Parental care or opportunism in South African Triassic cynodonts?

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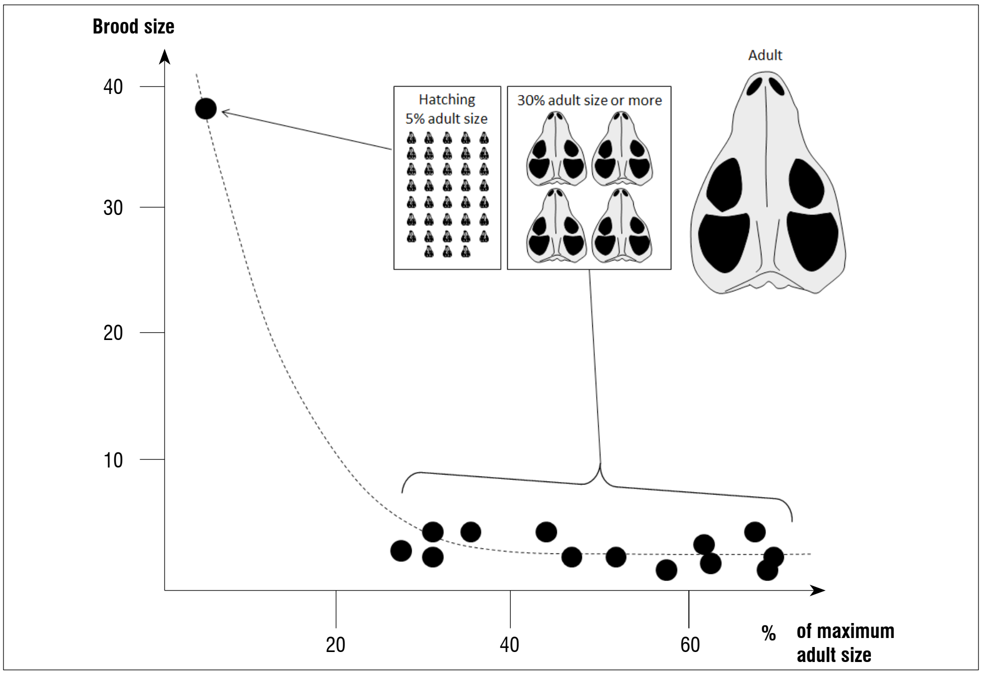
In a paper published in *Nature* in 2018, Hoffman and Rowe[1] describe the discovery of an adult tritylodontid cynodont, *Kayentatherium,* from the Jurassic of the Kayenta Formation (Arizona, USA), accompanied by at least 38 perinatal juveniles, all at the same very early stage of development. Such a high number of juveniles in one clutch is found only in a handful of oviparous reptiles, and never in viviparous or ovoviviparous species[1], suggesting that these cynodonts laid eggs. As tritylodontids are amongst the closest relatives to Mammaliaformes, and sometimes even reconstructed as their sister clade[2], this textbook changing discovery implies that all non-mammaliaform synapsids had an essentially reptilian-like reproductive biology[1].

Hoffman and Rowe's[1] discovery forces a reappraisal of the interpretation of the rich fossil record of parental care in South African non-mammaliaform cynodonts[3].

First, the implications of Hoffman and Rowe's[1] discovery for the evolution of parental care and lactation need to be discussed. With at least 38 hatchlings to feed, it can be safely assumed that lactation was not the main source of nutrients in *Kayentatherium* neonates (nor, by extension, in all more basal non-mammaliaform synapsids). Instead, perinatal juveniles of *Kayentatherium* already had functional teeth despite their early age, which (1) impedes lactation[4] and (2) strongly suggests that they were self-sufficient at birth and capable of foraging nearby vegetation[5]. Extensive parental care was thus most likely not essential to newborn survival in *Kayentatherium*. In contrast, early Mammaliaformes are characterised by (1) a diphyodont dentition, which indicates lactation[4], and (2) a remarkably smaller body mass compared to their non-mammaliaform cynodont ancestors, which imposes a physical limitation to the size of the eggs and, incidentally, the yolk they contain, thus enforcing parental care and lactation[6].



Sources: Data from Hoffman and Rowe[1] and Jasinoski and Abdala[3]

Figure 1: The drop in non-mammaliaform cynodont demographics.

The presence of an adult *Kayentatherium* next to perinatal juveniles indeed suggests that the eggs were incubated. This observation makes this specimen a landmark for any discussion about the origin of endothermy in mammalian ancestry, but more importantly for this discussion, it also suggests that a mammary gland could have produced a milk-like secretion as in modern monotremes that use their mammary glands to moisturise their leathery eggs to prevent desiccation.[7] Therefore, despite the fact that *Kayentatherium* likely did not suckle its young, the possibility that this taxon possessed an ancestral mammary gland that secreted a moisturising milk-like fluid cannot be excluded, thus not completely invalidating hypotheses that similar structures were already present in tritylodontids[8].

The high number of juveniles accompanying the *Kayentatherium* described by Hoffman and Rowe[1] sharply contrasts with the rest of the fossil record of non-mammaliaform cynodont adult–juvenile associations, primarily documented in the South African Karoo genera *Galesaurus* and *Thrinaxodon*[3]. Before Hoffman and Rowe's[1] discovery, the maximum number of juvenile non-mammaliaform cynodonts that were found associated with an adult was four[3]. Similarly, an adult–juvenile association is documented for *Heleosaurus*, a more basal pelycosaur synapsid, for which four juveniles were found together alongside an adult.[9] The *Kayentatherium* juveniles are substantially smaller, and most likely less mature, than any other juvenile non-mammaliaform cynodonts previously recovered in a parent and offspring association. The *Kayentatherium* juvenile skull size is about 5% of the maximum adult size for the taxon[1], whereas the skull size of the otherwise youngest non-mammaliaform cynodont recorded alongside an adult is 31% of the maximum adult size[3]. A burrow cast found with three juvenile *Langbergia* (but no adult) contains an individual with a skull 27% of the maximum adult size for this taxon.[3] Juvenile *Heleosaurus* are 39–54% the size of the associated adult.[9] All of these specimens are in a very advanced growth stage compared to the *Kayentatherium* perinates described by Hoffman and Rowe[1]. If these demographics are representative of the general condition in non-mammaliaform cynodonts, it means that from the time interval during which juveniles were growing from 5% to about 30% adult size, some 90% of the litter was lost. This high level of early juvenile mortality would further support the absence of lactation and parental care in non-mammaliaform cynodonts. In this case, far from evidencing parental care, the South African fossil record would actually support that non-mammaliaform cynodonts were not extensively taking care of their young beyond incubation.

A revised interpretation

Given that Mammaliaformes is a clade deeply nested within Cynodontia, so far the null hypothesis has historically been to consider the association of juveniles and adults in non-mammaliaform cynodonts as evidence for parental care. However, amongst the 12 specimens that show aggregation of many individuals (one in *Kayentatherium*, one in *Langbergia*, eight in *Thrinaxodon* and two in *Galesaurus*), only 4 actually include an adult associated with juveniles, whereas 3 show interspecific associations.[3,10] Thus, there is nearly as much evidence for parental care in non-mammaliaform cynodonts as there is evidence for interspecific shelter-sharing in the Triassic, advocating a case for the frequent co-occurrence of adults and juveniles actually being the result of opportunistic shelter-sharing (as some mammals do today[11]) as opposed to parental care. For the smallest individuals of any age or species, aggregation might have been advantageous as it provides protection against predators and extreme temperature changes in the dry and highly seasonal conditions of the Triassic.[3,10,12,13] The smallest individuals would be tolerated by the largest ones as they emit more body heat as a result of their high surface to volume ratio, thereby aiding in heat conservation during periods of hibernation or aestivation. Following this hypothesis, these fossils could instead suggest simple mutualistic behaviour rather than elaborate parental care.

Considering the facts presented above, a new interpretation of the aggregation of non-mammaliaform cynodonts is proposed here. Instead of parental care, these associations could instead actually offer evidence that opportunistic inter- and intraspecific shelter-sharing was tolerated as it provided a selective advantage to all participating parties.

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