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The oldest juvenile dinosaurs from Africa

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Abstract

Recently discovered juvenile dinosaur remains from the Lower Elliot Formation (Upper Triassic) of South Africa can be assigned to *Euskelosaurus browni* (Huxley), an early prosauropod dinosaur. The oldest known juvenile prosauropods, before this discovery, were those from the Upper Triassic of Patagonia in Argentina. Although a satisfactory age correlation between the Lower Elliot Formation of the Karoo Supergroup of South Africa and the El Tranquilo Formation of Argentina has not been done yet, the South African juvenile dinosaurs remain the oldest reported from Africa. This latest discovery contributes to the understanding of the development and reproductive behaviour of early dinosaurs.

Keywords: Juvenile prosauropod dinosaurs; South Africa; Upper Triassic; Karoo; Reproductive behaviour

1. Introduction

The archosaurs or ''ruling reptiles'' were the dominant terrestrial vertebrates during the Mesozoic. This diverse lineage had its origin with the thecodonts, the peg-toothed diapsid reptiles, which competed successfully with the synapsids or mammal-like reptiles, for dominance on land during the Triassic. Barring a very few exceptions, the majority of the thecodonts were carnivores and they soon took over the role of leading predators from the synapsids. From this lineage a wide variety of carnivorous and herbivorous animals originated – the crocodiles, the ornithischian (bird-hipped) dinosaurs, and the saurischian (lizard-hipped) dinosaurs from which the birds arose.

It is a matter of contention where and when the first dinosaurs arose, since both South Africa and South America have fossil material of thecodonts and basal dinosaurs. One can conclude that these dinosaur species were not the first to evolve because they seem to have been well established morphologically and ecologically already at the time of their existence. Unfortunately the number of basal dinosaur sites and species is limited, making it difficult to trace the origin, subsequent radiation and distribution of the early dinosaurs. Even less is known of their behaviour or initial ecological relationships. In the light of the above, every scrap of information that will aid us in understanding this group, which eventually dominated the continents for more than 130 million years, and which still live among us in the form of birds, is welcome.

Central to this study are the early lizard-hipped herbivorous dinosaurs – the prosauropods. The prosauropods, depending on the species, grew up to between 2.5 and 10 m long (Galton, 1990). They were herbivorous and had a long neck, presumably to reach the foliage of trees, and had simple serrated leaf-shaped teeth for shredding leaves, bark and cones. Their hands and feet retained the primitive thecodont design with elongated phalanges, tipped with claws, whereas their descendants, the sauropods had shorter phalanges, some of which developed hoof-like nails whereas the inner phalanges retained claws. The prosauropods moved about quadropedally like the later sauropods, but could also rear up on their hind legs, presumably when feeding.

Between 1995 and 1997, several new sites yielding fossils of the prosauropod dinosaur, *Euskelosaurus*, were discovered in Upper Triassic strata in the Northern Province of South Africa. Although *Euskelosaurus* fossils are not as abundant as its younger relative *Massospondylus*, sufficient fossils have been discovered elsewhere in South Africa to give us a good indication of its anatomy. The reproductive behaviour and allometric growth of these primitive dinosaurs were unknown before the discovery of juvenile *Euskelosaurus* remains

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alongside those of the adults at four of the sites discovered in the Northern Province.

Two previous discoveries of juvenile archosaur material are of great significance in the study of the latest discovery of juvenile dinosaurs, i.e., the eggs and juvenile *Mussaurus* fossils from Patagonia in South America and the embryo-containing eggs from Rooidraai in South Africa. The Patagonian fossils are of importance for this study because of their morphological and stratigraphic correlation with the South African fossils, while the Rooidraai fossils are important in our understanding of the reproductive behaviour and growth rates of archosaurs.

2. Fossil discovery, site locations and stratigraphic setting

During a palaeontological survey of the Northern Province of South Africa, numerous remains of the early prosauropod dinosaur *Euskelosaurus browni* were discovered at four localities (Fig. 1). The material collected correlates well with that described by Van Heerden (1979). Three of these localities are situated in the Kruger National Park. This region of the Park is normally inaccessible to both the public and vehicles due to its conservation status as an ecologically pristine wilderness area managed by the National Parks Board of South Africa. Limited access is granted twice weekly to this area, noted for its Mopane veld and elephants, to a small group of hikers under the guidance of a game ranger. A hiker, Mr Bearnard ORiain, discovered a dinosaur bone fragment in 1995. Subsequently thousands of disarticulated fossil bones and fragments were discovered at several localities in the region by game ranger Adriaan Louw (Durand, 1996).

Fossils of juvenile dinosaurs were discovered during a systematic palaeontological survey of the sites by a team consisting of members of the Council for Geoscience of South Africa and the South African Society for Amateur Palaeontologists, in 1996. Juvenile remains were found by this team at three separate localities within the

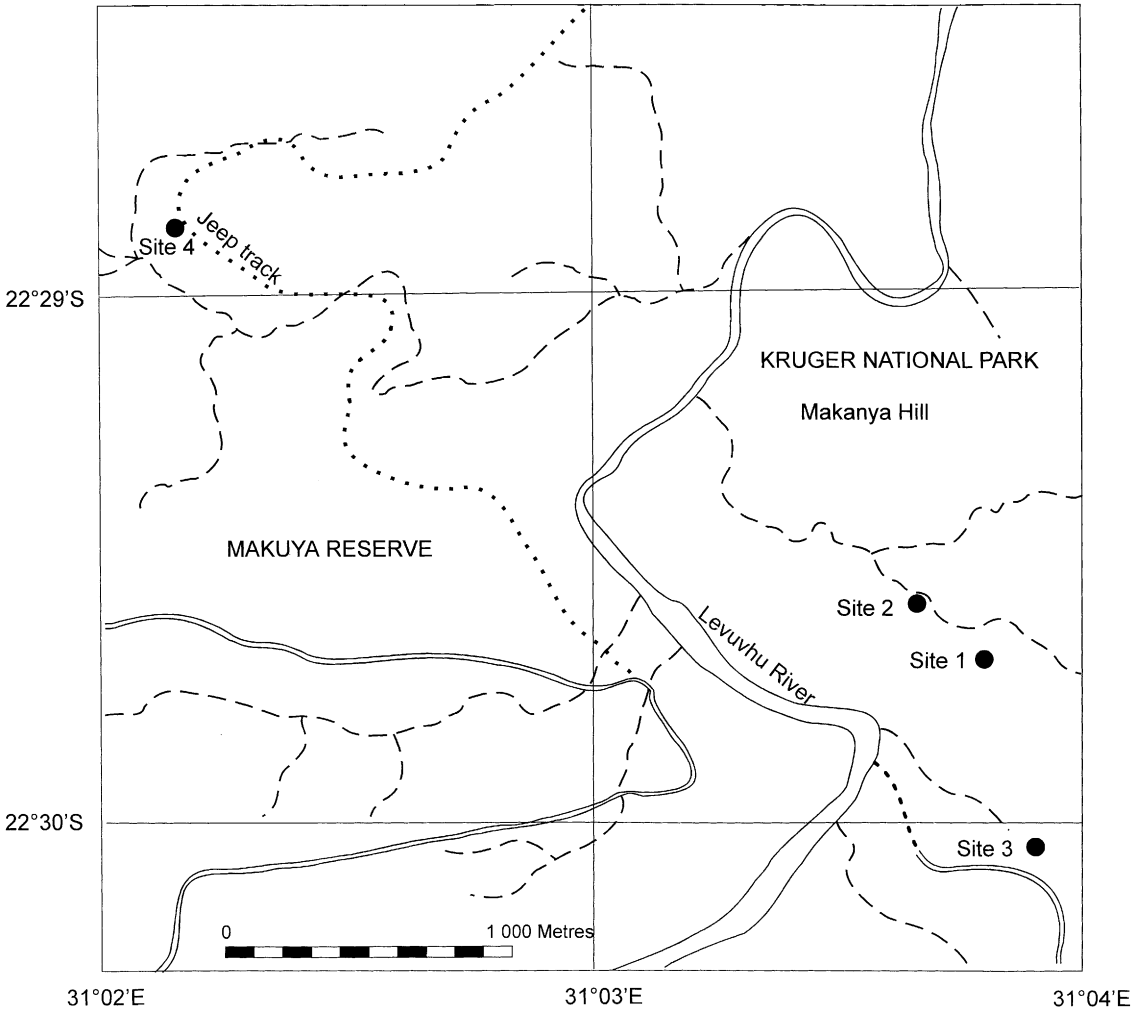

Fig. 1. Juvenile *Euskelosaurus* fossil sites.

Kruger National Park amongst adult *Euskelosaurus* remains. During a palaeontological survey of the Makuya Nature Reserve, managed by the Iron and Steel Corporation of South Africa, in 1997, more juvenile dinosaur remains were discovered by the team, found in close association with adult *Euskelosaurus* remains. This site is located approximately 4 km to the north west of those in the Kruger National Park.

According to the 1:2 500 002 230 MESSINA geological map (Geological Survey, 1981), the fossiliferous areas are located within the Solitude Formation that comprises mainly alternating multi-coloured shale and mudstone (Brandl, 1991). The Solitude Formation has been considered to be a contemporary of the Beaufort Group of the Main Basin, Karoo Supergroup, which is Upper Permian to Lower Triassic in age (Brandl, 1991). However, all the *Euskelosaurus* localities discovered thus far in the Northern Province are situated within a red-coloured siltstone. This correlates well with descriptions of the Bosbokpoort Formation (Van den Berg, 1980; Brandl, 1991) with its characteristic red mudstones and siltstones.

Euskelosaurus remains in the Main Karoo Basin are limited to the lower Elliot Formation that is dated as late Carnian or early Norian (Galton, 1990). The palaeontological and lithological correlation of the Bosbokpoort Formation with the Elliot Formation red beds of the Main Karoo Basin (Kitching and Raath, 1984) would confirm therefore the designation of the Bosbokpoort Formation as being Upper Triassic. The Bosbokpoort Formation seems to be quite attenuated in the study region, which would also explain the limited east–west distribution of the *Euskelosaurus* fossils. If Galton's dating of the Lower Elliot Formation as Late Carnian/Early Norian and the El Tranquilo Formation of Argentina as Norian were correct, it would follow that the *Euskelosaurus* fossils predate the *Mussaurus* specimens from Patagonia, which would make it not only the oldest dinosaur juveniles to be discovered to date in Africa, but also in the world (cf. Galton, 1990).

The fossils at Locality 1 occur mainly on a flat terrain sparsely covered by 1–3 m tall Mopane trees. The red mudrock weathers to form a sandy red soil, strewn with numerous fossil fragments. The fossils are covered with a dark red–brown layer of ferricrete and are generally quite fragmentary and weathered. Locality 2 is situated in a gully, at a slightly higher level than Locality 1. Only some of the better preserved or noteworthy fossils were collected from Localities 1 and 2, leaving the vast majority of adult fossils in situ. Locality 3 is separated from the main exposure by a fault and is situated in a clearing on the side of a mountain, adjacent to the Mopane veld. All the fossils in an area of approximately 100 m^2 were collected for a statistical survey of the bone accumulation. 370 fossil bone fragments, including 3 adult femoral heads and the proximal ends of 3 tibiae of different individuals, 45 vertebrae and one juvenile dinosaur femur fragment, were recovered from Locality 3.

Locality 4 is separated from the Kruger National Park localities by the Levuvhu River, which also forms the western border of the Park in this area. This site, which yielded a similar array of adult and juvenile *Euskelosaurus* long bone fragments, toe bones and vertebrae, is situated on a low ridge within the Mopane veld.

3. Existing upper triassic juvenile archosaur material

3.1. South Africa, Free state: the Rooidraai eggs

Although Africa is renowned for its wealth of prosauropod remains, very little is known of their reproductive behaviour due to the paucity of eggs and juvenile remains. The only exception, previous to the present discovery, was the discovery of clutches of fossilized eggs in the upper part of the Elliot Formation (Lower Jurassic) of South Africa by James Kitching of the University of the Witwatersrand. The clutch of eggs he discovered at the Rooidraai locality in the Free state was of particular interest since the eggs contained partially preserved embryos. Kitching (1979) tentatively suggested that they could be dinosaur embryos on the basis of the very short parietal region, the position of the postorbital, the parietal/supraoccipital suture, and the position and shape of the lacrimal of one of the exposed skulls. If this conclusion were correct, this find would not only mark the first amniote (taxon pertaining to reptiles, birds and mammals) eggs discovered in Africa, but also the first baby dinosaurs to be discovered in Africa.

3.2. South America, Patagonia: Mussaurus juvenile skeletons

Small dinosaur fossils from the El Tranquilo Formation of Patagonia have been reported by Bonaparte and Vince (1979). These dinosaurs were named *Mussaurus* (mouse dinosaur) due to their size. It was soon established that these were the remains of very young dinosaurs. There is some debate about whether the two eggs discovered in close association with the *Mussaurus* specimens belong to the same species, due to size discrepancies. Remains of approximately 3 m long adult prosauropod dinosaurs were later found in the same horizon as the juvenile skeletons and eggs (Casamiquela, 1980). The proximity to the juvenile specimens and comparable morphology strongly indicate that they could be adult *Mussaurus*. If this assumption were correct, *Mussaurus* is invaluable in our understanding of reproductive behaviour and allometric growth in early dinosaurs. These specimens are the oldest juvenile dinosaur remains found thus far in South America.

Fig. 2. Adult *Euskelosaurus* femora.

4. Fossil material from the Northern Province of South Africa

All the juvenile bones encountered at the sites were collected. The bulk of the juvenile material was discovered at Localities 1 and 4, but isolated juvenile femur fragments were also discovered at the other two localities. The juvenile material includes fragments of vertebrae, femora, tibiae and a humerus that are well-ossified and virtually identical in shape to their adult counterparts.

The most striking quality of the fossils is the pronounced size disparity between the adult and juvenile bones. The complete femur of an adult *Euskelosaurus*, which was discovered at Site 1, is 760 mm long (depicted at the bottom in Fig. 2). Several adult femoral portions were discovered at Site 1 (depicted at the top in Fig. 2), some of which were much bigger than the relevant region of the complete femur. It is estimated that the largest juvenile femur (depicted on the left, Fig. 3) would have been approximately 150 mm long and the smallest (depicted on the right, Fig. 3) approximately 70 mm long, if complete. This would imply that the *Euskelosaurus* juveniles collected varied between 583 and 1250 mm in length, using the femur/body length ratio of a 250 mm long *Mussaurus* as model. However, since the *Euskelosaurus* juveniles seem to be older than those of *Mussaurus*, in which case allometric growth differences could have already played a role, and due to the fact that *Mussaurus* seems to have had a relatively short neck for a prosauropod (Bonaparte and Vince, 1979), it is probable that the *Euskelosaurus* juveniles could actually have been slightly longer than this estimate.

Portions of dorsal vertebrae of presumably at least two different juveniles were discovered on the surface

Fig. 3. Juvenile *Euskelosaurus* femora.

Table 1
Dimensions of adult and juvenile *Euskelosaurus* bones from the Northern Province of South Africa

	Juvenile				Adult			
Femur head width	19.5	29	33	42.5	170	184	195	234
Femur length	(70)	(103)	(120)	(150)	(663)	(718)	760	(913)
Total body length	(583)	(858)	(1000)	(1250)	(6630)	(7180)	(7600)	(9130)
Vertebra centra	8 centra 14–25, average: 19.4				21 centra 65–150, average: 104			

Measurements in mm and estimated sizes in brackets.

close to the adult femur at Locality 1. The diameter of six of these juvenile vertebrae centra varies between 14 and 21 mm and the diameter of the other two is 25 mm. The centra of the 20 dorsal and sacral vertebrae found at Locality 3 measure between 65 and 148 mm, with an average value of 101.8 mm. The largest adult vertebra centrum from Locality 1 measures approximately 150 mm across (Table 1; Fig. 4). The vertebrae discovered at Localities 1 and 2 fall within the range of samples from Locality 3.

5. Discussion

There are certain indications that suggest the wisdom of a more cautious approach to the identification of the Rooidraai eggs. In a paper on the biozonation of the Elliot and Clarens Formations, Kitching and Raath (1984) list many archosaur fossils including those of crocodiles, thecodonts and ornithischian and saurischian dinosaur fossils that occur in the same stratigraphic horizon as the Rooidraai eggs. They prudently do not classify the eggs in this publication. Following the initial ambiguity as to the exact relationships of the embryos, Grine and Kitching (1987) concluded that the Rooidraai eggs probably belong to the prosauropod genus *Massospondylus*, merely because the eggs are too large to have been laid by the contemporaneous thecodont *Clarencea*. These authors come to the conclusion that "while the Rooidraai eggs resemble those of crocodilians in some respects, they are similar to those of avian (and later dinosaurian) taxa in others". In the light of this rather tenuous conclusion it would be advisable to treat the Rooidraai eggs with more circumspection than Galton (1990) and Weishampel and Horner (1994) did, who summarily accepted the Rooidraai eggs as belonging to *Massospondylus*.

There is also some controversy surrounding the individual age and size of the *Mussaurus* juveniles from Patagonia, described by Bonaparte and Vince (1979). Two eggs were discovered in close association with the *Mussaurus* specimens, the largest egg measuring 60 mm in length and 45 mm in diameter. These authors also mention specifically that the eggs were not big enough to house the collected juvenile *Mussaurus* specimens and that these were at least a couple of weeks old at the time of deposition, if the eggs were thought to have been laid by the same parent species.

Disregarding Bonaparte and Vince's conclusion, Weishampel and Horner (1994) bettered Galton's "very

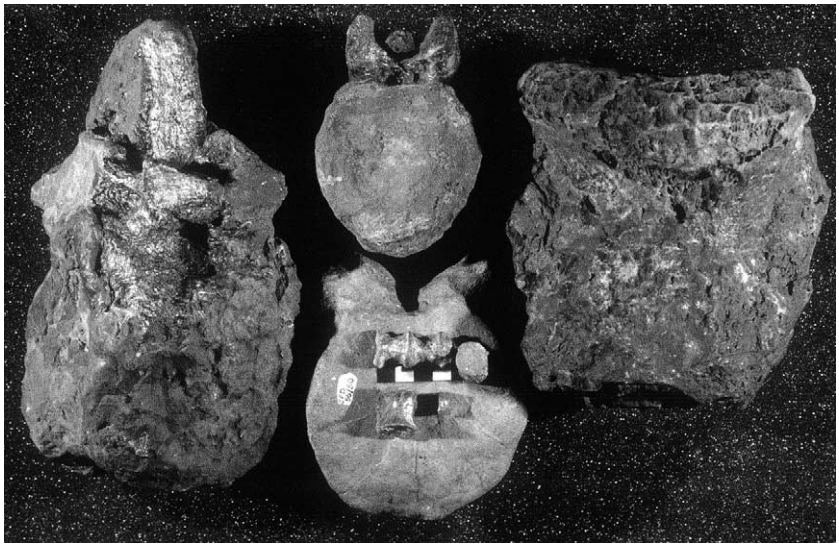

Fig. 4. Juvenile and adult *Euskelosaurus* vertebrae.

juvenile'', by referring to *Mussaurus* as ''hatchling material... weight approximately 1 kg'', whereas Carpenter and Alf (1994) refer to them as possibly being embryos (cf. Bonaparte and Vince, 1979; Galton, 1990). The given size of the *Mussaurus* juveniles also increased in subsequent publications. Bonaparte and Vince (1979) describe the *Mussaurus* juvenile as having been approximately 200 mm long in life. Galton (1990) gives the possible length for the *Mussaurus* juveniles as between 250 and 300 mm.

Weishampel and Horner (1994) infer that *Massospondylus* hatchlings weighed approximately 1 kg in life, the same weight they ascribe to *Mussaurus* hatchlings. This misunderstanding most probably arose due to a faulty scale in Kitching (1979, Fig. 3), which is approximately 0.16× what it should be, giving the impression that the embryological material in the Rooidraai egg is much larger than it actually is. In the text of his article, Kitching (1979) mentions the correct dimensions of the eggs, i.e., 65 mm along the long axis and 55 mm in diameter, making these eggs approximately as big as goose eggs, and just big enough to house a archosaur embryo of approximately 150 mm in length.

Weishampel and Horner (1994) calculated that both *Massospondylus* and *Mussaurus* hatchlings measured approximately 0.2–0.4% of the adult's length. Galton (1990) described the adults of *Massospondylus* as being approximately 5 m long and those prosauropods associated with the *Mussaurus* remains, described by Casamiquela (1980), as being 3 m long. Weishampel and Horner's calculation would therefore suggest hatchlings of 6–12 mm long for *Mussaurus* and 10–20 mm long for *Massospondylus* or inversely, taken that *Mussaurus* is a hatchling of 250 mm in length, that it would grow into an adult of 62–125 m in length (cf. Weishampel and Horner, 1994). There are two ways out of this quandary – either the juveniles hatched from goose-sized eggs and, as approximately 150 mm long individuals, they would be 5% of their adult length or otherwise, we must be looking for eggs that could have housed 250 mm long individuals which would be approximately 8% of their adult length.

From the evidence at our disposal, i.e., the lithology and the number, distribution, size ranges and ossification of the bones from the Northern Province sites discussed in this paper, as well as those in the literature reviewed above, one can draw certain conclusions. From the thousands of bones in certain mudstone strata, one can conclude that prosauropod herds were periodically killed by flash floods. The two different size ranges of bones would indicate that adult (maternal?) *Euskelosaurus* dinosaurs were accompanied by their precocious young, probably to protect them from predators such as big carnivorous thecodonts. It is suggested that the lack of intermediary sized bones from all four Northern Province localities may have been caused due to the dispersal of the individuals at the end of the breeding season as soon as the sub-adults could fend for themselves. Since it most probably took the sub-adult more than a year to reach sexual maturity it would not necessarily form part of a breeding herd during the breeding season before they were ready to mate. The absence of hatchling material, nests, eggs or egg shell fragments as well as the state of ossification of the juvenile bones, indicates that the juveniles were precocious and followed the mother around and that they were not tended in the nest by the mother dinosaur.

Another explanation for the absence of intermediary sized individuals could be that the sub-adults congregated in non-breeding herds, which for some ecological or behavioural reason were not present in the same region as the breeding herds during the time of deposition. The similarity in size of the juvenile material could probably be attributable to seasonal summer floods that coincided with the arrival of new generations of hatchlings. If the breeding herds kept to lushly vegetated river banks to facilitate the feeding habits of the young, their proximity to the rivers would make these herds especially susceptible to being inundated during seasonal floods.

6. Conclusions

The number of bones in the bone bed and the size discrepancy between adult and juvenile *Euskelosaurus* in the Northern Province mudstones examined here would suggest that breeding herds consisting of mothers, accompanied by their offspring, were killed by flash floods. The sizes of the juveniles varied between 583 and 1250 mm in length. This, together with the state of ossification, indicates that precocious juveniles could forage with their mothers. *Euskelosaurus* eggs probably hatched during spring and juveniles accompanied adult maternal herds during the summer months. The riverbanks would have provided easily accessible food and water for the young, but this in turn made these brood herds susceptible to summer floods. The maternal behaviour of prosauropods was probably like that of crocodiles and birds with precocious young. The proximity of these adults provides protection for the young – but the adults neither raise the young in nests nor do they feed the young.

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