the monophyletic hypothesis, that all Mammals, including Man, must be traced from a single mammalian parent form". Broom stated (1932, p.69.): "one small form in the upper Triassic gave rise to a mammal." And Simpson (1959) explained, "Evolutionary or so-called phylogenetic classification does not express phylogeny but is based on phylogenetic interpretation of the observational data. It is always necessary in a formal classification (so unlike an actual phylogeny) to compromise sooner or later between horizontal and vertical separation of taxa. *That each taxon sometime included only one species in its ancestry should be true*, but it is a completely impractical requirement that each taxon be so delimited and defined as to include and

begin with that species." So much for any lack of understanding on Simpson's part. He then goes on to say " In practice it is a sufficient principle for evolutionary taxonomy that each taxon arose wholly from one of lower categorical level, as Class Mammalia from Order Therapsida." It is for this view that Simpson is remembered and it has resulted in much confusion.

These old insights were explicitly rearticulated by Hennig in 1966, followed in 1972 by the *Punctuated Equilibrium* theory of Eldredge and Gould, which was a logical extension of Hennig's ideas. The following quotes state the case: As Hennig (1966) remarked, "A monophyletic group is a group of species descended from a single species, and which includes all species descended from this species." And Eldredge (1979) accordingly infers, "It is species that do the evolving. A genus or family cannot give rise to another genus or family."

In view of the above, it is interesting to see what palaeontologists have had to say about the origin of mammals. The first recent explicit proposal for the "monophyletic" derivation of Mammalia from Cynodontia is that of Hopson and Crompton (1969). They quote Simpson (1961 p.124), who defined monophyly as "the derivation of a taxon through one or more lineages from one immediately ancestral taxon of the same or lower rank." They rightly consider this polyphyletic and state, "Our criterion for the monophyletic origin of... the Class Mammalia would be derivation from an ancestral taxon (through one or possibly more lineages) of much lower rank, on the level of Family or perhaps even lower." Clearly the difference is one of degree only, and this is also polyphyly.

Hopson (1967, p.33): "I suggest that the ancestors of all the early mammals were very advanced Late Triassic cynodonts...", preceded (p.32) by this profound insight: " we must hypothesise the existence in the later part of the Triassic of a line of persistently small and dentally conservative cynodonts which were acquiring in parallel many of the mammalian features seen in their larger more specialised relatives."

I stated much the same thing in concluding my study of the braincases of cynodonts (Gow 1991): "What seems most probable is that Tritylodontoidea are the sister clade of another middle Triassic to lower Jurassic cynodont clade, which includes Mammalia, but several key members of which are not represented in the fossil record."

Hennig's influence led to the cladistic method of phylogenetic analysis, a method tailor-made for the computer age. The result is that relationships are nowadays presented as computer-generated cladograms.

Hopson (1994) continues to define Mammalia by the possession of a dentary-squamosal jaw articulation, in the traditional manner. Rowe (1988), following Hennig, defines Mammalia as the monophyletic group comprising Monotremata plus Theria, their most recent common ancestor, and all its descendants. This is the cladistic view, i.e. that one can only define taxa by genealogy, not defining characters. This is a theoretically excellent definition, but one can appreciate that the practicality issue remains a real concern.

Hopson (1994 p. 212) concludes a recent exhaustive cladistic analysis of the synapsids as follows "With our greatly improved knowledge of the phylogeny of non-mammalian synapsids, it has become clear that mammals arose from Triassic cynodonts, *in my view from animals similar to* Probainognathus *but with cheek teeth more like those of* Thrinaxodon" (my emphasis). Compare that with Crompton's (1972) view of the relationships of ictidosaurs "... These forms appear to have arisen from a primitive cynodont, perhaps even more primitive than *Thrinaxodon*." These intuitive views appear to suggest a conviction that key players have so far not been found in the fossil record and that the best cladograms currently available provide sister groupings which speak of relationships too distant to be intellectually satisfying.

These are encouraging signs and hopefully cladistics will in future be seen as part of the solution to phylogenetic studies in palaeontology, and not an end in itself as has tended to be the case.

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