Tetrapod burrows in the southwestern main Karoo Basin (Lower Katberg Formation, Beaufort Group), South Africa

Emese M. Bordy[1*], Orsolya Sztanó[2], Bruce S. Rubidge[3] & Adam Bumby[4]

[1]*Department of Geology, Rhodes University, Grahamstown, 6140 South Africa*
**Author for correspondence. E-mail: e.bordy@ru.ac.za*
[2]*Department of Physical and Applied Geology, Eötvös Loránd University, Pázmány Péter sétány 1/c, Budapest 1117, Hungary*
[3]*Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa*
[4]*Department of Geology, University of Pretoria, Pretoria, 0002 South Africa*

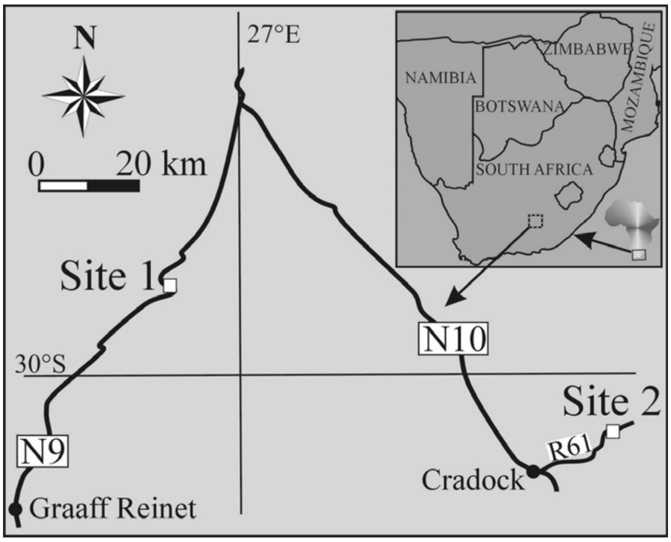

Figure 1. Locality map showing the two study sites in the Eastern Cape (South Africa). Site 1 (GPS 31°50′39.30″S, 24°52′15.54″E) is situated along the N9 national road, some 90 km from Site 2 (GPS 32°6′18.12″S, 25°47′ 42.78″E) which is found along road R61.

Introduction

Large, cylindrical, inclined tetrapod burrows are preserved in two stratigraphic zones immediately above of the Permo-Triassic (P/T) boundary as well as ~100–110 m above it in the southern main Karoo Basin (Eastern Cape, South Africa) (Fig. 1). Considering that the P/T boundary event is regarded as the most dramatic mass extinction in the Earth's Phanerozoic history, not only the environmental conditions that lead to it, but also those that followed this mass extinction and resulted in the Early Triassic biodiversity recovery, are of prime interest (Smith & Botha 2005).

Analysing the morphology and stratigraphic distribution of these burrows and associated sedimentary facies may improve (a) the understanding of the ethological reasons of the burrow making at and shortly after the P/T boundary event; as well as (b) the interpretation of the Early Triassic palaeoenvironment in the southwestern Karoo Basin. Some of these large, cylindrical burrows, especially those that are directly above the P/T boundary, have been mentioned (Retallack *et al.* 2003; Botha & Smith 2007a,b), but their morphology has never been described in detail. In this contribution, we document some of these large cylindrical burrows and consider their significance as environmental indicators in the Early Triassic of the main Karoo Basin.

The Katberg Formation

The described burrows are found in sandstones and siltstones of the Katberg Formation (Lower Triassic, Beaufort Group, Karoo Supergroup), at two localities situated some ~90 km apart (Fig. 1). The burrows are located at ~70 m from the base of the formation at Site 1 and ~45 m at Site 2, and in both sites, ~100–110 m above the P/T boundary, representing a sedimentary record of ~1 Ma in duration (Griesbachian to early Dienerian) (Ward *et al.* 2005; Szurlies 2007).

In the southern Karoo, the Katberg Formation is characterized by multistoried, fine- to medium-grained sandstones and mudstones (Fig. 2). The architecture of the sandstone stories shows lateral to downstream accretion of channel forms and bars. The accretionary surfaces are associated with channel lags overlain by intraformational mud-pebble and calcareous-nodule conglomerates. Main sedimentary structures in the sandstones include horizontal lamination, parting lineations, cross-bedding, soft-sediment deformations and massive beds with well-developed sole marks (Fig. 3). Mudstone intervals are either horizontally bedded with millimetre- to centimetre-thick intercalations of very fine sandstones or characterized by remnant horizontal bedding that alternates with irregular patches of sandy-clayey siltstones. The mudstones contain shallow and smooth erosional surfaces, as well as laterally traceable surfaces marked by sand-filled desiccation cracks at several levels (Fig. 4). These features are in agreement with previous palaeoenvironmental interpretations of the Katberg Formation that suggested a relatively high energy braided fluvial setting under relatively warm, dry climatic conditions (SACS 1980; Hiller & Stavrakis 1984).

Observations

Burrows consist of inclined shafts with a single opening that leads to a subhorizontal, rounded terminus (Fig. 5A, B,C,D). Burrow diameter range from ~25 to ~40 cm, with an average of ~30–35 cm. Individual burrow diameters are fairly consistent along the length of the burrow, and only very rarely seem to slightly taper downward (to an apparent minimum diameter of ~12 cm). Chambers or other enlargements are absent, and while the burrow terminus is rounded, it does not form a terminal chamber as it has the same diameter as the burrow itself. Cross-sectional burrow shape is circular-to-subcircular, and medial ridge in the burrow floor is absent.

These simple burrows are non-branching, non-connected, non-cross-cutting, and lack evidence for any coiling or spiralling, however may curve gently in any direction in the level of the terminus. Burrows descend at an angle of ~30° before levelling out in the rounded terminus. Burrow axis may have a deviation of up to 5°, but show no change in the inclination with depth. Preserved burrow lengths range from 0.5 m to greater than 3 m; maximum vertical depth is 1.5 m (average ~1 m, minimum 0.5 m).

Figure 2. Road-cutting in the Lower Triassic of Katberg Formation showing extended tabular sandstones and vertically accreted mudstones (siltstones and claystones). Person for scale.

Burrow sides and bases are well-defined as the massive and lithologically distinct burrow fill contrasts the lithology of the surrounding beds. These inclined structures are particularly apparent where they obliquely truncate the stratification of the host rocks (Fig. 5A,B,C).

Burrow fills are invariably unstratified (massive), and consist of coarse silt, very fine- to fine-grained sandstone and locally poorly-sorted, fine-grained claystone parabreccias. In spite of careful inspection, bone material has not been identified in the fill of the burrows. Burrow fills are surrounded by a <5 mm thin clay lining which in cross-section consists of packed clay flakes parallel to the burrow wall (and at high angle to the stratification in the host sediment).

The outer burrow walls are generally smooth with rare and subtle indentations of a few cm. Burrow walls are often covered by well-preserved transverse and longitudinal scratch marks which seem to be higher in density in the side of the burrow walls (Fig. 6A,B). The most common scratch marks are elongated triangular ridges (replicas of grooves) on the outer burrow wall with their long axis roughly perpendicular to the axis of the burrow.

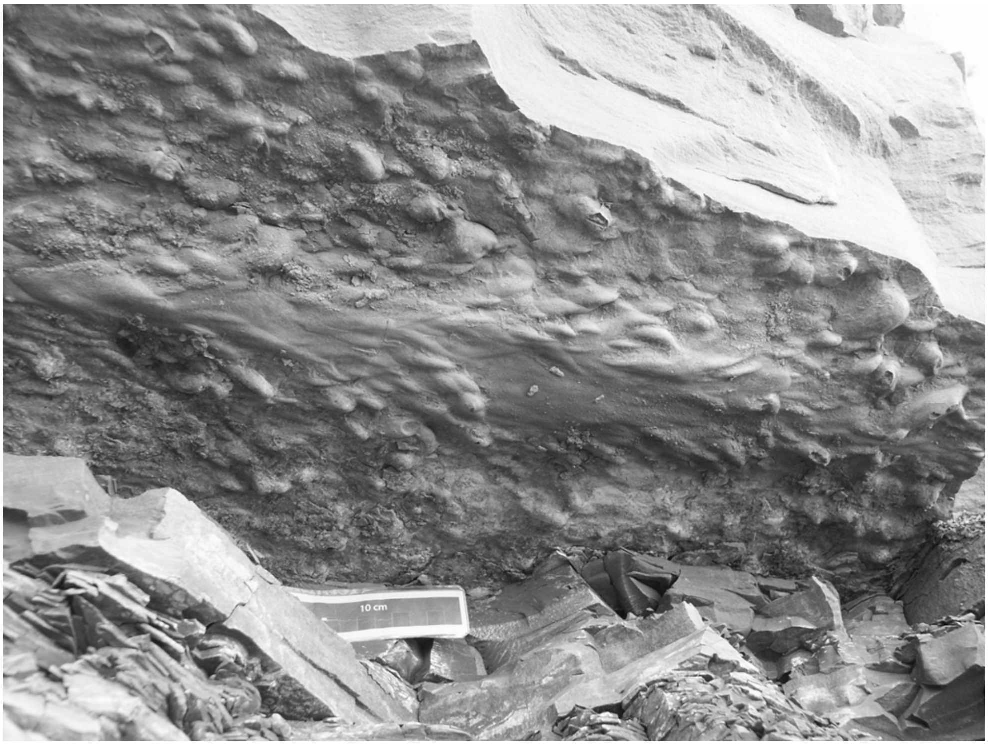

Figure 3. Sole marks at the base of medium-grained sandstones are most commonly flute marks and gutter casts. Scale in centimetres.

Figure 4. Mudstones both within and between the multistorey sandstones often contain desiccation cracks of up to 50 cm in depth. Person for scale.

Interpretation

Based on comparisons to fossil and modern burrows (e.g. Hasiotis *et al.* 1999; Groenewald *et al.* 2001; Miller *et al.* 2001; Damiani *et al.* 2003; Sidor *et al.* 2008), these structures are interpreted as burrows of vertebrates with fully or partly fossorial life style. The burrow morphology, in particular the uniform burrow diameter and lack of terminal chamber may suggest a reverse mode of excavation and that the burrow probably functioned as resting, hiding, aestivating shelter, and unlikely as a permanent dwelling, breeding or nesting structure.

Preservation of the burrows and scratch marks on their

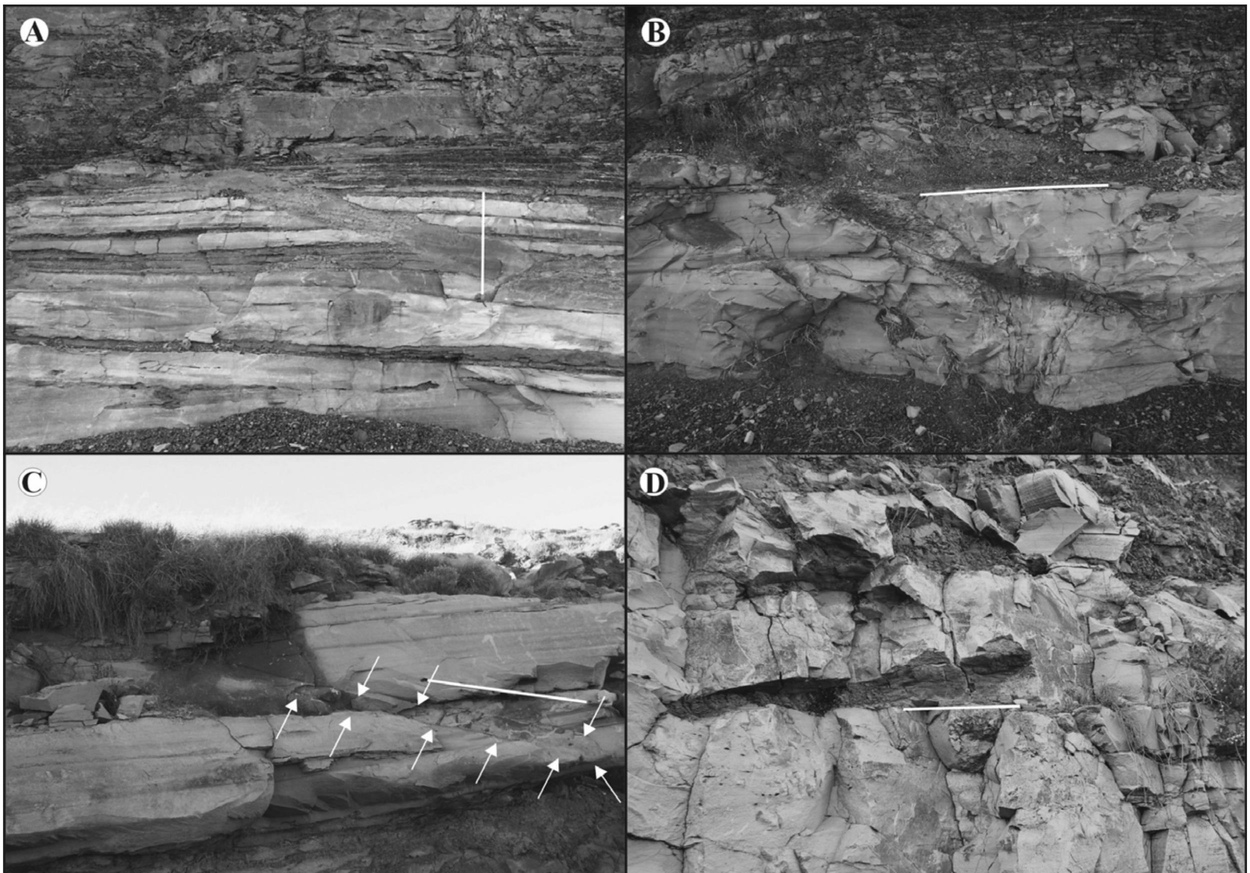

Figure 5. Large-diameter, low-angle inclined trace fossils in the lowermost Triassic Katberg Formation interpreted as subterranean therapsida burrows. Scale tape measure = 1 m in A, B, C and 0.5 m in D.

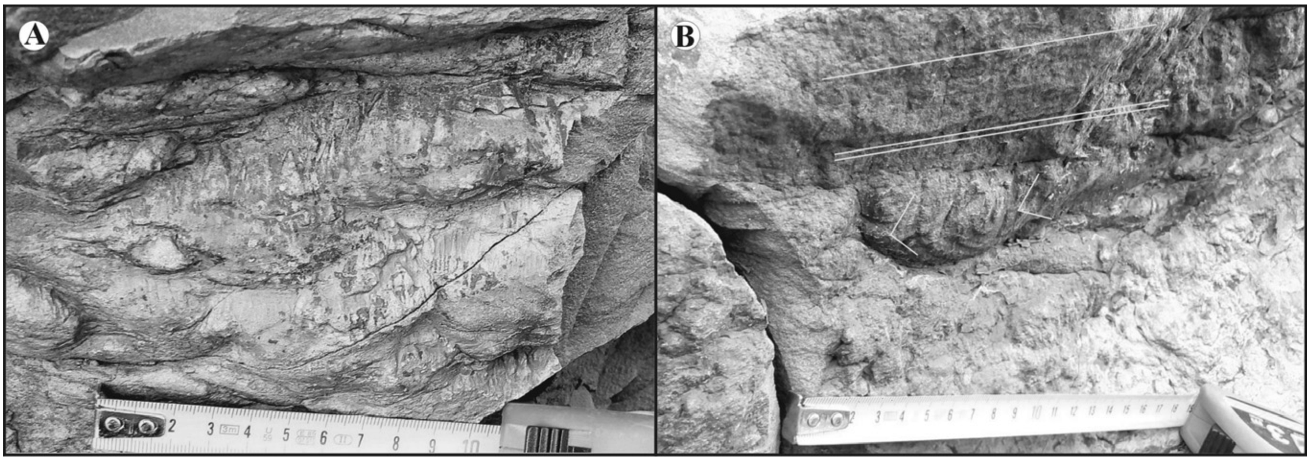

Figure 6. Vertical, triangular (**A**) and horizontal (**B**) scratch marks on burrow surfaces. Scale in centimetres.

outer burrow wall as well as absence of any deflected or offset laminae in the surrounding sediments suggest that the host medium was sufficiently firm to prevent the deformation of host strata or caving in of the open burrow, but moist enough to preserve scratch marks. Clay lining may indicate that the animals plastered their burrow internally, probably not only to reinforce the structure, but maybe also to slow dehydration of burrow, creating a buffered, sheltered (insulated) microenvironment at depths where daily temperature variations were less significant. Constructed burrow linings, massive burrow fill of sandstone and/or claystone parabreccias and lack of evidence for active backfilling (e.g. internal menisci) show that these lined structures were open burrows which were subsequently and passively filled in by probably in relatively high energy, rapid mass movement deposits.

Structures on the outer burrow wall record methods of excavation, and they indicate that penetration into the substrate occurred by scraping of the host sediment. The triangular ridge-like impressions on the outer burrow wall suggest a trace-maker animal with pointy claws and/or specialized beak or teeth with spikes of 2–3 mm terminus size for scratch digging. The orientation of scratch marks, and the apex of the scratch triangles pointing away from the direction of scratching movement collectively imply that excavation occurred sideways in a mostly downward direction within the burrow.

Possible tracemakers

Current palaeontological studies (e.g. Smith & Botha 2005; Botha & Smith 2007a,b; Abdala *et al.* 2006) suggest that in the Earliest Triassic of the main Karoo Basin, taxa including dicynodonts (*Lystrosaurus murrayi, L. declivis*) and cynodonts (e.g. *Thrinaxodon liorhinus, Galesaurus, Progalesaurus*), show features and preservational conditions congruent with fossorial lifestyle. Among these, prime burrow-maker candidates, however, remain *L. murrayi* and *L. declivis* not only based on their size, relative abundance and physiological adaptations (e.g. significant bone wall thickness, spatulate structure of the claws), but also due to fact that several of their articulated skeletons were found *in situ* in large, scratched, but undescribed burrows (Retallack *et al.* 2003). However, the lack of associated bone material within the structures described here only permits their attribution to mammal-like therapsids that possibly produced these structures to escape surface environmental conditions, which based on the associated sedimentary structures (e.g. high abundance of very large desiccation cracks) were, at least episodically, extremely hot.

Conclusion

In summary, these newly described structures are considered here possibly therapsid burrows that have been constructed as shelters to generate a microenvironment which allowed their occupants to extend the limits of their habitat under extreme ecological conditions characterized by lack of water and possibly episodic high temperatures. This is in agreement with previous suggestions (e.g. Smith 1987; Groenewald *et al.* 2001; Damiani *et al.* 2003; Retallack *et al.* 2003; Abdala *et al.* 2006; Botha & Smith 2007a,b) that large vertebrate burrows in the Earliest Triassic of South Africa assisted the tracemakers in surviving the harsh environmental conditions associated with the P/T mass extinction. The stratigraphic reoccurrence of these vertebrate burrows in spatially separated, but coeval sites in the South Africa, at some 100–110 m above the P/T boundary, may suggest that harsh environmental conditions have persisted at least on a semi-regional scale and reoccurred shortly after the P/T mass extinction event.

Research funds received from the Joint Research Committee of Rhodes University, the NRF Hungarian–South African Intergovernmental S&T Cooperation Programme (GUN 2072841) and M. Diop's field assistance are gratefully acknowledged. Thanks to F. Abdala, R. Smith, J. Botha-Brink and J. Neveling for the insightful discussions.

REFERENCES

ABDALA, F., CISNEROS, J. C. & SMITH, R.M.H. 2006. Faunal aggregation in the Early Triassic Karoo Basin: earliest evidence of shelter-sharing behavior among tetrapods? *Palaios* **21**, 507–511.

BOTHA, J. & SMITH, R.M.H. 2007. *Lystrosaurus* species composition across the Permo–Triassic boundary in the Karoo Basin of South Africa. *Lethaia*. **40**, 125–137.

BOTHA, J. & SMITH, R.M.H. 2007. Rapid vertebrate recuperation in the Karoo Basin of South Africa following the End-Permian extinction. *Journal of African Earth Sciences* **45**, 502–514.

DAMIANI, R.J., MODESTO, S.P., YATES, A.M. & NEVELING, J. 2003. Earliest evidence of cynodont burrowing. *Proceedings of the Royal Society of London, Series B, Biological Sciences* **270**, 1747–1751.

GROENEWALD, G.H., WELMAN, J. & MACEACHERN, J.A. 2001. Vertebrate burrow complexes from the Early Triassic *Cynognathus*

Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa. *Palaios* **16**, 148–160.

HASIOTIS, S.T., MILLER, M.F., ISBELL, J., BABCOCK, L.E. & COLLINSON, J.W. 1999. Triassic trace fossils from Antarctica: burrow evidence of crayfish or mammal-like reptiles? Resolving crayfish from tetrapod burrows. *Freshwater Crayfish* **12**, 71–81.

HILLER, N. & STAVRAKIS, N., 1984. Permo-Triassic fluvial system in the southeastern Karoo Basin, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **45**, 1–21.

MILLER, M.F., HASIOTIS, S.T., BABCOCK, L.E., ISBELL, J.L. & COLLINSON, J.L. 2001. Tetrapod and large burrows of uncertain origin in Triassic high paleolatitude floodplain deposits, Antarctica. *Palaios* **16**, 218–232.

RETALLACK, G.J., SMITH, R.M.H. & WARD, P.D. 2003. Vertebrate extinction across Permian-Triassic boundary in Karoo Basin, South Africa. *Geological Society of America Bulletin* **115**, 1133–1152.

SACS (South African Committee for Stratigraphy) 1980. Stratigraphy of South Africa Part 1 (Compiled by Kent, L.E.). Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia, and the Republics of Boputhatswana, Transkei and Venda. *Handbook of the Geological Survey of South Africa*, **8**, 1–690.

SIDOR, C.A., MILLER, M.F. & ISBELL, J.L. 2008. Tetrapod burrows from the Triassic of Antarctica. *Journal of Vertebrate Paleontology* **28,** 277–284.

SMITH, R.M.H. & BOTHA, J. 2005. The recovery of terrestrial vertebrate diversity in the South African Karoo Basin after the End-Permian extinction. *Comptes Rendus Palevol.* **4**, 555–568.

SMITH, R.M.H. 1987. Helical burrow casts of therapsid origin from the Beaufort Group (Permian) of South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **60**, 155–170.

SZURLIES, M. 2007. Latest Permian to Middle Triassic cyclo-magnetostratigraphy from the Central European Basin, Germany: implications for the geomagnetic polarity timescale. *Earth and Planetary Science Letters* **261**, 602–619.

WARD, P.D., BOTHA, J., BUICK, R.R., DE KOCK, M.O., ERWIN, D.H., GARRISON, G.H., KIRSCHVINK, J.L. & SMITH, R.M.H. 2005. Abrupt and gradual extinction among Late Permian land vertebrates in the Karoo Basin, South Africa. *Science* **307**, 709–714.