Earliest evidence of cynodont burrowing

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A 251 million year old partial burrow cast containing an articulated skeleton of the mammal-like carnivore *Thrinaxodon liorhinus* is the oldest evidence for burrowing by a cynodont synapsid. The burrow cast comes from terrestrial flood plain sediments close to the Permian–Triassic boundary in the Karoo of South Africa. Together with those of the later cynodont *Trirachodon*, the *Thrinaxodon* burrow cast indicates that burrow-making was broadly distributed in basal synapsids and has a long history in non-mammalian synapsid evolution. A reconstruction of its appendicular skeleton in cross-section indicates that *Thrinaxodon* was able to adopt a facultatively mammalian stance within its burrow shaft. Burrows of cynodont design are more common in Triassic rocks than previously realized, and suggest that burrowing may represent an adaptive response by cynodonts to the environmental conditions associated with the mass extinction event that punctuated the end of the preceding Permian period. The widespread occurrence of burrowing among extant mammals implies that the ancient synapsid ability to burrow conferred a strong adaptive value in the evolution of Mammalia.

Keywords: behaviour; burrow; cynodont; Permian–Triassic boundary; synapsid; *Thrinaxodon*

1. INTRODUCTION

Burrows are the most common type of shelter constructed by extant terrestrial vertebrates (Boucot 1990), but there are relatively few examples of burrow-making in the fossil record prior to the Cenozoic (Voorhies 1975). The earliest evidence of burrowing by terrestrial vertebrates is attributed to the dicynodont synapsid *Diictodon*, articulated skeletons of which have been preserved within large helically coiled burrow casts from the Upper Permian deposits of South Africa's Beaufort Group (Smith 1987). Similarly complex burrow systems from the Lower Triassic of South Africa (Groenewald *et al.* 2001) and the Middle Triassic of Namibia (Smith & Swart 2002) preserve skeletal remains of the cynodont synapsid *Trirachodon*. Lower Triassic burrow casts of simpler construction from contemporaneous deposits in South Africa (Stanistreet & Turner 1979; Groenewald 1991, 1996) and Antarctica (Hasiotis *et al.* 1999; Miller *et al.* 2001) have also been attributed to tetrapods, based largely on their presumed association with skeletal material from the same strata. However, there is no direct evidence of the maker(s) of these burrow casts as none preserve identifiable skeletal remains.

Fossils of the fox-sized cynodont *Thrinaxodon* are relatively common in the Lower Triassic deposits of South Africa (Kitching 1977), and are often found in characteristically curled-up positions (Brink 1958). Synapsid fossils preserved in this death pose are generally assumed to have died in a burrow, leading to widespread popular belief (e.g. Lambert *et al.* 2001) that such animals were indeed burrowers. However, unequivocal evidence of synapsids preserved within such structures exists only for the Permian dicynodont *Diictodon* (Smith 1987) and the Triassic cynodont *Trirachodon* (Groenewald *et al.* 2001). The *Thrinaxodon* burrow cast reported here is the oldest evidence for burrowing among cynodont synapsids, predating the burrows constructed by the more crownward cynodont *Trirachodon* (Groenewald *et al.* 2001) by *ca.* 5 million years (Myr). It also extends the antiquity of burrowing behaviour by cynodonts to the Permian–Triassic boundary (PTB), which marks the greatest extinction event in the history of life (Erwin *et al.* 2002). Together, the *Thrinaxodon* and *Trirachodon* burrow casts are indicative of a long history of burrowing behaviour in the fossil ancestors of Mammalia.

2. GEOLOGICAL SETTING

The *Thrinaxodon* burrow cast (specimen BP/1/5905 in the Bernard Price Institute for Palaeontological Research, Johannesburg), was found on the farm Elim 623 in the Bethulie District, Free State Province, South Africa. Three additional partial burrow casts (specimens BP/1/6095A–C) of similar construction were collected close to but not in association with the *Thrinaxodon* burrow cast, but these lack skeletal remains. All four burrow casts were found as surface 'float' (i.e. not embedded in the host rock), but the very low relief of the host mudrock at the Elim 623 locality precludes any possibility that the burrows were reworked from younger sediments. The mudrock at the Elim 623 locality belongs to the Palingkloof Member, which is the uppermost part of the Balfour Formation (Beaufort Group) and contains the PTB of *ca.* 251 Myr ago (Smith 1995; Ward *et al.* 2000; Smith & Ward 2001). The associated fauna includes the PTB index taxon *Moschorhinus*, the Permian genus *Dicynodon*,

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and the Permo–Triassic genus *Lystrosaurus* (Kitching 1977; Groenewald & Kitching 1995; Smith & Ward 2001). The combined sedimentological and faunal data suggest that the strata at the Elim 623 locality straddles the PTB, constraining the age of the *Thrinaxodon* burrow cast(s) to close to 251 Myr ago.

3. DESCRIPTION

The *Thrinaxodon* burrow cast (figures 1 and 2) represents the terminal chamber of a burrow as suggested by its expansion relative to the narrower opposing end (the presumed 'shaft'), its smoothly rounded distal edge and the curled-up attitude of the entombed *Thrinaxodon* skeleton. Judging from the clean break through the shaft, the terminal chamber was probably connected to the surface via a tunnel of indeterminate length. In cross-section near the break, the 'sides' and 'ceiling' of the burrow shaft have a rounded outline, whereas the burrow 'floor' bears a low central peak (figure 2*a*). Thus, the ceiling was vaulted and the floor of the shaft was divided into two equal sloping surfaces, as in many of the burrow shafts constructed by the later cynodont *Trirachodon* (Groenewald *et al.* 2001). *Thrinaxodon* had a semi-sprawling stance somewhat intermediate between that of the typical sprawl of lizards and more upright posture of mammals (Jenkins 1971). However, the width of the burrow shaft is narrower than the span required by the legs of a semi-sprawling animal the size of the interred *Thrinaxodon*, and this has necessitated our modification of an earlier reconstruction (Jenkins 1971) of the pelvic appendicular skeleton by bringing the knee in slightly (figure 2*b*). This, in turn, results in an inclined lower leg that is roughly perpendicular to the slope of the shaft floor, and a plantar foot surface that lies in the same plane as the sloped floor area on both sides of the shaft (figure 2). This modification of the normal semi-sprawling stance of a cynodont such as *Thrinaxodon* therefore accounts for the characteristic double-sloping floors of cynodont burrow shafts.

The surface morphology of the burrow cast includes areas of low parallel ridges mainly developed on the sides and lower parts of the ceiling of the burrow cast that generally converge slightly towards the long axis of the burrow (figure 1*a*). These presumably represent scratch marks made by the animal during excavation of the burrow, whereas their absence on the burrow floor may be attributed to wear by constant trampling. Similar surface markings on *Diictodon* (Smith 1987) and *Trirachodon* (Groenewald *et al.* 2001) burrow casts were also interpreted as scratch marks. The surface of the burrow cast also contains a number of small-diameter (less than 15 mm), rod-like invertebrate burrow casts of identical sedimentological structure. Invertebrate burrow casts of this morphology are abundant in mudrocks of Early Triassic age throughout South Africa (Groenewald 1991, 1996; Smith 1995).

The infill of the burrow is a uniform fine-grained sandstone, which contrasts strongly with the surrounding mudrock out of which the burrow cast appears to have weathered. These mudrocks represent flood plain deposits that accumulated under semi-arid climatic conditions (Smith 1995). Thus, the burrow appears to have been excavated originally into the silt and mud of an alluvial

flood plain adjacent to a stream or river, and subsequently filled with sand introduced during a flood event. The associated invertebrate burrows, which attest to moist soil conditions and the proximity to water, were dug on the interface between the *Thrinaxodon* burrow and the surrounding soil, and subsequently filled with sand alongside the larger burrow. As with the *Thrinaxodon* burrow cast, the tetrapod or presumed tetrapod burrows from South Africa (Smith 1987; Groenewald 1991, 1996; Groenewald *et al.* 2001) and Antarctica (Hasiotis *et al.* 1999; Miller *et al.* 2001) are from flood plain deposits and were preserved through casting by flood-introduced sand. The infill also shows evidence of stratification in the form of numerous rectangular mudchips that are concentrated near the floor of the burrow cast and are oriented horizontally within the sandstone infill. This suggests that flooding of the burrow was not instantaneous but occurred gradually, resulting in an incremental fill.

The entombed skeleton of *Thrinaxodon liorhinus* is of a large adult individual that is preserved on the lower surface (floor) of the burrow (figure 1*b,c*). The anterior portion of the skeleton displays the curled-up attitude that is characteristic of many *Thrinaxodon* specimens. The spatulate design of the terminal chamber presumably reflects the optimal room required by the animal to assume its resting position and the space it required to turn around in the chamber. The skeleton is complete save for the feet, which are probably preserved deeper within the burrow cast, and the tip of the tail, which is severed at the point where the burrow shaft is broken. Evidence of post-mortem desiccation and onset of skeletal disarticulation is indicated by dislocation of the mandibular bones and by displacement of the bones of the anterior part of the vertebral column, the shoulder girdle, and the front limbs. Six teeth (two caniniform and four incisiform teeth) are preserved *in situ* in the jaws. Fourteen disarticulated teeth of incisiform and post-caniniform morphology are scattered around the snout, and these appear to have fallen out of their sockets. Alternatively, such teeth may have been previously shed within the burrow during the animal's normal tooth replacement cycle (Crompton 1963), and ultimately preserved in association with the skull. As the skull is largely embedded in the burrow cast, we cannot confirm which of these two hypotheses is more likely, but we note that no empty sockets are visible in the upper jaws that are exposed. Overall, the degree of articulation of the skeleton suggests a relatively short post-mortem period prior to infilling of the burrow.

4. DISCUSSION

Not every burrow dweller is the original burrow-making species (Voorhies 1975), but *Thrinaxodon* is clearly the burrow maker in this case because the shaft design is shared with that of burrow shafts constructed by *Trirachodon* (Groenewald *et al.* 2001). In both cases, the shaft has a cross-section in which the floor has a central ridge that divides it into laterally sloping halves (figure 2). This floor design is unique to non-mammalian cynodonts as it is absent in the burrows excavated by the dicynodont *Diictodon* (Smith 1987) and those constructed by extant mammals (Voorhies 1975). As explained above, the bifaceted floor design appears to be a result of travel wear caused
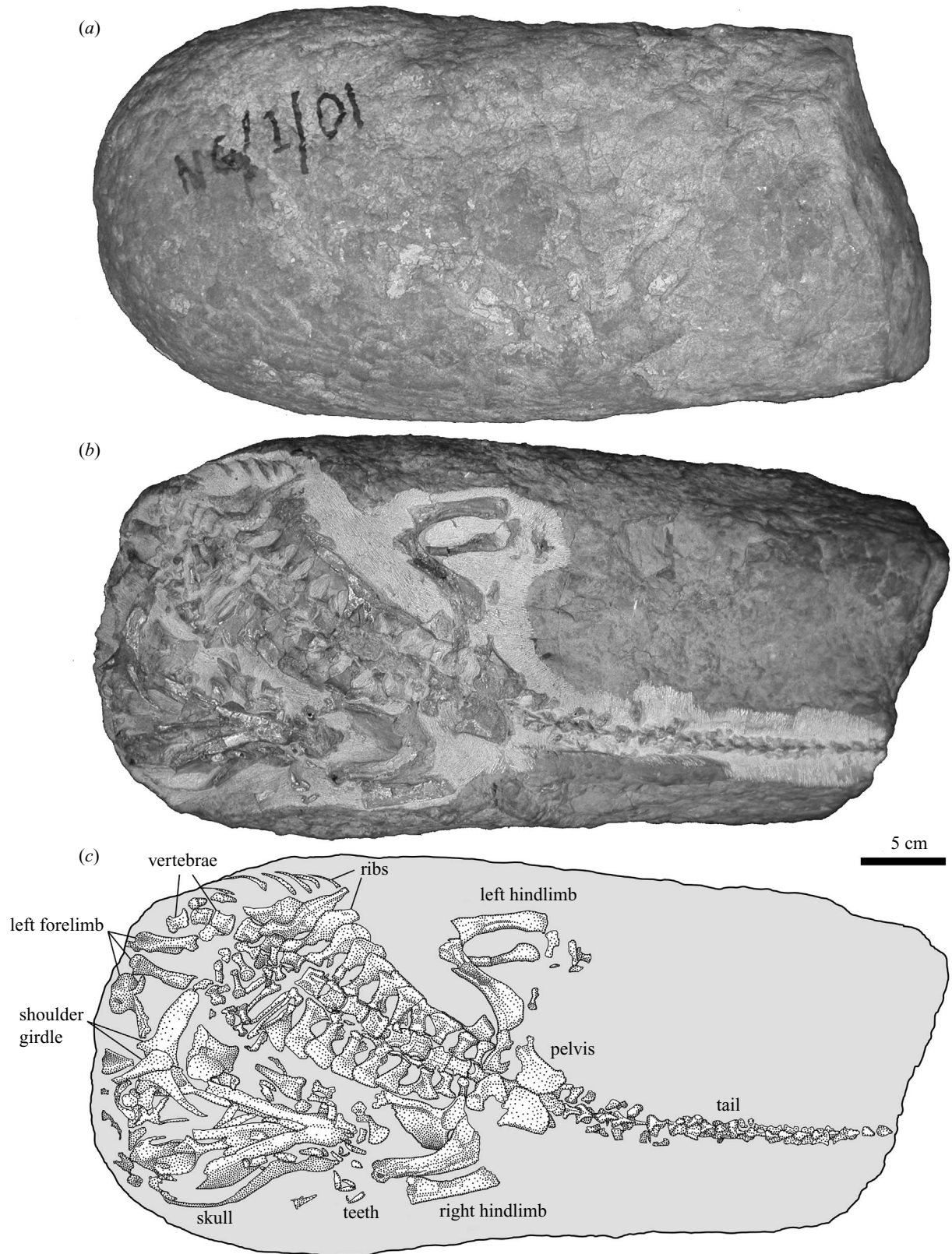
Figure 1. Burrow cast with entombed skeleton of the cynodont synapsid *Thrinaxodon liorhinus* (BP/1/5905) from the PTB of South Africa. (*a*) Dorsal view; (*b*) ventral view; and (*c*) interpretive drawing of (*b*).

by the facultatively mammalian locomotion of a normally semi-sprawling basal cynodont within its burrow. The relatively wide flat-floored shafts of the burrows constructed by the sprawling dicynodont *Diictodon* (Smith 1987) suggest strongly that the limbs of semi-sprawling dicynodont synapsids could not adopt the facultatively

modern mammalian stance that we infer for burrow-dwelling early cynodonts.

The *Thrinaxodon* burrow cast(s) are strongly suggestive of cynodont adaptation to possible deteriorating environmental conditions following the mass extinction event which marks the PTB. Although neither *Thrinaxodon* nor
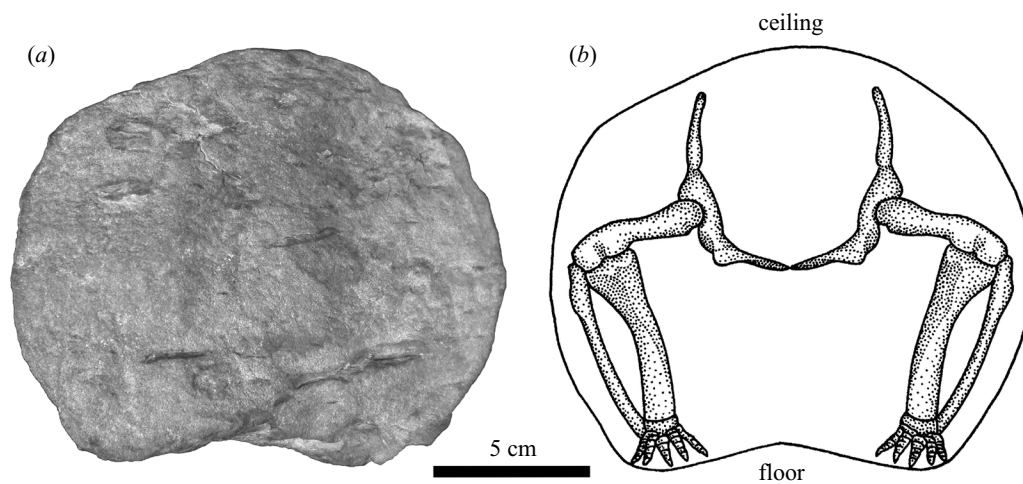
Figure 2. Burrow cast of the cynodont synapsid *Thrinaxodon liorhinus*. (*a*) Sectional end view showing the double-sloping floor design; and (*b*) interpretive reconstruction showing relationship between burrow-shaft outline and the pelvis and hindlimb skeleton.

Trirachodon display obvious osteological features that would indicate fossorial behaviour, burrow casts of cynodont design from South Africa (Stanistreet & Turner 1979; Groenewald 1991, 1996), Namibia (Smith & Swart 2002), Antarctica (Hasiotis *et al.* 1999; Miller *et al.* 2001) and the Elim 623 locality, as well as the curled-up attitude of many *Thrinaxodon* fossils, suggest that burrowing was widespread among Triassic non-mammalian cynodonts. One of the primary functions of burrowing is protection from environmental extremes, and it has been suggested that the increase in burrowing activity in Pleistocene mammals can be attributed to adverse climatic conditions associated with glaciation (Voorhies 1975). Much more severe climatic changes are thought to have characterized the Permian–Triassic extinction event (Erwin *et al.* 2002), and we find it significant that evidence for cynodont burrows is common to the Triassic rocks that record the time following the extinctions. This suggests that burrowing by early cynodonts may have been an adaptive response to the changing environmental conditions across the PTB. These changes included significantly altered fluvial environments and sweeping changes in terrestrial fauna and flora (Smith 1995; Ward *et al.* 2000; Erwin *et al.* 2002).

The recognition of non-mammalian cynodont burrowers suggests that the ability to burrow may be ancestral for mammals and ultimately may have played an important role in their origin (Voorhies 1975; Smith 1987; Groenewald *et al.* 2001). Intriguingly, it has been estimated (Voorhies 1975) that at least 50% of extant mammal species are burrowers. Indeed, all three extant monotreme species are burrowers (Voorhies 1975; Szalay 1994), and all but one of the major marsupial groups contain burrowing species (Voorhies 1975). However, insufficient ecological data for some putatively basal marsupial species (e.g. *Didelphis* (McManus 1974)), and the conflict between marsupial phylogenies based on morphological versus molecular characters (Springer *et al.* 1991; Luckett 1994; Szalay 1994), complicate a phylogenetic perspective on burrowing in marsupials. Placental phylogenies based on molecular studies are largely congruent with respect to the internal relationships of the major extant groups (Madsen *et al.* 2001; Murphy *et al.* 2001), but straightforward optimization of burrowing ability onto the available trees produces ambiguous results in that burrowing may or may not, in equal likelihood, be an ancestral trait for placentals. Similarly, a recent morphology-based phylogeny of placentals which included both extant and extinct taxa (Ji *et al.* 2002) proved inconclusive with respect to whether a scansorial or a terrestrial lifestyle was ancestral for placentals, although burrowers were not distinguished from other terrestrial therians. It is nevertheless intriguing that the most basal members of the major recognized placental clades, particularly Afrotheria, Glires and Laurasiatheria (Madsen *et al.* 2001; Murphy *et al.* 2001), are burrowers. It seems likely that burrowing has conferred some evolutionary advantage, perhaps in terms of survivorship, on the basal members of these placental groups.

Mammals are the only living representatives of a more inclusive group of amniotes called Synapsida, which has a history extending back *ca.* 310 Myr. It is thus significant that there is evidence for burrowing at *ca.* 251 Myr ago in the basal cynodont *Thrinaxodon*, as well as in the slightly younger cynodont *Trirachodon* (Groenewald *et al.* 2001). Elsewhere among non-mammalian synapsids, burrowing behaviour is known for the Permian dicynodont *Diictodon* (Smith 1987), there is strong osteological evidence for burrowing by the Permian dicynodont *Cistecephalus* and its close relatives (Cox 1972; Cluver 1974, 1978), and there is circumstantial evidence for burrowing in the latest Permian and Triassic dicynodont *Lystrosaurus* (Groenewald 1991, 1996; Miller *et al.* 2001) and its therocephalian contemporary *Bauria* (Groenewald *et al.* 2001). Dicynodonts and therocephalians occupy a more basal position within Synapsida than cynodonts (Rubidge & Sidor 2001), which suggests that burrowing may have been more common among synapsids than is implied by the few known burrow casts. Clearly, burrow-making is an ancient synapsid trait, one that probably had a strong adaptive value for the cynodont lineage that ultimately led to mammals.

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