Advanced Early Jurassic Termite (Insecta: Isoptera) Nests: Evidence From the Clarens Formation in the Tuli Basin, Southern Africa

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Sandstone pillars in the Lower Jurassic eolian strata of the Clarens Formation are concentrated in clusters, with up to four pillars within 25 m² in two localities in the Tuli Basin of northern South Africa and southern Zimbabwe. The pillars are generally vertical, have a preserved height of up to 3.3 m, and are elliptical in plan view. Pillars are grouped into two styles of architecture: those with oriented elliptical shapes and side buttresses, and those less well oriented with a smooth outer wall, internal open spaces, and vertical shafts cutting the pillar. The long axes of the elliptical pillars are generally oriented to the north. Northwards-oriented side buttresses also are associated with some of the pillars. The internal architecture of the pillars is characterized by intense bioturbation with two different burrowing styles. Type 1 burrows are composed of a network of randomly oriented, anastomosing sandstone-filled tubes, 0.3 to 0.8 cm in diameter. Type 2 burrows are rare, north-south oriented, and have a smaller diameter. Other associated features are back-filled tubes, open, vertical shafts, and open spaces between the interior and exterior of the pillars.

The pillars are interpreted as fossilized termite nests. Type 1 burrows are interpreted as termite passageways within the nest. Type 2 burrows may be related to invading ants. Back-filled burrows may be a result of either beetle predation on resident termites or backfilling by termites themselves. The strong north-south orientations are comparable with modern-day nest architecture of magnetic termites in northern Australia, where nest-orientation is related to cooling. The orientations and features reported here are interpreted to be modified for the high latitudes proposed for the Lower Jurassic Clarens desert. Complex nest architecture preserved in the Clarens Formation suggests that advanced eusocial behavior and ability to construct large nests had appeared in African termites by the Early Jurassic.

INTRODUCTION AND PREVIOUS RESEARCH

The paleontological record for the evolution of eusocial behavior of termites appears in the Late Triassic, as shown by simple fossil nests (Hasiotis and Dubiel, 1995). Complex nest architectures are well established by the Late Jurassic, as indicated by large, elaborate nests (Hasiotis et al., 1997; Hasiotis, 2000, 2002). This paper documents the external and internal architectural morphology and distribution patterns of large, complex termite nests preserved in Lower Jurassic eolian deposits of the Clarens Formation in southern Africa. This analysis also illustrates the significance of continental ichnofossils in reconstructing paleoenvironments and improving the knowledge of major evolutionary events in the fossil record.

The fossil termite nest localities described in this work are found in the Lower Jurassic Clarens Formation of the Tuli Basin, which straddles the borders of South Africa, Zimbabwe, and Botswana (Fig. 1). The South African locality (Site 1: S22°12.3′, E29°22.4′) is found on Greefswald farm, about 0.5 km south of the confluence of the Limpopo and Shashe Rivers. The Zimbabwean locality (Site 2: S21°58.3′, E29°47.5′) is situated on Mazunga Ranch, which is on the eastern banks of the Umzingwane River (Fig. 1).

Sandstone pillars in the Clarens Formation in Zimbabwe were reported, but not interpreted, by Thompson (1975) and Watkeys (1979). Sandstone pillars at the South African locality were first interpreted as termite nests by Bordy (2000) and Bordy and Catuneanu (2002a).

GEOLOGICAL SETTING

The Upper Carboniferous–Lower Jurassic continental sedimentary fill of the Tuli Basin is composed of four informal stratigraphic units, namely the Basal, Middle, and Upper units, and Clarens formation (Bordy, 2000; Bordy and Catuneanu, 2001; Bordy and Catuneanu, 2002a, b, c). These genetically distinct units are not in accordance with

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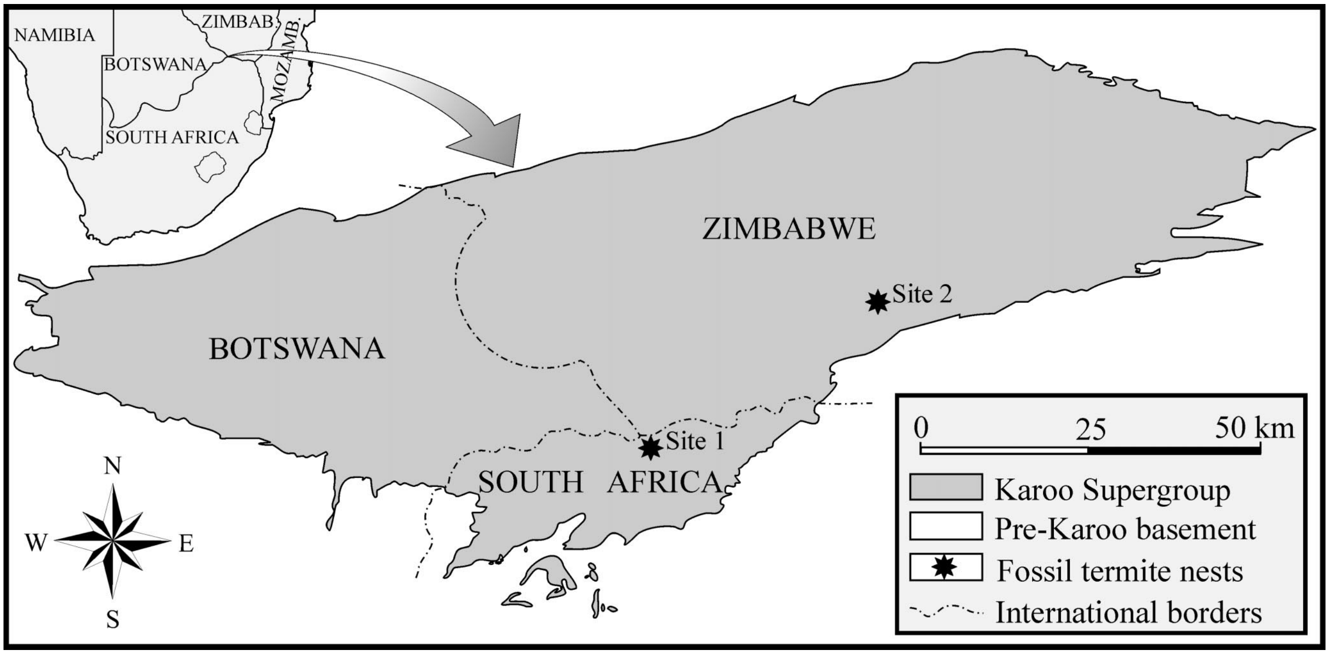

FIGURE 1—Geographical position of the Early Jurassic termite nest localities within the Karoo Supergroup-filled Tuli Basin.

the formal stratigraphic nomenclature of the area (S.A.C.S, 1980; Geological Map, Alldays, 2000). For instance, in the formal nomenclature, the Clarens Formation incorporates two genetically distinctive, regionally mappable members: the fluvial Red Rocks Member and the eolian Tshipise Member. The informal Clarens formation used here correlates with the formal Tshipise Member. Paleoenvironmental reconstructions of the arenaceous Clarens formation suggest an erg environment dominated by westerly winds, with migrating transverse dunes (Bordy, 2000; Bordy and Catuneanu, 2002a). In the lower part of the sequence, evidence suggests that the early stages of sedimentation occurred under semiarid desert conditions, where fluvial subenvironments are indicated by rare ephemeral-stream deposits. Petrified logs of *Agathoxylon* sp. wood and several insect and vertebrate trace fossils preserved in the South African part of the basin also form indirect evidence for semiarid desert conditions (Bordy, 2000; Bordy and Catuneanu, 2002a). The upper part of the Clarens formation lacks any evidence for fluvial settings, which suggests progressive aridification that led to the dominance of drier sand-sea conditions.

The Early Jurassic age of the Clarens formation is inferred from combined paleontological and radiometric data by Aldis et al. (1984). In the eastern part of the Tuli Basin, the lowermost lavas of the Drakensberg Group overlying the termite nest-bearing eolian strata have a minimum age of ~181 Ma and maximum age of ~195 to 200 Ma (Aldis et al., 1984).

DESCRIPTION OF SANDSTONE PILLARS

External Architecture

The external architecture of the enigmatic ichnofossils resembles pillars composed of sandstone identical to the host eolian deposits. The individual pillars are spaced between 10 and 0.5 m intervals, occupying an area of about 200 m^2 at Site 1 (Fig. 2). At Site 2 in Zimbabwe, the pillar density is less than at Site 1, with a total site area of about 100 m^2. At Site 1, preserved pillars are more clustered in the southwestern portion of the area (Fig. 2). In the most densely packed areas, up to 4 pillars may be found within 25 m^2 (Fig. 2). In peripheral areas to the north and west, spacing of preserved pillars is more widespread (Fig. 2). The freestanding structures are predominantly single, vertical columns (Fig. 3A, B), but S-shaped features (Fig. 3C), upward bifurcation, and twinning also are observed locally.

The true height of most of the pillars is unknown because the uppermost portions generally are missing and the lower parts are only rarely exposed. The greatest measured height of the preserved pillars is 3.3 m. Assuming that pillar height and circumference are directly related, the large measured circumferences of the pillars suggest that pillar heights of more than 3 m were not uncommon. The diameter along the preserved height tapers gradually from the larger basal circumference towards the upper part, from more than 1 m into a generally bullet-shaped peak (Fig. 3A, B). The cross-section of the pillars is elliptical (Fig. 3D), and the pillars have a horizontally squashed conical shape. At Site 1, 153 nests were measured, and the length of the measured long axis ranges from 11 to 170 cm (average 53 cm), and the length of short axis is between 7 and 120 cm (average 33 cm). At Site 2, 49 nests were measured, and the length of the long axis is between 10 and 80 cm (average 38 cm), and the short axis is 10 to 60 cm (average 24 cm) long. The short-to-long axis ratio reveals a prominent maximum at 0.5 to 0.6 (Fig. 4), which shows that most pillars are twice as elongated along their long axis than along their short axis. As shown in Figure 4, the

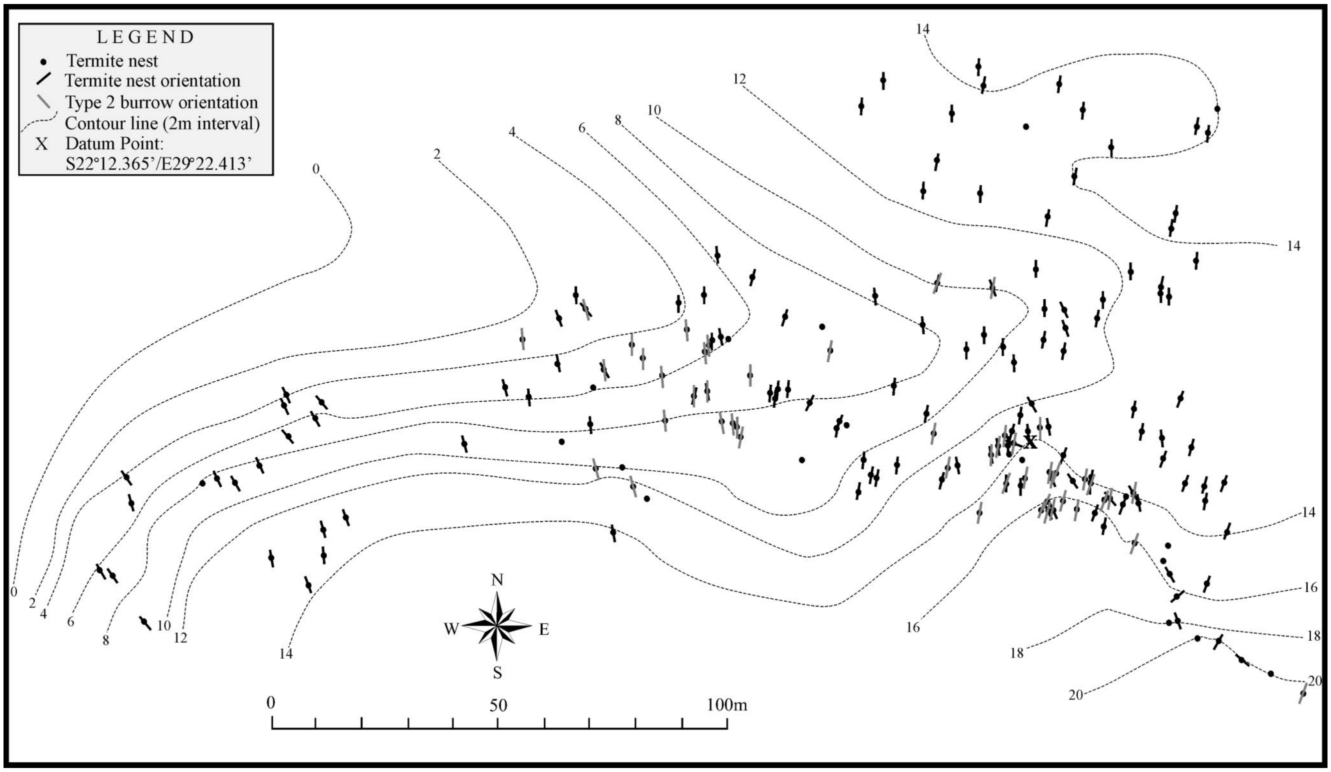

FIGURE 2—Map showing distribution of the Early Jurassic termite nests at Site 1, Greefswald Farm, Vhembe-Dongola National Park, Limpopo Province, South Africa.

long axis of the pillars is strongly north-south oriented. Calculated mean orientations for Site 1 pillars are 357° (Fig. 5A) and 349° for Site 2 (Fig. 5B). Detailed mapping of the pillar distribution at Site 1 shows that the orientation of the long axes of pillars varies throughout the locality (Fig. 2). Generally, pillars preserved in the west are oriented towards the north-northwest, whereas those in the east are predominantly oriented towards the north-northeast. In addition, some of the unbroken apices are distinctly inclined to the east (Fig. 3A).

The pillars are composed of bioturbated sandstone, although several oriented pillars at Site 1 have buttresses (Fig. 6A, B) situated and oriented to the north of the pillar. Buttresses are composed of massive sandstone with northward-trending lineations preserved along their flanks (Fig. 6B), in contrast to the heavily bioturbated pillars. Typically, buttresses are between 1 and 10 cm thick tapering away from the pillars, and locally reach up to 2 m in length. The proximal end of the buttresses is generally encased within the bioturbated sandstone of the pillar (Fig. 6A). Buttresses rarely bifurcate upwards.

In addition to the bioturbated conical, dome-like structures described in Bordy and Catuneanu (2002a), some of the pillars are connected to each other by straight, mostly north-south trending horizontal cylinders (Figs. 3B, 6C). Horizontal cylinders are 1 to 3 m long, often heavily bioturbated, and have an average diameter of 20 cm (maximum 30 cm). Cylinders weather locally to form troughs (Fig. 6D).

Internal Architecture

Internally, the sandstone pillars consist of intricately interwoven, simple burrows, larger shafts, and empty spaces. There are two different types of smaller, cylindrical burrows (Type 1 and 2). Type 1 burrows (Fig. 7A) are most common, resemble a web-like network of randomly oriented, sandstone-filled tubes, and have a consistent diameter between 0.3 and 0.8 cm (average 0.5 cm). Exposed segments of Type 1 burrows are slightly curved and are between 1 and 10 cm in length (Fig. 7A). True branching is rare, but the burrows often cross each other, forming an anastomosing pattern. The surficial morphology of the burrows is smooth. Most burrows are filled by massive, fine- to medium-grained sandstone, which is identical to that of the host substrate. Some of the Type 1 burrows are not filled (Fig. 7B), especially in the western portion of Site 1. Here, burrows resemble hollow tubes within the sandstone matrix. Type 2 burrows (Fig. 7C, D) are rare, smaller (about 0.3 cm diameter), straight, and very strongly north-south oriented. They are exclusively horizontal, parallel to one another, and lack any curves or branches (Fig. 7C, D). The burrow walls of these strongly oriented (Fig. 5D) linear features are smooth, and the burrows are also filled with massive, fine- to medium-grained sandstone. Locally, it appears that Type 2 burrows are superimposed on substrates already bioturbated with Type 1 burrows (Fig. 7D). An additional burrow type is represented by back-filled, straight or gently curving tubes that average 2 cm in diameter and 13 to 20 cm in length (Fig. 8A, B). These tubes

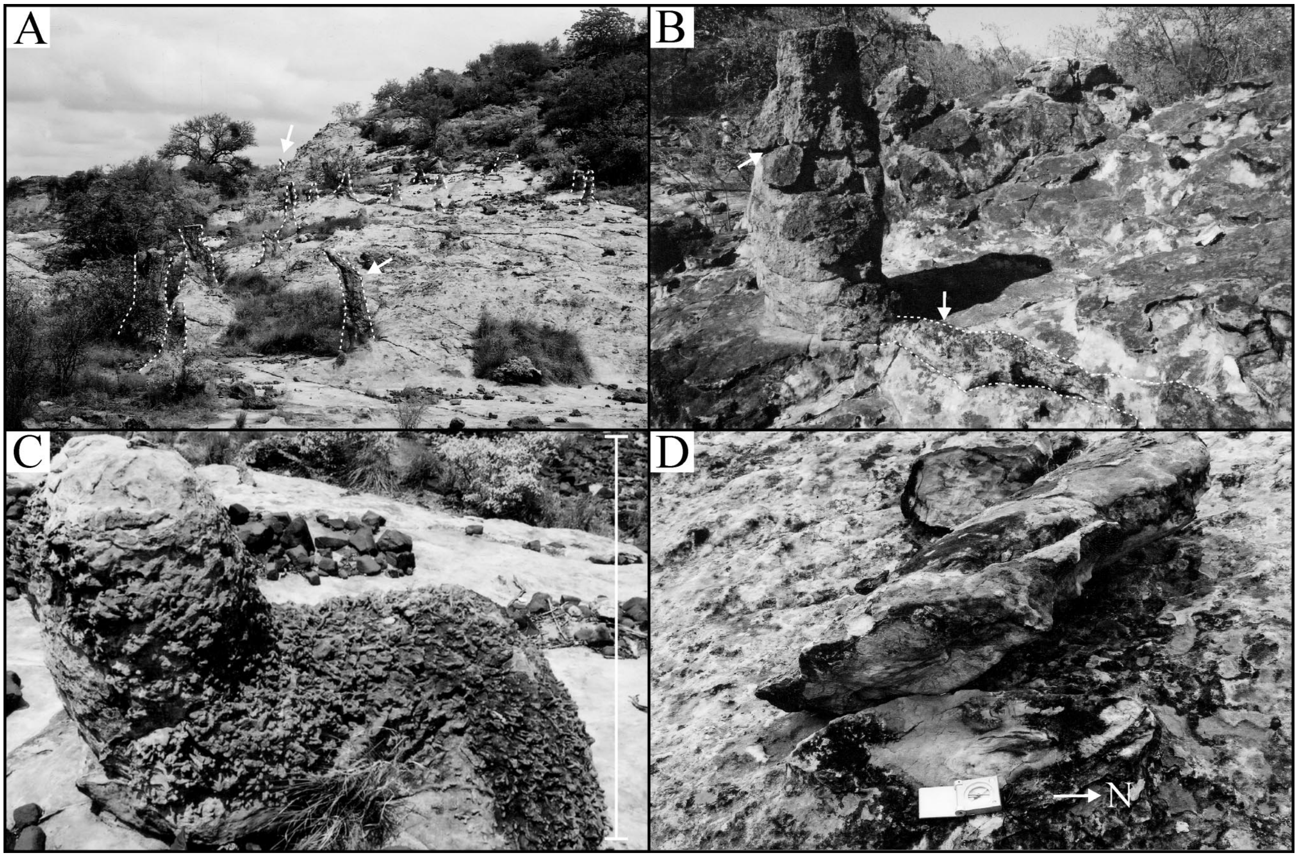

FIGURE 3—External architecture of the sandstone pillars. (A) Several freestanding, single, vertical columns, 0.5 to 3 m preserved height, densely distributed in certain areas of study site 1. Note eastwardly inclined pillars in the bottom and distant center of the picture (marked with arrows). (B) North-south oriented, upward-tapering single pillar with broken apex. Note the horizontal cylinder connecting the featured pillar to its neighbor (not in the picture); lens cap (see arrow) is 5.5 cm in diameter. (C) S-shaped, heavily bioturbated pillars are also present. Bar scale represents 80 cm. (D) Pillar cross-sections are rather elliptical, and their long axes are strongly north-south oriented (note compass bearing); open compass is 16 cm long.

lack wall structures, and are found both in the vertical pillars and interconnecting horizontal cylinders.

Open, straight shafts, 3 to 5 cm in diameter, are found locally within sandstone pillars (Fig. 8C, D). The observed shaft lengths are between 10 and 25 cm, and the shaft wall is 2 to 4 cm thick. These shafts, which are not preserved in all of the pillars at Site 1, are fairly common at Site 2 and generally penetrate the center of the pillars vertically (Fig. 8C). When shafts perforate the exterior of the pillars, they form cone-like features up to 10 cm in height (Fig. 8D).

Some of the broken sandstone pillars exhibit an internal, well-developed empty space between the heavily bioturbated central part and exterior wall of the pillar (Fig. 9A). The width of the space varies from 5 to 10 cm. This empty space is more common in pillars with smooth walls perforated by the above shafts (Fig. 9B).

Major Pillar Types

Based on external and internal architectural characteristics, there are at least two types of different sandstone pillars. Most of the pillars at Site 1 and a few at Site 2 are characterized by definite orientation, heavily bioturbated exteriors and interiors, and locally with associated buttresses (none at Site 2). This type of pillar has few internal shafts and occasionally an inner empty space (Figs. 3A–D, 6A–B). In contrast, in the western part of Site 1 and eastern part of Site 2, the bioturbated inner pillars are more irregular and surrounded by a 2-to-4-cm thick, hardened, smooth wall giving an intact appearance to the pillars (Fig. 9B). The only connection between the pillar interior and hardened exterior are the cone-shaped perforations of the massive wall that are external continuations of the internal shafts (Fig. 8D). The empty space in the pillar interior is a common feature.

DISCUSSION

The complex external and internal architecture of the structures described above is strikingly consistent with the nest architecture of some recent termite mounds found in the savanna close to the study area. Thus, the sandstone pillars were interpreted as termite nests by Bordy (2000) and Bordy and Catuneanu (2002a). It is perhaps also possible that the pillars are related to nest building by some other unknown Jurassic social organisms that constructed nests very similar to termites.

The web-like network of Type 1 burrows previously was interpreted (Bordy, 2000; Bordy and Catuneanu, 2002a) as sand-filled passageways used by termites to give access

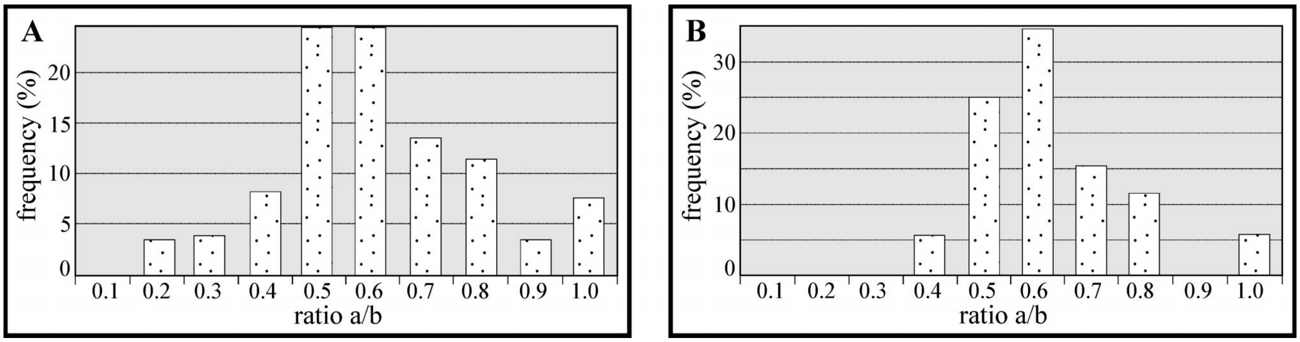

FIGURE 4—Histograms showing short versus long axis ratios. (A) Site 1. (B) Site 2.

to storage chambers or to dumping sites where waste material was deposited (Bown, 1982). The open shafts were interpreted as part of an internal chamber system constructed for several purposes, such as a dwelling place for the king and queen, nursery for eggs, fungus gardens, or ventilation canals (chimneys) designed to maintain the microclimate of the nest (Genise and Bown, 1994). The bioturbated dome-like structures that surround the sandstone columns likely accounted for the exposed subterranean part of the nest system (Bordy, 2000; Bordy and Catuneanu, 2002a).

The strong north-south preferred orientation of the nests may be interpreted as an external architectural morphology that enabled protection from extreme diurnal temperature variations that likely existed in the sand-sea environment in the Early Jurassic of the Tuli Basin. Grigg (1973) experimentally demonstrated that the roughly 9° E orientation of some wedge-shaped northern Australian termite nests (Fig. 5C) is designed to deflect the midday heat and enhance gas exchange across the walls of the nests. Roughly north-south oriented, slab-shaped nests of *Tumulitermes* and *Amitermes* of northeast Australia are the classical examples of such architectural behavior in recent termite nests (Spain et al., 1983; Noirot and Darlington, 2000). An equally popular explanation for the nest orientation is based on the hypothesized ability of the termites to utilize the earth's magnetic field (Grigg et al., 1988, and references therein). To date, possible reasons for nest orientations are inconclusive, and no modern studies conclusively show that termites use magneto-perception to construct nests with preferential orientation (Grigg et al., 1988). The recorded variation in mound orientation, where more westerly clusters are oriented towards the north-northwest and easterly clusters towards the north-northeast (Fig. 2), is consistent with observations of some modern-day termite mounds that form clusters of homogonous orientation within the study areas (Grigg and Underwood, 1977).

It is clear the measured north-south nest alignments originally were oriented more towards the Early Jurassic north-northeast (Parrish, 1990; Scotese et al., 1999), and thus the vector means were pointing to about 10° to 20° E. This result is somewhat comparable with the angular mean orientation of recent northern Australian termite nests, which also differ from geographic and magnetic north (Grigg and Underwood, 1977; Spain et al., 1983; Grigg et al., 1988). For instance, the calculated mean vector of 248 nests is 9.4° (Fig. 5C, recomputed from Grigg and Underwood, 1977) in the Maningrida area, and hundreds of mounds have a mean vector of 8° in the Darwin area (Grigg et al., 1988), both in northern Australia. A further possible explanation for the discrepancy reported here lies in the high paleolatitude calculated for southern Africa in the Early Jurassic. At such high latitudes, the mid-day azimuth of the sun would be considerably lower in the sky than that experienced in low latitudes by the modern Australian termites. Thus, more northeastwardly oriented nests would provide a greater degree of shading

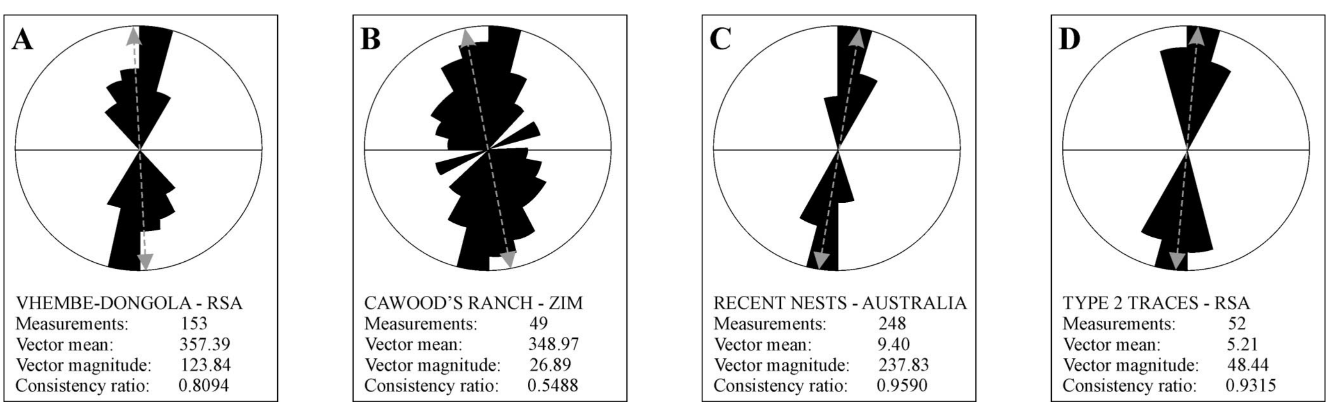

FIGURE 5—Orientation rose diagrams. (A) Measured orientation data of the Tuli termite nests at Site 1. (B) Measured orientation data of the Tuli termite nests at Site 2. (C) Orientation data of modern Australian termite nests (recomputed from Grigg and Underwood, 1977). (D) Rose diagram of the strongly oriented Type 2 burrows. Note the high consistency ratio.

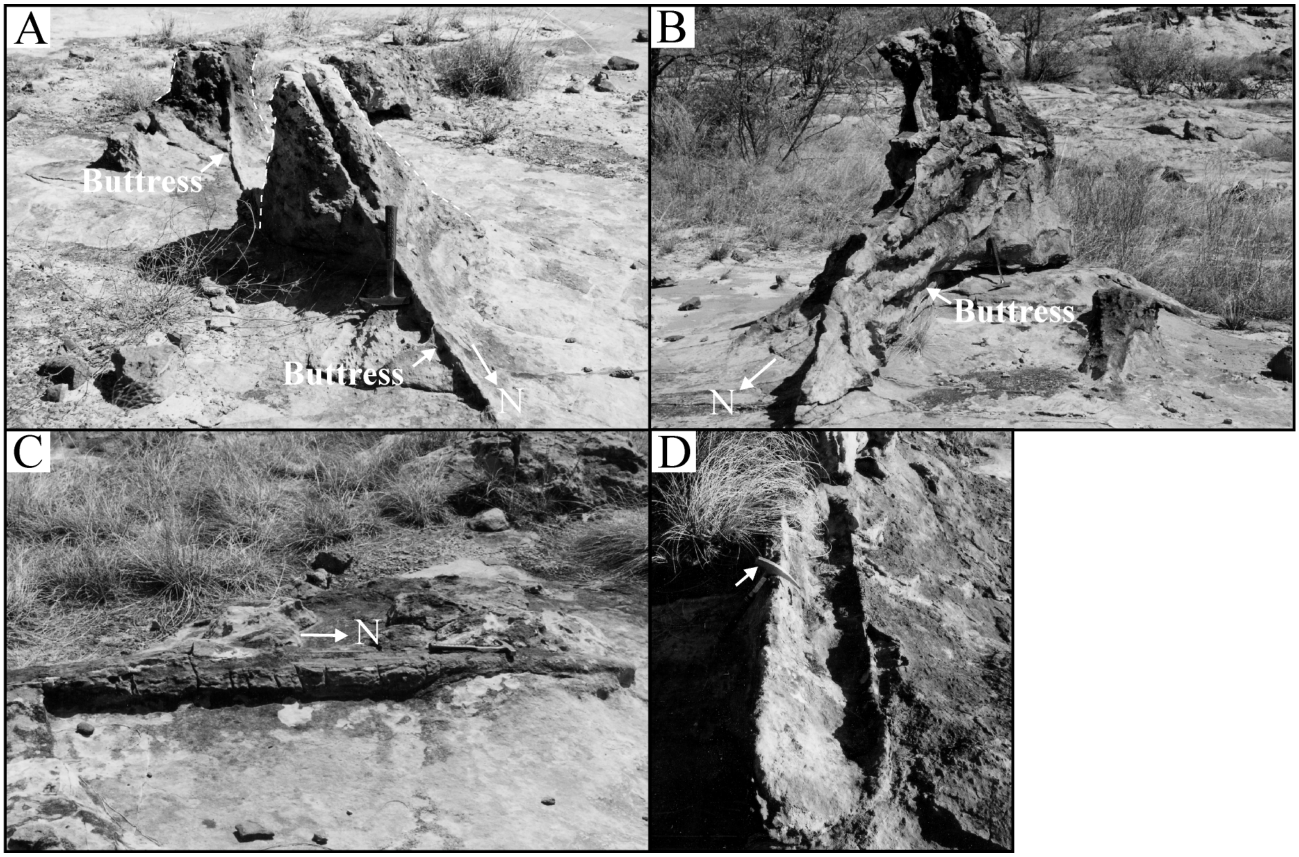

FIGURE 6—External architecture of the sandstone pillars. (A) Massive, northward-oriented buttress tapering away from northern side of bioturbated pillar. Note that the proximal end of the buttress cast is surrounded by the pillar; hammer is 28 cm long. (B) About 10-cm-thick and 1.2-m-long buttress shows northward-trending lineations along its flanks; hammer is 28 cm long. (C) North-south oriented, straight, horizontal cylinder, ~2.5 m long, 25 cm in diameter. These cylinders interconnect the neighboring pillars and are often heavily bioturbated; hammer is 28 cm long. (D) Trough-shaped weathering feature of a horizontal cylinder leading to a broken sandstone pillar; hammer head (see arrow) is 18 cm long.

to the south of the nests at midday compared to a more northerly oriented mound.

Additionally, at such high latitudes, solar radiation is likely to have been less than at low latitudes, reducing the importance of precise north-south orientation. Low consistency in nest orientation (Fig. 5A, B) may be a reflection of this, or may indicate that nests were not built contemporaneously, but were constructed in different orientation in response to short-term climate changes in order to maintain ideal internal temperatures. However, in a comparative study of some recent nests of open savanna and woody savanna, the influence of environmental conditions was demonstrated not to be significant since the two, environmentally distinct populations showed no major differences in nest orientation (Grigg and Underwood, 1977). Similarly, environmental influence on variation of orientation of the termite mounds of northern Australia was excluded by Spain et al. (1983). Interpretations that account for the variance in orientation within the Tuli termite nests by varying magnetic declination during long periods of termite residence are less likely to be accurate, as the susceptibility of modern termites to magnetic fields has yet to be determined. It appears that instead of environmental influences, genetic factors (i.e., different species) are the ultimate regulators of the consistency of mound orientations.

Strongly northward-oriented buttresses are not bioturbated, suggesting that although termites may have constructed them, they did not form a residential part of the termite nest. Buttresses may have acted as windbreakers (foreset directions in the proximal eolian Clarens formation suggest westerly paleowinds) to enhance cooling of the nest. Alternatively, buttresses may have acted as a system for casting shade over subterranean parts of the nest when the sun was not directly overhead. Diurnal shading by buttresses would supplement temperature regulation of the oriented nests. Generally, nests associated with buttresses do not exhibit preserved ventilation shafts. Thus, an alternative interpretation is that buttresses were constructed simply to increase the surface area of the mound. According to Monteith (2000), oxygen and carbon dioxide must permeate through the walls of the mounds efficiently for respiration of the occupant termites. Increasing the ratio of mound surface to volume is thought to increase the area over which the exchange of gasses occurs. In modern nests, such as those constructed by *Amitermes laurensis* in northern Australia, thin buttresses are also present (P. Jacklyn, written communica-

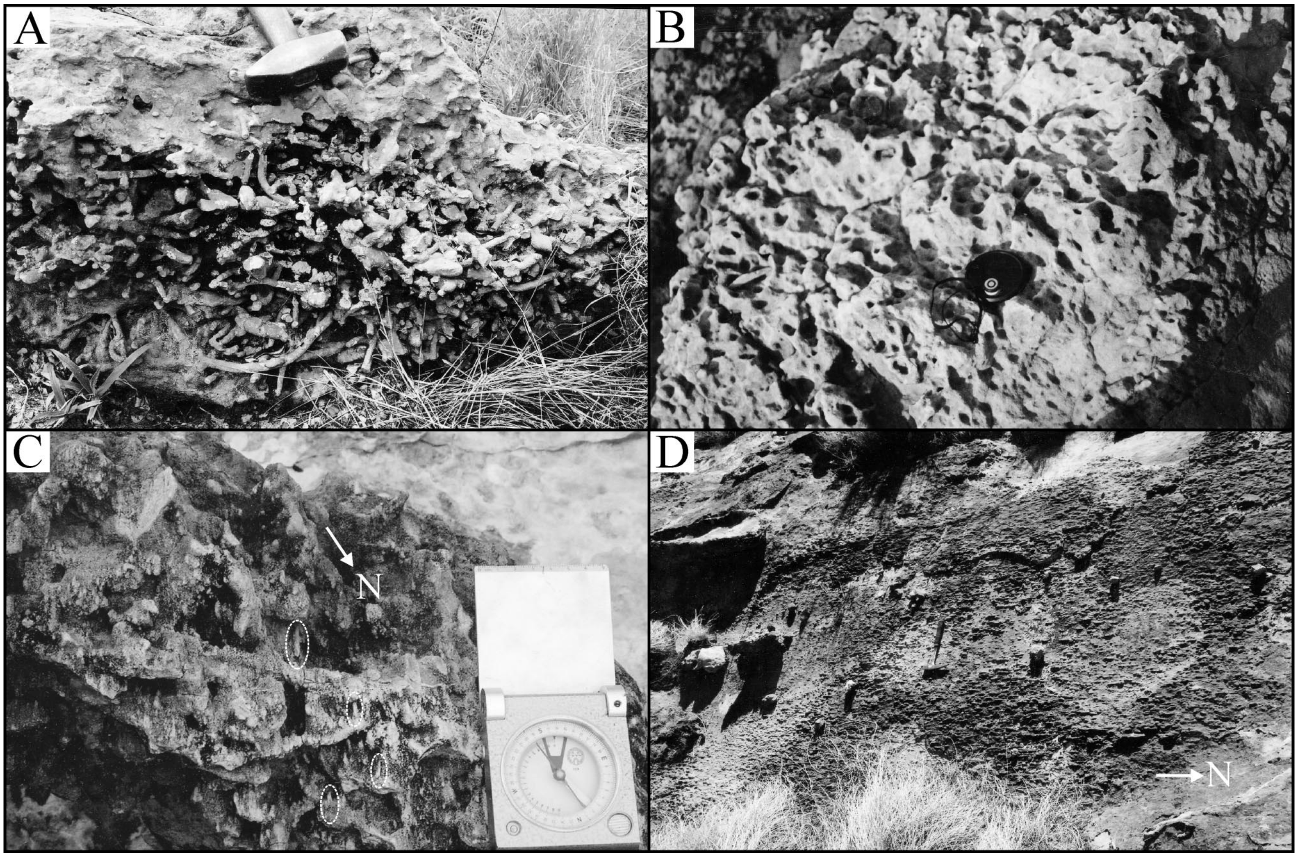

FIGURE 7—Internal architecture of the sandstone pillars. (A) Intricately interwoven, cylindrical burrows of Type 1 forming network of randomly oriented tubes with consistent diameter and gentle curving inside the pillars. The burrows have smooth surfaces and massive sandstone filling; hammer head is 12 cm long. (B) Local variation of open Type 1 burrows gives a sponge-like appearance to the host sandstone bed; lens cap is 5.8 cm in diameter. Photo shows cross-sectional view of the bed. (C) Strongly oriented, horizontal, simple Type 2 burrows (see circles) are smaller and less common than Type 1 burrows. Note their straight shape, smooth surface, and massive fill; open compass is 16 cm long. View shows a horizontal surface through the nest. (D) Superposition of Type 2 burrows on surfaces already bioturbated by Type 1 burrow makers is found only at Site 1; hammer is 32 cm long. View shows an upper bedding surface.

tion, 2002), therefore, northward-oriented buttresses similarly accommodated enhanced gas exchange in the Tuli termite nests. Although buttresses are only rarely found associated with the Jurassic nests, modern nests of *Amitermes laurensis* in Northern Territory of Australia similarly may or may not contain side buttresses (P. Jacklyn, pers. comm., 2002).

The pronounced inclination to the east of some of the nest apices in the Tuli termite nest strongly resembles the inclined apices of some recent termite mounds in the study area. Similar apex-inclination of some north-south aligned *Amitermes vitiosus* nests in northern Australia were reported by Spain et al. (1983).

Straight, mostly north-south trending, 1 to 3 m long, bioturbated horizontal cylinders are interpreted as connecting tunnels between a main and satellite nests. The interleading tunnels might be explained in terms of polycalism, where a large termite colony has several satellite nests that usually are connected to one another by subterranean or covered galleries (Noirot and Darlington, 2000).

The smaller diameter Type 2 traces with distinct parallel, north-south orientation are tentatively interpreted as ant galleries. This interpretation is based upon the invariable diameter (0.3 cm) of the traces, which form a simple, parallel pattern (Bown et al., 1995, 1997). The superposition of Type 2 traces on surfaces bioturbated by Type 1 burrows may be explained by the fact the modern ants are predators of termites, commonly invading their nest to prey on them (Lepage and Darlington, 2000; Noirot and Darlington, 2000). Although ants are thought to have originated in the Early Jurassic (Crozier et al., 1997), the oldest reported ant nests are from the Late Triassic (Hasiotis, 2002), followed by Late Jurassic findings (Hasiotis and Demko, 1996; Hasiotis, 2000, 2002), and the oldest known ant fossils are Late Cretaceous (92 Ma ago) (Agosti et al., 1998).

Undetermined, larger organisms, possibly beetles that invaded the nests and preyed on the termites, may have produced the larger, back-filled horizontal tubes. Hasiotis (1999) similarly reported co-occurrence of termite nests and beetle burrows from the Upper Jurassic Morison Formation (USA) and Genise et al. (2000) from the Lower Miocene Pinturas Formation (Argentina). Alternatively, these back-filled burrows may be explained as backfilling of chambers and passages by termites themselves, based

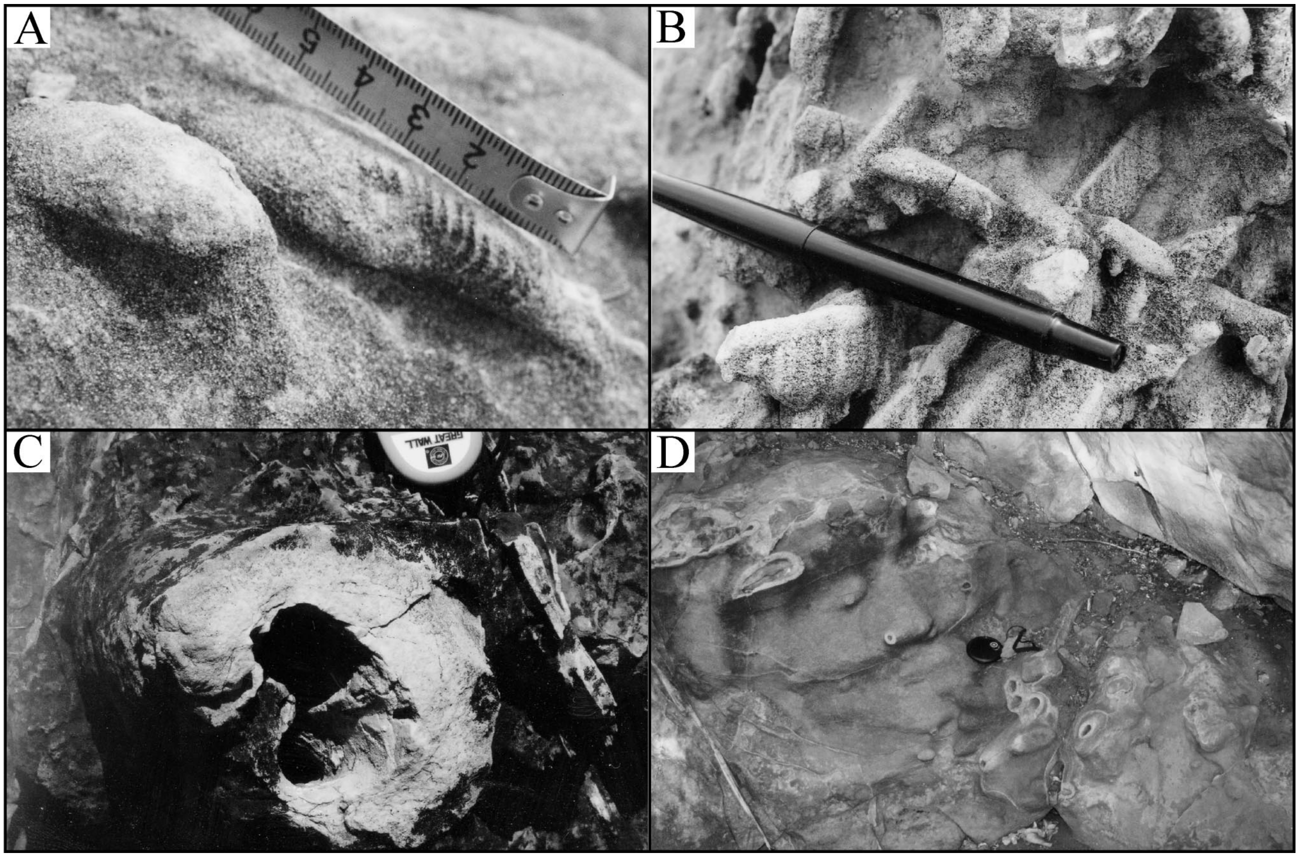

FIGURE 8—Internal architecture of the sandstone pillars. (A), (B) Back-filled, straight burrows with no wall structures often form tubes of average 2 cm in diameter and 13 to 20 cm in length; units are in centimeters; pen is 13.5 cm long. Oblique view of nest surface. (C) Open, vertical, straight shaft with 5 cm diameter penetrates the center of some pillars. Internal shafts are more common in the irregular pillar types compared to those with more explicit north-south orientation; tape measure is 6 cm wide. (D) Cone-like features on the smooth, hardened wall of the pillars result from perforation by internal shafts. This feature is characteristic of the irregular pillar-types; lens cap is 5.8 cm in diameter. Oblique view of nest surface.

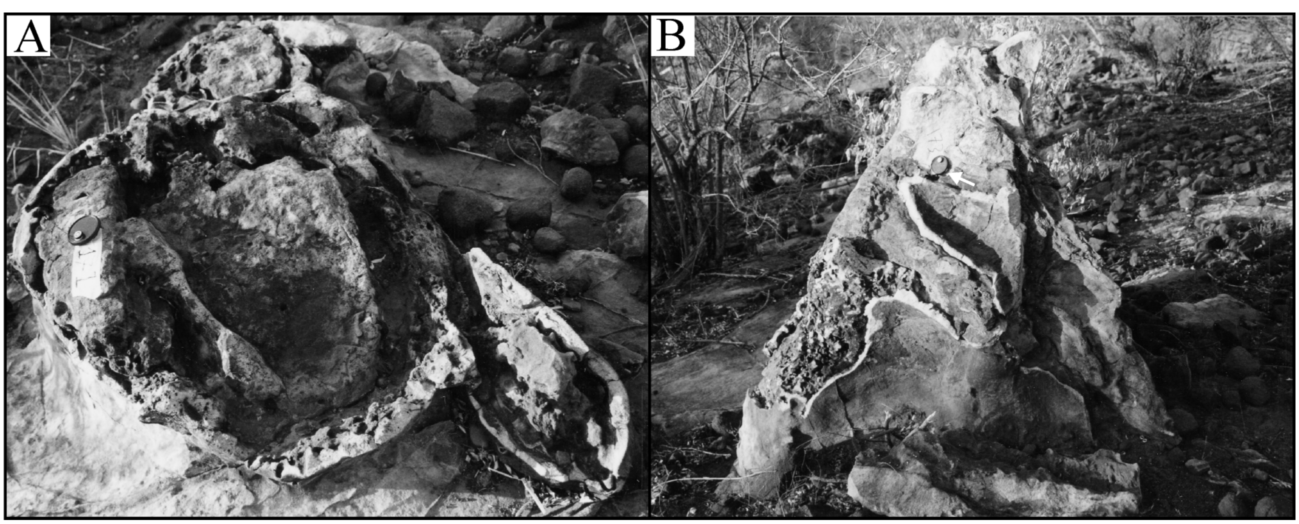

FIGURE 9—Internal architecture of the sandstone pillars. (A) Well-developed empty space between the heavily bioturbated central part and exterior wall of the pillar is not exclusive to the irregular pillar types, but is less common in the oriented pillar types; lens cap is 5.8 cm in diameter. (B) Irregular pillar type with a heavily bioturbated inner part and smooth hardened wall that is commonly perforated by the cone-shaped openings (latter feature not visible on this photo, but featured in Fig. 8D); lens cap (see arrow) is 5.8 cm in diameter.

on recent observations of termite behavior (S.T. Hasiotis, written communication, 2003).

Based on the presence of ventilation shafts and the upward tapering and bifurcating nature of the pillars, the Tuli termites were likely fungus-growing rather than wood-dwelling, despite the fact that the eolian deposits of the Tuli Basin contain fossilized wood logs (Bordy, 2000; Bordy and Catuneanu, 2002a). According to Lepage and Darlington (2000), open-air passages are constructed in modern nests in order to maintain a favorable nest microclimate for fungal metabolism and nymphal growth. The harsh climactic conditions recorded by the sedimentary features of the eolian deposits in the study area (Bordy, 2000; Bordy and Catuneanu, 2002a) further support the idea that the Tuli nests were built by fungus-growing termites, which are considered typically drought-enduring species (e.g., Lepage and Darlington, 2000).

The empty space between the nest and exterior wall observed in some of the structures may be interpreted as the paraecie (Noirot and Darlington, 2000). This feature is found in present-day termite nests and acts as a protective barrier between the exterior and the nest itself. Noirot and Darlington (2000) suggest that predators managing to break through the external wall of the termite mound might become disoriented in the paraecie. In addition to predator exclusion, the paraecie may also serve as the climate regulator of the nest (Noirot and Darlington, 2000).

Modern entomological observations show that termite behavior during the construction of the nest is genetically determined (Grigg and Underwood, 1977; Bignell and Eggleton, 2000; Noirot and Darlington, 2000), and few recent termite species build more than one type of nest (Noirot and Darlington, 2000; Hasiotis, 2002). It is equally possible that the two architecturally different types of Tuli termite nests were constructed either by a single termite taxon or by two taxa constructing nests independently. Construction of the two types of nest could have been either contemporaneous or penecontemporaneous.

IMPLICATIONS AND CONCLUSIONS

Paleoenvironment

The occurrence of clusters of termite nests in the eolian paleodunes of the Clarens formation is consistent with the interpretation of a semiarid desert milieu (Bordy, 2000; Bordy and Catuneanu, 2002a), where periods of higher rainfall occurred. It is possible that the clusters of Tuli nests occupied temporarily moist interdune areas. The environments reconstructed from certain parts of the Morrison Formation (New Mexico, USA), which also bears fossil termite nests, are excellent Late Jurassic analogues of the Clarens scenario. Those rocks also document an erg setting in a semiarid climate where termite nests indicate vegetated and well-drained soils (Hasiotis, 1999). Spain et al. (1983) reported that certain clusters of modern, oriented termite mounds of northern Australia are associated with seasonally inundated drainage hollows.

The elongated, north-south oriented nests of the Tuli Basin also indicate that the diurnal temperature variations were rather extreme in the Clarens desert. Thus, the nests were designed to deflect the midday heat—architectural behavior still used in some recent termites of northern Australia (Grigg, 1973; Grigg and Underwood, 1977; Spain et al., 1983; Grigg et al., 1988; Noirot and Darlington, 2000).

Isopteran Evolution

The Tuli termite nests are, so far, the only reported occurrences of social insect trace fossils with sophisticated nesting behavior from Jurassic continental deposits of the African continent and Gondwana. The large nests of these insects are predated only by a primitive termite nest from the lower part of the Upper Elliot Formation (earliest Jurassic) in the main Karoo Basin (Smith and Kitching, 1997). Worldwide, the Tuli termite nests are probably the third-oldest reported occurrence after the termite nests of the Upper Triassic Chinle Formation (Petrified Forest National Park, Arizona; Hasiotis and Dubiel, 1995) and the earliest Jurassic Elliot Formation structures. Undoubtedly, the Tuli findings are the oldest reported occurrence of large, elaborate termite nests in the world. Similar large termite nests from eolian environments were found in the Upper Jurassic Morrison Formation (New Mexico, USA; Hasiotis and Demko, 1996; Hasiotis et al., 1997, 2002). Interestingly, advanced construction behavior exhibited by the Tuli termites appears to have modern analogues in the magnetic termites of the Northern Territories in Australia.

In accordance with the American findings of advanced isopteran eusocial behavior (Hasiotis and Bown, 1992; Hasiotis and Dubiel, 1995; Hasiotis, 1998, 2000, 2002), the Tuli termite nests reinforce the interpretation that the evolution of eusocial behavior in insects predate the appearance of the flowering plants in the Early Cretaceous (Traverse, 1988; Labandeira and Sepkoski, 1993, Hasiotis and Dubiel, 1995; Hasiotis, 1998, 2002). In addition, these Early Jurassic African termite nests bridge the break in the evolutionary history of insects that existed between the reported Late Triassic and Late Jurassic occurrences from the USA, clearly supporting the idea that the beginnings of the evolution of the Isoptera took place prior to the breakup of Pangea (Emerson, 1955, 1968; Emerson and Krishna, 1975; Krishna, 1990; Hasiotis and Dubiel, 1995; Hasiotis, 1998, 2002).

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