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## ENIGMATIC TRACE FOSSILS FROM THE AEOLIAN LOWER JURASSIC CLARENS FORMATION, SOUTHERN AFRICA

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### ABSTRACT

The Lower Jurassic aeolienites of the Clarens Formation in southern Africa contain unique sedimentary structures that are unlikely to be non-biogenic. They are also unlike any known modern or ancient trace fossils. Here, some enigmatic, horizontal, regularly-oriented sedimentary structures are described, which occur in association with other trace fossils as well as features that were previously interpreted as nests of termites or termite-like ancient social insects. These spectacular structures are exposed in enormous profusion as straight, ~5 mm cylinders with strong compass orientation, in parallel alignment with one another and to ancient horizontal bedding planes. Their fill is identical to that of the host rock: clean, well-sorted, very fine- to fine-grained quartz-arenite. In cross-section, each structure is defined by a subtle, ~0.1 mm thin, concentric gap.

Without comparable modern biogenic structures, the biological origin of the structures is uncertain. Their strong compass orientations are, however, also inconsistent with an inorganic origin, even though they may resemble pipey concretions generated by flowing groundwater. Nonetheless, this paper, based on spatiotemporal distribution patterns of the oriented structures, their locally high abundance and association with obvious trace fossils, as well as other sedimentological and palaeontological lines of evidence, argues that the compass structures may be products of ancient social invertebrates living in a resource-limited, semi-arid to arid environment. Furthermore, the compass structures as well as the accompanying structures of the predominantly aeolian Clarens Formation collectively imply the recurrence of favourable ecological parameters (e.g., moist substrates) related to episodic climate fluctuations in the Early Jurassic of southern Pangaea (i.e., southern Gondwana).

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**KEY WORDS:** enigmatic trace fossils; horizontal, regularly-oriented structures; aeolian deposits; Early Jurassic; Karoo

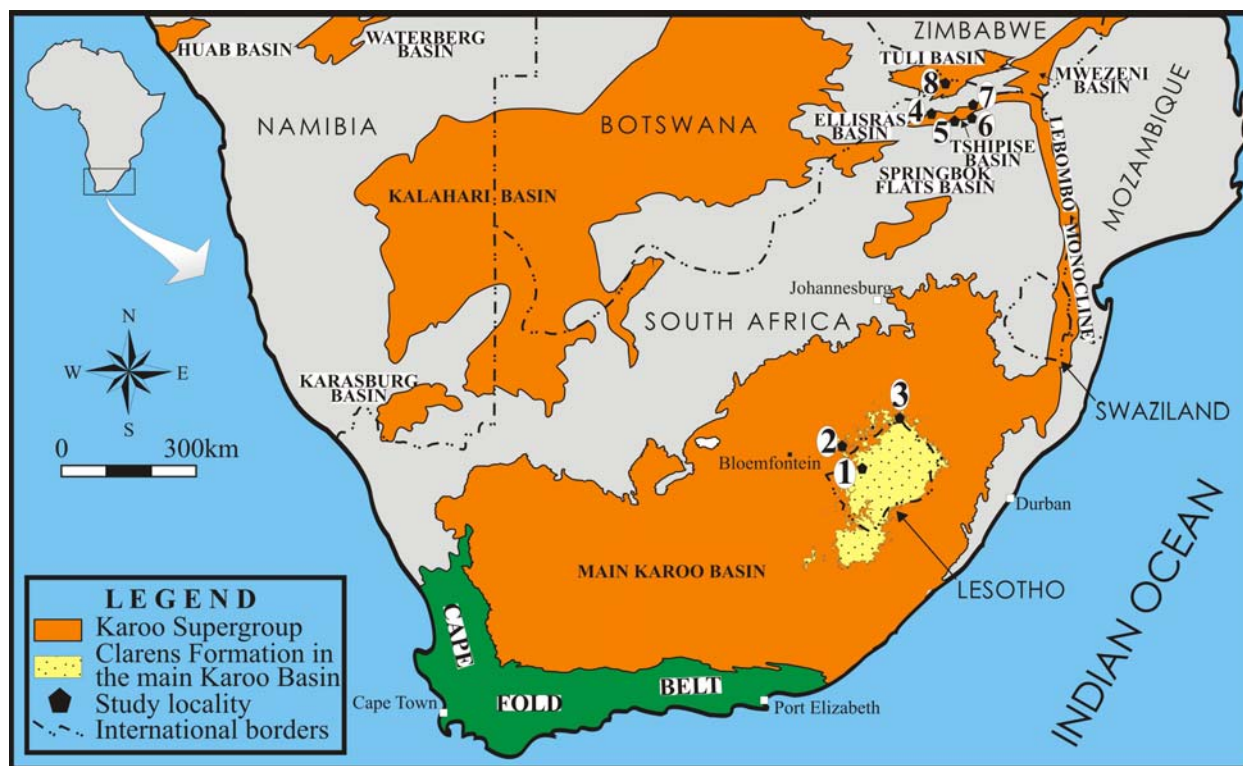
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**Figure 1.** Map of southern Africa, showing the distribution of the Karoo-age deposits and the location of the eight study sites (map modified after Johnson et al. 1996). Note that due to scale limitation, the Lower Jurassic Clarens Formation is only indicated in the main Karoo Basin.

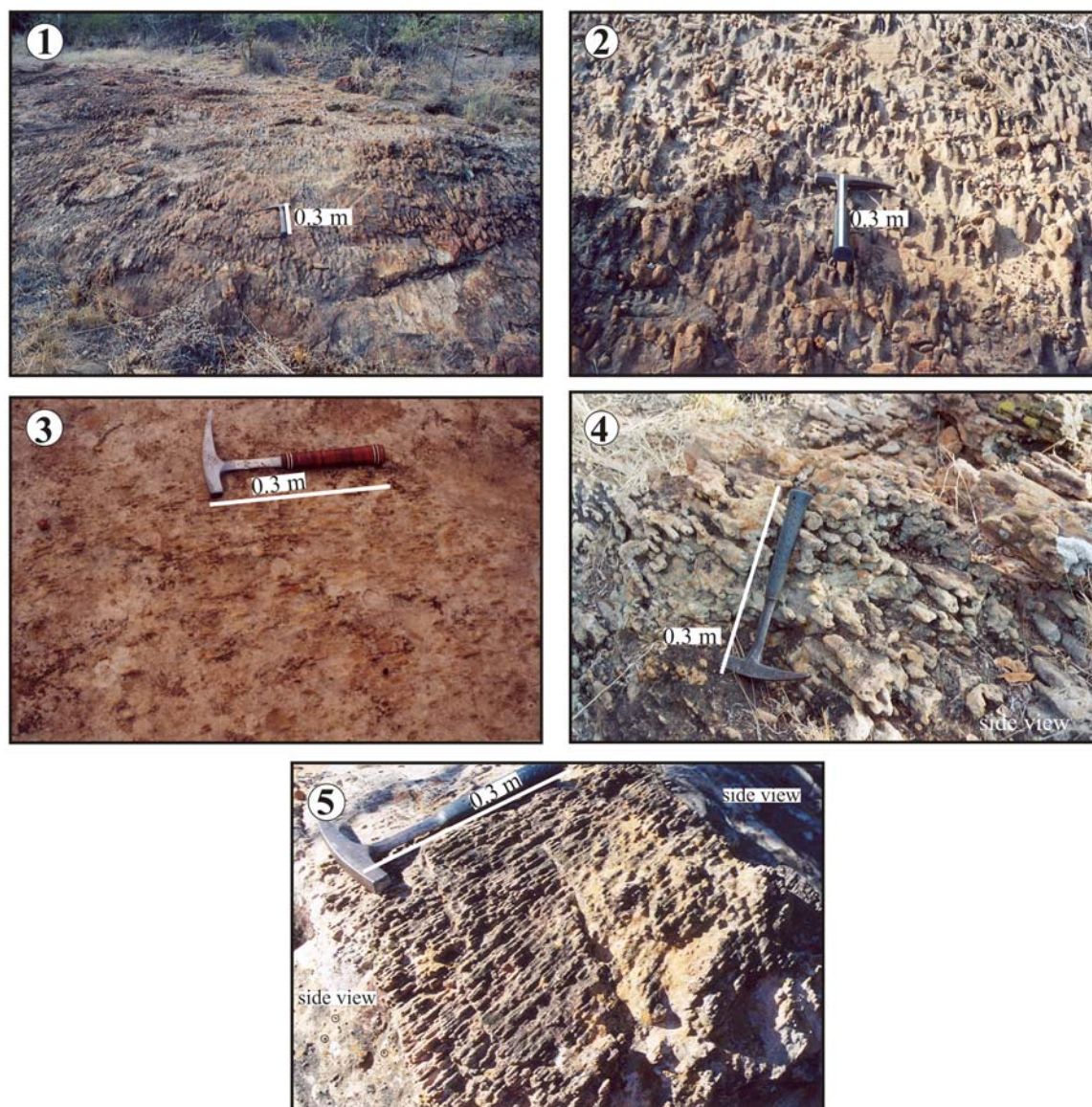
## INTRODUCTION

One of the most fascinating geological features of the mainly aeolian Lower Jurassic Clarens Formation of southern Africa (Figure 1) comprises the presence of unbranched, unornamented, cylindrical, exclusively horizontal structures, which show strong compass orientation and locally occur in enormous numbers on weathered surfaces (Figure 2). These bizarre features were first described from the Tuli Basin (South Africa) as Type 2 burrows accompanying some other unusual bioturbation features that were tentatively interpreted as Early Jurassic termite nests (Bordy and Catuneanu 2002; Bordy et al. 2004). Since this initial discovery, the horizontal, regularly-oriented structures have been observed in numerous other outcrops of the same stratigraphic unit in widely separated regions of southern Africa (Figure 1). In spite of these large spatial distances, the structures remain consistent in their physical appearance, and occur in clean quartz-arenites, reflecting substrates with homogeneous compositions and textures (Beukes 1970; Eriksson 1981, 1986; Johnson 1991 and personal observation).

The aim of this paper is to present detailed morphologic descriptions, some possible interpretations and geological implications (especially for the predominantly aeolian Lower Jurassic systems of southern Africa) of these unusual structures. This contribution is intended to stimulate the recognition of similar ancient and modern structures worldwide, and to lead to an eventual breakthrough regarding their true genesis.

### Geological Background of the Clarens Formation

The Clarens Formation is a buff-coloured, fine-grained arenite that ranges in thickness from a maximum of about 300 m in the main Karoo Basin, to less than 100 m in the Springbok Flats, Lebombo, Tuli, Tshipise and Ellisras Basins (Figure 1) (Johnson 1994 and personal observation). The gross lithological uniformity of the Clarens Formation led some casual interpretations of the unit (e.g., Truswell 1977) as product of an overly dry, sand sea, in spite of detailed investigations (e.g., Beukes 1970; Eriksson 1981, 1986) presenting evidence for episodic wetter phases during the predominant aeolian deposition.



**Figure 2.** Field occurrences of the enigmatic horizontal, regularly-oriented structures from the Lower Jurassic Clarens Formation of southern Africa. The structures commonly occur in great profusion, en masse on horizontal surfaces up to 100 m<sup>2</sup> (1 - 2) as well as in localized, smaller (eroded) patches (5). The density of the structures is typically extremely high (1 - 2), but locally only a few, rather loosely spaced structures are present (3). Side views (4 - 5) show that the structures have spherical cross-sections (see black circles in E), uniform diameters (~5 mm) and are preserved as full relief (4 - 5) or epirelief (1, 2, 3, 5). Also note that the thickness of the strata in which these structures occur varies from a few cm to over 0.5 m (4). 1-3 bedding plane views; 4 side view; 5 mainly bedding plane view, upper right and lower left corners side views.

Throughout southern Africa, the arenaceous Clarens Formation is characterized by massive units interbedded with sandstones (Figure 3) containing small- to very large-scale cross-bedding (planar, trough, low-angle), horizontal lamination, desiccation cracks, etc. (Beukes 1970; Van Dijk et al. 1978; Eriksson 1981, 1986; Bordy and Catureanu 2002). Evidence of soil formation is virtually

absent, with the exception of a single report of root-lets in a silty sandstone facies in the northeastern main Karoo Basin (Van Dijk et al. 1978). The described horizontal, regularly-oriented structures as well as other associated ichnofossils are preferentially found in structureless, massive facies.

The Early Jurassic age of the Clarens Formation is based largely on dinosaur biostratigraphy



**Figure 3.** Sedimentary structures (Sp – planar cross-bedding; Sh – horizontal lamination) in the Clarens Formation. This unit is a moderately to well-sorted, predominantly fine-grained (0.2 mm), massive, silica-cemented, clean quartz-arenite. Note the tangential to angular contact of the cross-beds.

and geochronology of the conformably overlying continental flood basalts, which were dated  $183 \pm 1$  Ma (late Early Jurassic) in the main Karoo Basin (Duncan et al. 1997), and 181-178 Ma in the north (e.g., Tuli Basin) (Le Gall et al. 2002; Jourdan et al. 2004).

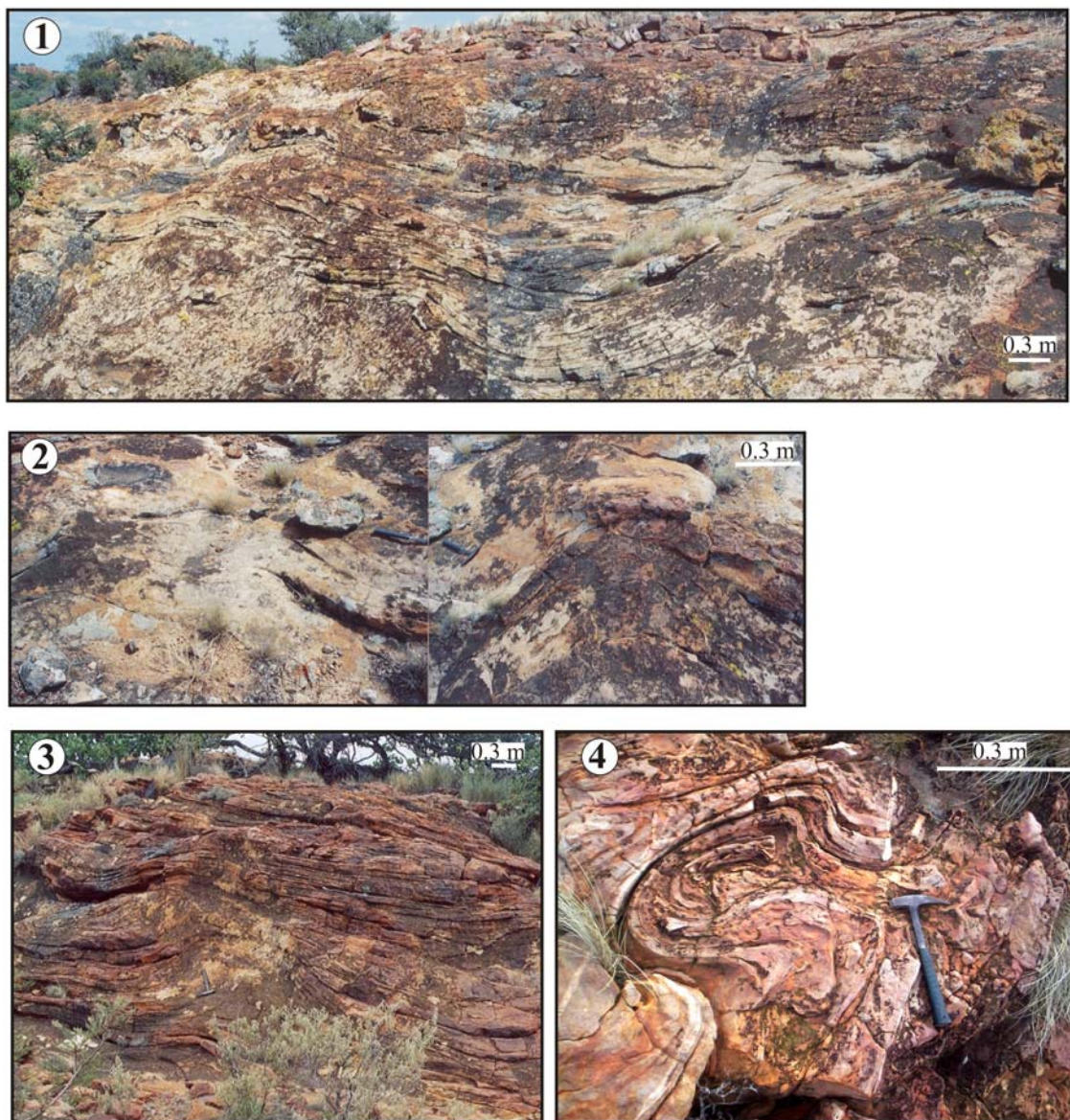
The palaeontological record of the Clarens Formation consists of invertebrate (e.g., crustaceans, insects), vertebrate (e.g., fish, dinosaurs, cynodonts), plant (e.g., sphenophytes, conifers) and numerous ichnofossils (e.g., gastropod trails, arthropod and vertebrate tracks) (Meijs 1960; Beukes 1970; Ellenberger 1970; Van Dijk et al. 1978; Kitching and Raath 1984; Tasch 1984; Olsen and Galton 1984; Smith 1990; Van Dijk 2001; Bamford 2004). This palaeontological diversity alone implies that the palaeoenvironments of the Clarens Formation were capable of sustaining, at least episodically, a relatively varied biota, and therefore could have not been overly resource-limited, harsh settings throughout the deposition of the unit. This interpretation is further corroborated by integrated sedimentary facies analyses (Beukes 1970; Van Dijk et al. 1978; Eriksson 1981, 1986; Eriksson et al. 1994; Bordy and Catuneanu 2002; Holzförster 2007), which suggest that the Clarens Formation was deposited in an overall aeolian environment, with wetter interludes during which ephemeral streams, lakes and wet interdune areas existed. The development of this arid to episodically semi-arid setting was most probably linked not only to the Early Jurassic latitudinal position of southern Africa within Gondwana ( $\sim 45^\circ$  south – Veevers 2004), but also to the rain shadow effect of the Cape Fold Belt (Figure 1), which formed a continuous mountain range along the southern margin of the study area.

The episodic drying and wetting of the climate across southern Africa during this time is substantiated by the large-scale spatiotemporal distribution

of wet aeolian conditions in the main Karoo Basin (Beukes 1970; Eriksson 1981, 1986) and in the smaller basins further north. For instance, in the Tuli Basin (Figure 1), both the lowermost and uppermost parts of Clarens Formation show sedimentary lithofacies indicative of deposition in ephemeral streams and ponds, as well as evidence of plant and animal life (e.g., channel fills, carbonaceous mudstones, coal seamlets, petrified tree trunks with growth rings, vertebrate tracks) (Bordy and Catuneanu 2002; Brandl, personal commun., 2005). Similarly, in the Tshipise Basin (Figure 1), there is evidence showing that the deposition of the aeolian Clarens Formation was also interrupted by wetter intervals, during which the previously deposited sediments became water-saturated. Large- to small-scale soft-sediment deformation features (Figure 4) attest to these water-saturated conditions. These features occur within a 3 m stratigraphical vicinity of the described horizontal, regularly-oriented structures, both in the over- and underlying aeolian strata.

### THE HORIZONTAL, REGULARLY-ORIENTED STRUCTURES

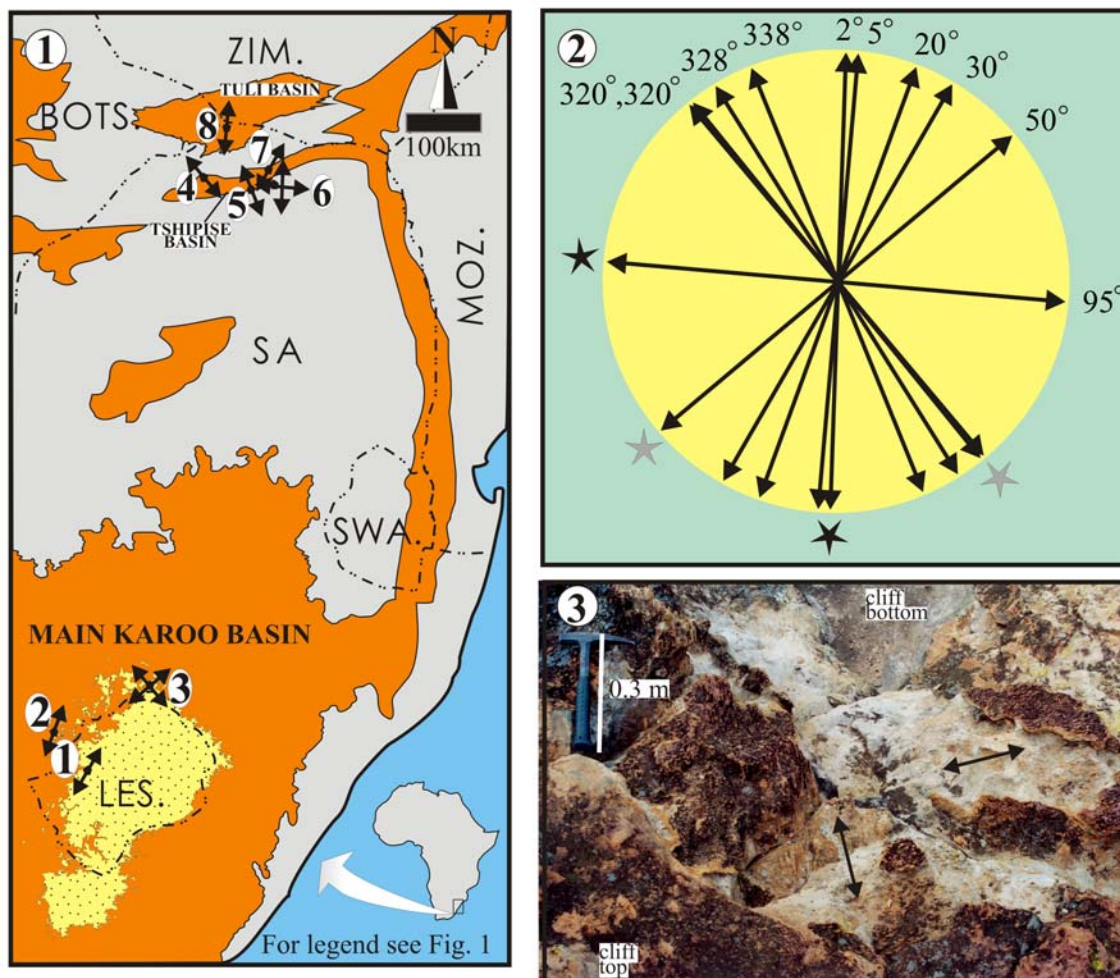
The morphological uniqueness of these structures is related to their repeated, uniform size and shape, as well as their strictly horizontal and aligned appearance (Figure 2). While the most spectacular occurrences are those where the density is more than one hundred structures per meter square along well-exposed horizontal surfaces of up to  $100 \text{ m}^2$  (Figure 2.1, 2.2), the structures are found in relative isolation as well (Figure 2.3). Individual structures can be followed for 50 to 150 mm; however, it is not clear whether their terminations are natural or due to weathering. In vertical exposures (Figure 2.4, 2.5), the diameters of these unbranched, cylindrical (tube-like) and virtually straight structures vary only slightly from 3 to 5



**Figure 4.** Large- to small-scale soft sediment deformation features (1 - 4) in the Tshipise Basin, attesting to water-saturated conditions during the deposition of the Clarens Formation. Such contorted beds are traceable for 20-30 m laterally in the individual outcrops, which occur in the same stratigraphic horizon. The structures show strong, irregular undulations and swirled bedding in the form of intraformational folds, in which the layers thicken and thin irregularly. Such features are interpreted as evidence of lateral flowage because of a sudden increase in the intensity of the hydrostatic pressure of pore waters.

mm. The diameter is maintained over the entire length of the individual structure (hence the cylindrical shape), and within a given exposure. The structures show no evidence of overlapping or crosscutting one another, and show no external sculpture or internal grain arrangements. The structures are preserved both in full relief (Figure 2.4, 2.5) within the host rock, and positive (convex) relief on flat surfaces (epirelief) (Figures 2.1-2.3,

2.5, 5.3). These flat surfaces are difficult to classify as bedding planes or weathering surfaces. Nonetheless, it is clear that the inclinations of these surfaces are parallel to the bedding planes of the over- and underlying strata. The zones containing full relief structures are variable in thickness, ranging from a few centimeters up to 0.6 m (Figures 2.4, 2.5, 5.3).

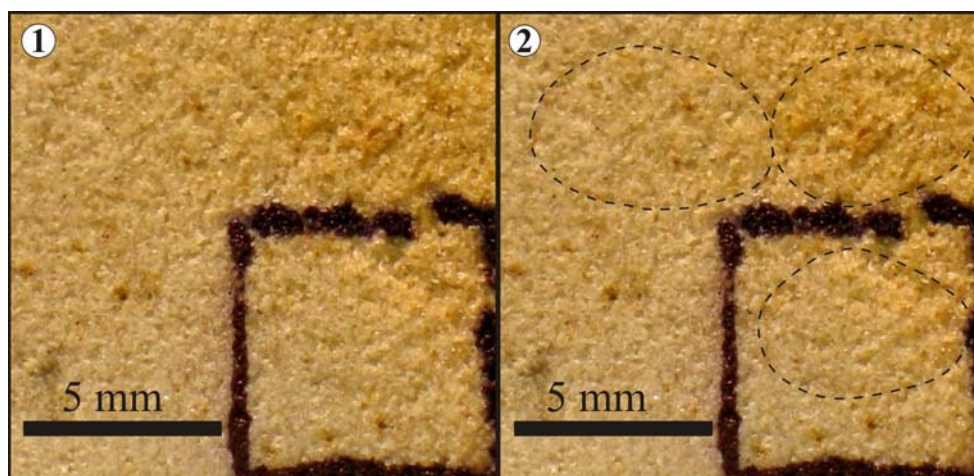


**Figure 5.** Plan view (1) and rose diagram (2) of the orientation of the long axes of the horizontal, regularly-oriented structures in the Clarens Formation of southern Africa. Note that at locations 3 and 6, the mean vectors (arrowed lines) in successive stratigraphic units lie at right angles to each other (see pairs of grey and black stars in 2). 3) A field example of the above case, shows a step-like cliff face in plan view, capturing two successive horizontal surfaces in which the structures are at right angles to one another.

The long axes of these structures are invariably parallel to one another and to the major horizontal bedding planes in the surrounding stratigraphic units. This spatial relationship of the structures is consistent throughout the studied outcrops in southern Africa; however directional scattering of the mean vectors is evident laterally between outcrop areas (Figure 5.1). The most common orientations are north-northwest - south-southeast (40% of the measurements), and north-northeast - south-southwest (30% of the measurements) but east-west oriented structures are also present in one locality (Figure 5.2). Furthermore, at localities 3 and 6 (Figure 5.1), the mean vectors of the horizontal, regularly-oriented structures found in two vertically successive zones occur at right

angles to one another (see Figure 5.3 and star markings on Figure 5.2). Note that at Locality 3, the structures occur towards the upper part of the Clarens Formation, approximately 20 m below the first Karoo flood basalts. Owing to the massive appearance of the host rock, there is no indication of any obvious stratigraphic gap (e.g., erosion surface, discordant strata) between the consecutive layers containing the differently oriented horizontal structures.

While in most occurrences, the outlines of the structures are well-defined due to differential weathering of the massive infilling and surrounding host rock (Figures 2.3, 2.5, 5.3), in some outcrops, the true outline of the tubes is poorly defined macroscopically as they are surrounded by an indu-



**Figure 6.** Close-up, cross-sectional image, showing three extremely subtle,  $\sim 0.1$  mm thick gaps, which typically surround the 5 mm diameter horizontal, regularly-oriented structures (1 – non-interpreted; 2 – interpreted image).

rated zone of well-cemented sediment which causes the structures to appear much larger (e.g., up to 25 mm in diameter) than it is. In fact, some of the structures shown in Figures 2.1 and 2.2 comprise two or three structures that are fused together by a zone of stronger cementation, and thus form thicker elongated features. The much smaller, true diameter of these weathered specimens is clearly visible in cross-sectional views (Figure 2.4, 2.5). That is especially true upon magnification, where the structures become even more evident because of textural discontinuities in form of extremely subtle,  $\sim 0.1$  mm thin gaps surrounding each of the  $\sim 5$  mm diameter cylinders (Figure 6). This small gap separates the massive infilling of the structures from the surrounding host rock, both of which comprise the same, moderately to well-sorted, predominantly fine-grained (0.2 mm), massive, silica-cemented, quartz-arenite, which contain mainly subrounded and subangular, monocrystalline quartz grains,  $<1\%$  feldspar, and a few chert fragments.

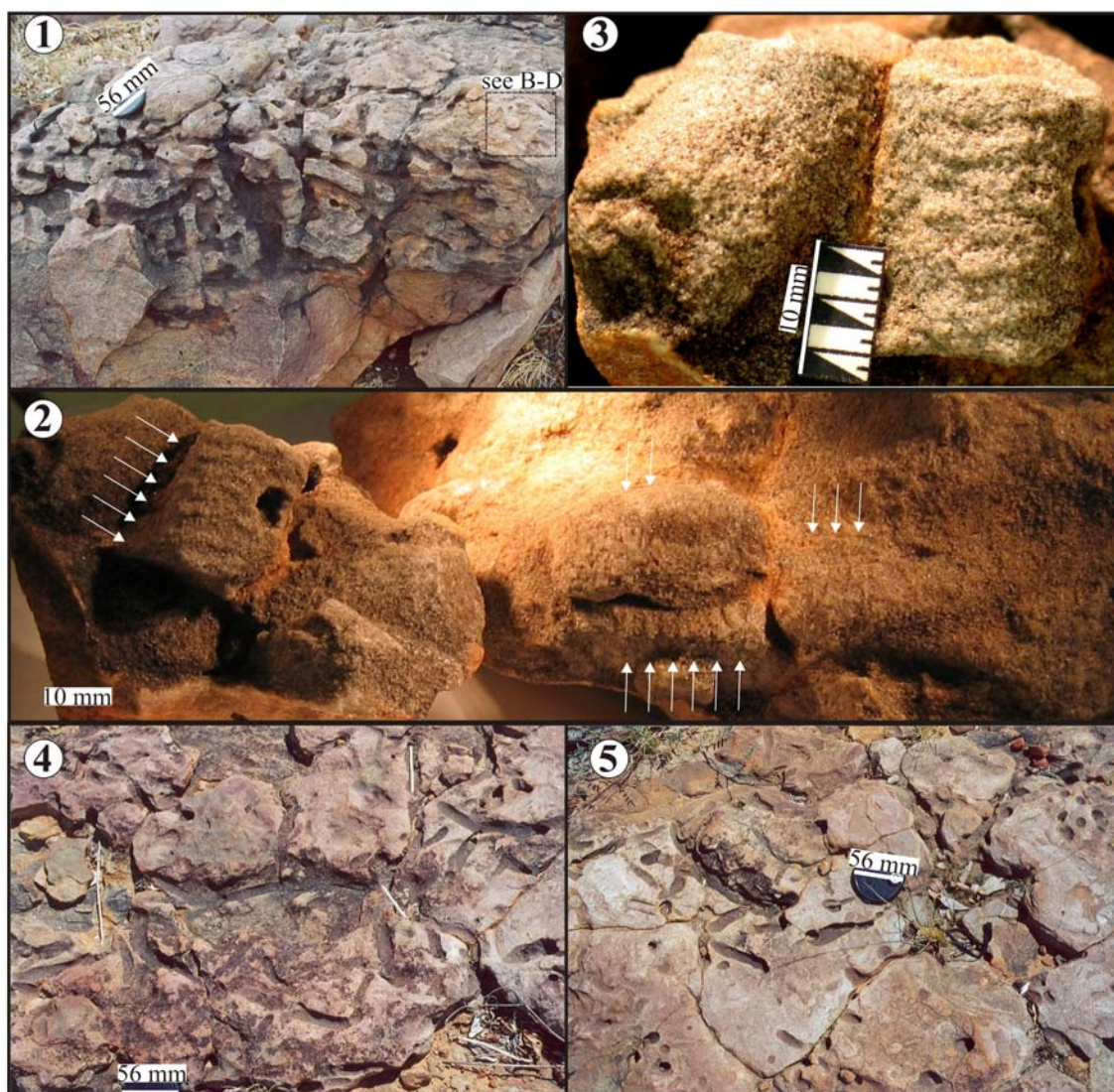
#### ASSOCIATED PROBABLE TRACE FOSSILS

In close stratigraphic association with these enigmatic structures, each study locality contains a number of probable trace fossils of various shapes, sizes, and vertical and lateral distributions (Figures 7, 8, 9). Although present elsewhere in the Clarens Formation, no vertebrate tracks or body fossils of other organisms were found in close proximity ( $< 1$  km radius) to the regularly-oriented horizontal structures at any of the study localities.

The most conspicuous biogenic structures among the associated features are some straight

to gently curved, irregularly branching, internally distinctly laminated, randomly oriented tubes with uniform  $\sim 10$  mm diameter and distinct ornamentation in the form of a ribbed outer surface (Figure 7.1, 7.2). The tubes, which lack chamber-like terminations, are filled by alternating laminae of 0.1 and 0.25 mm diameter sand grains (Figure 7.2, 7.3). The coarser laminae are 1.1 mm, while the finer ones are 0.1 mm thick. The consecutive laminae seem to end abruptly against the massive host rock, and in thin-sections, no constructed walls or linings are visible.

Another cylindrical feature, identical in size to the internally laminated, randomly oriented tubes, are straight to gently angled, locally irregularly branched, randomly oriented, 40-50 mm long open (unfilled) tubes that are  $\sim 10$  mm in diameter (Figure 7.1, 7.4, 7.5). In addition to these, thinner, 3 to 5 mm tubes, with massive fill, but otherwise similar morphological characters, are also common as positive, negative and full relief structures (Figure 8.1-8.6). Unlike the enigmatic structures, these features are relatively abundant, form well-developed network of tubes and give the host sandstones a sponge-like (bioturbated) texture. Locally, these complex mazes of tubes form  $\sim 0.5$  to 0.8 m thick layers, and where the outcrop continuity permits, they can be traced laterally for several tens of meters in (Figure 8.1, B). In addition to the stratified form, the tube network also occurs in various sizes and more or less distinct forms (e.g., blobs, domes, pears) (Figure 8.3-8.6). These tube networks are surrounded by either massive (Figure 8.4, 8.5) or well-stratified host rock (Figure 8.6) (see Bordy et al. 2004 for further details).



**Figure 7.** Associated trace fossils and bioturbate textures. Ribbed tubes with well-developed, laminated fill often co-occur with the horizontal, regularly-oriented structures (1 – field view; 2 - 3 - close ups). Note the well-developed boxwork of tubes in 1, and the rectangle that shows the sample enlarged in 2 - 3. In 2, the white arrows highlight the ribbed surface of the tubes. 4 - 5) Negative epirelief of randomly oriented traces, which have similar diameters and distributions as the ribbed tubes with laminated fill. These might represent another trace fossil type, but they could also be preservational variations of the ribbed tubes. For a positive epirelief image, rotate the figure 180°.

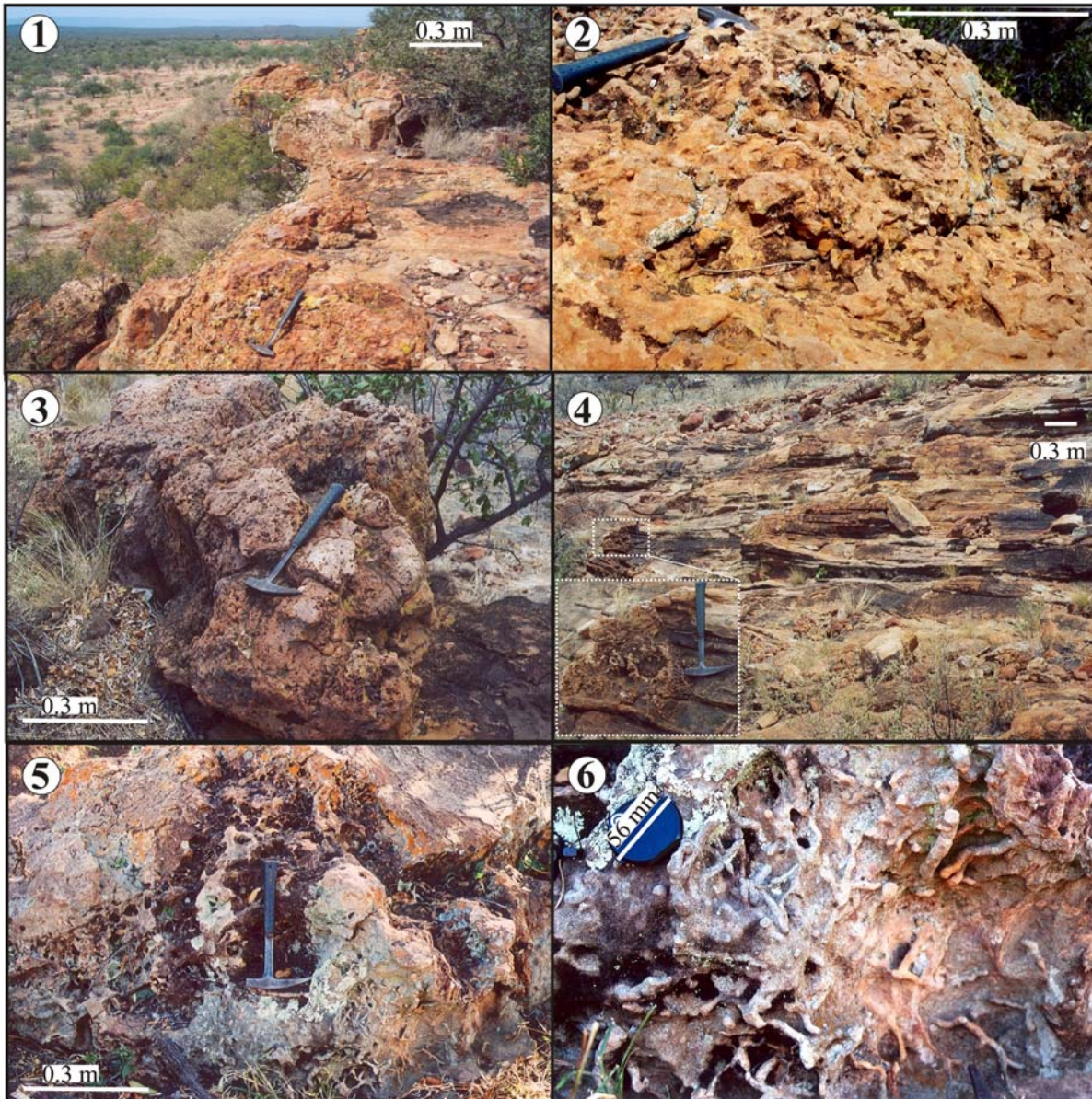
In the ichnological literature, tube-like structures of similar size, random distribution pattern and surficial morphology are commonly interpreted as organism-produced burrows and are attributed to a range of organisms from earthworms to arthropods (Bromley and Asgaard 1972; Ekdale et al. 1984; Hasiotis 2002).

#### ASSOCIATED UNIDENTIFIED STRUCTURES

A common structure associated with the horizontal, regularly-oriented structures are spherical

features (Figure 9.1-9.6) that are uniform in diameter, but whose populations show wide ranges in size from 5 to 40 mm in diameter. Unlike most inorganic concretions in the Clarens Formation, these spheres show no internal textures of any kind. They generally have smooth exteriors, but locally display rough, ornamented surfaces consisting of small, 3-4 mm humps (Figure 9.3, 9.4). At one locality, one humped horizontal cylinder 20 mm in diameter is also preserved (Figure 9.4) among the humped spheres. The spheres occur both in isola-

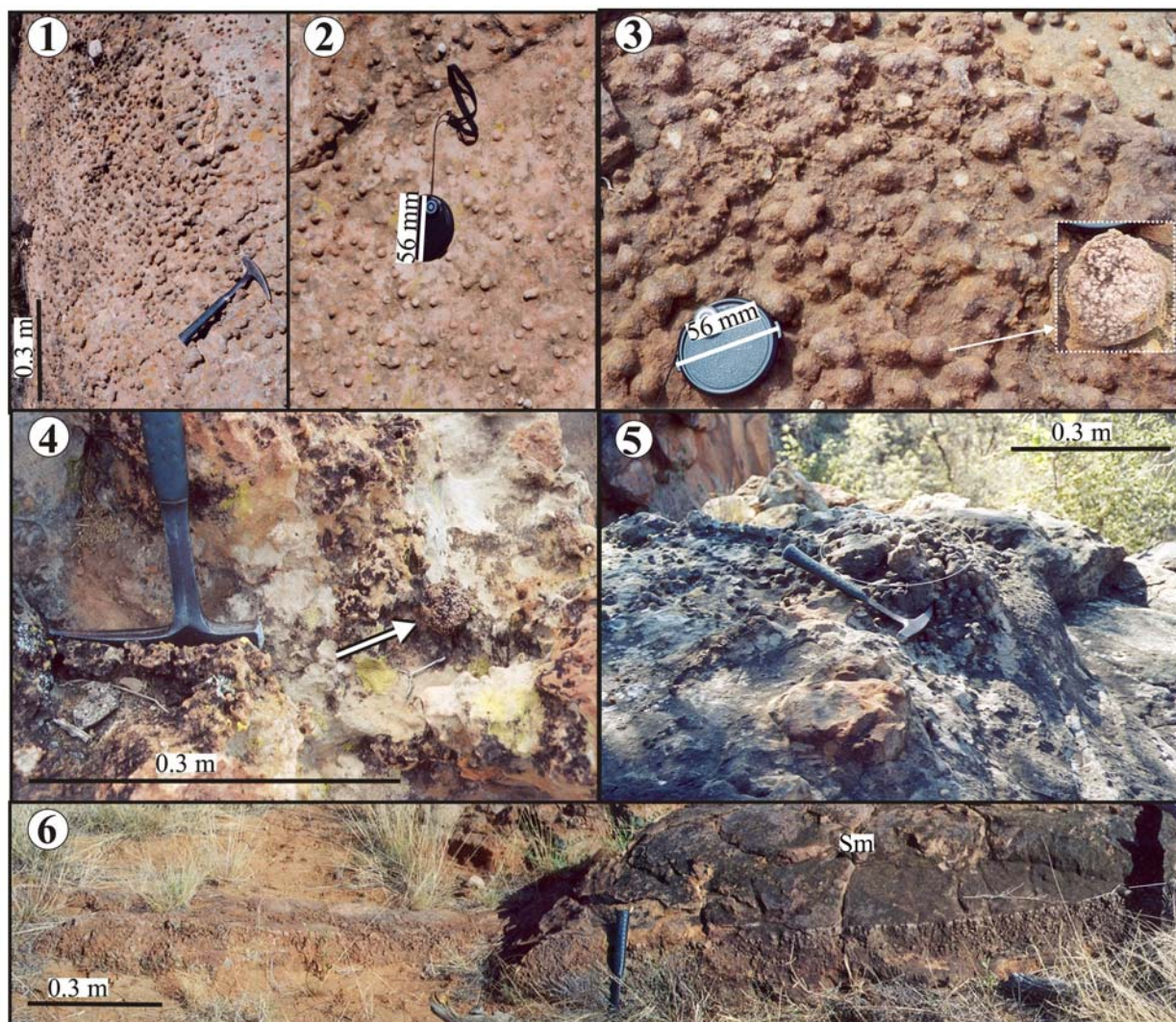




**Figure 8.** Associated trace fossils and bioturbate textures. 1 - 2) Sandstones with non-descript bioturbated textures resulting from a boxwork of randomly oriented tubes are locally confined to laterally continuous strata in which the original stratification is totally obscured by abundant, indistinct burrows (2 close-up image of 1). 3) Irregular-shaped occurrence of indistinct tube network. 4 -6) Pear-shaped occurrence of networks of indistinct, interconnected tubes enveloped in massive (4 - 5; 5 close-up image of 4) and well-stratified (6) Clarens Formation sandstone (For more detailed description and interpretation of these features, see Bordy et al. 2004).

tion (Figure 9.4) and in large masses, where their abundance is typically sufficient to form column-like structures 0.2-0.3 m in diameter (Figure 9.5). In some exposures, the vertical distribution of the spheres shows a very sharp upper boundary (Fig-

ure 9.6). In thin-section, the spherical features show no distinctive textural characteristics with the exception of some irregular mottles of fine- and very fine-grained massive quartz sand grains.



**Figure 9.** Associated trace fossils and bioturbate textures. **1 - 3**) Different populations of uniformly sized, spherical features most commonly show smooth exteriors (**1 - 2**), but locally display rough, ornamented surfaces consisting of small, 3-4 mm humps (**3**). Note that A and B are both landscape images. **4**) Rare, humped horizontal cylinder (diameter: 20 mm) at the hammer head. The spheres occur both in isolation (see white arrow in **4**) and en masse (**1, 2, 3, 5**), and where their densities are high (**5**), they may form column-like structures (see white circle indicating the eroded base of a possible column). **6**) Outcrop distribution of spheres in vertical section. Note the sharp upper boundary above which the host Clarens Formation is massive (Sm – massive sandstone).

## INTERPRETATION OF THE HORIZONTAL, REGULARLY-ORIENTED STRUCTURES

### Biogenic or Abiogenic

The orientation of the primary physical sedimentary structures (e.g., azimuth of the cross-beds) and structural features (e.g., local faults, joints) in the study areas do not resemble the orientation of the enigmatic horizontal and preferentially aligned structures. Most of the primary sedimentary and tectonic structures display east-

west orientations especially in the basins north of the main Karoo (Geological Survey 1984). At this stage, no known inorganic sedimentary or structural process could plausibly explain the generation of these horizontal, regularly-oriented structures, or the differential weathering associated with them. Although the structures may superficially resemble the appearance of elongate concretions, the diversity of orientation of the enigmatic structures at a single outcrop is inconsistent with that of elongate concretions which form diagenetically in groundwa-

ter that migrates preferentially along flow paths with highest host rock permeability, and are usually subparallel to palaeocurrent directions (cf. Mozley and Davis 1996). In relative terms, however, there are clear morphological characteristics associated with these structures that are more consistent with a biogenic origin. In particular, the delicate ~0.1 mm concentric gap surrounding each uniform-diameter tube; the recurrence of these structures with respect to their identical shapes, sizes and orientations in geographically separated regions; their regular co-occurrence with other organism-produced (e.g., ribbed tubes) traces support the contention that these features are biogenic sedimentary structures. The differential weathering associated with these structures is also consistent with differential cementation recording permeability variations between the host material and the fill of the biogenic structures (cf. Pemberton et al. 2001:63).

The delicate gap that surrounds the horizontal, regularly-oriented structures is interpreted here as a mechanical artifact produced by an Early Jurassic organism. It is envisaged that this organism purposefully constructed the horizontal structures as discrete, three-dimensional and horizontal tunnels. While direct evidence for the organic linings of these tunnels was not found, the presence of such organic material could be inferred, based on the small circular opening surrounding the tubes (cf. Johnston et al. 1996:515). This small gap, which possibly represents the weathered remnant of the original, likely clay lining of the tunnels, together with the massive infilling, most likely increased the preservation potential of the structures. The original lining may have been instrumental in the peculiar and preferential preservation of the structures, by locally altering the permeability patterns. Whether these tunnels were constructed above or excavated below the surface is not obvious from the preserved biological and sedimentological evidence, however, given that the structures form up to half a meter thick units, it seems very likely that they were excavated below the surface. Otherwise, in order to generate the thick accumulation of burrows, very thin increments of new sediment would have to be individually added and then promptly modified by the tunnel-makers before the arrival of next thin increment of sediment. This sedimentation rate would be at odds with aeolian systems where layers typically accumulate as thicker increments (cf. Hunter 1977).

### What Could Have Made Them?

Horizontal, preferentially-oriented trace fossils are rare in continental deposits and have been attributed to fresh-water molluscs (Pryor 1967), arthropods (notostracan branchiopods) (Ekdale et al. 1984), and crane fly larvae (Ahlbrandt et al. 1978; Ekdale and Picard 1985). The traces of these organisms are, however, significantly different from the horizontal, regularly-oriented structures of the Clarens Formation. Molluscs leave behind surface trails rather than burrowed tunnels; the tiny notostracan crustaceans have diminutive burrows, and the crane fly larvae burrows are meniscate and commonly irregular. None of these organisms are, therefore, plausible tracemakers of the horizontal, regularly-oriented structures observed in the Clarens Formation.

Without known ancient or modern counterparts, the identity of the original tracemaker of these peculiar structures remains elusive. The integration of all sedimentological and palaeontological evidence encountered from these deposits does permit, however, the following argument to be made. The large number of these geometrically extremely regular structures argues in favour of a great density of coeval, behaviourally sophisticated organisms, which burrowed in an orchestrated manner and were capable of profoundly impacting the Clarens sediments. This interpretation leads to the possibility that the tracemakers were, in fact, social organisms that followed a straight, linear foraging pattern, probably to prevent crossing their own path, and ensuring maximum foraging efficiency. Given that arid and semi-arid environments are characterized by episodic abundance irregularly distributed food resources, systematic linear foraging strategies during the Early Jurassic could have ensured reliable access to nutrients (cf. Bernstein 1975; Faulkes et al. 1997; Wolf 2008).

Bordy et al. (2004) tentatively assigned these regular burrows to Early Jurassic ants. This interpretation considered, first of all, that at one locality (Tuli Basin) the horizontal, regularly-oriented structures are superimposed on randomly bioturbated surfaces which were attributed to termites, and secondly, that modern ants are predators of termites. These assignments were subsequently disputed (Genise et al. 2005; Bordy et al. 2005), mainly based on the age discrepancy between the interpreted insect trace fossils in the Clarens Formation and the earliest known body fossils of social insects. Although ants were suggested as tracemakers of Late Jurassic ichnofossils (Hasiotis 2002; 2003; 2004) and recent phylogenetic and

molecular clock analyses of ant DNA showed that ant phylogeny commenced much earlier (in the Late Cretaceous) than previously thought (Moreau et al. 2006), it is known that ants less commonly alter their environments to the extent seen in these rocks. Given the foregoing, the most likely social tracemakers were either extinct unknown social organisms without any body fossil record or possibly termites, which are known to be the greatest ecosystem engineers of all sediment reworking insects (cf. Jones et al. 1994; Hasiotis 2003; Hutchins et al. 2004; Jouquet et al. 2006).

### Spatiotemporal Orientation Differences

Given the biogenic origin of the horizontal, regularly-oriented structures, their orientation variations within and between the different localities may signal behavioural adjustments in repose to changes in the physico-chemical conditions of an otherwise stable ecological niche.

As demonstrated through field- and laboratory-based experimental studies, as well as detection of internal biomineralized magnetite, certain extant termite genera are capable of receiving geomagnetic information, able to utilize it for navigational purposes and even generate structures aligned with the present geomagnetic field (Rickli and Leuthold 1988; Maher 1998; Becker 1989; Jacklyn and Munro 2002; Alves et al. 2004; Esquivela et al. 2004). Consequently, it may be *hypothesized* that if the tracemakers were termites, whom were guided during foraging by the orientation of the geomagnetic field, the different burrow orientations in successive strata *might* represent adjustments in burrowing direction triggered by changes in the geomagnetic field orientation during the Early Jurassic. Such perturbances of the Earth's natural magnetic field take place during geologically "brief" geomagnetic excursions or polarity reversals, which occur at highly variable frequencies (from <1 to >10 reversals per Ma) (Pavlov and Gallet 2001; Constable and Korte 2006).

## DISCUSSION

### Palaeoenvironmental Implications

Irrespective of behavioral interpretations of the regularly-oriented structures, their biogenic origin, in conjunction with other palaeontological evidence, implies that at least episodically, the Early Jurassic southern African palaeoenvironment was capable of supporting a diverse ecosystem. Furthermore, contrasting with previous perceptions of

low preservation potential of continental trace fossils (e.g., Ekdale et al. 1984), and in line with more recent reports of occasional high trace fossil diversity in aeolian systems (Loope and Rowe 2003; Ekdale et al. 2007), the ichnological record of Clarens Formation suggests that this Early Jurassic aeolian ecosystem was also suitable to preserve such biogenic sedimentary structures.

Given a biogenic origin for the structures, their occurrence, distribution, and morphology suggest episodic changes in the physico-chemical parameters of their habitat. Some of the environmental changes were most likely related to perturbations in an otherwise arid climate (e.g., changes in the local hydrogeological conditions and nutrient availability). The presence of water and temporal as well as spatial fluctuations in substrate moisture levels are indicated by both organic and inorganic evidence. For instance, considering that the surface ornamentations on the associated ribbed tubes are likely scratches on the outer surface of the burrows, their presence implies that excavation of the burrows occurred in a firm, possibly moist substrate. Lack of lining and horizontal lamination of the fill suggest that the burrows were left open, and subsequently filled by coarse and fine sand laminae, which imply several depositional events with variable energy levels. In addition, the analysis of growth rings in rare large woody taxa testifies to periods during the deposition of the Clarens Formation when good growth rates occurred in a climate with some seasonal variation, but without dramatic water shortage (Meijs 1960; Bordy and Catuneanu 2002:309). Furthermore, the vertical distribution of the spheres (i.e., upward increase in abundance - Figure 9.6) and the well-defined, straight, horizontal upper surface in their distribution may reflect vertical moisture level variations along the hydrological profile and the position of the capillary zone of the water table, respectively (cf. Hasiotis et al. 2007). In case of assuming a biogenic origin for these spheres, such vertical distribution may suggest that the activities of their tracemakers were dependent on the vertical changes in substrate moisture levels which in turn limited the vertical dimension of the niche area.

A further evidence for temporal increase in substrate moisture levels is the repeated occurrence of large-scale, dramatically contorted Clarens Formation strata in the Tshipise Basin which also indicate that: (1) the disturbance of the water-saturated strata occurred prior to lithification; and (2) their rather violent disturbance occurred rapidly (cf. Horowitz 1982; Alvarez et al. 1998; Netoff

2002) most likely in an active tectonic setting (Bordy and Catuneanu 2001).

The water needed for the moist, semi-cohesive (i.e., “burrowable”) substrate, the growth ring development in woody taxa, and the large-scale soft-sediment deformations, was most likely derived from episodic (seasonal?) precipitation, possibly in the form of low-frequency, high-intensity storms and from groundwater brought to the depositional sites by basinal groundwater migration systems (i.e., discharge areas). Therefore, the occurrence of trace fossils in the climate-sensitive sedimentary succession of the Clarens Formation implies episodic changes in the climate (e.g., increased substrate moisture rates) in this part of Gondwana, and thus the findings may aid the refining of the Early Jurassic global palaeoclimate zones/ patterns.

### **Spatiotemporal Distribution and Co-occurrence with Other Traces**

The regular co-occurrence of the horizontal, regularly-oriented structures with other organism-produced traces (e.g., ribbed tubes) may suggest that they could have formed as related, structural elements of a compound trace fossil (cf. Miller III 2003) or as traces left behind by a contemporaneous biotic community of unrelated organisms. The great abundance of the oriented structures and their recurring association in geographically distant regions of southern Africa, be it as part of a complex trace fossil or as discrete, biologically unaffiliated trace fossil associations, indicate that ecological circumstances (e.g., favourable nutrient amount, palaeohydrologic regime) conducive to the generation of such biogenic sedimentary structures were widespread in southern Gondwana (cf. Hasiotis et al. 2007). More specifically, they suggest that the predominantly aeolian Early Jurassic of this region was at least episodically capable of supporting a diverse ecosystem (cf. Ekdale et al. 2007). Intermittent moist conditions in this Early Jurassic ecological system are also supported by independent indicators of water (e.g., plant and vertebrate fossils, soft-sediment deformations) throughout southern Africa. Furthermore, if the tracemaking activity related to the generation of the oriented structures was depth dependent, it can be inferred that the individual layers of horizontal traces represent consecutive tracemaking events (i.e., horizontally adjacent structures are approximately coeval), during which the tracemakers kept pace with the supposedly lower sedimentation rates. If, indeed, this increase in biological activities

occurred when other physical sedimentary processes (sedimentation rates, erosion, etc.) were less dominant, presenting stable environmental niches for the burrowing organisms, then the intensely bioturbated strata may represent climate-linked localized diastems or regional unconformities. Unfortunately, the current stratigraphic resolution of the Clarens Formation is inadequate for the determination of the relative ages of the various sites or direct correlation between the geographically distant exposures. Thus, the question as to whether or not the preserved biotic communities were secluded in time and space, and flourished only in certain favourable landscape mosaics of the more arid Clarens palaeoclimate, remains open for future research. Hence, it is not possible at this time to determine the exact nature (i.e., repetitive progressive changes or near-random episodic events), number, duration and geographical extent (local vs. regional) of these climate fluctuations and related variations in the depositional system.

### **The Termite Issue**

Without comparable modern biogenic structures of similar dimensions and spatial arrangement to the Clarens structures, the identity of the tracemakers as well as why and how these bizarre, Early Jurassic biogenic sedimentary structures were generated, remain to be found. This highlights the pressing need for neoichnological studies in arid environments, for without them, the usefulness of continental ichnotaxa for identifying physico-chemical palaeoenvironmental changes remains limited, despite the fact that such trace fossils are fairly abundant, varied and often well-preserved in lithofacies associations of continental depositional systems (cf. Hasiotis 2002; Hasiotis et al. 2007).

The identification of the tracemakers as termite-like insects is clearly tentative in this study, and it is chiefly based on the similarity of these structures to termite-made galleries in their vast abundance, strict directional orientation as well as size and overall burrow morphology. The profusion of the structures suggests an enormous number of individuals with well-coordinated and oriented behavior, a typical characteristic of social insects, especially that of some modern termites (cf. Jacklyn and Munro 2002). The interpretation of these oriented structures as ichnofossils of termite-like insects, together with the previously interpreted termite nests of the Clarens Formation (Bordy et al. 2004) would have important ramifications for the appearance of sociality in these insects. In particu-

lar, the fact that the four earliest (Late Triassic to Late Jurassic) fossil termite nest occurrences are exclusively reported from rocks formed in arid and semi-arid environments (e.g., Hasiotis and Dubiel 1995; Smith and Kitching 1997; Hasiotis 2004; Bordy et al. 2004) may imply that the onset of sociality in these insects was a behavioural response to environmental triggers. More specifically, in such stressful habitats with episodic and irregular nutrient distribution, the appearance of the evolutionary novelty of sociality seems more practical, as it may have assisted organisms in a more successful foraging. Similar explanations (i.e., aridity food-distribution hypothesis) for the evolution of sociality in the African mole-rats were offered by Faulkes et al. (1997).

### CONCLUSION

The morphology, orientation and abundance of the horizontal, regularly-oriented structures suggest a biogenic origin, and a likely social insect-like (termitic?) architect. The ethological reason for the preferred alignment of these biogenic structures of the Clarens Formation remains unknown to date. The dearth of similar modern features leads to speculation as to the exact functional interpretation of the traces, as well as the role of their tracemakers in the Early Jurassic ecosystem. Nonetheless, these findings, together with the other Early Jurassic palaeontological and sedimentological records of southern Africa, contain important clues regarding changes in the depositional environment that were most likely related to episodic variations in climate as well as intermittent sedimentation rates. The recurrence of moisture indicating biogenic and sedimentary structures in the Lower Jurassic aeolian successions in this part of Gondwana may be used to enhance the resolution Early Jurassic global climate models. In particular, with improved stratigraphic and geochronological studies, the strongly oriented biogenic structures that show ethological pattern adaptations to changing ecological parameters may prove to be valuable constraints in reconstructing the duration and periodicity of Early Jurassic climate changes. Finally, it is hoped that this morphologic description detailing their physical appearance, geological context and associated trace fossils will aid the recognition of similar ancient structures, and advance the quest for identifying modern organisms capable of producing similar structures.

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### REFERENCES

- Ahlbrandt, T.S., Andrews, S., and Gwynne, D.T. 1978. Bioturbation in eolian sediments. *Journal of Sedimentary Petrology*, 48:839-848.
- Alvarez, W., Staley, E., O'Connor, D., and Chan, M.A. 1998. Synsedimentary deformation in the Jurassic of southeastern Utah - A case of impact shaking? *Geology*, 26:579-582.
- Alves, O.C., Wajnberg, E., de Oliveira, J.F., and Esquivela, D.M.S. 2004. Magnetic material arrangement in oriented termites: a magnetic resonance study. *Magnetic Resonance*, 168:246-251.
- Bamford, M.K. 2004. Diversity of the Woody Vegetation of Gondwanan Southern Africa. *Gondwana Research*, 7:153-164.
- Becker, G. 1989. Communication between termites by means of biofields and the influence of magnetic and electric fields on termites, p. 116-127. In Popp, F.A., Warnke, U., König, H.L., and Peschka, W. (eds.), *Electromagnetic Bio-Information, Urban and Schwarzenberg*: Baltimore, MD.
- Bernstein, R. 1975. Foraging strategies of ants in response to variable food density. *Ecology*, 56:213-219.
- Beukes, N.J. 1970. Stratigraphy and sedimentology of the Cave Sandstone stage, Karoo System, p. 321-342. In Haughton, S.H., (ed.), *Proceedings and Papers, 2<sup>nd</sup> Gondwana Symposium*, Pretoria, South Africa.
- Bordy, E.M., and Catuneanu, O. 2001. Sedimentology of the upper Karoo fluvial strata in the Tuli Basin, South Africa. *Journal of African Earth Sciences*, 33:605-629.
- Bordy, E.M., and Catuneanu, O. 2002. Sedimentology and palaeontology of upper Karoo aeolian strata (Early Jurassic) in the Tuli Basin, South Africa. *Journal of African Earth Sciences*, 35:301-314.

- Bordy, E.M., Bumby, A., Catuneanu, O., and Eriksson, P.G. 2004. Advanced Early Jurassic Termite (Insecta: Isoptera) Nests: Evidence from the Clarens Formation in the Tuli Basin, Southern Africa. *Palaios*, 19:68-78.
- Bordy, E.M., Bumby, A., Catuneanu, O., and Eriksson, P.G. 2005. Reply to a Comment on Advanced Early Jurassic Termite (Insecta: Isoptera) Nests: Evidence from the Clarens Formation in the Tuli Basin, Southern Africa. (Bordy et al. 2004). *Palaios*, 20:308-312.
- Bromley, R.G., and Asgaard, U. 1972. Freshwater Cruziana from the Upper Triassic of Jameson Land, East Greenland. *Grønlands Geologiske Undersøgelse Rapport 49*, 15-21.
- Constable, C., and Korte, M. 2006. Is Earth's magnetic field reversing? *Earth and Planetary Science Letters*, 246:1-16.
- Duncan, R.A., Hooper, P.R., Rehacek, J., Marsh, J.S., and Duncan, A.R. 1997. The timing and duration of the Karoo igneous event, southern Gondwana. *Journal of Geophysical Research*, 102:18127-18138.
- Ekdale, A.A., and Picard, M.D. 1985. Trace fossils in a Jurassic eolianite, Entrada Sandstone, Utah, USA. In Curran, H.A., (ed.), *Biogenic Structures: Their Use in Interpreting Depositional Environments: SEPM Special Publication*, 35:3--12.
- Ekdale, A.A., Bromley, R.G., and Loope, D.B. 2007. Ichnofacies of an ancient erg: A climatically influenced trace fossil association in the Jurassic Navajo Sandstone, southern Utah, USA, p. 562-574. In Miller, W. III. (ed.), *Trace Fossils: Concepts, Problems, Prospects*. Elsevier, Amsterdam.
- Ekdale, A.A., Bromley, R.G., and Pemberton, S.G. 1984. Ichnology: The use of trace fossils in sedimentology and stratigraphy: SEPM Publication, Tulsa, OK, 317 pp.
- Ellenberger, P. 1970. Les niveaux paleontologiques de premiere apparition des manmiferes primordiaux en Afrique de sud et leur ichnology, p. 343-370. In Haughton, S.H., (ed.), *Proceedings and Papers 2<sup>nd</sup> Gondwana Symposium*, South Africa.
- Eriksson, P.G. 1981. A palaeoenvironmental analysis of the Clarens Formation in the Natal Drakensberg. *Transactions of the Geological Society of South Africa*, 84:7-17.
- Eriksson, P.G. 1986. Aeolian dune and alluvial fan deposits in the Clarens Formation of the Natal Drakensberg. *Transactions of the Geological Society of South Africa*, 89:389-394.
- Eriksson, P.G., McCourt, S., and Snyman, C.P. 1994. A note on the petrography of upper Karoo sandstones in the Natal Drakensberg: implications for the Clarens Formation palaeoenvironment. *Transactions of the Geological Society of South Africa*, 97:101-105.
- Esquivela, D.M.S., Wajnberg, E., Cernicchiaro, G.R., and Alves, O.C. 2004. Comparative magnetic measurements of migratory ant and its only termite prey. *Journal of Magnetism and Magnetic Materials*, 278:117-121.
- Faulkes, C.G., Bennett, N.C., Bruford, M.W., O'Brien, H.P., Aguilar, G.H., and Jarvis, J.U.M. 1997. Ecological constraints drive social evolution in the African mole-rats. *Proceedings of the Royal Society London B*, 264:1619-1627.
- Genise, J.F., Bellosi, E.S., Melchor, R.N., and Cosarinsky, M.I. 2005. Comment—Advanced Early Jurassic Termite (Insecta: Isoptera) Nests: evidence from the Clarens Formation in Tuli Basin, Southern Africa (Bordy et al. 2004). *Palaios*, 20:303-308.
- Geological Survey 1984. Geological map of the Republics of South Africa, Transkei, Bophuthatswana, Venda and Ciskei and the Kingdoms of Lesotho and Swaziland. Scale 1: 1000000. Pretoria: Geological Survey of South Africa (Council for Geoscience).
- Hasiotis, S.T. 2002. Continental Trace Fossils. SEPM Short Course Notes, n. 51, 132 pp.
- Hasiotis, S.T. 2003. Complex ichnofossils of solitary and social soil organisms: understanding their evolution and roles in terrestrial paleoecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192:259-320.
- Hasiotis, S.T. 2004. Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain region, USA: environmental, stratigraphic, and climatic significance of terrestrial and freshwater ichno-coenoses. *Sedimentary Geology*, 167:277-368.
- Hasiotis, S.T., and Dubiel, R.F. 1995. Termite (Insecta: Isoptera) nest ichnofossils from the Triassic Chinle Formation, Petrified Forest National Park, Arizona. *Ichnos*, 4:119-130.
- Hasiotis, S.T., Kraus, M. J., and Demko, T. M. 2007. Climatic controls on continental trace fossils, p. 172-195. In Miller, W. III. (ed.), *Trace Fossils: Concepts, Problems, Prospects*. Elsevier, Amsterdam.
- Holzförster, F. 2007. Lithology and depositional environments of the Lower Jurassic Clarens Formation in the Eastern Cape, South Africa. *South African Journal of Geology*, 110:543-560.
- Horowitz, D.H. 1982. Geometry and origin of large-scale deformation structures in some ancient wind-blown sand deposits. *Sedimentology*, 29:155-180.
- Hunter, R. E. 1977. Basic types of stratification in small eolian dunes. *Sedimentology*, 24: 361-387.
- Hutchins, M., Evans, A.V., Garrison, R.W., and Schlager, N., (eds.) 2004. *Insects: Volume 3: Grzimek's animal life encyclopedia*: Detroit: Gale Group, Inc.: Farmington Hills, MI. 2<sup>nd</sup> edition.
- Jacklyn, M.P., and Munro, U. 2002. Evidence or the use of magnetic cues in mound construction by the termite *Amitermes meridionalis* (Isoptera: Termitinae). *Australian Journal of Zoology*, 50:357-368.
- Johnson, M.R. 1991. Sandstone petrography, provenance and plate tectonic setting in Gondwana context of the southeastern Cape-Karoo Basin. *South African Journal of Geology*, 94:137-154.
- Johnson, M.R., ed. 1994. *Lexicon of South African Stratigraphy. Part 1: Phanerozoic Units*: Council for Geoscience, South Africa, 56 pp.

- Johnson, M.R., Van Vauuren, C.J., Hegenberger, W.F., Key, R., and Shoko, U. 1996. Stratigraphy of the Karoo Supergroup in southern Africa: an overview. *Journal of African Earth Sciences*, 23:3-15.
- Johnston, P.A., Eberth, D.A., and Anderson, P.K. 1996. Alleged vertebrate eggs from Upper Cretaceous red beds, Gobi Desert, are fossil insect (Coleoptera) pupal chambers: *Fictovichnus* new ichnogenus. *Canadian Journal of Earth Sciences*, 33:511-522.
- Jones, C.G., Lawton, J.H., and Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos*, 69:373-386.
- Jouquet, P., Dauber, J., Lagerlöf, J., Lavelle, P., and Lepage, M. 2006. Soil invertebrates as ecosystem engineers: intended accidental effects on soil and feedback loops. *Applied Soil Ecology*, 32:153-164.
- Jourdan, F., Fe'raud, G., Bertrand, H., Kampunzu, A.B., Tshoso, G., Le Gall, B., Tiercelin, J.J., and Capiez, P. 2004. The Karoo triple junction questioned: evidence from Jurassic and Proterozoic  $^{40}\text{Ar}/^{39}\text{Ar}$  ages and geochemistry of the giant Okavango dyke swarm (Botswana). *Earth and Planetary Science Letters*, 222:989-1006.
- Kitching, J.W., and Raath, M.A. 1984. Fossils from the Elliot and Clarens Formations (Karoo Sequence) of the northeastern Cape, Orange Free State and Lesotho, and a suggested biozonation based on Tetrarapods. *Palaeontologia Africana*, 25:111-125.
- Le Gall, B., Tshoso, G., Jourdan, F., Fe'raud, G., Bertrand, H., Tiercelin, J.J., Kampunzu, A.B., Modisi, M.P., Dymont, J., and Maia, M. 2002.  $^{40}\text{Ar}/^{39}\text{Ar}$  geochronology and structural data from the giant Okavango and related mafic dyke swarms, Karoo igneous province, Botswana. *Earth and Planetary Science Letters*, 202:595-606.
- Loope, D.B., and Rowe, C.M. 2003. Long-lived pluvial episodes during deposition of the Navajo Sandstone. *Journal of Geology*, 111:223-232.
- Maher, B.A. 1998. Magnetite biomineralization in termites: Proceedings of the Royal Society of London B, 265:733-737.
- Meijs, L. 1960. Notes on the occurrence of petrified wood in Basutoland. Roma, Basutoland: Pius XII University Collage, Papers No. 2, 8 pp.
- Miller, W., III 2003. Paleobiology of complex trace fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192:3-14.
- Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B., and Pierce, N.E. 2006. Phylogeny of the Ants: Diversification in the Age of Angiosperms. *Science*, 312:101-104.
- Mozley, P.S., and Davis, J.M. 1996. Relationship between oriented calcite concretions and permeability correlation structure in an alluvial aquifer, Sierra Ladrones Formation, New Mexico. *Journal of Sedimentary Research*, 66:11-16.
- Netoff, D. 2002. Seismogenically induced fluidization of Jurassic erg sands, south-central Utah. *Sedimentology*, 49:65-80.
- Olsen, P.E., and Galton, P.M. 1984. A review of the reptile and amphibian assemblages from the Stormberg Group of southern Africa with special emphasis on the footprints and the age of the Stormberg. *Palaeontologia Africana*, 25:87-110.
- Pavlov, V., and Gallet, Y. 2001. Middle Cambrian high magnetic reversal frequency (Kulumbé River section, northwestern Siberia) and reversal behaviour during the Early Palaeozoic. *Earth and Planetary Science Letters*, 185:173-183.
- Pemberton, S.G., Spila, M., Pulham, A.J., Saunders, T., MacEachern, J.A., Robbins, D., and Sinclair, I. K. 2001. Ichnology and Sedimentology of Shallow to Marginal Marine Systems: Ben Nevis & Avalon Reservoirs, Jeanne d'Arc Basin: Geological Association of Canada Geological Association of Canada Short Course Notes, 15, 343 pp.
- Pryor, W.A. 1967. Biogenic directional features on several recent pointbars. *Sedimentary Geology*, 1:235-245.
- Rickli, M., and Leuthold, R.H. 1988. Homing in harvester termites: evidence of magnetic orientation. *Ethology*, 77:209-216.
- Smith, R.H.M. 1990. A review of the stratigraphy and sedimentary environments of the Karoo Basin of South Africa. *Journal of African Earth Sciences*, 10:117-137.
- Smith, R.M.H., and Kitching, J. 1997. Sedimentology and vertebrate taphonomy of the Tritylodon Acme Zone: a reworked palaeosol in the Lower Jurassic Elliot Formation, Karoo Supergroup, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 131:29-50.
- Tasch, P. 1984. Biostratigraphy and palaeontology of some conchostracan-bearing beds in southern Africa. *Palaeontologia Africana*, 25:61-85.
- Truswell, J.F. 1977. The Geological Evolution of South Africa: Purnell, Cape Town, 218 pp.
- Van Dijk, D.E., Hobday, D.K., and Tankard, A.J. 1978. Permo-Triassic lacustrine deposits in the eastern Karoo basin, Natal, South Africa. In Matter, A., and Tucker, M.E., (eds.), Modern and ancient lake sediments, International Association of Sedimentologists, Special Publication, 9:229-235.
- Van Dijk, E.D. 2001. Jurassic bipeds that could hop? perch? pounce? fly? *South African Journal of Science*, 97:373-374.
- Veevers, J.J. 2004. Gondwanaland from 650–500 Ma assembly through 320 Ma merger in Pangea to 185–100 Ma breakup: supercontinental tectonics via stratigraphy and radiometric dating. *Earth-Science Reviews*, 68:1-132.
- Wolf, H. 2008. Desert ants adjust their approach to a foraging site according to experience. *Behavioral Ecology and Sociobiology*, 62:415-425.