

KATBERGIA GEN. NOV., A NEW TRACE FOSSIL FROM UPPER PERMIAN AND LOWER TRIASSIC ROCKS OF THE KAROO BASIN: IMPLICATIONS FOR PALAEOENVIRONMENTAL CONDITIONS AT THE P/TR EXTINCTION EVENT

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Abstract: A new ichnogenus and ichnospecies of burrow, *Katbergia carltonichnus*, are described from Upper Permian and Lower Triassic rocks of the Karoo Basin, South Africa, where they are preserved in pedogenically modified overbank deposits that are interpreted as inceptisols subsequently gley-sol overprinted. Sigmoidal burrows consist of a long (≥ 0.5 m) cylindrical tube, ranging from 1–2 cm in diameter, terminating in a slightly larger living chamber. The burrows are unlined and passively filled, preserving a hierarchy of scratch patterns on the burrow walls. Scratch patterns include longitudinal, transverse, and crescent-shaped markings found around the circumference of the burrow, but which are less densely concentrated on the burrow floor. Calcareous concretions are associated with burrowed siltstone intervals, generally restricted to the lowermost decimetre,

with nodules nucleating around burrows. Stable $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotope data on calcite cement in the burrow fill, entombing siltstone, and associated calcareous nodules all cluster together when plotted, indicating that nodule formation occurred following burrow horizon abandonment and a rise in regional water table. Isotopic data reflect calcite precipitation under a semi-closed system in saturated conditions. A model for burrow emplacement, abandonment and infill, and subsequent cementation by calcite is presented demonstrating that previous interpretations of Late Permian and Early Triassic palaeosol types associated with the P/Tr extinction event must be re-evaluated.

Key words: Karoo Basin, palaeosol, carbon isotope, oxygen isotope, palaeoecology.

THE Karoo Basin of South Africa records what has been described as continuous continental sedimentation across the Permian/Triassic (P/Tr) boundary (Smith *et al.* 1993; Smith 1995), providing a rare opportunity to study the Late Palaeozoic mass extinction event that occurred at this stratigraphic horizon (Erwin 1994). The exact placement of the P/Tr boundary is a subject of contention, and various authors place it in different locations throughout the Palingkloof Member (Smith 1995; Smith and Ward 2001; Retallack *et al.* 2003) and the Katberg Formation (Steiner *et al.* 2003). The Palingkloof Member is composed primarily of siltstone and is overlain by the Katberg Formation, a complicated sandstone-dominated interval placed biostratigraphically in the early Triassic. A characteristic of the boundary-interval siltstones is the presence of cylindrical inclined burrows (Smith and Ward 2001). These are preserved both above and just below the P/Tr boundary, and deciphering the palaeoenvironment

in which they formed will aid in understanding the change that so dramatically altered the landscape.

Smith and Ward (2001) described these unassigned burrows as a feature of the so-called 'dead zone' (Ward *et al.* 2000) above the P/Tr boundary at Bethulie. Subsequently, they were reported to be a consistent character of the Upper Permian and Lower Triassic interval at Bethulie, Carlton Heights, and elsewhere (Smith and Botha 2005). Retallack *et al.* (2003) identified them as *Macanopsis* and used the burrows to define several Triassic palaeosols (Retallack *et al.* 2003) interpreted to represent river or lakeside environments (Retallack *et al.* 2003; Smith and Botha 2005). Potential trace makers include crab, spiders, beetles, and shrimps (Retallack *et al.* 2003; Smith and Botha 2005).

Although the placement of the P/Tr boundary in these sections has been revised repeatedly in the literature, usually it has been placed somewhere in the Palingkloof

Member. Smith (1995) placed the transition from Permian to Triassic deposits within the Upper Balfour Formation, with the boundary occurring above the base of the Palingkloof Member in the southern Karoo Basin. Subsequently, Ward *et al.* (2000), MacLeod *et al.* (2000), and Smith and Ward (2001) also placed the P/Tr boundary in the Palingkloof Member, above a distinct layer of brown-weathering calcareous nodules (Smith and Ward 2001). This boundary is identified on the basis of vertebrate palaeontological remains preserved within the concretions, above which is a siltstone-dominated interval identified as the 'dead zone' (Smith and Ward 2001). Retallack *et al.* (2003, fig. 4) placed the boundary within the 'dead zone' based on the occurrence of pedogenic carbonate nodules, laminated beds, and weakly developed palaeosols, as well as the last appearance of *Moschorhinus*, a Permian theropcephalian. Ward *et al.* (2005) continued to assert that the boundary lay within the concretionary bed below the 'dead zone'. The only agreement that has been reached in the literature, as far as the stratigraphic position of the bed used to mark the extinction event is concerned, is that it lies somewhere within the Palingkloof Member (Retallack *et al.* 2003; Ward *et al.* 2005).

The burrow described as *Macanopsis* from Carlton Heights and Bethulie is an 'oblique, silt-filled, irregularly scratched burrow with a terminal chamber' (Retallack *et al.* 2003, p. 1143), but a problem exists with the generic assignment. The type specimen, *Macanopsis pagueyi*, was described by Macsotay (1967) as a straight-to-curved tube with a circular-to-oval cross-section ranging between 10 and 40 mm in diameter. This marine burrow enters the substrate at an angle of 90 degrees and slowly curves in a J-shape, ending in an enlarged chamber. The Karoo burrows are not J-shaped, the diagnostic morphology of *Macanopsis*. Hence, this contribution will characterize the morphology and composition of these Late Permian–Early Triassic burrows, and evaluate them within a sedimentological and stratigraphical context. A suite of burrows is described morphologically, the scratch patterns detailed, and their fill and surrounding matrix analyzed geochemically. Stable isotopic data from the carbonate (micrite and spar) fraction of the burrow fill, matrix, and the carbonate nodules associated with the bioturbated intervals provide evidence to discern the nature of the environmental system in which the burrows were created and subsequently preserved.

LATE PERMIAN AND EARLY TRIASSIC DEPOSITS

The Palingkloof Member and Katberg Formation are lithostratigraphic units of the Karoo Supergroup, which represents deposition that began in the Permo-Carbonif-

erous and continued into the Jurassic. The Karoo Basin formed in the Late Carboniferous, first as a passive margin and subsequently as a retroarc-foreland basin resulting from the collision of the palaeo-Pacific with the Gondwanan plate (Smith 1995). The impact of convergence resulted in the orogenesis of the Cape Fold Belt and its emplacement at the south-eastern edge of the basin (Veevers *et al.* 1994; Catuneanu *et al.* 1998). Following deglaciation in the Late Permian, the basin was filled with terrestrial sediments derived from the Cape Fold Belt (Johnson *et al.* 1997). Continental deposits of the Karoo Supergroup in the south-western part of the basin are assigned to the Beaufort Group (Johnson *et al.* 1997), which is further subdivided into the Adelaide and Tarkastad subgroups. Fully continental deposits in the Adelaide sequence are assigned to the Balfour Formation, which is dominated by high sinuosity fluvial regimes (Smith 1995; Ward *et al.* 2000). The base of the overlying Katberg Formation marks the boundary of the Tarkastad Subgroup (Johnson *et al.* 1997). Overall, the Beaufort Group is interpreted as a fluvio-lacustrine system characterized by a change from meandering fluvial geometries to braided regimes (Smith *et al.* 1993). This changeover is attributed by some authors to the regional vegetation extinction associated with the P/Tr boundary event (Ward *et al.* 2000), although this interpretation has been called into question (Gastaldo *et al.* 2005).

MATERIAL AND METHODS

Burrows were collected from two locations in the Karoo Basin, Bethulie (GPS 30.422472° S, 26.254167° E) and Carlton Heights (GPS 31.29228° S, 24.95152° E; WGS84 Cape Datum), both of which have been the focus of numerous publications (e.g. Ward *et al.* 2000; Smith and Ward 2001; Retallack *et al.* 2003; Gastaldo *et al.* 2005; Smith and Botha 2005). The section at Bethulie from which burrows were collected includes the laminated beds first described by Smith (1995) in the Palingkloof Member of the Balfour Formation above the P/Tr boundary. Subsequently, Smith and Ward (2001) redefined this same interval as the laminated 'event' beds, while Retallack *et al.* (2003) redescribed the interbedded interval as consisting of 'laminites' in which palaeosols could be recognized. The presence of *Macanopsis* was used as a criterion for recognizing Zam palaeosols at this locality (Retallack *et al.* 2003). The burrows occur in three discrete intervals within the short stratigraphic 'laminite' section. Sandstone-cast burrows occur in very fine, greenish grey (5 GY 7/1) lithic wacke (litharenite) whereas siltstone-cast burrows occur in a greenish grey, coarse siltstone that fines upwards to siltstone. These burrows are in association with nodular concretions, and the upper contact is

defined by a dispersed nodule layer in which remains of *Moscarinus* are reported (Retallack *et al.* 2003; R. Smith, pers. comm. 2004).

The section at Carlton Heights in which burrows are preserved occurs in both the Palingkloof Member and the Katberg Formation (Text-figs 1–2; Gray *et al.* 2004; Pace *et al.* 2005). Burrows in the Palingkloof Formation crop out within a section of interbedded sandstone and siltstone exposed in the railway cutting north of where the N9 crosses the railway (31.30700° S, 24.95450° E). These beds occur stratigraphically below the P/Tr boundary of Smith and Ward (2001) and Retallack *et al.* (2003; Gastaldo *et al.* 2005; Text-fig. 2). Here, the facies reflect shifts between shallow sandstone channels and overbank deposits of siltstone and sandstone (Gray *et al.* 2004). Burrows are restricted to the siltstone facies and are siltstone filled.

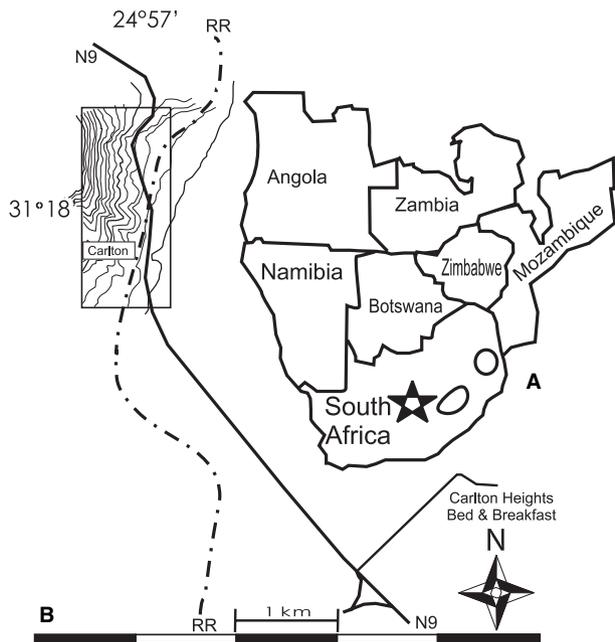
The lithofacies within the overlying Katberg Formation are related genetically to each other in an overall fining-upward sequence. Each genetic sequence begins with a basal fine-grained, channel sandstone unit, in which there may be a concretionary lag that grades upwards into an interval of burrowed siltstone in which carbonate nodules occur (Text-figs 2–3). This in turn is overlain by alternating thin beds of fine-grained sandstone and siltstone, in which desiccation cracks may be preserved. The contact

with the overlying genetic sequence is erosional and records degradation of the Early Triassic landscape by fluvial incision, with loss of a minimum of 3 m of stratigraphic section in many instances (Pace *et al.* 2005). Sandstone-channel bases often contain rip-up mudclasts and pedogenic nodule conglomerate (Pace *et al.* 2005; Smith and Botha 2005; Text-fig. 3). These fining-up sequences are repeated throughout the section and can be tracked laterally and vertically. The intercalated bioturbated siltstone intervals occur throughout the lowermost 100 m of section. As sandstone thickness increases up-section owing to amalgamation of superposed channel systems (Pace *et al.* 2005), intervals of bioturbated siltstone are not as common in donga (erosional gully) sections, although they may be found in laterally correlated outcrop.

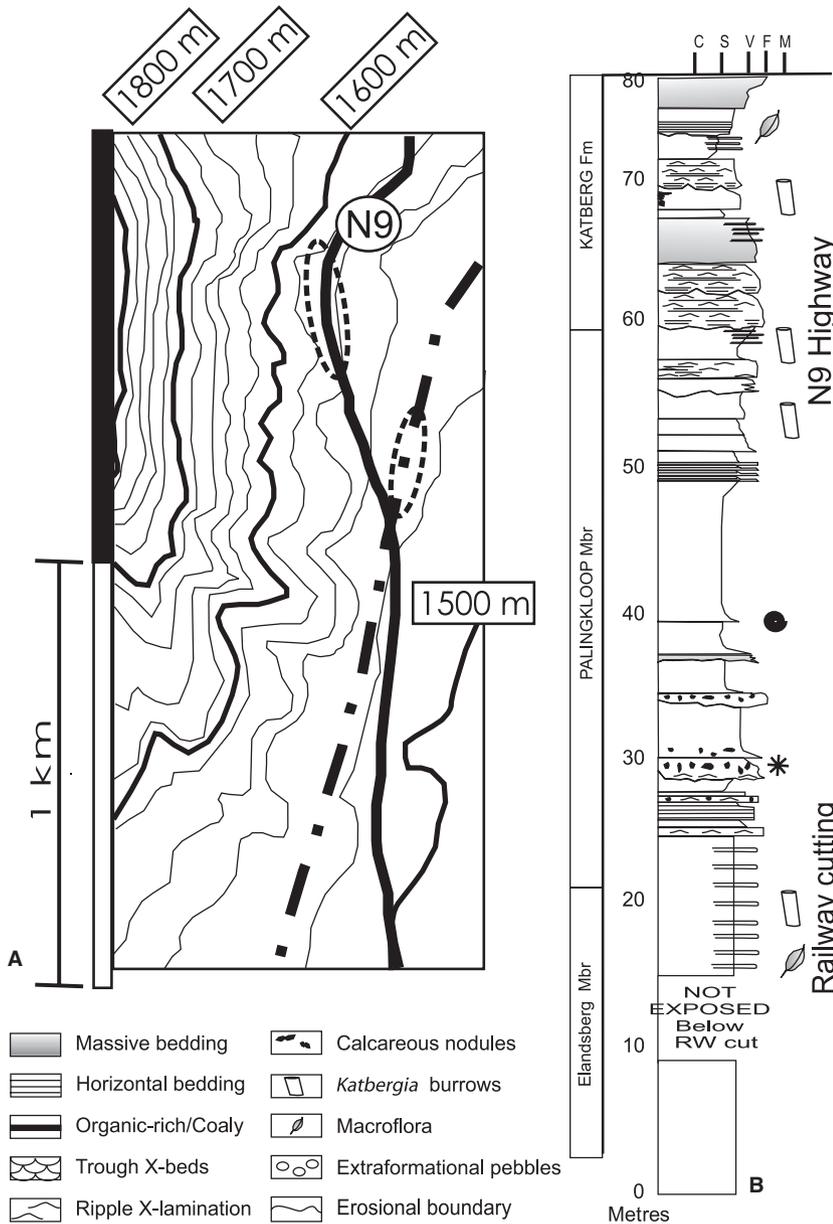
Burrows and associated carbonate nodules were examined *in situ* and then collected from Carlton Heights (06/2005) and Bethulie (06/2003–05). Standard field methods were employed to describe the sedimentological context and lithologic attributes, and stratigraphic relationships of each bioturbated interval were detailed. Before removal, exposed length, diameter, and angles of inclination at different points along the exposed burrows were recorded. Some of the longer burrows could not be removed intact. These were taken out of the substrate and numbered as individual burrow segments that were reconstructed following unpacking.

Laboratory procedures included an analysis of cross-sectional shape and diameters along the length of the burrow segments. Thin sections, both longitudinal and transverse, were made for analysis of burrow fill and examined using fluorescence microscopy to identify any residual organic matter content. Optical microscopy was not effective in determining the mineralogy because of the fine-grained nature of the burrow fills. Hence, mineralogical composition of burrows and adhering matrix were evaluated using 5 mm well-slides in a Rigaku 3000 D-Max two-axis XRD equipped with Jade MDI-7 software. The presence and quantity of carbon and nitrogen were analyzed using an Exeter 440 CHNO analyzer.

The scratch patterns preserved on the outside of the burrow were examined by sequential photography of the best preserved burrow segment, rotating the specimen approximately 60 degrees between images. Images were superimposed into a composite using Photoshop and enlarged, resulting in an unrolled image of the burrow and external scratch patterns. First, the total composite of the scratches was traced onto an overhead transparency. Next, hierarchies of scratch-pattern sets were determined by shape, length, and the orientation along and across the burrow. The composite was divided into sets of scratches, each traced onto their own transparency with registration



TEXT-FIG. 1. Locality maps of the main study area in South Africa. A, outline map of southern Africa with the location of Carlton Heights marked by a star. B, collections were made in the Late Permian Palingkloof Member along the railway cutting (dashed and dotted line) and outcrops of the Early Triassic Katberg Sandstone adjacent to the N9 highway (solid black line; see Text-fig. 2 for details).



TEXT-FIG. 2. The Permo-Triassic section at Carleton Heights, South Africa. A, enlargement of topographic map with 20 m contour intervals. Collection sites are indicated by dashed ellipses along the N9 motorway and the railway cutting (dashed and dotted line) north of the train station. B, stratigraphic section across the P/Tr boundary at Carleton Heights (after Gastaldo *et al.* 2005). The concretionary bed used by Ward *et al.* (2000), MacLeod *et al.* (2000), Smith and Ward (2001), and Ward *et al.* (2005) as the P/Tr boundary is marked with an asterisk; the horizon marking the P/Tr boundary used by Retallack *et al.* (2003) is indicated by a spiral icon. The placement of the boundary by Steiner *et al.* (2003) is within the N9 highway outcrop exposure.

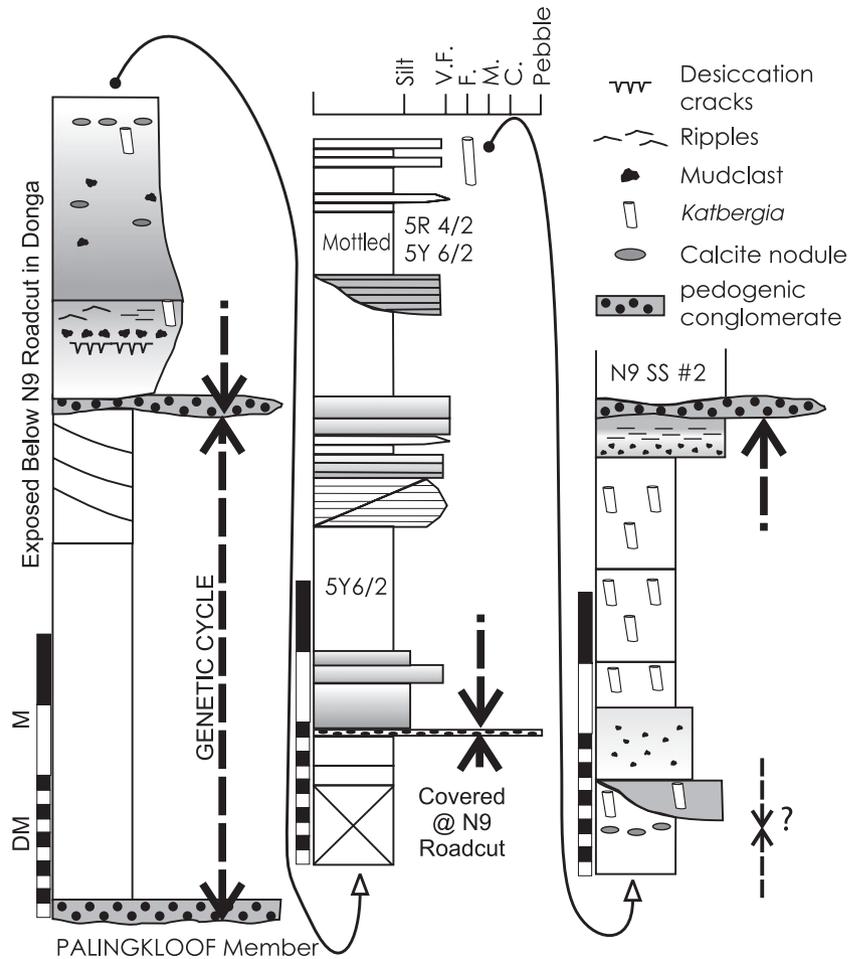
marks for compilation. This provided detail that allowed for recognition of distinct scratch trends in the burrow.

Analyses of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopes from calcite cement in the burrows and matrix were carried out in the Department of Geological Sciences, Southern Methodist University (SMU), Dallas, Texas. Samples were powdered in a cleaned corundum mortar and pestle, loaded into reaction vessels, and atmospheric gases evacuated. Samples then were dissolved in 100% H_3PO_4 at 25°C for c. 16 hours to produce CO_2 . Carbon dioxide samples were cryogenically purified and analyzed for carbon- and oxygen-isotope compositions using a Finigan MAT 252 isotope ratio mass spectrometer, and are reported relative to standard delta notation:

$$\delta^{13}\text{C}(\text{or }^{18}\text{O}) = (\text{R}_{\text{sample}}/\text{R}_{\text{standard}} - 1) * 1000 \quad (1)$$

where R is the ratio of heavy to light stable isotope present in the sample or standard. Delta values are reported relative to the PeeDee Belemnite standard (Craig 1957) for carbon isotope values, and standard mean ocean water (SMOW; Gonfiantini 1978) for oxygen isotope values. Extraction processes were run on seven samples; one matrix sample from the N9 highway (matrix), two burrow-fill samples from Bethulie (B-1 and B-2), and four burrow-fill samples from Carlton Heights (CH-1 to CH-4). Stable isotope values for associated carbonate nodules from the Carlton Heights section were taken from Tabor *et al.* (2007, fig. 4) for comparative purposes.

TEXT-FIG. 3. Measured stratigraphic section beginning at the base of the Katberg Sandstone within a donga section below the N9 highway. Burrows assigned to *Katbergia* gen. nov. are found at several stratigraphic levels, with a concentrated assemblage near the top of a fining-upward sequence. Conspicuous genetic, fining-upward cycles are indicated by arrows.



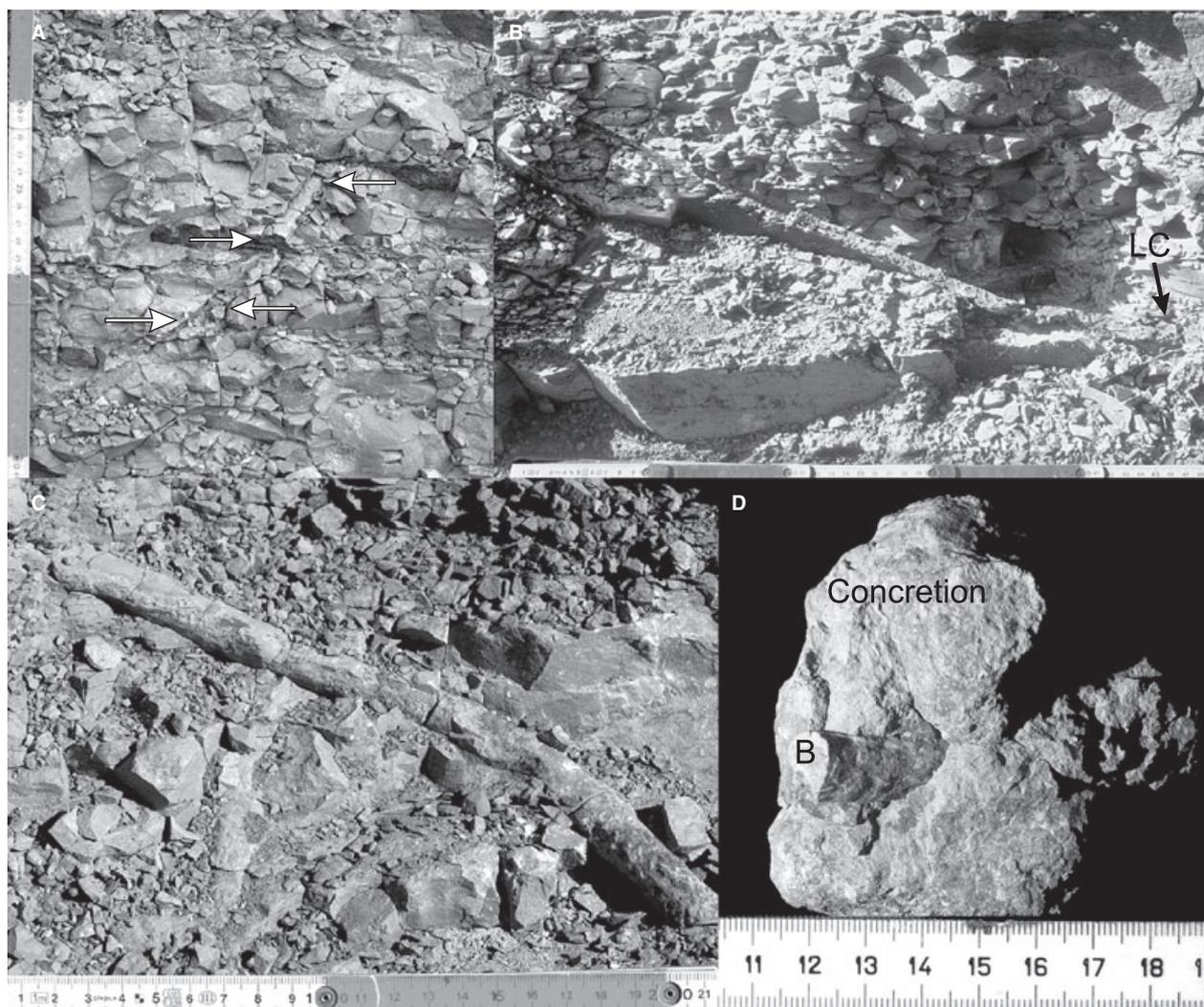
SEM analysis was used at SMU to evaluate the mineralogical composition of interesting mineral grains associated with the burrows, matrix, and concretions.

BURROW CHARACTERIZATION

Burrows recovered from Carlton Heights and Bethulie display the same morphological and dimensional features. All exhibit a consistent diameter of 1–2 cm throughout recoverable lengths of 5 – >40 cm (n = 98) in outcrop terminating in a slightly enlarged chamber; no tapering of the burrow diameter was observed in either distal or proximal regions (Text-fig. 4A). The overall shape is cylindrical, with a circular to ovate cross-section when completely filled (Text-fig. 5A); when fill is incomplete, cross-sectional shapes vary from elliptical to flattened. Burrows are inclined in the substrate where the angle ranges between 20 and 30 degrees; there is no evidence of branching. Longer examples display a change in inclination over the exposed length; the most complete burrow is sigmoidal in geometry (Text-fig. 4B), exhibiting a soft

S-shape as it descends into the substrate (Text-fig. 4C). The angle of inclination decreases towards the basal terminus (Text-fig. 4A) where a slightly enlarged chamber is preserved. In general, the upper burrow sections are inclined at angles of 21 degrees (n = 35; range 20–24°) and then change to a steeper 28-degree angle at mid-depth (n = 38; range 27–35°). As the burrow comes towards the lower terminus it slopes to a more gradual angle of inclination averaging 15 degrees (n = 27; range 11–18°). Hence, the difference in angle of inclination of individual burrow segments exposed in outcrop is a result of the change in configuration over the course of the sigmoidal trace. Steeply inclined sections indicate mid-burrow exposure, whereas more proximal or distal burrow segments show more shallow angles of inclination.

A maximum density of six burrows per m² occurs in the N9 highway exposure where they cross-cut lithological changes. Burrows may cross-cut a sandstone bed and are sandstone filled, whereas others that cut across thin beds of alternating sandstone and siltstone are generally siltstone-filled. A small proportion of burrows exhibit an exposed enlarged basal chamber that, while not exagger-



TEXT-FIG. 4. Outcrop and laboratory photographs of *Katbergia* gen. nov. in matrix. A, a more vertically orientated *in situ* shaft extending for >25 cm in length (N9 outcrop). Incompletely exposed burrows are a typical occurrence of *Katbergia*. B, an extensive burrow orientated at a more acute angle with an intact terminal living chamber (LC). This sigmoidal burrow was exposed in the railway cutting below the P/Tr boundary. Scale is in dm. C, the holotype burrow of *Katbergia* (specimen BP/6/687) that shows a sinuoid curvature of the cylinder, twisting downwards into the matrix. This architecture is characteristic of the upper parts of the burrow trace (N9 outcrop). Scale in dm and cm. D, *Katbergia* burrow (B) around which an early diagenetic carbonate concretion formed subsequent to the filling of the burrow. Scale in cm.

ated, may be 3–4 cm in diameter (compared to the 1–2 cm diameter) and extend 5–6 cm (Text-fig. 4B).

Calcareous nodules of various shapes and sizes co-occur within the bioturbated siltstone; none is pisolith-sized. These nodules occur in horizons rather than being dispersed in the matrix, and are found near the base of the burrowed interval, usually within the lowermost 10 cm. The close relationship between nodules and burrows is illustrated best by one example where a burrow crosscuts a nodule of spherical to elongate shape (Text-fig. 4D). Both nodules and burrows are in sharp contact with the matrix. No gradational boundaries exist between the burrow fill, walls, and the entombing siltstone.

Most burrows from Carlton Heights and Bethulie were siltstone-filled, but several were sandstone-filled. Burrow-fills are a homogeneous mixture of silt-sized clasts of quartz, feldspar, and calcite. The absence of visible primary or secondary structures in both transverse and longitudinal thin section in most samples indicates passive burrow-fill (Text-fig. 5). Burrows appear unlined, although the contact between burrow margin and matrix may appear diagenetically modified (Text-fig. 5A). Marginal rim alteration is not found in all thin sections, and thin section examination under epifluorescence microscopy indicated an absence of organic matter within and surrounding the burrow. Small scale, fining-up sequences

comprise the burrow-fill where preserved, with bedding surfaces well defined in longitudinal thin section (Text-fig. 5). Primary structures are tangential to the cylindrical burrow, indicating that they were filled on an incline. Fining-upward sequences include mm-sized siltstone clasts aligned along bedding planes, indicating that burrow fill was accomplished through multiple, repetitive depositional events from suspension load (Gastaldo *et al.* 1989).

The burrow walls preserve a series of intricate scratch patterns that can be separated into three distinct hierarchical categories (Text-figs 6, 7A). The primary set includes long marks, obliquely angled to the longitudinal axis of the burrow. These are up to 2.3 cm in length, straight, and appear to occur in pairs (Text-fig. 7B). The

second set consists of short, transverse scratches up to 1 cm in length, and also are paired (Text-fig. 7C). Lastly, a pattern of small, curved, crescent-shaped scratch marks exists, each of which may be 0.9 cm in length (Text-fig. 7D). This tertiary set is characterized by their crescent shape, also occurring as paired markings. Paired longitudinal and transverse scratches exhibit parallel, convergent and divergent patterns, with the orientation of these markings in both directions along the length of the burrow. Scratches are concentrated around the sides and top of the burrow, with a reduced density along the burrow floor (Text-fig. 7).

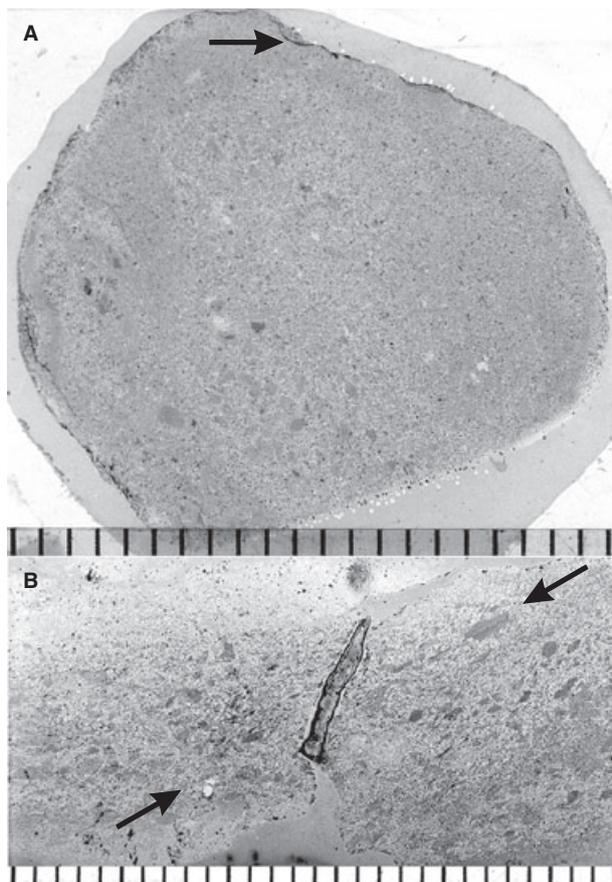
Mineralogy, organic carbon, and stable isotopes

The mineralogy of the matrix and the siltstone and sandstone burrow-fills are almost identical, consisting of feldspar, quartz and calcite, with the last of these found in trace quantities. SEM examination with EDAX revealed that several clasts may be zircon and apatite, or bone chips. There is no difference in the Total Organic Carbon (TOC) and Total Organic Nitrogen (TON) values of the matrix and the burrow fill. TOC values for the matrix range from 0.07 to 1.18% (N = 18), whereas TOC values in the burrows range between 0.02 and 0.95% (N = 15).

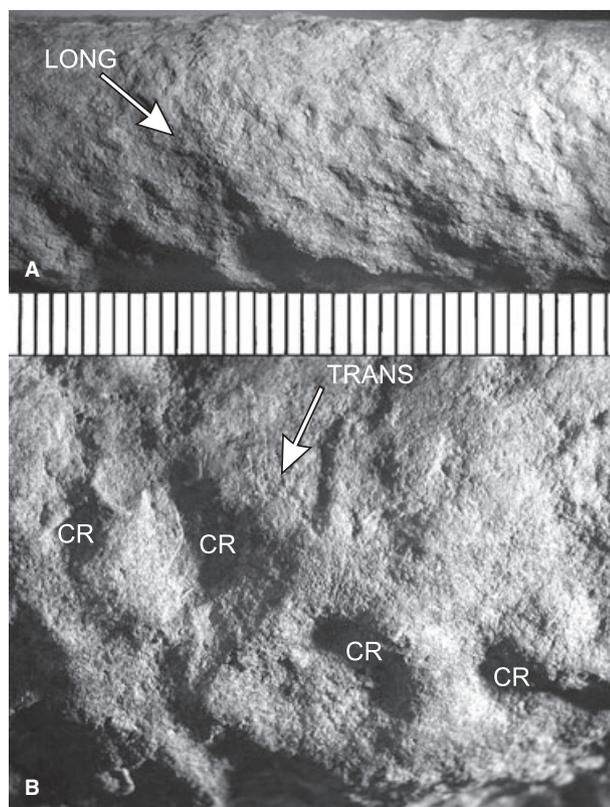
Stable isotope data for the matrix and burrow fills are presented in Table 1. The stable oxygen-isotope data from Carlton Heights matrix- and burrow-fills fall within a narrow range from -14.6 to -23.3 $\delta^{18}\text{O}$, with the lowest value from a matrix sample (Text-fig. 8). There is a greater range in $\delta^{13}\text{C}$ values from -4.7 to -23.3 for burrows. Burrow-fills from Bethulie plot within the spread of Carlton Height values, and fall approximately midway within that range.

COMPARISON WITH *MACANOPSIS*

The genus *Macanopsis* has grown to include several species since the type, *M. pagueyi*, was published (Macsoy 1967) from lithologies interpreted to represent fully marine conditions. *Macanopsis erewhonensis* (Retallack, 1979), *M. astreptum* (Bown and Kraus, 1983), and *M. plataniformis* (Muniz and Mayoral, 2001) are morphologically quite different from each other, as well as from the holotype (Table 2). *Macanopsis erewhonensis* is a burrow 2–3 cm in diameter, 3–4 cm in length, with a distinct entrance and living chamber (Retallack 1979). The angle of inclination is described as ‘steep’, but the overall shape of the burrow is not described. Broad scratch marks of undefined length or morphology are preserved on the burrow floor and in the living chamber. The inferred burrower is a brackish to marine invertebrate with rounded swimmerets, which were



TEXT-FIG. 5. Thin sections of burrows in transverse and longitudinal views in transmitted light. A, transverse section of burrow in which a rim of diagenetic colour alteration can be seen at arrow. No evidence has been found for a burrow lining, armouring, or ornamentation. Several fining-upward sequences can be seen within the section (basal bed consisting of 0.5–1-mm mudclasts fining into silt). Specimen BP/6/697. B, longitudinal section showing the alignment of mm-scale clasts on inclined bedding planes (at arrows). Specimen BP/6/696. Both scales in mm.



TEXT-FIG. 6. Scratch patterns preserved on the exterior of *Katbergia* burrows. A, longitudinal scratches (LONG) run at an angle to the burrow, and can be found partially to encircle it. Scale in mm. B, crescent (CR) and transverse (TRANS) scratches of holotype (specimen BP/6/687) are intermixed with longitudinal scratch patterns. See Text-figure 7 for scratch-pattern hierarchy.

responsible for the creation of the broad scratch patterns (Retallack 1979). Hence, this ichnotaxon is characteristic of an organism with a fully aquatic marine habit. The ichnotaxon *M. astreptum* has a distinctive short, vertical tube shape with a bulbous termination (Bown and Kraus 1983). The holotype is 1.2 cm in diameter and only 3–4 cm in length. No scratch pattern is described nor is a burrower inferred for this common Cretaceous floodplain (Bown and Kraus 1983) and Tertiary point-bar ichnotaxon (Bown 1982). *Macanopsis plataniformis* is a ‘banana-shaped burrow’, 3.4–13 cm in diameter and 8–45 cm in length, with a subvertical shaft that opens into a broad elongated chamber (Muniz and Mayoral 2001). It differs by possessing a 0.25-cm-thick lining. Scratch marks are poorly preserved and restricted to the floor of the burrow (Muniz and Mayoral 2001). *Macanopsis plataniformis* is admittedly different from *M. pagueyi* and *M. astreptum* in overall burrow shape and size, and it is reported only from shallow sublittoral marine facies. Hence, the taxon responsible for this burrow was a marine invertebrate. Because of the dissimilarities

between their ichnotaxon and other ichnospecies, Muniz and Mayoral (2001) proposed that *M. plataniformis* was similar to the ichnotaxon, *Psilonichnus upsilon*, to which it often is compared. Frey *et al.* (1984) compared *Macanopsis* to *Psilonichnus* and *Skolithos*, two genera that share some characteristics with *M. pagueyi*. *Psilonichnus* has a J-shaped tubular form, but differs from *Macanopsis* by the presence of a terminal hemispherical chamber and the absence of the bifurcated morphology of *Psilonichnus*, and does not share anything besides a cylindrical shape with *Macanopsis*. A comparison of the features of the South African material and the above ichnotaxa (Table 2) demonstrates that although it shares some similarities with *Macanopsis*, the overall sigmoidally shaped burrow, in which shaft orientation changes with depth, along with a hierarchy of paired scratch marks preserved on burrow walls (but not floors), makes this form different. Hence, the creation of a new taxon for these late Permian and early Triassic burrows is warranted.

SYSTEMATIC PALAEOLOGY

Ichnotaxon KATBERGIA gen. nov.

Text-figures 4–5

- 1995 Unassigned invertebrate burrows; Smith, p. 93.
- 2001 Unassigned callianassid-like burrow; Smith and Ward, p. 1148.
- 2003 *Macanopsis*, ?crustacean; Retallack *et al.*, p. 1143, fig. 10, table 2.
- 2003 Sub-horizontal, cylindrical burrows; Steiner *et al.*, p. 407.
- 2005 Unassigned callianassid-like burrow; Smith and Botha, pp. 559–560.

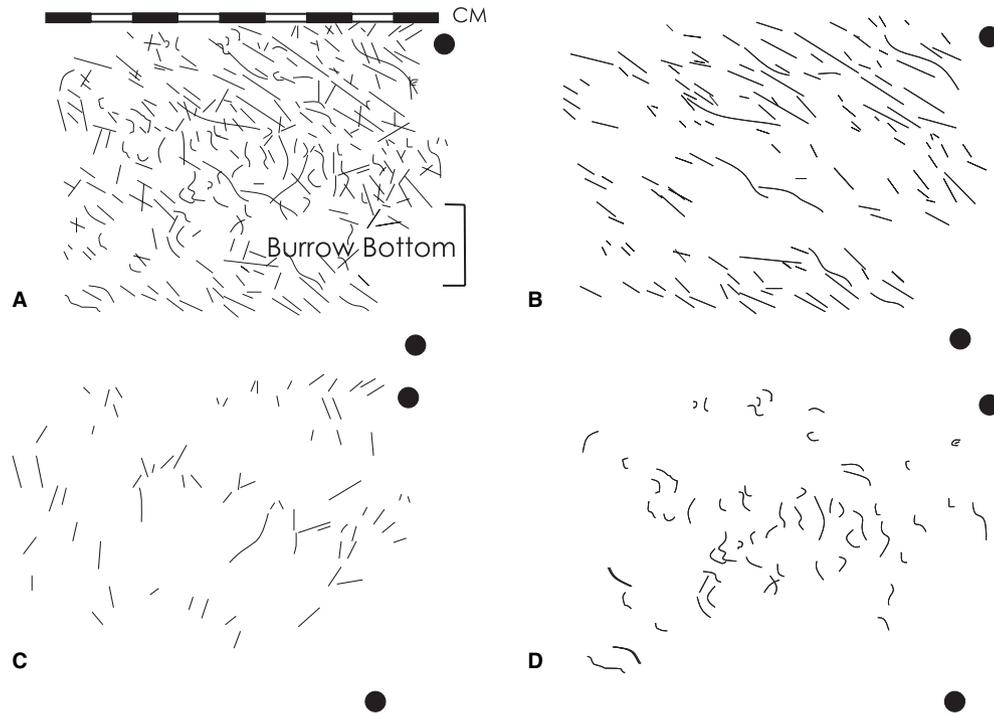
Diagnosis. Long, cylindrical, unlined, non-branching burrow with a terminal chamber; terminal chamber *c.* 2–3 × cylinder diameter, extending 4–6 cm beyond end of cylindrical geometry; inclined at angles ranging from 11 to 35 degrees, straight to sinusoidally curved, overall sigmoidal geometry; burrow wall characterized by paired scratches.

Katbergia carltonichnus sp. nov.

Text-figures 4C, 6–7

Diagnosis. Presence of three scratch-pattern hierarchies: longitudinal, transverse, and elliptical (crescent-shaped); less concentrated on burrow floor.

Type locality. Carlton Heights, South Africa (31.29228° S, 24.95152° E).



TEXT-FIG. 7. Scratch-pattern hierarchy as determined from tracings of burrow photomosaics that have been unrolled; holotype (specimen BP/6/687). A, composite of all scratch types as observed on the burrow exterior. B, the longitudinal scratch pattern. C, the transverse scratch pattern. D, the crescent scratch pattern. Black dots are registration marks.

Other localities. Bethulie (31.30700° S, 24.95450° E), Lootsberg Pass (31.50867° S, 24.52712° E), Graaff-Reinet area, South Africa (Smith and Botha 2005).

Types. Holotype, Text-figures 4C, 6–7, BP/6/687, curated at the Bernard Price Institute of Palaeontology, Witswatersrand University, Johannesburg, South Africa. Paratype, BP/6/688. Lectotypes, BP/6/689–BP/6/697.

Stratigraphic position. Upper Permian–Lower Triassic Palingkloof Member, Balfour Formation, and Lower Triassic Katberg Formation.

Age. Late Permian–Early Triassic.

DISCUSSION

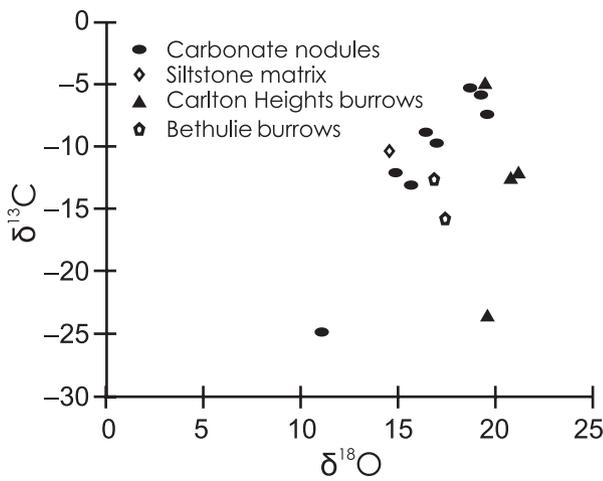
The burrows described here have received some attention in previously published literature. The casts were first assigned to the genus *Macanopsis* by Retallack *et al.* (2003), although they were noted by Ward *et al.* (2000) and used as a criterion to identify an Early Triassic ‘dead zone’. Retallack *et al.* (2003) used their presence to define the Budi, Patha, Zam, and Pawa palaeosols, all of which were interpreted to have developed under an ‘unknown’ palaeoclimate with a vegetational cover consisting of horsetail marsh, riparian bushland, or quillwort marsh.

Smith and Botha (2005) recently described the same burrows but chose not to assign them to either *Macanopsis* or another ichnotaxon. Instead, they reiterated an earlier interpretation that they are callianassid-like burrows that have scratch marks that are either irregular (Retallack *et al.* 2003) or possibly present on the outer surface (Smith and Botha 2005). *Katbergia* from Carlton Heights and Bethulie, however, displays an indisputable hierarchy of paired scratch patterns and cannot be considered as callianassid-type burrows. Callianassid-type burrows are a J- to Y-shaped crustacean trace and assigned to the ichnotaxon *Psilonichnus upsilon* (Frey *et al.* 1984). *Psilonichnus* is considered indicative of shoreface and estuarine settings (Nesbitt and Campbell, 2006) and shares few of the same characteristics as the continental burrow casts described from the Karoo Basin.

The Karoo burrows were filled by passive means; hence, the casting lithology is a record of what sediments were deposited after the burrow was abandoned. The substrate in which the burrow was excavated was firm enough to maintain a constant cylindrical diameter to an uncompressed depth of at least 0.5 m, as well as allowing for the preservation of detailed scratch marks along the entire burrow length. The orientation and variety of paired scratch marks on the burrow wall (Text-fig. 6) indicate that as the animal tunnelled in and out of the inclined burrow no part of the structure broke the plane of the

TABLE 1. Stable $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ isotope values for Matrix and Burrow samples analyzed from Carlton Heights (CH) and Bethulie (BE), and Carlton Heights concretions (data from Tabor *et al.* 2007).

Sample	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	CH Concretions	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$
CH matrix	14.6	-10.3	CH Microspar	15.0	-12
CH Burrow	19.8	-23.3	CH Radiaxial	11.3	-24.4
CH Burrow	21.1	-12.4	CH Radiaxial	16.6	-8.8
CH Burrow	19.7	-4.7	CH Microspar	15.9	-12.8
CH Burrow	21.3	-12.2	CH Radiaxial	19.6	-7.3
BE Burrow	17.1	-12.5	CH Radiaxial	17.2	-9.5
BE Burrow	17.5	-15.6	CH Micrite	19.0	-5.2
			CH Micrite	19.4	-5.7



TEXT-FIG. 8. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values are plotted for carbonate nodules recovered from burrowed siltstone facies (data from Tabor *et al.* 2007), siltstone matrix from adjacent to a burrow (present study), and *Katbergia* burrows from Carlton Heights and Bethulie (present study).

water table. It remained below the terminal living chamber during inhabitation because water-table fluctuations would have resulted in a periodically flooded burrow, wherein scratch patterns along the wall would have been smeared or obliterated upon subsequent activity. Clark and Ratcliffe (1989) noted that sediment cohesion and grain size are the limiting factors affecting burrow construction, and burrows that are used over time as permanent dwellings are constructed in a substrate that is sufficiently firm to prevent collapse (Bryson 1939). In a fine-grained substrate that is too wet or saturated, there will be insufficient grain cohesion to maintain an open burrow, and when the substrate is too dry, the sediment is incompressible and prone to roof failure as the animal moves throughout the course of the burrow. Abandonment by the burrower occurred when pore-water conditions in the silt substrate changed, resulting in an

TABLE 2. Comparative characteristics of the ichnotaxa assigned to *Macanopsis* Macsotay (1967), '*Macanopsis*' as described from the Karoo Basin (Smith 1995; Smith and Ward 2001; Retallack *et al.* 2003; Steiner *et al.* 2003; Smith and Botha 2005), *Psilonichnus upsilon*, and *Katbergia carltonichnus* gen. and sp. nov.

Ichnotaxon	Branched	Diameter (cm)	Length (cm)	Lining (mm)	Shape	Inclination	Scratches	Terminal chamber
<i>M. pagueyi</i>	No	1-3	15.7	N/R	J-shaped	N/R	N/R	spherical
<i>M. astreptum</i>	No	1.2	4.6	N/R	Vertical tube	90°	none	roughly spherical
<i>M. erewhonensis</i>	No	2-3	3-4	N/R	N/R	'steep'	broad scratches	living chamber
<i>M. plataniiformis</i>	No	3.4-13	8-45	0.25	Banana-shaped	70-80°	poorly preserved on floor	most of trace fossil is chamber, with only small entrance burrow
' <i>Macanopsis</i> '	No				'oblique'		'irregularly scratched'	yes
<i>P. upsilon</i>	Yes	2.5-4.5	≤120	No	J- or Y-shaped	gently inclined	none	terminus not preserved
<i>Katbergia</i> gen. nov.	No	1-2	≥50	No	Sinusoidal	varied; differs proximal, medial, distal	longitudinal, transverse, and crescent-shaped	2-3 times wider than burrow width; 2-3 times longer than burrow width

inhospitable domicile. After the structure was abandoned, the burrow would have remained open and filled with whatever sediments were transported by suspension load and deposited by settling into the tube (Gastaldo 1992).

A variety of exterior scratches is preserved on the burrow casts and can be used as clues to behavioural patterns of the burrow dweller. The longest, most longitudinally orientated scratches are paired and represent normal traffic in the burrow. Several scratch pairs converge, while others diverge along the sides and top, showing that the movement was in two directions up and down the length of the cylindrical burrow (Text-fig. 7B). The shorter, transverse scratches also are paired and restricted primarily to the burrow sides (Text-fig. 7C). These may represent repairs made to the inside of the tunnel in the event of sediment collapse. The small crescent-like marks are found concentrated on the burrow floor and may represent either routine maintenance to the inside of the burrow or indentations by appendages to stabilize the animal within the inclined burrow. Hence, these may be resting traces (cubichnia), while longitudinal and transverse scratches may represent locomotion traces (repichnia) within a burrow that acted as a domicile (dominichnia).

To produce a paired scratch pattern on the inside of the burrow, an appendage consisting of two parts that lie in parallel is required. Such appendages include pincers (modified pedipalps) or claws that may result in a repetitive and consistent pattern. Reported potential tracemakers of *Katbergia* include spiders (Chelicerata), beetles (Uniramia), and crabs and shrimps (Crustacea; Retallack *et al.* 2003; Smith and Botha 2005). Alf (1968) described a spider trackway from the Permian Coconino Formation, Arizona, preserved in sandstone wherein the impressions consist of three points in a forward line with a single point behind the inner of the three forward points. There is no evidence of any additional appendage that may have acted in consort to produce a paired trace within a burrow system. Hence, an arachnid can be excluded from potential *Katbergia* trace makers. Permian beetles are known primarily from remains of elytra (Ponomarenko and Mostovski 2005), although body fragments including pronota (dorsal plate of the prothorax) have been recovered from the Kuznetsk Basin (Aristov 2004). To date, there is no evidence for paired appendages in the families of Late Permian and Early Triassic beetles that could have produced these traces. Burrowing decapod crustaceans include shrimps, crabs, and crayfish, the latter two taxa equipped with pincers or claws capable of leaving paired scratch marks on a burrow interior. Although the oldest decapod crustacean was reported from Early Permian deposits in Antarctica and identified on the basis of a fossil claw (Babcock *et al.* 1998), the specimen has been reinterpreted recently as a euthycarcinoid arthropod (Hasiotis 2002). Miller *et al.* (2001) could not discount

the burrows associated with these body fossils as having been made by crayfish, because surface scratch marks are diverse, including chevron-shaped scratches within a basal groove, and are associated with a knobby texture. Antarctic burrows are characterized as having a lining and/or mudchip exterior surface, typical of crayfish burrows (Hasiotis and Mitchell 1993). The characters of the L-burrows of Miller *et al.* (2001) differ from the burrow morphology described for *Katbergia*.

Endemic, Southern Hemisphere freshwater crayfish belong to a monophyletic group assigned to the superfamily Parastacidae (Crandall *et al.* 2000). Burrows consist of several morphologies (depressions, U-shaped, and networks; Grow 1981), but the most common is an angular pit consisting of a simple tunnel that ends in a terminal chamber (Lawrence 2001). In general, there is a single entrance to each cylindrical burrow that averages 0.5 m in depth (max. 1.48 m) with the enlarged chamber or cavern that is 2.4 times the mean-tunnel diameter (Lawrence 2001). As in other crayfish taxa, the burrow wall may have a mud and lag liner and is ornamented with knobby and hummocky surfaces. If the animal that excavated *Katbergia* burrows was a decapod crustacean, the burrow morphology of that unknown taxon is consistent with the general aspect of burrow morphology and may be a variant not recorded in any of the three recognized Recent superfamilies.

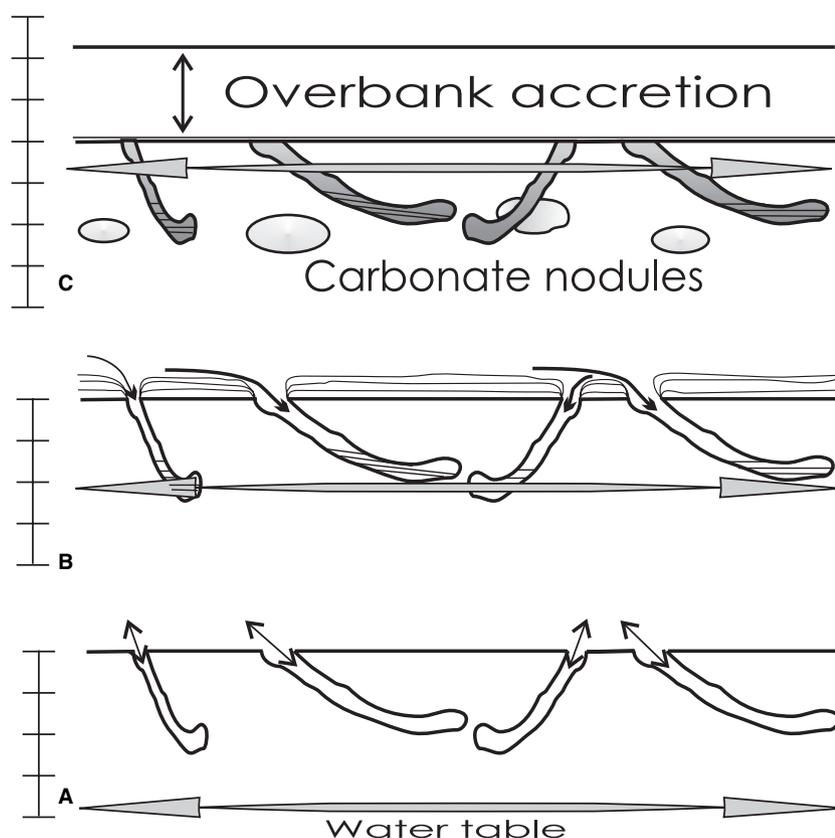
Burrow-fill and substrate mineralogy are very similar, which is not surprising because of the passive nature in which the burrows were filled and the restricted sediment facies in the system (Pace *et al.* 2005). What is unique at the P/Tr boundary sites in the south-western Karoo (Carlton Heights, Bethulie, Lootsberg Pass, and presumably elsewhere; e.g. Graaff Reinet; Smith and Botha 2005) is that the burrows are associated with horizons of carbonate nodules. At times they are preserved between nodule horizons, sometimes they are above them, and in at least one case the nodule formed around the burrow (Text-fig. 4D). Hence, there is a temporal gap between the time of colonization and burrow formation, subsequent abandonment and fill, and the development of the carbonate nodules. This differs from the interpretation of Retallack *et al.* (2003) and others about the relationship between burrows and calcite concretions in these palaeosols, who indicate contemporaneity of these features.

Calcite cement is found within the siltstone matrix and burrow-fills, and their stable isotope signatures cluster together with those of the calcareous nodules found in the same stratigraphic horizons (Text-fig. 8), indicating that the cement is diagenetic. Tabor *et al.* (2007) have reported stable isotope data on a suite of calcareous nodules from Carlton Heights consisting of samples from two separate populations of concretions. One concretion population originated from channel-lag deposits recovered

from the base of sandstone channel forms, whereas the second population consists of the larger concretions within the bioturbated siltstone (Text-fig. 3). Concretions within the pebble conglomerate display micritic cement whereas nodules in association with *Katbergia* are characterized by radially and microspar calcite. They concluded that channel-lag concretions formed in equilibrium with atmospheric $p\text{CO}_2$ (open system), representing allochthonous residuals from calcsols as suggested by Pace *et al.* (2005), whereas the stable isotopic signatures of the larger nodules do not reflect calcite precipitation that was in equilibrium with the atmosphere. Rather, these values are indicative of calcite crystallization under poorly drained, waterlogged soil conditions within a semi-closed system (Tabor *et al.* 2007). Hence, the calcite cement found in the siltstone, burrow-fills and associated concretions was formed after the burrows were abandoned, filled, and

shut off from atmospheric gases (Text-fig. 9). These conditions indicate that the regional water-table had risen above the level of the burrows before initiation of calcite precipitation. This is supported by the cross-cutting relationships of concretions and burrows (Text-fig. 4D). Hence, burrow formation and nodule precipitation were not contemporaneous.

Retallack *et al.* (2003) interpreted the occurrence of *Katbergia* and the presence or absence of calcite nodules, along with sediment colour and grain size, as representing distinct Late Permian and Early Triassic palaeosol types in the Carlton Heights sequence. Subsequent literature has refrained from using the classification system (Ward *et al.* 2005; Smith and Botha 2005), calling into question their utility in the Karoo Basin. Late Permian bioturbated soils include the Zam type described as a bedded purple-grey siltstone with root traces, burrows, and pale-yellow



TEXT-FIG. 9. A model for the temporal development of the *Katbergia*-bioturbated siltstone facies found at Carlton Heights, Bethulie, and elsewhere in Late Permian and Early Triassic deposits of the Karoo Basin. A, overbank deposits are colonized during an interval of landscape stasis by an invertebrate, with the burrows excavated deep into the substrate. A terminal living chamber is established above the local/regional water table in a poorly developed soil (inceptisol). B, initiation of landscape aggradation results in the rise of the local/regional water-table wherein burrows are abandoned. This is followed by the passive fill of burrows that occurs during short-term depositional events. Graded bedding preserved within burrows attests to the slow and episodic nature of overbank deposition. C, landscape aggradation continues at a more rapid rate, resulting in accumulation of overbank deposits within which burrowing animals are unable to colonize extensively. Local/regional water table rises and reaches the stratigraphic position of the burrows. Calcite cement and calcitic nodules within the siltstone matrix are precipitated in and around filled *Katbergia* burrows resulting in the development of calcic gleysol features.

nodules (Retallack *et al.* 2003, table 2, fig. 6), and interpreted as a protosol. Weakly developed Early Triassic palaeosols include Budi, which are green-grey, bedded sandstones in which root traces and burrows are preserved, and Patha soils, which are reddish brown silty clay or clay with relict bedding, root traces, and burrows. Sedibos are more well-developed, grey clay soils with calcareous concretions found at depth, interpreted as aridisols and calcic gleysols. The depth at which these concretions are found was used as evidence that the water table dropped low in the profile for part of the year. Burrows are either noted as a characteristic of Sedibo palaeosols (Retallack *et al.* 2003, p. 1143) or not (Retallack *et al.* 2003, table 2), and their presence in these horizons appears to be an overprint onto the soil horizon (Retallack *et al.* 2003, fig. 6). Stable isotopic data presented herein indicate that carbonate concretions within bioturbated siltstone are a diagenetic feature that is subsequent to colonization and abandonment of the substrate by a population of *Katbergia*-excavating organisms. Hence, bioturbation is the primary alteration of the aggradational siltstone, not the formation of carbonate nodules at depth in response to aridity, making recognition of the Sedibo-palaeosol type untenable.

Fine-grained lithologies in which *Katbergia* are preserved have been interpreted as either lake-margin sediments, where the water-table would have been high, within a saturated soil (Retallack *et al.* 2003), or playa-lake deposits (Smith and Botha 2005). Such interpretations appear to be predicated on an interpretation that the burrow maker was a callianassid-type crustacean. The physical conditions necessary to excavate and maintain *Katbergia* burrows preclude saturated sediment and a high water-table, although the sediment must have been sufficiently moist (Bryson 1939). There is no physical evidence within any bioturbated siltstone interval for coeval desiccation cracks that would reflect dry periods that had affected the burrowers. Such features occur either below (Text-fig. 3) or above bioturbated zones (Pace *et al.* 2005). Hence, colonization of a playa-lake setting cannot be corroborated. The repetitive occurrence of *Katbergia*-bioturbated siltstone within each genetic sequence identified in the Carlton Heights section (and elsewhere, including Lootsberg Pass; unpublished 2006 field data) demonstrates that similar environmental conditions prevailed over space and time within the aggradational phase of the Karoo landscape (Pace *et al.* 2005). The environment in which *Katbergia* burrows are preserved is interpreted as overbank-floodplain deposits that were incipient soils that had undergone progressive saturation. Burrowing occurred in an inceptisol (Mack *et al.* 1993) that was overprinted as the water-table rose and the sediments were altered to gleysols (Mack *et al.* 1993) in which the calcite precipitated (Tabor *et al.*

2007). This interpretation is in accord with the broad generalizations of previous authors identifying alluvial soils (Retallack *et al.* 2003) in the Late Permian and Early Triassic (budi, protosol; sedibo, calcic gleysol), but the results of the present study refine the timing and sequence of soil formation in the Palingkloof and Katberg formations, requiring a re-evaluation of characterized soil types in the Karoo Basin.

CONCLUSIONS

A new ichnogenus, *Katbergia*, is described and characterized as a long, untapering, cylindrical burrow that changes trajectory from the surface to the deep subsurface, ending in a slightly enlarged living chamber. A distinct suite of hierarchical scratches line the burrow walls of this sigmoidal trace, indicating several behavioural activities of a probable decapod crustacean. The burrows are characteristic of poorly developed inceptisols where the water-table was maintained below the level of the living chamber. Abandonment and burrow infill reflect aggradational phases of the interfluvial areas with an accompanying rise in the water-table. The result of aggradation and water-table rise was the development of gleysols in which calcite precipitated as cement in burrow-fills and enclosing silt matrix, and calcareous nodules that grew around burrows. These conditions prevailed before, during and after the P/Tr extinction event in the Karoo Basin, indicating relatively constant environmental factors that prevailed during this interval.

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