Check for updates

JOURNAL OF QUATERNARY SCIENCE (2026) **41**(6) 933–949 ISSN 0267-8179. DOI: 10.1002/jqs.70089

JQS Journal of Quaternary Science QRA Quaternary Research Association

Columnanidus calitzdorpensis ichnogen. ichnosp. nov: A new Middle Pleistocene subterranean termite trace fossil from South Africa

MIENGAH ABRAHAMS,[1]* ROBERT A. MUIR,[2] JORGE F. GENISE,[3] JOHN E. ALMOND,[4] GCINAMAHLUBI HADEBE,[1] JOHN C. HELLSTROM,[5] RABIA JACOBS[1] and CHRIS HARRIS[1]

[1]Department of Geological Sciences, University of Cape Town, Cape Town, South Africa
[2]Department of Earth Science, University of the Western Cape, Cape Town, South Africa
[3]Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
[4]Natura Viva cc, Cape Town, South Africa
[5]School of Geography, Earth and Atmospheric Sciences, University of Melbourne, Victoria, Australia

Received 25 July 2025; Revised 22 May 2026; Accepted 26 May 2026

ABSTRACT: Termites are landscape geo-engineers whose nesting activities substantially modify the physical and chemical properties of soils. Fossilised termite nests commonly constitute the only identifiable evidence of ancient termite activity and represent valuable trace fossil archives for reconstructing past environments. Here, we describe a new ichnogenus and ichnospecies, *Columnanidus calitzdorpensis* ichnogen. ichnosp. nov., from Quaternary alluvial deposits near Calitzdorp, South Africa. The subterranean nests are subcylindrical structures, reaching ~1 m in height and ~65 cm in diameter, and are characterised by a ~12 cm wide, shelved nest wall surrounding an empty central cavity. Within the nest wall, the gallery and chamber morphology and abundance vary between the inner and outer zones. The nests are preserved as calcretised features, composed of inter-laminations of clastic sediment and pedogenic carbonate precipitate. U-series dating of the carbonate laminations yields robust age peaks at 401 ± 46 ka and 323 ± 12 ka, indicating a Middle Pleistocene minimum age for nest formation. These ages coincide with intervals favourable for pedogenic carbonate development under semi-arid to arid climatic conditions. Hardpan calcretes capping the nests suggest prolonged periods of semi-arid conditions and sustained pedogenic stability during the Middle Pleistocene in the Calitzdorp region. © 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

KEYWORDS: *Columnanidus calitzdorpensis*; fossil termite nests; ichnology; Middle Pleistocene; South Africa

Introduction

Ants and termites have independently evolved complex eusocial behaviours, in which colonies function as a single, cohesive 'superorganism' working together to improve their survival and reproductive success. This advanced behaviour is mostly evident in the construction and excavation of their large nest structures, for which above-ground mound features can reach up to 10 m (Pullan, 1979). Whereas the delicate bodies of termites are rarely preserved in the fossil record (e.g., Emerson, 1938; Jarzembowski, 1981; Nel et al., 2004), their nest structures, reinforced by saliva or stercoral material, have a higher preservation potential and are often the only preserved indication of ancient termite activity (e.g., Genise and Bown, 1994a; Rohr et al., 1986; Pickford and Senut, 2000, 2002; Darlington, 2005; Duringer et al., 2007; Roberts et al., 2016). Termite nests may comprise easily identifiable above-ground (epigeous) mounds, but also hidden below-ground (hypogeous) boxworks with minimal surface expression. Although below-ground networks are prevalent, well-documented examples of subterranean termite nest architecture are less common than those of above-ground features in both the modern and fossil records (e.g., Coaton and Sheasby, 1974; Miller and Mason, 2000; Schuster et al., 2000; Darlington, 1985, 2005).

In South Africa, extant termites are geographically widespread and ecologically important (e.g., Coaton, 1958; Coaton and Sheasby, 1974), with their above-ground mounds extensively documented, particularly in terms of spatial density and ecosystem impact (e.g., Coaton and Sheasby, 1974; Meyer et al., 1999). Similar accounts have also focused on subfossil above-ground mound features, locally known as heuweltjies, but while they may sometimes be linked to present-day termite activity (e.g., Moore and Picker, 1991; Francis et al., 2024), their origin and formation are controversial (e.g., Cramer and Midgley, 2015; McAuliffe, 2023). Conversely, reports of fossil specimens identified as termite nests are only limited to a handful of studies (e.g., Coaton, 1981; Miller and Mason, 2000; De Beer et al., 2002; Roberts et al., 2008; Almond, 2011, 2014, 2020; Helm et al., 2025), of which even fewer (Coaton, 1981; Miller and Mason, 2000) provide the detailed morphological analyses and comparison necessary for understanding the overall nest architecture (e.g., above or below ground, central hive) and identifying the tracemaker. Whether modern, subfossil or fossil, despite the prevalence of termites in South Africa, systematic documentation of subterranean nest architecture is scarce and, when present, often does not provide sufficient detail to satisfy modern ichnological standards (e.g., Duringer et al., 2007).

Here, we present comprehensive macro- and micro-morphological analyses for eight well-preserved, *in situ* fossil structures from Calitzdorp, South Africa (Fig. 1), and provide robust evidence that they represent a new ichnogenus of Pleistocene subterranean nests that are likely attributable to termites. By understanding their geological context and

*Correspondence: M. Abrahams, as above.
Email: Miengah.abrahams@uct.ac.za

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.
This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

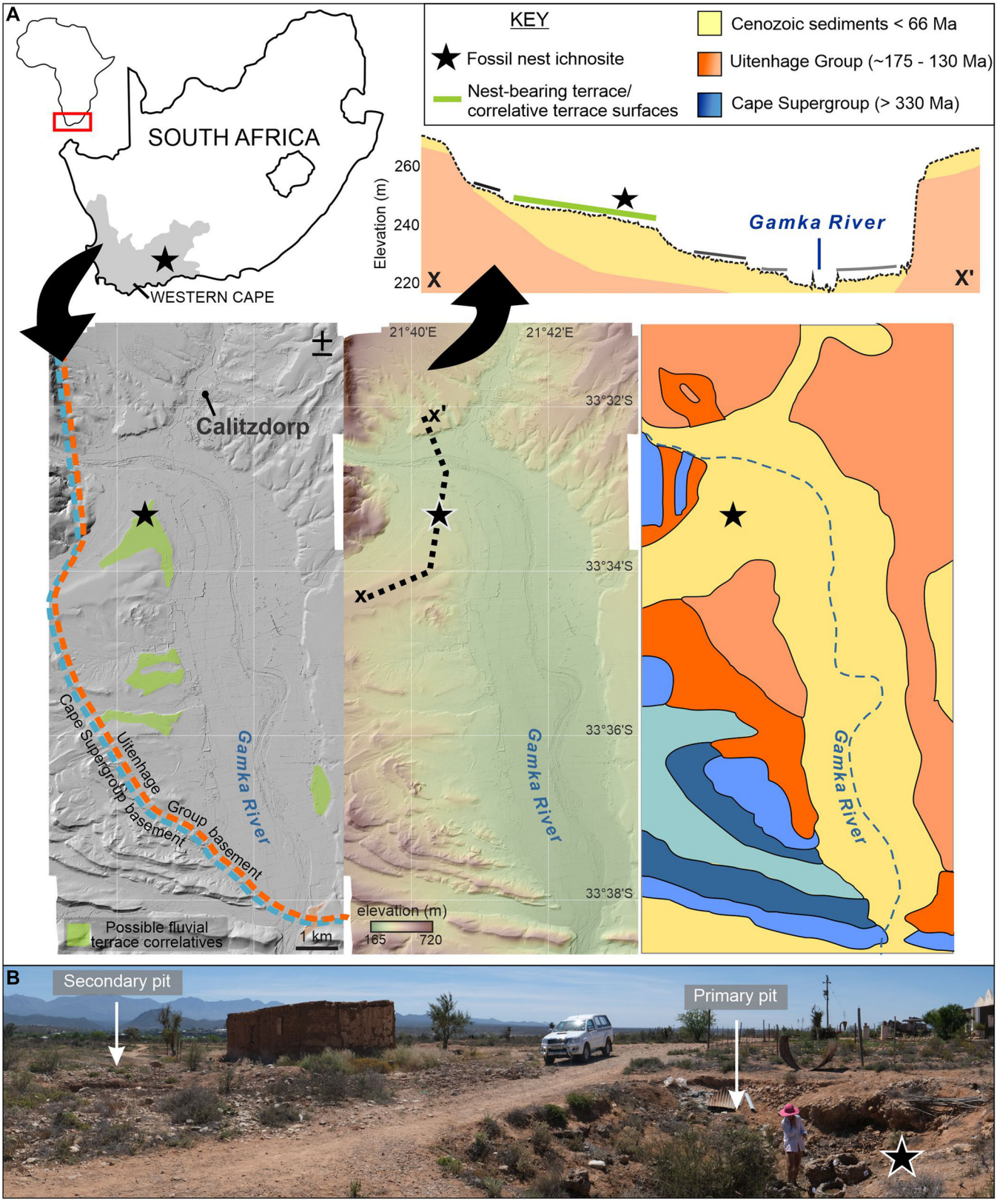


Figure 1. Overview of the ichnosite, indicated by the star. (A) Geographical, geomorphological and geological context. (B) Photograph of the fluvial terrace surface with two artificial pits, of which the primary pit exposes the fossil nests. [Color figure can be viewed at wileyonlinelibrary.com]

confirming their termite affinity, these structures offer important insights into the local palaeoenvironment.

Site history

In the early 2000s, numerous striking and unusual pipe-like features were excavated near the South African small town Calitzdorp by Mr Tim Robson, a local artist (Fig. 1). He thought that these features, preserved as resistant, calcretised structures, were ovens used by early humans (personal communication to JEA by Tom Barry, Bob Wood 2003–2004). Unfortunately, no formal documentation about the circumstances of the excavation exists, and we have no information about the initial motivation for

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

digging or whether the features had a visible surface expression. Several specimens were removed from the site, and one was deposited at the Calitzdorp Museum, where it is still housed. JEA briefly documented the site for a palaeontological heritage study (Almond, 2005) and though he posited that the features may be fossil termite nests, no detailed description or follow-up study was undertaken.

Geological context

The Calitzdorp fossil nests (33°33′18.4″ S 21°40′24.3″ E) are preserved within upward fining alluvium capping a relict fluvial terrace along the Gamka River, near Calitzdorp, Western Cape Province, South Africa (Fig. 1). To date, these Late Cenozoic alluvial deposits, which locally unconformably overly sedimentary bedrock of the ~175–130 Ma Uitenhage Group (Muir et al., 2020), have received little to no attention. The fluvial terraces along the Gamka River are flat geomorphological features, and it is only due to two artificial pits excavated into one of these terrace surfaces that the fossil nests and their host sediments are exposed and observable (Figs. 1 and 2). The two pits, which are ~10 m apart, share similar sedimentological features, though there are noteworthy differences between the two, and only the primary pit preserves fossil nest material.

The succession that outcrops within the primary pit, showing vertical sections through the terrace deposits, is poorly exposed. Here, we describe the best exposure along the pit's southern margin. The primary pit is characterised by an upward fining succession with basal clast-supported gravel deposits that grade into fine sands (Fig. 2(A), (B)). The gravel clasts are cobbles (between 7 and 18 cm in length) composed of quartzite, and are sub-rounded, moderately sorted and commonly have calcified fine sand coatings and matrix. They are overlain by a 40.5 cm horizon of calcareous fine sand, which, at its base, is clast-rich, containing sporadic quartzite gravel clasts, and then grades into a nodular-rich facies, devoid of clastic clasts and instead comprising spherical to irregularly shaped carbonate nodules ranging between 0.5 and 8.5 cm in length (Fig. 2(C)). The nodule size and density increase up-stratigraphy, until they ultimately amalgamate to form a 16.5 cm thick honeycomb calcrete, which is capped by a 28 cm thick hardpan calcrete (Fig. 2(D), (E)). Based on X-ray diffraction analyses, calcite is the only carbonate mineral present in the calcareous sands (3%), nodules (25%–65%) and hardpan (42%; Table S1).

The fossil nest structures are preserved within the primary pit and their vertical extent is strongly controlled by the host lithology (Fig. 2). The nests are found within the clast- and nodular-rich sand horizons, interpreted to be an ancient soil profile. Their base corresponds to the top of the gravel deposit and the upper limit of the taller nests correlates with the honeycomb, amalgamated nodule layer.

The secondary pit has clearly defined vertical sections and has been dug more neatly and deeply, allowing for better exposure of the terrace deposits (Figs. 1 and 2(B)). The secondary pit comprises most of the same lithologies as the primary pit: basal gravel deposits that grade into calcareous fine sands that become nodular-rich upwards (Fig. 2(A), (B)). Notably, although only ~10 m away from the primary pit, the secondary pit preserves no honeycomb or hardpan calcrete. An important sedimentological feature observed in the secondary pit is the vertical variation in the calcareous sand unit thickness (Fig. 2(B)), a feature that is also inferred to be present within the primary pit.

Trace fossil description

Eight concentrated fossil nests with the same overall morphology are preserved *in situ* within 4.5 m of each other at the Calitzdorp ichnosite (Fig. 2(F); Table 1). The nests are preserved as resistant, calcretised features (with bulk samples containing between 14 and 26 wt % calcite and dolomite; Table S1) and are easily distinguished from their soft, calcareous sand host sediment. The nest structures are vertical, subcylindrical features, with exposed heights ranging from 36 to 104 cm, and are defined by a discrete wall (average width of ~12 cm) comprising externally of well-developed to poorly-developed boxworks of galleries and chambers and internally of shelved chambers that surround an empty central space (Figs. 2(F) and 3; Table 1). There is no correlation between nest height, wall width and the empty centre (Table 1). Along the height of the nest, the total diameter of the nest may either be consistent, vary slightly or, as for the tallest nest (#4), taper (Fig. 2(F)). The interior and exterior surfaces of the nest wall have distinct features (Figs. 3 and 4). The interior surface displays clear, systematic, closely spaced, horizontal shelving made up of flat chambers that are vertically stacked (Figs. 3(D) and 4(B)). The chambers are wider than high (average width of 6.39 cm, average height of 0.73 cm; horizontally elongate 'rectangles'), have smooth floors and ceilings, and are separated by narrow partition pillars (Figs. 3(D) and 4(A), (B); Table 1). Across the partition pillars, individual chambers can be traced along a horizontal plane around the circumference of the interior surface of the nest wall. Vertical and inclined ramps, connecting various horizontal chamber levels, are observed on the interior surface (Fig. 3(D)). Conversely, the appearance of the exterior surface of the nest wall is more variable and the features are generally less systematic and more poorly defined than on the interior surface (Figs. 3 and 4(B), (C)). The exterior surfaces preserve either high, intermediate or no morphological detail: surfaces with high morphological detail preserve well-defined chamber and gallery structures, whereas surfaces with no morphological detail are undulated with no clear chamber or gallery structures (Fig. 3(E)). High morphological detail exterior surfaces are dominated by irregular 'oval'-shaped galleries that are wider than high and have smooth walls and ceilings (average gallery width of 2.96 cm, average gallery height of 1.02 cm; Figs. 3(F) and 4(C); Table 1). Chambers, similar to those on the interior surface, are present on the exterior surface but are less prevalent. Vertical, inclined and sinuous ramps connecting horizontal levels are also observed on the exterior surface, and their size tends to exceed those on the interior surface (Fig. 3(C)–(E)).

Relative to the interior surface, the chambers and galleries on the exterior surface have greater heights (maximum chamber height of 1.26 and 1.91 cm, respectively), shorter lengths (maximum chamber width of 20.82 and 4.37 cm, respectively) and are more sparsely spaced (Figs. 3 and 4; Table 1). Furthermore, whereas the interior surface chambers are systematically organised with uniform morphology, the exterior surface galleries and chambers appear more random (Fig. 4(B), (C)).

Although clustered near each other in the primary pit, the fossil nests are predominantly preserved as isolated, independent structures, although some have walls built up against each other and some share walls (Figs. 2(F) and 3(B)). Embedded within the vertical extent (height) of the nests are sub-rounded, cobble-sized quartzite clasts indistinguishable from those in the gravel deposits underlying the nests

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License



Figure 2. Sedimentary context of the fluvial terrace deposits preserving fossil nests. (A) Sedimentary log of the upward fining successions exposed in the artificial primary and secondary pits. Notably, the primary pit preserves lithologies (e.g., amalgamated nodules and hardpan) and trace fossils that are absent in the secondary pit. (B) Upward fining succession of basal conglomerates grading into fine sand preserving sporadic clastic clasts and carbonate nodules. Note: the thickness variation of the fine sand unit. (C) Carbonate nodule-rich horizon. (D) Amalgamated or honeycomb nodular calcrete. (E) Hardpan calcrete. (F) Overview of the primary pit highlighting the fossil nests preserved below the hardpan level, with the upper limit of taller nests corresponding to the base of the hardpan. Individual fossil nests within the cluster are numbered (#1 to #8). Abbreviations: f, fine sand; c, coarse sand. [Color figure can be viewed at wileyonlinelibrary.com]

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 1. Measurements of macro-morphological features of the Calitzdorp trace fossils. To see the numbered nests' position at the site, refer to Fig. 2. Nest 2 has been broken and therefore no measreuments were obtained from it.

Nest #	Exposed height (cm)	Total diameter (cm)	Empty centre diameter (cm)	Average wall width (cm)
Nest structure				
1	39.6	57.8	43.1	11.7
2				
3	39.0	67.6	57.0	8.3
4	103.6	46.0	27.0	12.0
5	58.6	66.2	47.0	5.0
6	89.0	58.0	36.0	15.5
7	36.0	48.0	34.4	8.9
8	51.0	48.0	35.0	8.6
		Height (cm)	Width (cm)	Height/Width
Interior surface chambers				
Minimum		0.28	0.89	0.03
Maximum		1.26	20.82	0.43
Average		0.73	6.39	0.16
Inner zone chambers				
Minimum		0.37	1.38	0.13
Maximum		1.01	4.37	0.57
Average		0.65	2.76	0.27
Exterior surface galleries and chambers				
Minimum		0.61	1.28	0.13
Maximum		1.91	8.67	0.96
Average		1.02	2.96	0.45
Outer zone galleries and chambers				
Minimum		0.54	1.25	0.10
Maximum		1.12	5.31	0.75
Average		0.90	2.63	0.46

(Fig. 3(C)). The inclusion of cobbles throughout the height of the nest walls suggests that the nests were originally entirely subterranean features within an ancient soil profile. The basal morphology of the Calitzdorp nests is uncertain: for nests in which we were able to remove the infilled sediment, no basal feature was observed and the nest-defining wall simply ended.

Cross-sections through the nest walls, extending from the interior to the exterior surface, reveal differences in both the abundance and morphology of chambers, as well as variation in the lithologies associated with those chambers. (Figs. 3(A), 4(D), (E), 5, S1, and S2). Based on these differences, the nest wall can be divided into an inner zone adjacent to the interior surface of the nest wall and an outer zone adjacent to the exterior surface of the nest wall. The changes in features from the inner zone to the outer zone are transitional and there is no defined boundary between the two.

The inner zone is characterised by abundant, systematically stacked chambers that can be directly correlated with the chambers visible on the interior surface of the nest wall. The floors and ceilings of the inner zone chambers are undulating, and the chambers are wider than they are high, with their height gradually tapering from the nest interior surface towards the exterior surface until they terminate in smooth, curved walls (Figs. 4(E) and 5). Closest to the interior surface of the nest wall, the chambers are horizontal but along their extent, towards the outer zone, they may incline gently upwards. CT imaging shows that around the circumference of the nest wall, the morphology of the inner zone chambers is consistent (Figs. 4(E) and S2; Vid. S2). The morphology of the inner zone chambers is highly apparent due to stark lithological contrasts (Fig. 5); the chambers are lined with distinct dark organic material and their infill predominantly consists of light brown clastic sediment (sand), whereas the nest wall comprises convoluted interlaminations of cream-coloured carbonate precipitate with minor darker brown clastic sediment (sand). The carbonate-rich laminations are thicker and more abundant adjacent to the chambers, and both the carbonate laminations and organic linings tend to mirror the chamber morphology. The dense clustering of the chambers and their associated organic linings suggest that nest construction by the trace-maker was prevalent within the inner zone.

The outer zone is characterised by more sparsely spaced, irregular and rounded oval galleries of variable size with minor chambers, both of which cannot necessarily be traced to features visible on the exterior surface of the nest wall (i.e., the exterior surface may have low morphological detail; Figs. 3(E), 4(E), 5, and S2; Video S2). CT imaging shows that at given cross-section surfaces through the nest wall, the galleries have varied orientations but across the circumference nest wall, these galleries are preferentially horizontal or inclined towards the nest interior surface (Figs. 4(E), 5, and S2). Overall, the outer zone features are less uniform. Unlike the inner zone, the outer zone is dominated by brown clastic sediment (sand) with minor cream-coloured carbonate-rich laminations (Fig. 5). In fact, the galleries and chambers are difficult to observe with the naked eye because of the rather slight lithological differences between the nest wall and gallery infill (Figs. 4 and 5). Within the outer zone, few organic linings are associated with the chambers and galleries and the minor carbonate laminations present do not always follow the gallery or chamber morphology. The dispersed arrangement of galleries and chambers, together with the low presence of organic linings, suggests that excavation by the tracemaker was dominant in the outer zone.

Micro-morphological analysis of the fossil nests shows distinct textural and compositional features reflective of both the initial excavation/construction (lining) of the nest and the subsequent taphonomic processes (Fig. 6). Within the nest, there is clear zonation of non-clastic and clastic material. Non-clastic zones are characterised by laminations of micritic and organic material, and where empty pore spaces are present, thicker carbonate laminations coat the pore (Fig. 6(B), (C)). Where organic bands are interlaminated with clastic-rich horizons, the clasts commonly have a preferred orientation, with their long axis running parallel to the organic bands (Fig. 6(A), (D), (E)). A similar observation is made within the bow-like microtextures and multiple generations of terminal walls directly associated with the nest galleries (Fig. 6(A), (E)). Here, the grains within the sediment-rich horizons are also closely packed, which is distinct from the loose packing of the passive gallery infill. The preferred orientation and dense packing of grains diminish with distance from the chamber and gallery walls, suggesting that the compaction and grain alignment are likely the result of the excavation and construction activities by the tracemaker. Within the clastic component of the nest, there is an absence of large calcite or dolomite grains and, where carbonate is present, it is as interstitial material or grain coatings. This suggests that the nests were not initially built in carbonate-rich soils but rather that the carbonate precipitation post-dates the nest-building activity.

Age constraints

The trace fossil-bearing alluvial sediments that form terraces along the Gamka River have not yet been dated using radiometric methods, and the only relative age constraints are that they directly overlie, and are therefore younger than the Upper Mesozoic Uitenhage Group. To provide more refined age

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

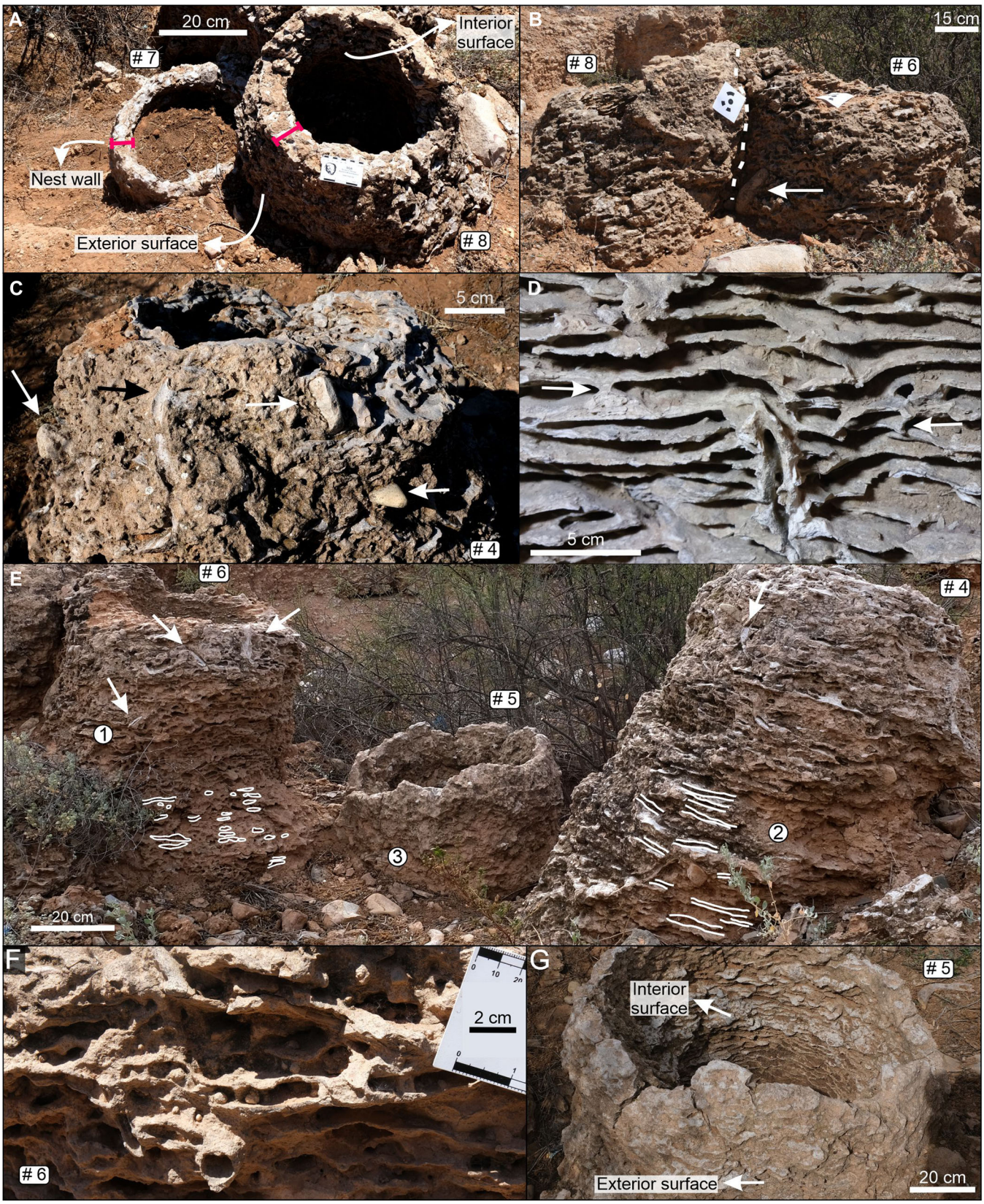


Figure 3. Overview of the fossil nests and their macro-morphological features. For the relative position of the numbered nests, see Fig. 2. (A) Labelled nest wall and its interior and exterior surfaces. (B) Nest walls built up against each other are marked with a dashed line. Arrow points to a clastic clast incorporated into the nest structure. (C) Clastic cobbles within the nest structure (white arrows) and a large sinuous ramp on the external surface (black arrow). (D) Interior surface showing its characteristic systematic, closely spaced, horizontal shelving, which has been cross-cut by a vertical ramp. Narrow partition walls separating chambers are indicated by white arrows. (E) Three nests with varying morphological details preserved on their exterior surface: 1—high-detail, 2—intermediate-detail and 3—low-detail. On high-detail exterior surfaces, galleries and chambers are clear, on intermediate-detail exterior surfaces, an overall layered, horizontal pattern is evident, while low-detail exterior surfaces simply preserve uneven surfaces with no evidence of bioturbation. Arrows point to inclined ramps and outlines show the general gallery orientation. (F) Close-up of a high-detail exterior surface. Note the round gallery extending out from the surface. (G) Close-up of a low-detail exterior surface. Note that although the external surface lacks detail, clear shelving is evident on the interior surface and can be traced across the inner circumference of the nest. [Color figure can be viewed at wileyonlinelibrary.com]

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

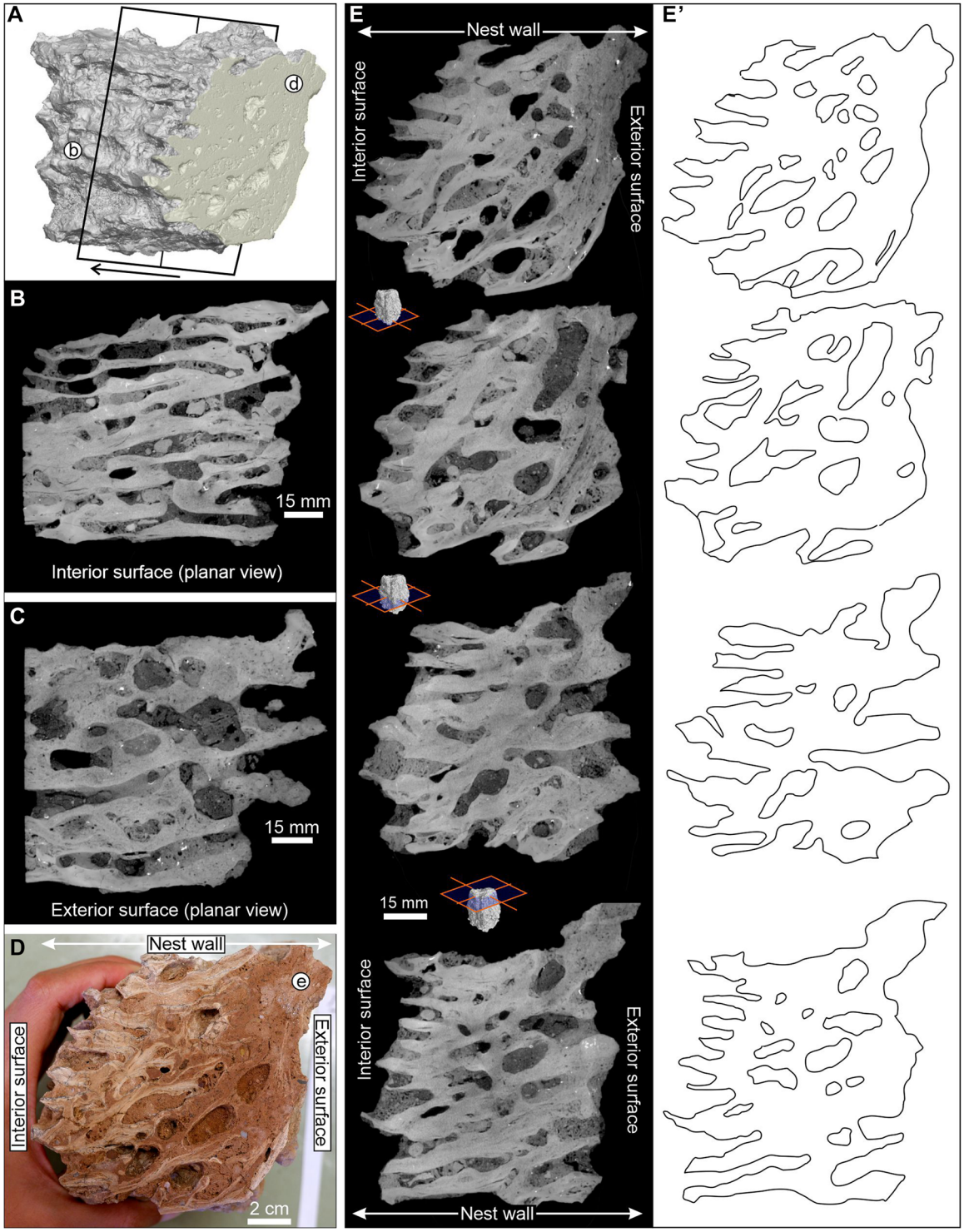


Figure 4. Morphology and distribution of chambers and galleries within the nest wall. (A) 3D view of a collected *ex situ* specimen of nest wall with the yellow shaded area highlighting a cross-section surface of the nest wall. The black plane shows the CT imaging direction for E. (B) CT image of the planar view of the interior surface. (C) CT image of the planar view of the exterior surface. (D) Photograph of a cross-sectional surface through the nest wall, that is, a cross-section from the interior to exterior surface. The cross-sectional surface in D is perpendicular to the planar surfaces shown in B and C. This surface corresponds to the yellow shaded area in A. (E, E′) Progressive CT images, and chamber or gallery interpretive outlines, of successive cross-section surfaces through the nest wall. For all CT images, lighter colours correspond to more cemented lithologies and darker colours relate to more porous sediments (infill). For more CT images and videos, see Figs. S1, S2; Videos S1, S2). [Color figure can be viewed at wileyonlinelibrary.com]

constraints for the Calitzdorp fossil nests, pedogenic carbonates within the nests were dated by the U–Th method (Hellstrom, 2003) following the carbonate geochemical pre-screening and sample selection outlined by Pickering (2015) and Von der Meden et al. (2022). For details of the methods and prescreening results, see Appendix S1, Tables S2–S6 and Fig. S3.

Eleven cream-coloured, non-porous carbonate laminations were analysed and the results are presented in Table S7 and Fig. 7. Of these, nine analyses resulted in reliable dates, while two yielded dates with unreasonably large uncertainties and were removed from further consideration (CF1-4 and 2CL-1). These two samples have the lowest $^{238}U/^{232}Th$ ratios and very low (<5) $^{230}Th/^{232}Th$ ratios, indicating that a significant detrital component was included during sampling (Table S7).

The remaining nine samples yield dates that range from 422 ± 49 to 206 ± 8 ka (Fig. 7; Table S7). These dates define

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

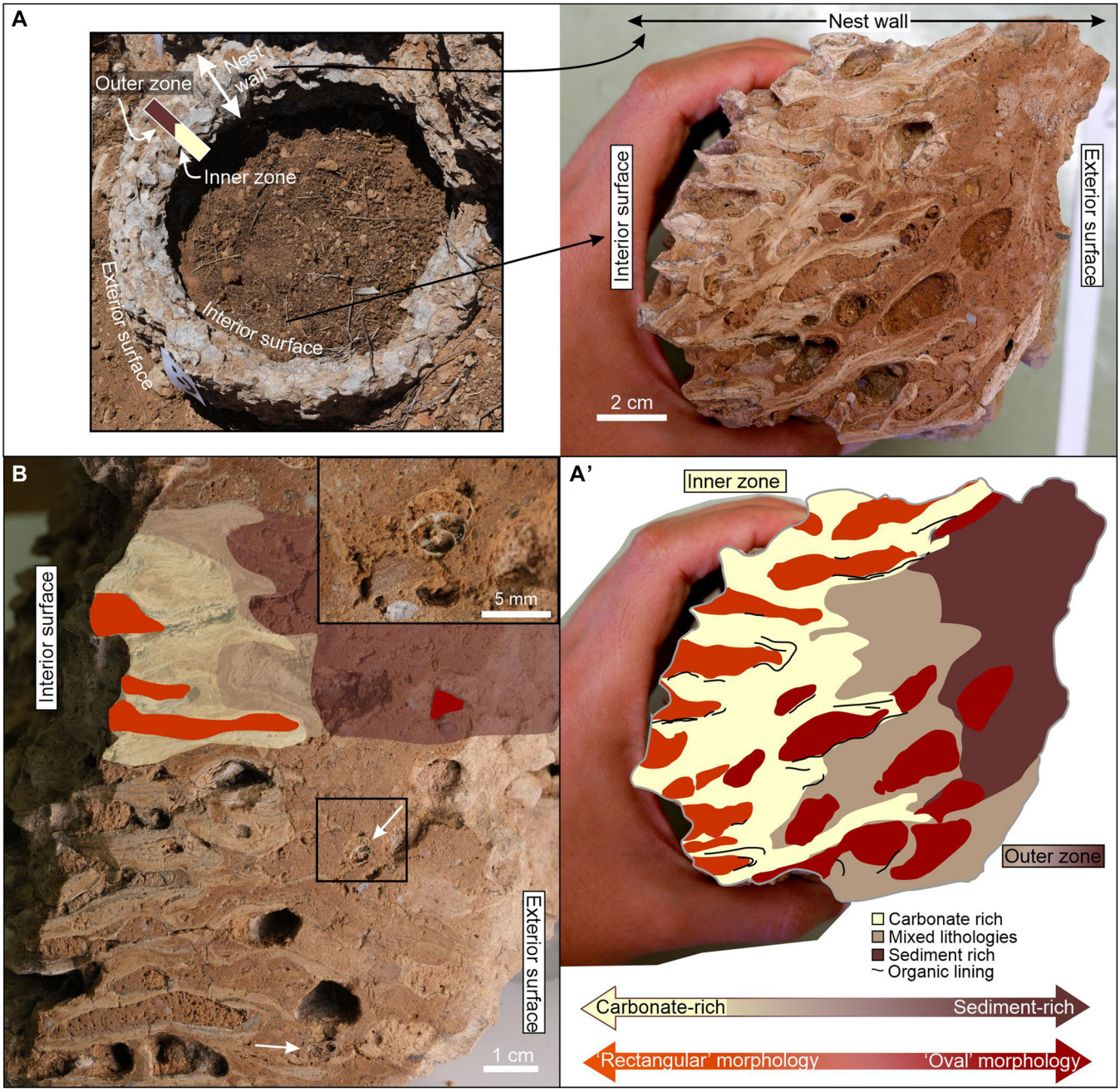


Figure 5. Cross-section of fossil nest walls highlighting lithological and bioturbation differences across the wall. (A, A′) Densely stacked chambers associated with dark organic linings and carbonate-rich lithologies are characteristic of the inner zone, whereas irregular-shaped, rounded galleries and sediment-rich lithologies characterise the outer zone. (B) As indicated in A, but showing that elongate chambers are also present in the outer zone. A close-up of a gastropod shell incorporated into the nest structure. [Color figure can be viewed at wileyonlinelibrary.com]

three discrete age peaks, at 401 ± 46 ka ($n = 3$), 323 ± 12 ka ($n = 5$) and 206 ± 8 ka ($n = 1$), identifying at least three phases of carbonate precipitation associated with the fossil nests. The youngest peak (206 ± 8 ka), represented by a single date, is linked to chaotically orientated laminations that do not mirror the chamber morphology, whereas the two older peaks (401 ± 46 and 323 ± 12 ka), each represented by multiple dates, are linked to carbonate laminations that follow the nest chamber morphology. Given that carbonate laminations that do not follow the chamber morphology do not have a clear relation to the nest structure and that the youngest peak is only represented by a single date, we consider 206 ± 8 ka unlikely to be the minimum age for the fossil nests. The two older peaks are more robust because they comprise multiple dates that are sourced from carbonate laminations that mirror the chamber morphology. Consequently, they represent two different periods of precipitation that post-date the construction of the nest at 401 ± 46 and 323 ± 12 ka. Of these two peaks, the younger component (323 ± 12 ka) contains our most precise and largest number ($n = 5$) of dates (Fig. 7; Table S7). Therefore, we interpret the minimum age of the Calitzdorp fossil nests to be 323 ± 12 ka, implying that nest-building activities occurred within or before the Middle Pleistocene (Chibanian).

Discussion

Comparative ichnotaxonomy

Based on their overall morphology and internal organisation, the Calitzdorp trace fossils are assigned herein to the

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

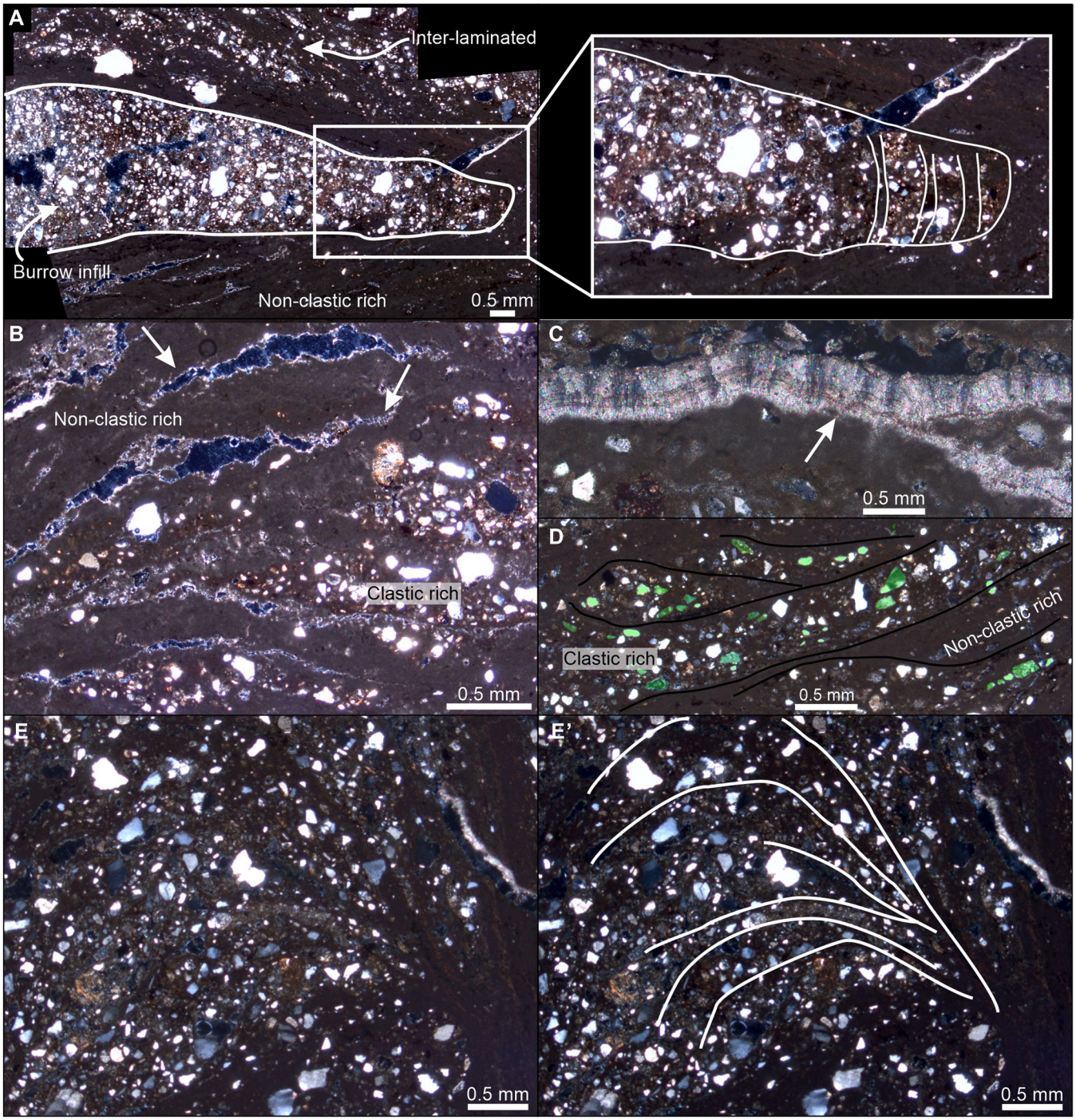


Figure 6. Micro-morphological characteristics of the fossil nests. (A) Cross-section through an infilled gallery highlighting the thick non-clastic, carbonate-rich horizons surrounding the gallery. Note the termination of the gallery comprises alternating laminations of non-clastic and clastic-rich material. Here, unlike the burrow infill, the clastic component is sorted and closely packed. (B) Clastic versus non-clastic composition. Note laminations of distinct carbonate precipitate, indicated by white arrows, are associated with the dark brown, non-clastic laminations. (C) Close-up of a thick carbonate lamination, indicated by the white arrow, coating a pore space. (D) Alternating laminations of non-clastic and clastic-rich materials, with the long axis of numerous elongate clasts, highlighted in green, aligning parallel to the non-clastic material. (E, E′) Bow-like microtexture alternating between clastic sediment-rich and non-clastic-rich laminations. [Color figure can be viewed at wileyonlinelibrary.com]

Ichnofamily Krausichnidae, which is characterised by nests composed of interconnected chambers and galleries, attributed to eusocial insect activity (for a review of the Krausichnidae, see Genise, 2017). While no single diagnostic feature unequivocally distinguishes termite nests from those of ants (e.g., Wheeler, 1910; Grasse, 1984; Tschinkel, 2003; Cosarinsky et al., 2005; Cosarinsky, 2011; Genise, 2017), the combination of macro-morphological and micro-morphological characteristics of the Calitzdorp trace fossils aligns closely with known termite nest structures. The Calitzdorp trace fossils are preserved as subterranean structures, comprising a complex morphology, with the inner zone of the nest consisting of tiered chambers that are frequently associated with dark organic linings observable to the naked eye (Figs. 3–5). These features are consistent with termites that are known to excavate and construct (line) more architecturally complex nests than ants (e.g., Darlington, 1984; Bown and Laza, 1990; Duringer et al., 2007; Genise et al., 2013a) and, while we now know that ants also occasionally utilise organic linings to reinforce their burrow walls (Genise et al., 2013b), this behaviour is significantly more prevalent in termites. The empty centre, which is a

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

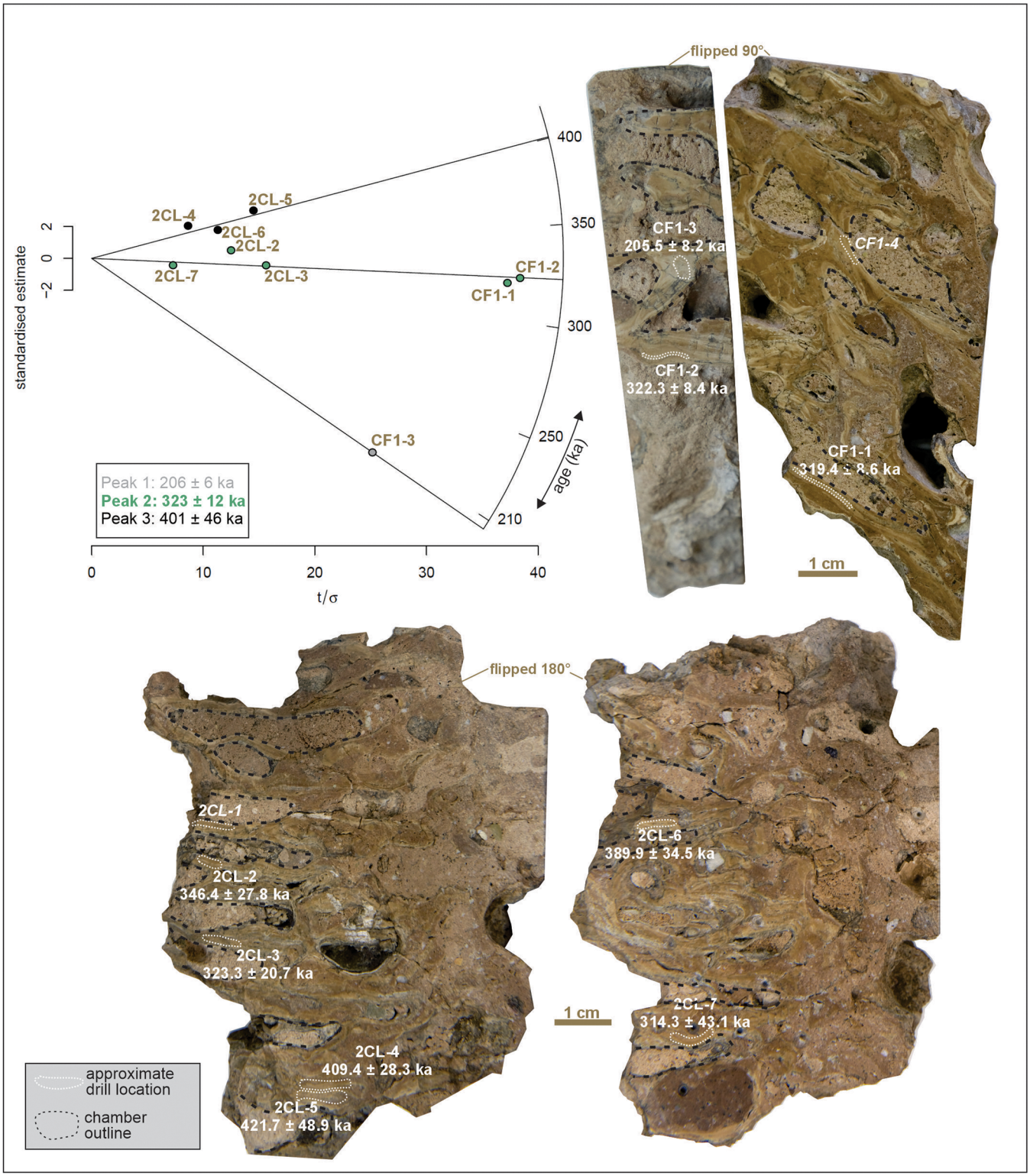


Figure 7. U-series (U–Th) pedogenic carbonate dates from the Calitzdorp fossil nests. The dates presented in the radial diagram (plotted in IsoplotR, Vermeesch et al., 2018) correspond to data presented in Table S7 and to the drilling locations indicated in the cut and polished nest fragments. [Color figure can be viewed at wileyonlinelibrary.com]

consistent feature for all eight Calitzdorp fossil nests, is curious and not understood. The nests may have contained an organic-rich central component, for example, a hive, that has low preservation potential and decayed (e.g., Pickford, 2006), or, like arboreal and epigeal termite nets, they may have been constructed around existing features, for example, tree trunks (see Genise, 2017). At the micro-morphological scale, the presence of bow-like and lamellar microtextures as well as grain sorting and alignment within the fossil matrix is consistent with soil modifications produced by termites and are commonly observed in termite-related laterites (e.g., Cosarinksy et al., 2005; Cosarinsky, 2011; Francis et al., 2013; Genise, 2017).

Attributing trace structures to termites specifically becomes contentious in older sequences (e.g., Triassic traces—Hasiotis and Dubiel, 1995; Smith and Kitching, 1997; Jurassic traces—Bordy et al., 2004; Genise et al., 2005). Fossil nests with robust evidence supporting termites as tracemakers are typically more recent, becoming prevalent since the Palaeogene (e.g., Genise and Bown, 1994b; Miller and Mason, 2000; Pickford and Senut, 2000; Laza, 2006; Darlington, 2011; Roberts et al., 2016).

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

For the ichnotaxonomic assignment of the Calitzdorp traces, we exclusively focus on ichnogenera that show rounded macro-morphologies and are composed of systematic, horizontally stacked shelves—specifically *Coatonichnus globosus* (Early Pliocene; Schuster et al.., 2000; Duringer et al., 2007) and *Termitichnus schneideri* (Late Miocene–Early Pliocene; Duringer et al., 2007).

Both *Coatonichnus globosus* (Schuster et al., 2000; Duringer et al., 2007) and the Calitzdorp trace fossils are preserved in groups (>10 and >8 nests, respectively), consist of horizontally stratified shelves with flat floors and are interpreted to be subterranean features. Although both have a broadly rounded micro-morphology, in horizontal section, *C. globosus* is defined by its flattened ovoid shape, being wider than tall, with its maximum width at the equator, whereas the Calitzdorp nests are characterised by their subcylindrical shape, being taller than they are wide, with no fixed height-to-width ratio (Fig. 8). Furthermore, the Calitzdorp subcylindrical structures have a distinct empty central space that is absent from *C. globosus*. Given the significant macro-morphological differences, the Calitzdorp trace fossils cannot be assigned to *C. globosus* and are instead considered to represent a separate ichnogenus.

Both *Termitichnus schneideri* (Duringer et al., 2007) and the Calitzdorp trace fossils represent excavated, subterranean nest systems composed of horizontally tiered shelves connected by large ramps, with undulating external surfaces that reflect the systematic internal shelving (Figs. 3 and 8). No detailed cross-sectional analysis of *T. schneideri* nests is currently available, limiting direct comparison of the complex internal morphologies. Despite the similarities in macro-morphological features, there are notable morphological differences between *T. schneideri* and the Calitzdorp trace fossils: *T. schneideri*—like *C. globosus*—is subspherical and wider than tall, whereas the Calitzdorp nests are subcylindrical and taller than wide. Additionally, a diagnostic feature of *T.schneideri* is the presence of tunnels at its base, a feature that has not been identified for the Calitzdorp structures (Fig. 8). It is likely that for the Calitzdorp traces, this feature is genuinely absent, but we must note that the basal morphology is not clearly exposed at the ichnosite and is therefore poorly understood. Given these limitations and the macro-morphological differences, the Calitzdorp trace fossils are considered to be distinct from *T. schneideri*.

Although the Calitzdorp traces have superficial similarities with these *C. Globosus* and *T. schneirderi*, and much more distantly with others showing shelved structures like *Microfavichnus* and *Krausichnus* (Duringer et al., 2007, Genise et al., 2016; Genise, 2017), they possess unique features that distinguish them (Figs. 2, 3, 4, 5, and 8). Consequently, we propose a new ichnogenus and ichnospecies for the nest structures described herein.

Columnanidus ichnogen. nov.

Etymology: Columna, derived from the Latin columna, meaning column or pillar. This reflects the distinct macromorphology of the trace fossil. Nidus, derived from Latin, meaning nest or dwelling. This acknowledges the inferred behaviour of the tracemaker.

Type ichnospecies: *Columnanidus calitzdorpensis*, isp. nov.

Holotype: Housed at the Calitzdorp Museum—accession number 93/01/01.

Type locality and horizon: The ichnosite is in Calitzdorp, South Africa (33°33′18.4″ S 21°40′24.3″ E), within Late Cenozoic alluvium.

Diagnosis: Subterranean, vertical to sub-vertical, pipe-like structures defined by a wall that surrounds an empty central cylindrical space. The nest wall interior and exterior preserve different features. The interior is composed of systematic, densely packed, horizontal, shelved, flat chambers connected by inclined or vertical ramps. These chambers, which are wider than high, show dark organic linings, gently incline and taper until they terminate in a U-shaped chamber wall. The exterior has more irregular aspects from absolutely structureless to preserving sparsely spaced, irregular oval galleries and, more

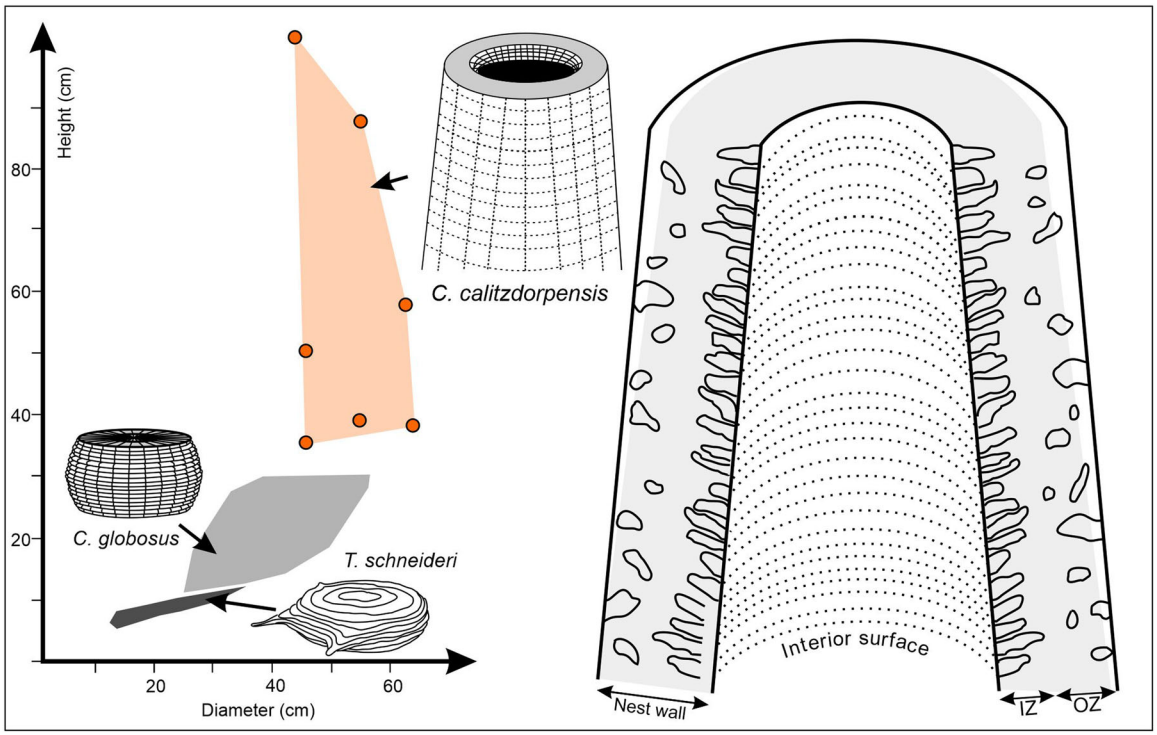


Figure 8. Comparison of macromorphological features, including dimensions, of *Columnanidus calitzdorpensis, Coatonischnus globosus* and *Termitichnus schneideri*. Modified after Duringer et al., 2007. Abbreviations: IZ, inner zone; OZ, outer zone. [Color figure can be viewed at wileyonlinelibrary.com]

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

rarely, rectangular chambers that are horizontally elongated. Features on the exterior have more random orientations and are rarely associated with dark organic linings.

Columnanidus calitzdorpensis ichnosp. nov.

Etymology: Latinised, from Calitzdorp. The ichnospecies is named after the type locality, the town Calitzdorp in South Africa.

Examined material: Eight complete fossil nests preserved *in situ* (33°33′18.4″ S 21°40′24.3″ E).

Distribution: Pleistocene. U-series dating herein indicates a ~320 ka minimum age for the nests.

Diagnosis: It is the only known ichnospecies; this is the same as for the ichnogenus.

Description: *Columnanidus calitzdorpensis* isp. nov. is preserved as a vertical to subvertical (up to ~1 m exposed height), sub-cylindrical or pipe-like trace fossil defined by an ~12 cm thick nest wall with a complex morphology that surrounds a central empty space (average diameter of 40 cm). The overall structure is taller than it is wide, with no consistent relationship between height and diameter. The interior surface of the nest wall shows well-defined, stacked horizontal chambers, whereas the nest exterior surface preserves irregular-shaped 'rounded' galleries and few chambers. In cross-section, the nest wall is differentiated into two distinct zones. The inner zone displays a high density of systematically arranged, horizontally tiered chambers with undulating floors and ceilings that are stacked into discrete layers. The chambers, which are commonly associated with organic linings, are horizontal at the nest wall interior surface but may incline gently upwards towards the exterior surface. The outer zone preserves sparsely spaced irregular-shaped galleries with minor chambers, both of which reach greater heights and smaller widths than the chambers of the inner zone. The gallery orientation of overlying features is variable, but a preferred horizontal or incline downwards towards the nest wall interior surface is observed. Few organic linings are observed in the galleries or chambers of the outer zone.

Pedogenic carbonate and nest preservation

Both fossil and extant termite nests are often preserved, with accumulations of carbonate material within their structures (e.g., Coaton, 1981; Moore and Picker, 1991; Genise and Bown,1994a; Monger, 2002; Pickford, 2006; Darlington, 2011; Mujinya et al., 2011; Roberts et al., 2016; Francis and Poch, 2019), but the origin of this carbonate remains the subject of ongoing debate (e.g., Hesse, 1955; Liu et al., 2007; Mujinya et al., 2011). In studies of fossil termite nests, the presence and, occasionally, the carbonate mineralogy may be noted in relation to preservation style but it typically receives little attention as most studies focus on the ichnological or biological aspects of the nests, for example, characteristic morphology, behavioural implications, etc. At Calitzdorp, all the recorded fossil termite nests are preserved as carbonate-bearing features, comprising both calcite and dolomite, within a calcareous palaeosol that exclusively contains calcite (Figs. 2 and 3; Table S1). Such soil carbonates may either be inherited, with carbonates sourced from the parent material, or pedogenic, meaning that the carbonates formed in place within the soil (Monger, 2002; Wright and Tucker, 2009; Alonso-Zarza and Wright, 2010, Zamanian et al., 2016). Pedogenic carbonates have widely accepted and established features (Gile et al., 1966; Netterberg, 1980; Wright and Tucker,1991) and at Calitzdorp, many of these features have been observed: (i) At the landscape scale, the carbonate bodies occur as subsurface horizons that run parallel to the land surface (Fig. 2). The lithologies exposed within the primary pit can be mapped across the pit walls, with the gravels, calcified sands and nodular sands traceable for an additional 10 m into the secondary pit. (ii) In profile, distinct carbonate morphological stages are preserved, typical of pedogenic carbonates in gravel and sandy deposits: the basal gravels have carbonate coatings and are overlain by calcareous sands that grade into nodular sands that amalgamate into larger nodules that are capped by a hardpan (Fig. 2). (iii) At the micro-morphological scale, carbonate is primarily present as pervasive interstitial material (micrite) and there are no large clasts of carbonate minerals present (Figs. 5 and 6).

The pervasive calcretisation at the Calitzdorp ichnosite is likely to be complex, consisting of multiple periods of precipitation (of which at least three phases are identified at 401 ± 46, 323 ± 12 and 206 ± 6 ka), and, possibly, subsequent recrystallisation. However, we are able gain insights into the relative timing for most of the calcretisation at the ichnosite which we summarise here: (i) The calcretisation of the host sediments occurred after nest-building activities for two key reasons: First, the hardpan overlying the nests is impenetrable, meaning that the nests must have already existed by the time it formed (Fig. 2). Second, the nests contain only micritic and pore-infill carbonate, with no large carbonate grains incorporated from the host sediments (Fig. 6). (ii) The precipitation of carbonate within the nests occurred after, or a minor amount concurrently with, the nest-building activities. This is indicated by the strong association between termite activity and carbonate precipitation (Fig. 5). Within the inner zone of the nest, where there is a higher density of stacked chambers, a greater proportion of carbonate-rich laminations is observed. Additionally, these laminations tend to be thicker directly adjacent to the chamber wall. Notably, similar to the organic linings along the chamber walls, the carbonate-rich laminations follow the curved morphology of the chamber itself (Fig. 5). This relationship between chamber morphology and lamination pattern suggests that, in the Calitzdorp nests, most carbonate precipitation occurred after the nests (chambers) were constructed. (iii) The bulk of carbonate precipitation for both the host sediments and the fossil nests likely occurred at the same time. This is supported by the previously observed timing relationships, as well as the fact that the upper surfaces of some nests preserve carbonate nodules that are similar in size to those found within the nodular sands and these nest tops correspond stratigraphically to the nodular sand horizon (Figs. 2 and 9).

There are four accepted models to describe pedogenic carbonate precipitation (for a review see Zamanian et al., 2016): (i) The *per descendum* model with a top-down movement of carbonate within meteoric water; (ii) the *per ascendum* model with the bottom-up movement of calcium and bicarbonate through capillary action from groundwater sources; (iii) the *in situ* model involving the dissolution and re-precipitation of calcium carbonate within the soil; and (iv) the biogenic model, where biological activities enrich in the soil in the relevant cations. Studies based on extant termite nests have shown that carbonate accumulations within nests may be attributed to a combination of biotic and abiotic processes (e.g., Genise and Bown, 1994a; Monger 2002; Liu et al., 2007; Mujinya et al., 2011; McAuliffe et al., 2014, 2019; Francis et al., 2022) and this is also our interpretation for this study. Although pedogenic carbonate is pervasive across the fluvial terrace at Calitzdorp, the locally enhanced degree of calcretisation at the ichnosite can be attributed to the termite activity (Figs. 2 and 9). This is evident both within the nests, where carbonate precipitation is clearly associated with the

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

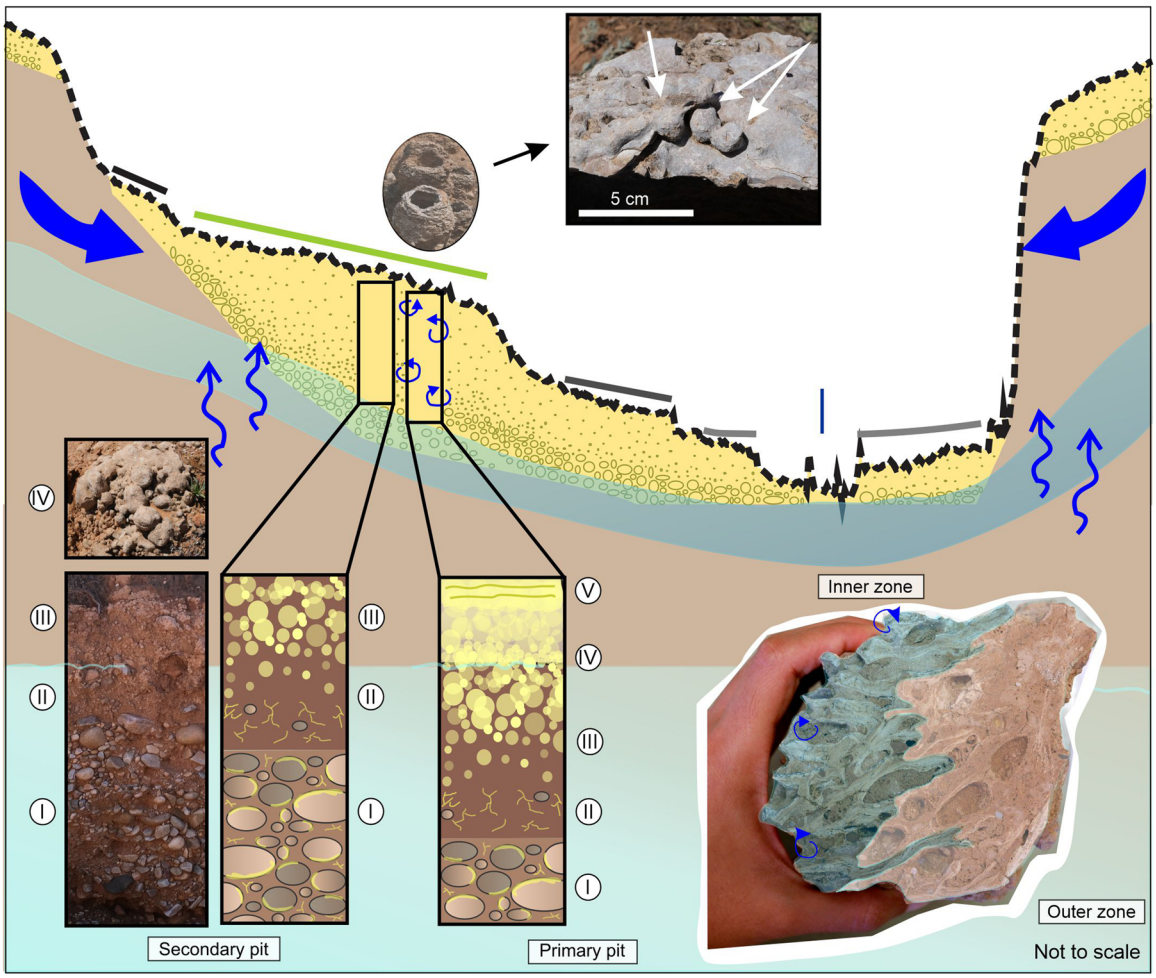


Figure 9. Overview of the calcretisation at the Calitzdorp ichnosite, with a focus on the link between calcretisation and the fossil nests. In support of biological factors affecting the degree of calcretisation—1. morphologically advanced stages of calcrete are exclusively associated within the nest-bearing primary pit and 2. within the nest, greater amounts of carbonate precipitation are associated with higher densities of burrowing activity. Blue arrows indicate that the nest systems would locally improve the hydrological properties of the soils by increasing permeability and porosity. Additionally, the trace-bearing terrace would also receive moisture from higher lying terrace surfaces. I-V represent the different lithological units: I - carbonate coated gravels, II - sands with clastic nodules, III - sands with carbonate nodules, IV - amalgamate nodules, V - hardpan. [Color figure can be viewed at wileyonlinelibrary.com]

high-density, stacked chambers (Fig. 5), and at the outcrop scale (Figs. 1(B) and 2), where more advanced morphological stages of pedogenic carbonates (i.e., amalgamated nodules and hardpan) are exclusively associated with the fossil nests in the primary pit and tellingly disappear along strike within 10 m in the secondary pit. The termite activity probably facilitated this enhanced carbonate precipitation through several mechanisms, including modification of the soil chemistry, alteration of the local soil porosity and localised increase in moisture retention (Lee and Wood, 1971; Asawalam et al., 1999; Holt and Lepage, 2000; Turner et al., 2006). Termites selectively incorporate material into their nests, combining it with saliva or faecal matter (e.g., Genise and Bown, 1994a), enriching nest structures in exchangeable cations such as Ca and Mg (e.g., Mujinya et al., 2011; Singh et al., 2017), which are necessary for calcite and dolomite precipitation. Additionally, complex burrowing networks within nests alter the hydrological properties of soils, increasing porosity and permeability, and promoting greater moisture flow throughout the nests (Lee and Wood, 1971; Turner et al., 2006; Clarke et al., 2022). Furthermore, clays used in nest construction are more absorbent than the surrounding sediments, further enhancing moisture retention capabilities within nests (Lee and Wood, 1971). While no evidence for fungi has been observed within the Calitzdorp trace fossils, enhanced carbonate cementation possibly associated with fungi has been observed for fossil ant nests (Genise et al., 2013a) and rhizolith features tentatively attributed to ant activity (Genise et al., 2010). The presence of fungi need not be due to active cultivation by the insects but may simply be due to fungi exploiting the good living conditions afforded by empty chambers (e.g., humidity and oxygen level; Martin and Bennett, 1977; Richardson, 1983).

For whichever of these reasons, the termite activity at Calitzdorp appears to have significantly increased the preservation potential of these unique structures by enhancing localised carbonate precipitation over a substantial time interval (at least 401 ± 46 to 323 ± 12 ka, and possibly to 206 ± 8 ka). The differing carbonate mineralogy of the host sediments and fossil nests (calcite vs. calcite and dolomite, respectively) may also be influenced by the termite activity, but available data from this ichnosite are too limited to explore this further. However, our research group is currently investigating similar compositional patterns at additional sites in South Africa, which may provide broader insights into these processes.

Palaeoenvironmental implications

The geographic complexity of South Africa, combined with the influence of atmospheric and oceanic currents and the limited availability of continuous palaeoclimate proxies, makes it challenging to reconstruct local climatic trends during the

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Quaternary (Walker, 1990; Hewitt, 2000; Chase and Meadows, 2007; Holzkämper et al., 2009; Bruch et al., 2012; Hare and Sealy, 2013; Quick et al., 2015; Dupont et al., 2022; Strobel et al., 2022). Furthermore, most research has focused on specific intervals, such as the last glacial maximum and the Plio–Pleistocene boundary, which have significant implications for climate change and faunal, particularly human, evolution (e.g., Partridge et al., 1990; Reynolds, 2007; Hopley and Maslin, 2010; Cooper et al., 2018). The local Middle Pleistocene record is particularly sparse and often contradictory, with some studies suggesting warmer and drier conditions during the Middle to Late Pleistocene, while others propose cooler climates (e.g., Bar-Matthews et al., 2010; Dupont et al., 2022; Quick et al., 2015; Compton, 2016; Strobel et al., 2022). Currently, there are no Pleistocene climatic data available for Calitzdorp; therefore, the fossil nest site described herein offers a potential opportunity to provide insights into the ambient local climate.

Modern termites are widespread in the tropics and subtropics, occupying humid or semi-arid to arid environments (Kemp, 1955; Noirot and Darlington, 2000; Roisin, 2000; Jones et al., 2011). In addition to offering protection from predation, providing nurseries for reproduction and storing resources, termite nests serve to create habitable micro-environments in otherwise suboptimal conditions by locally regulating factors such as humidity and temperature within the nest (e.g., Oberst et al., 2020). As a result, nests constructed in different climatic conditions show varying functions and morphologies (e.g., Harris, 1956; Turner et al., 2006; Korb, 2011). Additionally, nest site location is controlled by access to moisture and avoidance of periodic flooding (Miller et al., 1994), which further influences the nest architecture. In warmer semi-arid to arid environments, the groundwater table typically lies deeper than that in a humid setting (10–80 m below surface vs. 0.25–5 m below surface, Fan et al., 2013). Consequently, termites excavate and construct subterranean components of their nests to greater depths to access soil moisture (e.g., West, 1965). This moisture facilitates evaporative cooling within the nest, buffering internal nest temperatures against ambient heat (e.g., Klingner et al., 2005). For example, the modern *Hodotermes mossambicus*, which occupies semi-arid to arid environments, excavates nests up to ~3.5 m below surface (Coaton and Sheasby, 1974). A similar observation is made for above-ground nest components that reach greater heights in semi-arid to arid environments (Mège and Rango, 2009; Davies et al., 2014). Therefore, the subterranean *Columnanidus calitzdorpensis* nests, which have a preserved vertical extent of up to ~1 m, but likely had termite activity for greater heights, as the burrowing activities may have extend into the 28 cm thick overlying hardpan and below into the gravels, are consistent with nests built in warmer, drier climates.

It is well-established that advanced calcrete development occurs in settings where evaporation typically exceeds precipitation, limiting leaching and promoting the upward movement of moisture and the concentration of solutes (i.e., *per ascendum* model, Wright and Tucker, 1991; Alonso-Zarza and Wright, 2010). As such, the presence of advanced morphological stages of pedogenic carbonate, for example, the amalgamated and hardpan calcretes observed at Calitzdorp (Fig. 2), strongly suggests prolonged semi-arid to arid conditions during their formation (Gile et al., 1966; Birkeland, 1984; Mack et al., 1993; Retallack, 2001; Wright and Tucker, 2009; Zamanian et al., 2016). Carbonate precipitation within the nests occurred during distinct phases at 401 ± 46 and 323 ± 12 ka, and possibly at 206 ± 6 ka, reflecting semi-arid to arid conditions during those periods (Fig. 7). It is likely that the host lithologies, especially the nest-bearing sands, underwent calcification during these periods as well. Given that the termite nesting activities predate the overlying sediments altering into impenetrable amalgamated and hardpan calcretes, prolonged calcretisation under semi-arid to arid conditions occurred after nest construction. This suggests either (i) discrete periods of semi-arid to arid palaeoclimatic conditions during which pedogenic carbonate precipitated or (ii) a prolonged period (~100 000 years) of semi-arid to arid conditions punctuated by pedogenic carbonate precipitation.

Conclusion

This study demonstrates the value of fossil termite nests not only in ichnotaxonomic frameworks but also as proxies for improving geochronological constraints, reconstructing past environmental conditions, biotic interactions and pedogenic processes in continental settings.

- *Columnanidus calitzdorpensis* ichnogen. ichnosp. nov is a new Middle Pleistocene subterranean termite nest structure preserved as a calcretised feature. It has a distinct cylindrical morphology, defined by a wall surrounding a hollow centre.
- CT imaging is a useful tool for visualising the internal architecture of the nest walls. *C. calitzdorpensis* nest walls preserve differing characteristics between their inner surface and outer surface, where the inner zone preserves more defined, densely stacked horizontal shelved chambers, whereas the outer zone preserves poorly defined shelves and rounded galleries that have a sparse distribution.
- Laminations of carbonate precipitation within the nest wall are suitable for U/Th dating, and yielded a robust minimum age of 323 ± 12 ka for the nest traces at Calitzdorp. Understanding the precipitate laminations relative to the chamber morphology is vital for interpreting age data.
- There is a correlation between termite nesting activities and the degree of carbonate precipitation, both within the nest and at the outcrop scale. It is therefore likely that the soil modifications caused by the termites facilitated the preservation of the nests at Calitzdorp.
- Fossil termite nests can offer insights into ancient climate. The calcretised Calitzdorp nests, from which two phases of carbonate precipitation are identified, are preserved within calcified alluvium that is capped by a hardpan calcrete. This indicates periods of semi-arid to arid conditions, at times prolonged to allow for advanced morphological phases of calcrete to form.

Acknowledgements. We thank Emese Bordy (UCT) for first drawing our attention to the Calitzdorp trace fossils, Tom Barry (Cape Nature) for discussions regarding the early excavation of the site and for guiding us in the field and Paul Bos (Calitzdorp Museum) for assistance. We thank the Editor, John Tibby, and anonymous reviewers for their feedback which greatly improved the manuscript. For lab assistance, we thank Megan Purchase-Wellman for XRD analysis at the University of Free State, Muofhe Tshibalangada for CT scanning at the Central Analytical Facilities—Stellenbosch University and research assistants of the UCT CONTRAST (continental trace studies) group for measuring the chamber and gallery features. The research component of this project was supported through the following research grants obtained by MA as principal investigator: DSI-NRF Centre of Excellence (GENUS) [grant number 86073]; NRF Thuthuka [grant number 138151]; DST-NRF Research development grant for new generation of academics programme [grant number 119694]; and Palaeontolgoical Scientific Trust, Johannesburg, South Africa. GH and RJ were recipients of postgraduate funding from the Mining Qualifications Authority (2020), DSI-NRF Centre of Excellence (GENUS; 2022–2024) and NRF Thuthuka (grant number 138151; 2023–2024).

Conflicts of Interest—The authors declare no conflicts of interest.

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Data Availability Statement

The data that support the findings of this study are available in the supplementary material of this article.

Supporting information

Additional supporting information can be found in the online version of this article.

Appendix S1. Detailed methods for U/Th dating.

Figure S1. CT-scanning photographs of successive slices through the fossil termite nest, as viewed from the interior surface to the exterior surface. See Video S1.

Figure S2. CT-scanning photographs of successive slices through the fossil termite nest, as viewed in cross-section showing the variation within the inner and outer zones. See Video S2.

Figure S3. Selected results from trace-element pre-screening (Tables S2–S5) of representative samples of the hardpan calcrete and fossil nest. (A) Cut and polished sample of laminated calcrete host sediment and corresponding Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS) profile with plots of U and Th concentrations. (B) Cut and polished sample of laminated carbonate in a fragment of the fossil termite nest and corresponding LA-ICP-MS profiles with plots of U and Th concentrations. Pre-screening and dating methods closely follow those described in Pickering (2015) and Hellstrom and Pickering (2015).

Table S1. Mineral proportions determined by XRD analysis.

Table S2. Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS) meta data with instrumental conditions, internal and external standards used during pre-screening procedures (Fig. S3(A), (B); Tables S3–S6).

Table S3. Results of Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS) pre-screening of nest fragment CFF1, displayed in Fig. S3(B).

Table S4. Results of Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS) pre-screening of nest fragment CFF2, displayed in Fig. S2(B).

Table S5. Results of Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS) pre-screening of nest fragment CFF3, displayed in Fig. S2(B).

Table S6. Results of Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS) pre-screening of laminated hard-pan carbonate in the primary pit (Fig. 1(B) and displayed in Fig. S2(A)).

Table S7. U and Th isotope ratios measured in pedogenic carbonate samples from fossil termitaria. Errors on all isotope activity ratios are reported with 2σ uncertainty. All ages have been corrected to account for the effect of detrital Th, assuming an estimate for initial 230Th/232Th of 0.4 ± 0.4 and calculated using the 230Th-238U decay constants of Cheng *et al.* (2013) and Equation 1 from Hellstrom (2006). Data presented in grey are considered unreliable due to extreme error and/or negative age calculations.

Video S1. CT-scanning through the fossil termite nest, as viewed from the interior surface to the exterior surface. See Fig. S1.

Video S2. CT-scanning through the fossil termite nest, as viewed in cross-section showing the variations within the inner and outer zones. See Fig. S1.

References

Almond, J.E. (2005) *Geology of the Gamkaberg-Rooiberg conservation area, Little Karoo. Cape Nature*. Cape Town: Heritage Assessment. p. 155.

Almond, J.E. (2011) Proposed photo-voltaic solar power plant on farm Nuwerus, No. 450, Portion 6, Worcester, Western Cape Province. *Natura Viva* cc, 19pp.

Almond, J.E. (2014) Steenkampskraal Monazite Mine on farms Steenkampskraal no. 70, Brandewynskraal no. 69 & Nabeeb no. 102 near Vanrhynsdorp, Matzikama Municipality, Western Cape. Palaeontological specialist assessment: combined desktop and field-based study, Natura Viva cc, Cape Town, 41.

Almond, J.E. (2020) *Proposed Development of Nine 175 MW Solar Photovoltaic Facilities and Associated Electrical Grid Infrastructure Near Touwsriver, Witzenberg Local Municipality, Western Cape*. Palaeontological input to heritage scoping assessment. Cape Town, p. 70.

Alonso-Zarza, A.M. & Wright, V.P. (2010) Calcretes. In: Alonso-Zarza, A.M. & Tanner, L.H. (Eds.) *Developments in sedimentology. Carbonates in continental settings: facies, environments, and processes*. Amsterdam: Elsevier, pp. 225–267.

Asawalam, D.O., Osodeke, V.E., Kamalu, O.J. & Ugwa, I.K. (1999) Effects of termites on the physical and chemical properties of the acid sandy soils of southern Nigeria. *Communications in Soil Science and Plant Analysis*, 30, 1691–1696.

Bar-Matthews, M., Marean, C.W., Jacobs, Z., Karkanas, P., Fisher, E.C., Herries, A.I.R. et al. (2010) A high-resolution and continuous isotopic speleothem record of paleoclimate and paleoenvironment from 90 to 53 ka from Pinnacle Point on the south coast of South Africa. *Quaternary Science Reviews*, 29, 2131–2145.

De Beer, C.H., Gresse, P.G., Theron, J.N. & Almond, J.E. (2002) *The geology of the Calvinia area, explanation to 1:250 000 geology sheet 3118 Calvinia*. Pretoria: Council for Geoscience, 92. pp.

Birkeland, P.W. (1984) *Soils and geomorphology*. New York: Oxford University Press.

Bordy, E.M., Bumby, A.J., Catuneanu, O. & 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.

Bown, T.M. & Laza, J.H. (1990) A Miocene termite nest from southern Argentina and its paleoclimatological implications. *Ichnos: An International Journal of Plant and Animal*, 1, 73–79.

Bruch, A.A., Sievers, C. & Wadley, L. (2012) Quantification of climate and vegetation from southern African Middle Stone Age sitesa—an application using Late Pleistocene plant material from Sibudu, South Africa. *Quaternary Science Reviews*, 45, 7–17.

Chase, B.M. & Meadows, M.E. (2007) Late Quaternary dynamics of southern Africa's winter rainfall zone. *Earth-Science Reviews*, 84, 103–138.

Clarke, C.E., Vermooten, M., Watson, A., Hattingh, M., Miller, J.A. & Francis, M.L. (2022) Downward migration of salts in termite-affected soils: implications for groundwater salinization. *Geoderma*, 413, 115747.

Coaton, W.G.H. (1958) The hodotermitid harvester termites of South Africa. *Department of Agriculture Science Bulletin*, 375, 1–112.

Coaton, W.G.H. (1981) Fossilised nests of Hodotermitidae (Isoptera) from the Clanwilliam district, Cape province. *Journal of the Entomological Society of Southern Africa*, 44, 79–81.

Coaton, W.G.H. & Sheasby, J.L. (1974) National survey of the Isoptera of southern Africa 10. The genus *Hodotermes Hagen* (Hodotermitidae). *Cimbebasia*, 3, 105–137.

Compton, J.S. (2016) Quaternary environmental change on the southern African coastal plain. In: Knight, J. & Grab, S.W. (Eds.) *Quaternary environmental change in Southern Africa: physical and human dimensions*. Cambridge: Cambridge University Press, pp. 88–97.

Cooper, J.A.G., Green, A.N. & Compton, J.S. (2018) Sea-level change in southern Africa since the Last Glacial Maximum. *Quaternary Science Reviews*, 201, 303–318.

Cosarinsky, M.I. (2011) The nest growth of the Neotropical mound-building termite, *Cornitermes cumulans*: a micromorphological analysis. *Journal of Insect Science*, 11(122), 1–14.

Cosarinsky, M.I., Bellosi, E.S. & Genise, J.F. (2005) Micromorphology of modern epigean termite nests and possible termite ichnofossils: a comparative analysis (Isoptera). *Sociobiology*, 45, 745–778.

Cramer, M.D. & Midgley, J.J. (2015) The distribution and spatial patterning of mima-like mounds in South Africa suggests genesis

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

through vegetation induced aeolian sediment deposition. *Journal of Arid Environments*, 119, 16–26.
Darlington, J.P.E.C. (1984) Two types of mound built by the termite *Macrotermes subhyalinus* in Kenya. *International Journal of Tropical Insect Science*, 5, 481–492.
Darlington, J.P.E.C. (1985) The structure of mature mounds of the termite *Macrotermes michaelseni* in Kenya. *International Journal of Tropical Insect Science*, 6, 149–156.
Darlington, J.P.E.C. (2005) Distinctive fossilised termite nests at Laetoli, Tanzania. *Insectes Sociaux*, 52, 408–409.
Darlington, J.P.E.C. (2011) Trace fossils interpreted in relation to the extant termite fauna at Laetoli, Tanzania. In: Harrison, T. (Ed.) *Paleontology and geology of Laetoli: human evolution in context: Volume 2: Fossil hominins and the associated fauna*. Dordrecht: Springer, pp. 555–565.
Davies, A.B., Levick, S.R., Asner, G.P., Robertson, M.P., van Rensburg, B.J. & Parr, C.L. (2014) Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment. *Ecography*, 37, 852–862.
Dupont, L.M., Zhao, X., Charles, C., Faith, J.T. & Braun, D. (2022) Continuous vegetation record of the Greater Cape Floristic Region (South Africa) covering the past 300 000 years (IODPU1479). *Climate of the Past*, 18, 1–21.
Duringer, P., Schuster, M., Genise, J.F., Mackaye, H.T., Vignaud, P. & Brunet, M. (2007) New termite trace fossils: galleries, nests and fungus combs from the Chad Basin of Africa (Upper Miocene–Lower Pliocene). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 251, 323–353.
Emerson, A.E. (1938) Termite nests—a study of the phylogeny of behavior. *Ecological Monographs*, 8, 247–284.
Fan, Y., Li, H. & Miguez-Macho, G. (2013) Global patterns of groundwater table depth. *Science*, 339, 940–943.
Francis, M.L. & Poch, R.M. (2019) Calcite accumulation in a South African heuweltjie: role of the termite *Microhodotermes viator* and oribatid mites. *Journal of Arid Environments*, 170, 103981.
Francis, M.L., Clarke, C.E., van Gend, J., Vermooten, M., Maponya, M.G. & Mashimbye, E. et al. (2022) *The relationship between Heuweltjies and 70 saline groundwater along the West Coast of South Africa* Department of Earth Sciences, Stellenbosch University, Water Research Commission, 13, p. 93.
Francis, M.L., Ellis, F., Lambrechts, J.J.N. & Poch, R.M. (2013) A micromorphological view through a Namaqualand termitaria (Heuweltjie, a Mima-like mound). *Catena*, 100, 57–73.
Francis, M.L., Palcsu, L., Molnár, M., Kertész, T., Clarke, C.E. & Miller, J.A. et al. (2024) Calcareous termite mounds in South Africa are ancient carbon reservoirs. *Science of the Total Environment*, 926, 171760.
Genise, J.F. (2017) *Ichnoentomology: insect traces in soils and paleosols*. Cham: Springer, 707. pp.
Genise, J.E. & Bown, T.M. (1994a) New trace fossils of termites (Insecta: Isoptera) from the late Eocene-early Miocene of Egypt, and the reconstruction of ancient isopteran social behavior. *Ichnos: An International Journal of Plant & Animal*, 3, 155–183.
Genise, J.F. & Bown, T.M. (1994b) New Miocene scarabeid and hymenopterous nests and early Miocene (Santacrucian) paleoenvironments, Patagonian Argentina. *Ichnos: An International Journal of Plant & Animal*, 3, 107–117.
Genise, J.F., Alonso-Zarza, A.M., Krause, J.M., Sánchez, M.V., Sarzetti, L., Farina, J.L. et al. (2010) Rhizolith balls from the Lower Cretaceous of Patagonia: just roots or the oldest evidence of insect agriculture? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 287, 128–142.
Genise, J.F., Bellosi, E.S., Melchor, R.N. & Cosarinsky, M.I. (2005) Comment—advanced early Jurassic Termite (Insecta: Isoptera) nests: evidence from the Clarens formation in the Tuli Basin, Southern Africa (Bordy et al., 2004). *Palaios*, 20, 303–308.
Genise, J.F., Cantil, L.F. & Bellosi, E.S. (2016) Lower Paleogene complex ant nests from Argentina: evidence for early polydomy in ants? *Palaios*, 31, 549–563.
Genise, J.F., Cuezzo, F., Gonzalez, M.G. et al. (2013b) Organic linings in nests of the fire ants *Solenopsis electra* Forel and *Solenopsis nr. macdonaghi* Santschi from Argentina. *Insectes Sociaux*, 60, 87–91.
Genise, J.F., Melchor, R.N., Sánchez, M.V. et al. (2013a) *Attaichnus kuenzelii* revisited: a Miocene record of fungus-growing ants from Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 386, 349–363.
Gile, L.H., Peterson, F.F. & Grossman, R.B. (1966) Morphological and genetic sequences of carbonate accumulation in desert soils. *Soil Science*, 101, 347–360.
Grassé, P. (1984) *Termitologia, Tome II*. Paris: Masson. p. 613
Hare, V. & Sealy, J. (2013) Middle Pleistocene dynamics of southern Africa's winter rainfall zone from $\delta^{13}C$ and $\delta^{18}O$ values of Hoedjiespunt faunal enamel. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 374, 72–80.
Harris, W.V. (1956) Termite mound building. *Insectes Sociaux*, 3, 261–268.
Hasiotis, S.T. & Dubiel, R.F. (1995) Termite (Isoptera) nest ichnofossils from the Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona. *Ichnos: An International Journal of Plant and Animal*, 4, 119–130.
Hellstrom, J. (2003) Rapid and accurate U/Th dating using parallel ion-counting multi-collector ICP-MS. *Journal of Analytical Atomic Spectrometry*, 18, 1346–1351.
Helm, C.W., Carr, A.S., Cawthra, H.C., De Vynck, J.C., Dixon, M.G., Gräbe, P.J. et al. (2025) Pleistocene aardvark (*Orycteropus afer*) burrow traces on South Africa's Cape coast. *Quaternary Research*, 124, 139–152.
Hesse, P.R. (1955) A chemical and physical study of the soils of termite mounds in East Africa. *Journal of Ecology*, 43, 449–461.
Hewitt, G. (2000) The genetic legacy of the quaternary ice ages. *Nature*, 405, 907–913.
Holt, J.A. & Lepage, M. (2000) Termites and soil properties. In: Abe, T., Bignell, D.E. & Higashi, M. (Eds.) *Termites: evolution, sociality, symbioses, ecology*. Dordrecht: Springer, pp. 389–407.
Holzkämper, S., Holmgren, K., Lee-Thorp, J., Talma, S., Mangini, A. & Partridge, T. (2009) Late pleistocene stalagmite growth in Wolkberg cave, South Africa. *Earth and Planetary Science Letters*, 282, 212–221.
Hopley, P.J. & Maslin, M.A. (2010) Climate-averaging of terrestrial faunas: An example from the Plio-Pleistocene of South Africa. *Paleobiology*, 36, 32–50.
Jarzembowski, E.A. (1981) An early cretaceous termite from southern England (Isoptera: Hodotermitidae). *Systematic Entomology*, 6, 91–96.
Jones, D.T. & Eggleton, P. (2011) Global biogeography of termites: a compilation of sources. In: Bignell, D.E., Roisin, Y. & Lo, N. (Eds.) *Biology of termites: A modern synthesis*. Dordrecht: Springer, pp. 477–498.
Kemp, P.B. (1955) The termites of north-eastern Tanganyika: their distribution and biology. *Bulletin of Entomological Research*, 46, 113–135.
Klingner, R., Richter, K., Schmolz, E. & Keller, B. (2005) The role of moisture in the nest thermoregulation of social wasps. *Naturwissenschaften*, 92, 427–430.
Korb, J. (2011) Termite mound architecture, from function to construction. In: Bignell, D.E., Roisin, Y. & Lo, N. (Eds.) *Biology of termites: a modern synthesis*. Dordrecht: Springer, pp. 349–374.
Laza, J.H. (2006) Termiteros del Plioceno y Pleistoceno de la provincia de Buenos Aires. RepArgent Signif paleoambiental paleozoogeogr. *Ameghiniana*, 43, 641–648.
Lee, K.E. & Wood, T.G. (1971) *Termites and soils*. London, UK: Academic Press, p. 251.
Liu, X., Monger, H.C. & Whitford, W.G. (2007) Calcium carbonate in termite galleries–biomineralization or upward transport? *Biogeochemistry*, 82, 241–250.
Mack, G.H., James, W.C. & Monger, H.C. (1993) Classification of paleosols. *Geological Society of America Bulletin*, 105, 129–136.
Martin, L.D. & Bennett, D.K. (1977) The burrows of the Miocene beaver Palaeocastor, Western Nebraska, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 22, 173–193.
McAuliffe, J.R (2023) Earthen mounds (heuweltjies) of South Africa and their termite occupants: applicability of concepts of the extended phenotype, ecosystem engineering and niche construction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 378, e20220150.
McAuliffe, J.R., Hoffman, M.T., McFadden, L.D., Bell, W., Jack, S., King, M.P. et al. (2019) Landscape patterning created by the southern harvester termite, *Microhodotermes viator*: spatial disper-

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

sion of colonies and alteration of soils. *Journal of Arid Environments*, 162, 26–34.
McAuliffe, J.R., Timm Hoffman, M., McFadden, L.D. & King, M.P. (2014) Role of aeolian sediment accretion in the formation of heuweltjie earth mounds, western South Africa. *Earth Surface Processes and Landforms*, 39, 1900–1912.
Von der Meden, J., Pickering, R., Schoville, B.J., Green, H., Weij, R., Hellstrom, J. et al. (2022) Tufas indicate prolonged periods of water availability linked to human occupation in the southern Kalahari. *PLoS One*, 17, e0270104.
Mège, D. & Rango, T. (2010) Permanent groundwater storage in basaltic dyke fractures and termite mound viability. *Journal of African Earth Sciences*, 57, 127–142.
Meyer, V.W., Braack, L.E.O., Biggs, H.C. et al. (1999) Distribution and density of termite mounds in the northern Kruger National Park, with specific reference to those constructed by *Macrotermes Holmgren* (Isoptera: Termitidae). *African Entomology*, 7, 123–130.
Miller, L.R. (1994) Amitermes arboreus Roisin in Australia, with notes on its biology (Isoptera: Termitidae). *Australian Journal of Entomology*, 33, 305–308.
Miller, W.R. & Mason, T.R. (2000) *Stellavelum arborensis* igen., sp. nov., *Stellavelum uncinum igen.*, isp. nov. and *Termitichnus namibiensis* isp. nov.; New Ichnofossils from Cenozoic deposits of Namaqualand, South Africa. *Ichnos: An International Journal of Plant & Animal*, 7, 195–215.
Monger, H.C. (2002). Pedogenic carbonate: links between biotic and abiotic $CaCO_3$. In: *17th World Congress of Soil Science, 14–21 August 2002, Bangkok, Thailand*, Symposium No. 20, pp. 891.
Moore, J.M. & Picker, M.D. (1991) Heuweltjies (Earth Mounds) in the Clanwilliam District, Cape Province, South Africa: 4000-year-old termite nests. *Oecologia*, 86, 424–432.
Muir, R.A., Bordy, E.M., Mundil, R. & Frei, D. (2020) Recalibrating the breakup history of SW Gondwana: U–Pb radioisotopic age constraints from the southern Cape of South Africa. *Gondwana Research*, 84, 177–193.
Mujinya, B.B., Mees, F., Boeckx, P., Bodé, S., Baert, G., Erens, H. et al. (2011) The origin of carbonates in termite mounds of the Lubumbashi area, DR Congo. *Geoderma*, 165, 95–105.
Nel, A., Perrault, G., Perrichot, V. & Néradeau, D. (2004) The oldest ant in the Lower Cretaceous amber of Charente-Maritime (SW France) (Insecta: Hymenoptera: Formicidae). *Geologica Acta*, 2, 23–29.
Netterberg, F. (1980) Geology of southern African calcretes: 1: terminology, description, macrofeatures, and classification. *South African Journal of Geology*, 83, 255–283.
Noirot, C. & Darlington, J.P. (2000) Termite nests: architecture, regulation and defense. In: Abe, T., Bignell, D.E. & Higashi, M. (Eds.) *Termites: evolution, sociality, symbioses, ecology*. Dordrecht: Springer, pp. 121–139.
Oberst, S., Lai, J.C.S., Martin, R., Halkon, B.J., Saadatfar, M. & Evans, T.A. (2020) Revisiting stigmergy in light of multi-functional, biogenic, termite structures as communication channel. *Computational and Structural Biotechnology Journal*, 18, 2522–2534.
Partridge, T.C., Avery, D.M., Botha, G.A. et al. (1990) Late Pleistocene and Holocene climatic change in Southern Africa. *South African Journal of Science*, 86, 302–306.
Pickering, R. (2015) U–Pb dating small, buried stalagmites from Wonderwerk Cave, South Africa: a new chronometer for earlier stone age cave deposits. *African Archaeological Review*, 32, 645–668.
Pickford, M. (2006) A termite tale of climate change. *Quest*, 2, 28–31.
Pickford, M. & Senut, B. (2000) *The geology and palaeobiology of the central and southern Namib Desert, southwestern Africa*. Volume 1: Geology and history of study, Geological Survey of Namibia Memoir, 18. Windhoek, p. 155.
Pickford, M. & Senut, B. (2002) *The Fossil Record of Namibia*. Windhoek: Geological Survey of Namibia. p. 39
Pullan, R.A. (1979) Termite hills in Africa: their characteristics and evolution. *Catena*, 6, 267–291.
Quick, L.J., Carr, A.S., Meadows, M.E., Boom, A., Bateman, M.D., Roberts, D.L. et al. (2015) A late Pleistocene–Holocene multi-proxy record of palaeoenvironmental change from Still Bay, southern Cape Coast, South Africa. *Journal of Quaternary Science*, 30, 870–885.
Retallack, G.J. (2001) *Soils of the past: an introduction to paleopedology*. Oxford: Blackwell Science, p. 404.
Reynolds, S.C. (2007) Mammalian body size changes and Plio-Pleistocene environmental shifts: implications for understanding hominin evolution in eastern and southern Africa. *Journal of Human Evolution*, 53, 528–548.
Richardson, A.M.M. (1983) The effect of the burrows of a crayfish on the respiration of the surrounding soil. *Soil Biology and Biochemistry*, 15, 239–242.
Roberts, D.L., Bateman, M.D., Murray-Wallace, C.V., Carr, A.S. & Holmes, P.J. (2008) Last Interglacial fossil elephant trackways dated by OSL/AAR in coastal aeolianites, Still Bay, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 257, 261–279.
Roberts, E.M., Todd, C.N., Aanen, D.K., Nobre, T., Hilbert-Wolf, H.L. & O'Connor, P.M. et al. (2016) Oligocene termite nests with in situ fungus gardens from the Rukwa Rift Basin, Tanzania, support a Paleogene African origin for insect agriculture. *PLoS One*, 11, e0156847.
Rohr, D.M., Boucot, A.J., Miller, J. & Abbott, M. (1986) Oldest termite nest from the Upper Cretaceous of west Texas. *Geology*, 14, 87–88.
Roisin, Y. (2000) Diversity and evolution of caste patterns. In: Abe, T., Bignell, D.E. & Higashi, M. (Eds.) *Termites: evolution, sociality, symbioses, ecology*. Dordrecht: Springer, pp. 95–119.
Schuster, M., Duringer, P., Nel, A. et al. (2000) Discovery of fossil termite mounds in Chadian Pliocene vertebrate sites: description, identification and paleoecological implications. *Comptes Rendus de l'Académie des Sciences-Series IIA—Earth and Planetary Science*, 331, 15–20.
Singh, S., Chaudhary, A., Handique, S., Singh, S.K. & Tripathi, J.K. (2017) Biological weathering and geochemical fractionation by termites: a case study of loessic sediments from Jawaharlal Nehru University, New Delhi, India. *Earth Science India*, 10, 94–107.
Smith, R. & 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.
Strobel, P., Bliedtner, M., Carr, A.S., Struck, J., du Plessis, N. & Glaser, B. et al. (2022) Reconstructing Late Quaternary precipitation and its source on the southern Cape coast of South Africa: a multi-proxy paleoenvironmental record from Vankervelsvlei. *Quaternary Science Reviews*, 284, 107467.
Tschinkel, W.R. (2003) Subterranean ant nests: trace fossils past and future? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 192, 321–333.
Turner, J.S., Marais, E., Vinte, M. et al. (2006) Termites, water and soils. *Agricola*, 16, 40–45.
Vermeesch, P. (2018) IsoplotR: a free and open toolbox for geochronology. *Geoscience Frontiers*, 9, 1479–1493.
Walker, N.D. & Shillington, F. (1990) The effect of oceanographic variability on South African weather and climate. *South African Journal of Science*, 86, 382–386.
West, W.F. (1965) Some unconventional ideas on prospecting. *Chamber of Mines Journal*, 7, 40–42.
Wheeler, W.M. (1910) *Ants: their structure, development and behaviour*. New York: Columbia University Press, 663 pp.
Wright, V.P. & Tucker, M.E. (1991) Calcretes. The international association of Sedimentologists, *Reprint Series*, 2. Oxford: Blackwell Scientific Publications, p. 380.
Wright, V.P. & Tucker, M.E. (2009) *Calcretes: an introduction*. Hoboken, NJ: John Wiley & Sons, p. 363.
Zamanian, K., Pustovoytov, K. & Kuzyakov, Y. (2016) Pedogenic carbonates: forms and formation processes. *Earth-Science Reviews*, 157, 1–17.

© 2026 The Author(s). *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

10991417, 2026, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/jqs.70089 by South African Medical Research Council, Wiley Online Library on [12/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License