

Comment—Advanced Early Jurassic Termite (Insecta: Isoptera) Nests: Evidence from the Clarens Formation in the Tuli Basin, Southern Africa (Bordy et al., 2004)

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“The characteristics of termite nests are better understood if the main requirements of these insects are kept in mind (Noirot, 1970, p. 102). More than the gross architecture, some details may be significant. . . A very precise description of the chambers and galleries would be necessary. . .” (Noirot, 1977, p. 179)

Insect paleoichnology, being a young discipline, needs to gain acceptance and recognition as a sister counterpart of paleoentomology and entomology. Accordingly, the analyses and discussions to ascertain the attribution of continental trace fossils to insects should be carried out very carefully. Such analysis (e.g., Machado, 1983; Sands, 1987) for fossil termite nests, which is lacking in the recent contribution by Bordy et al. (2004) on supposed Jurassic termite nests, is critical, because their results are at odds with our previous knowledge of the evolutionary history of termites and their relationship with coevolving groups of plants and fungi.

Many invertebrate trace fossils are more preservable than their constructors are. For example, fossil bee nests predate the oldest known bees by about 25 My (Elliot and Nations, 1998; Genise, 2000; Engel, 2000), which is an expected gap. In contrast, the gap between the oldest termites, which come from the Lower Cretaceous (Jarzembowski, 1981; Martínez-Delclòs and Martinell, 1995), and the supposed termite nests described by Bordy et al. (2004) would be about 60 My. However, it is neither the time involved nor the difficulties of imagining fungus-growing termites in an early Jurassic environment deprived of Basidiomycotina and grasses that promoted this comment. Instead, it is the understanding that the description and affinities of the Tuli structures are not treat-

ed with the necessary detail and their termitic origin was not demonstrated. Termite nests comprise closed and dynamic systems, largely isolated from the external environment, within which the microclimate can be controlled, food can be stored, and protection from enemies achieved (Lee and Wood, 1971). Some termite nests are considered the most complex constructions of the animal kingdom (Noirot, 1970). Such morpho-functional complexity is accomplished by the spatial arrangement of different morphological parts, following distinct basic bauplans, according to the biology of the species and the environment. The internal morphology of the Tuli structures does not exhibit any of these basic termitic bauplans. The important evolutionary conclusions to which the paper seems to arrive are based on controversial and weak evidence—as is the case with other records of supposed Triassic and Jurassic termite nests mentioned in the bibliography (see Genise, 2004 for discussion). At present, the body and ichnofossil record shows that the appearance of eusocial insects and flowering plants occurred during the early Cretaceous (Jarzembowski, 1981, 2003; Labandeira, 1998; Grimaldi, 1999; Engel, 2000, 2001; Genise, 2004).

Insect paleoichnology is a fortunate branch of ichnology because frequently, insect trace fossils can be attributed to modern taxa, contributing to knowledge of the evolutionary history of producers. However, the degree of reliability of such attributions has been uneven. Several fossil termite nests are undisputable, such as those described by Coaton (1981), Schuster et al. (2000), or *Krausichnus trompitus* (Genise and Bown, 1994), whereas other claims need further analysis and confirmation; and still others are unlikely (Genise, 2004). The reliability of attributions depends on the complexity of the described trace fossils, the methodology applied for their study, the existence of a sound ichnotaxonomy, and particularly, the control by the body-fossil record (Genise, 2004). Even evolutionary hypotheses based on objective evidence, such as molecular clocks, are calibrated or contrasted with the body-fossil record (Brochu et al., 2004).

The contribution by Bordy et al. (2004) lacks the pertinent macro- and micromorphological analyses and comparisons of the structures that would allow their attribution to termites. In exhaustive analyses (e.g., Machado, 1983; Sands, 1987), the external and internal (macro- and micro-) morphologies of the structures are extensively compared with modern termite nests—a first hand comparison that is lacking in the paper by Bordy et al. (2004). The micromorphology of the Tuli structures was not studied at all, even when these data would be a primary tool to determine their termitic origin (Stoops, 1964; Machado, 1983; Mermut et al., 1984; Sands, 1987; Cosarinsky et al., 2004). In addition, Sands (1987) had to appeal to the complex distribution of the possible termite nests in the deposits to demonstrate that they were as old as the host rocks—a possibility completely absent in Bordy et al.’s (2004) discussion. In contrast, Bordy et al. (2004, p. 71) stated “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.” This statement is followed by a short paragraph in which only two paleoichnological references are mentioned as comparison with modern examples. The whole paper should have been

focused on demonstrating the termitic origin of the structures, however, this origin is claimed from the very beginning of the discussion without a proper analysis.

PALEOENVIRONMENT

Bordy et al. (2004) suggested that the occurrence of termite nests in eolian facies of the Clarens Formation was consistent with the interpretation of a semiarid desert environment (Bordy, 2000; Bordy and Catuneanu, 2002). However, Bordy and Catuneanu (2002) used bioturbation, including the supposed termite nests, as evidence (along with fossil wood remains and rare ephemeral-stream deposits) to infer this semiarid paleoenvironment. To demonstrate the termitic origin of the Tuli structures while avoiding circularity in reasoning, it should have been necessary to: (1) exclude their supposed affinities when inferring the paleoenvironment; and (2) show that the supposed nest morphology matches with the inferred paleoenvironment, given present knowledge of termite architecture and biology. In addition, Bordy and Catuneanu (2002) previously stated that the Tuli structures were preserved in massive eolian sand-dune deposits (facies Sm) that originated in an ancient erg with probable vegetation-free areas (i.e. an arid paleoenvironment). However, recently Bordy et al. (2004) suggested that these structures occur in interdune areas (i.e. ephemeral streams and oases) represented by facies Sc, Sh, St and Sl, which underlie the Sm facies.

Few termites inhabit eolian dunes, such as those described from the Clarens Formation, even the moister interdunes and oasis. Termites that do occupy such habitats include Psammotermitinae and *Anacanthotermes* (Hodotermitinae), which construct completely subterranean nests without mounds (Lee and Wood, 1971; Grassé, 1984). This behavior is related to the strong dependence on water by termites (Collins, 1969). In such dune environments, rather than constructing epigeous mounds, termites migrate downwards, seeking the water table, and avoiding high temperatures and desiccation (Grassé and Noirot, 1948a). In contrast, mound-building behavior is typical of termites inhabiting savannas, steppes, sclerophyll forests, grasslands, woodlands, and rain forests, but never deserts (Lee and Wood, 1971; Grassé, 1984). Previous studies show that mound-building behavior is more likely related to wet lowlands and seasonally flooded environments (Coaton, 1947; Lee and Wood, 1971; Matthews, 1977). Mound-building termites, such as *Cubitermes fungifaber* (Grassé and Noirot, 1948a) or *Trinervitermes trinervius* (Grassé, 1984), migrate to the hypogeous part of the nests during hot periods, demonstrating that mounds are not structures constructed particularly to deal with the extremely hot and dry climate of deserts. In addition, such a dry environment, probably supporting scarce vegetation, would be incompatible with the presence of abundant and large societies of termites.

INTERCONNECTING BIOTURBATED CYLINDERS

Bordy et al. (2004) interpreted horizontal cylinders having an average diameter of 20–30 cm as interconnecting tunnels among nests. Although these structures are neither properly described nor illustrated, they are nonethe-

less incomparable with any known termite gallery. Only very exceptionally do termite nests show complex interconnecting galleries composed of a number of individual parallel tunnels along the main axis (*cylindres maçonnés*, Grassé and Noirot, 1948b; Genise and Bown, 1994). However, such morphology was not described for the Tuli structures. The *cylindres maçonnés* are restricted to nests of the single modern species, *Sphaerotermes sphaerothorax*, which constructs polycalic, subterranean nests (Grassé and Noirot, 1948b).

In fact, interconnecting galleries are present only in polycalic nests, which are composed of a network of chambers and tunnels (Noirot, 1970; Lee and Wood, 1971; Grassé, 1984), whereas in concentrated nests, such as those supposed for the Tuli structures, the periecie (peripheral tunnels) basically reach food, clay, and water sources and are composed of simple tunnels (Grassé, 1984). There are only exceptional cases of termite mounds connected by tunnels, but none is comparable with the Tuli structures. For instance, species of the genus *Trinervitermes* construct nests having relatively small mounds connected by tunnels. However, they represent polycalic nests (not concentrated nests) having important subterranean components (Grassé, 1984). Fontes (1998) recorded nests composed of a large mound connected by tunnels with small ones for *Cornitermes cumulans*, which represent nests in an early stage of development. Such is not the case for the Tuli structures.

Finally, the diameter of the interconnecting cylinders, 20–30 cm, is unlikely for peripheral galleries. Even for the large nests of *Bellicositermes*, which reach 2–3.80 meters high, the galleries range from 1–3 cm in diameter. In nests of *B. rex*, having mounds of 28 meters in diameter, peripheral galleries are less than 2 cm in diameter (Grassé, 1937; Boyer, 1975). In a few species of *Coptotermes*, *Nasutitermes*, *Apicotermes* and *Acanthotermes*, which construct small or no mounds, the interconnecting galleries are up to 5 cm in diameter (Hill, 1915; Ratcliffe and Greaves, 1940; Grassé and Noirot, 1951; Grassé, 1984). Consequently, the large size of the Tuli cylinders seems to be incompatible with the average dimensions of extant termite galleries.

ORIENTATION OF STRUCTURES

The cross section of the Tuli structures at site 1 is elliptical and oriented approximately north–south. Despite devoting an important part of the discussion for extensive comparison of the orientation of the towers with those of some Australian modern termite nests, the conclusion was “low consistency of nest orientation (Bordy et al., 2004, p. 73).” In any case, orientation of the structures is not diagnostic of termite nests, and can be considered only as a secondary character.

Non-bioturbated, planar structures, interpreted as buttresses by Bordy et al. (2004), are also oriented. As Bordy et al. (2004) noted, buttresses are unusual for termite mounds (they noted a single report, in a written communication, of thin lateral buttresses in nests of an Australian species). The structure illustrated in Bordy et al., 2004, Figure 6A, interpreted as a windbreaker, is a thick ridge intersecting two contiguous towers—a morphology that is not compatible with termite-nest architecture. The

groove in the first tower suggests that the buttress penetrates deeply, which would make it part of the internal structure. Should a supposed windbreaker be important enough to compose part of the internal mound architecture? A single planar structure (interpreted as a buttress) seems to cut both towers (Bordy et al., 2004, Fig. 6A). Would termites of two different nests construct a common windbreaker for both? Actually, these planar structures resemble structural joints; however, that possibility apparently was not analyzed. Horizontal external cylinders, interpreted as interconnecting tunnels between satellite nests, also are oriented north–south. Is it possible to imagine a row of satellite termite nests distributed along a single north-south oriented line?

The most striking aspect of these features, which is impossible to explain in terms of termite biology, is that all of them—long axis of towers, buttresses, and horizontal external cylinders—are oriented north–south. Could all these structures have any relationship with the presence of oriented structural joints, to the heterogeneity in the fabric of the deposits enhanced by diagenetic processes, or with the direction of any post-Jurassic erosive agent?

TYPE 1 BURROWS

The Type 1 burrows are described as “intricately interwoven, simple burrows” resembling “a web-like network of randomly oriented, sandstone filled tubes” in which “true branching is rare, but the burrows often cross each other, forming an anastomosing pattern” by Bordy et al. (2004, p. 70). Is it a true network, originally constructed as such, or the result of the random crossing of burrows made by solitary organisms? It is impossible to attribute individual burrows to social or solitary organisms, even less to termites, without a detailed description and interpretation of the relationships among them. Termites excavate and construct true branched, three-dimensional, burrow systems (i.e., boxworks, *sensu* Ekdale et al., 1984). True anastomosing systems are also common (i.e., branching burrows join repeatedly) in termite nests, where in some cases the whole system shows a definite orientation (Grassé, 1937, 1984; Ruelle, 1964).

However, true networks do not necessarily indicate social behavior. Solitary crustaceans commonly make networks (i.e., Bromley, 1990), whereas true cooperative organisms, such as bees, can use a common single burrow (Michener, 1974). Termite (as well as ant) nests show boxworks combined with chambers that are constructed cooperatively. Commonly, such work is reflected by tunnels showing diameters that differ by an order of magnitude: individual passages have small diameters related to the sizes of individual workers, whereas communal tunnels, which are constructed cooperatively, do not relate directly to the sizes of the workers (Machado, 1983; Sands, 1987; Genise, 1997). Such characters also are found in fossil termite nests (i.e., Bown and Laza, 1990; Genise and Bown, 1994; Genise, 1997).

In nests of fungus-growing termites, such boxworks commonly are found in the mound wall. The royal chamber and the fungus garden, which are made of delicate layers of clay material and supported by pillars and lateral attachments (Noirot, 1970; Grassé, 1984), are located in the central part of the mound, surrounded by the paraecie.

There is no evidence of these typical central structures of fungus-growing termite nests in the Tuli structures, where the same boxwork seems to be present in all parts of the structure.

OTHER INTERNAL CHARACTERS

Type 2 burrows, attributed to ants by Bordy et al. (2004), also are present in the internal structure. They are straight, parallel to one another, and north–south oriented, which is a completely unknown pattern for ant burrows. In addition, the oldest known ants come from the Cretaceous (Nel et al., 2004).

In termite nests, the width of the external wall is related to the height of the mound. In mounds of ~3 meters high, as in the Tuli structures, the wall is 35–60 cm wide, which probably is the ratio necessary to provide to the whole structure with the essential strength and isolation from the exterior (Grassé, 1984). In contrast, the wall in the Tuli structures is only 2–4 cm wide.

Fungus-growing termites, the proposed constructors of the Tuli towers, use clay material mixed with saliva as mortar (Grassé, 1984), whereas most termites use fecal material. In addition, the habitacle where the larvae are reared is constructed completely with clay because of the hygroscopic character of this material (Lee and Wood, 1971; Grassé, 1984). Therefore, the clay content of soils is critical for construction of Macrotermitinae mounds, which can be constructed in any soil with the appropriate proportion of clay. In contrast, Bordy and Catuneanu (2002) and Bordy et al. (2004) did not mention the presence of clay matrix in the lithofacies Sm where the Tuli structures occur, which is consistent with the proposed eolian dune origin of the deposits.

CO-EVOLUTIONARY ASPECTS

Bordy et al. (2004) proposed fungus-growing termites (Macrotermitinae) as possible producers of the Tuli structures. However, these termites have a strict symbiotic relationship with the fungal genus *Termitomyces* (Sands, 1969), which belongs to the Basidiomycotina, whose oldest record comes from the Eocene (Taylor and Taylor, 1993). In addition, the Macrotermitinae also depend on grass leaves, which compose the main part of their diet, particularly in arid environments (Emerson, 1949; Grassé, 1982, 1986). The oldest Poaceae are of Maastrichtian–Paleocene age, and the appearance of grasslands occurred in the late Oligocene–early Miocene (Macphail and Hill, 2002) or in the Eocene (Retallack, 2004). Emerson (1949) had proposed the origin of Macrotermitinae in the Eocene or Oligocene based on the oldest record of grasses. Recently, Schaefer (2001), in a broader scenario, proposed a close interdependence between the origins of angiosperms, latosols, and termites during Cretaceous–early Tertiary times. The presence of Macrotermitinae or their nests in the early Jurassic, without grasslands and the appropriate fungus, is unlikely. Even if termites had appeared in the Jurassic, such elaborate nests, similar to those of the extant Macrotermitinae, which are among the most derived, would not be expected; however, nests in wood would be likely (Abe, 1984).

CONCLUSIONS

It is not the purpose of this comment to find alternative interpretations to the Tuli structures. These alternative interpretations cannot be made without the proper field studies and detailed observations, including microscopic analyses. However, it should be stated emphatically that not every network found in subaerial facies should be attributed to termites or ants in the absence of a better explanation. The fossil record of ants and termites is a critical topic for entomology and paleoentomology and, accordingly, termite and ant fossil nests are of primary interest. Positive termitic diagnostic characters should be shown clearly.

The Tuli structures show features that are similar to other bioturbated erosive remnants, which are not treated by Bordy et al. (2004). They resemble giant rhizoliths (up to 3.5 meters high) currently exposed at the Pinnacle desert of the Nambung National Park (Tamala Limestone, Western Australia). They are free-standing, bioturbated structures that are mound shaped, with some orientation, elliptical cross-sections, and upward bifurcation (McNamara, 1995). These structures are interpreted as erosive remnants of tree roots grown in a Quaternary calcrete (McNamara, 1995).

Another analysis that is lacking is that of the contemporaneity of structures and host rocks. It seems that Tuli structures have never been found included in the overlying deposit, but always as emergent structures from exposed rocks. Moreover, they roughly resemble similar extant nests in the study area, as noted by Bordy et al. (2004). In such a scenario, an assessment of the possibility of these being modern structures made with ancient sediments should have been made. There are classical examples of termites burrowing in ancient rocks that have generated much discussion (e.g., Cloud et al., 1980). The nature of the filling of burrows, diagenetic studies, and cross-cutting relationships can be used to distinguish the structures made during soil formation from those that originated after its exhumation (Retallack, 1990).

Different elements, such as the inferred paleoenvironment, presence of buttresses, orientation of structures, morphology of internal burrows, wall width, horizontal cylinders, clay content, absence of habitacle, and absence of Basidiomycetes and grasses in the Jurassic, all argue against the attribution of these structures to termites, much less to fungus-growing, advanced termites. Even for those isolated elements that may resemble termite constructions, such as the tower-shaped structure, internal empty spaces, and shafts, it is necessary to emphasize that a termite mound is not a random combination of structural elements of termite architecture. It is a complex and functional unit that strongly depends on and interacts with the environment in which it is constructed. An analysis should not be restricted to the single comparison of isolated morphological elements, but also to the interpretation of them within the context of termite biology, architecture, and environment. The Tuli structures seem to be a reconstruction of a supposed termite nest composed of different parts of known nests, but, when combined together, do not match with any known nest and consequently, do not match with the functional morphology of those elements in relation to the inferred paleoenviron-

ment. It is important to note that even though modern and fossil traces of the same group do not necessarily have to match, the morphology of the fossil structures still have to fit with the biology of the supposed producer(s).

The contribution by Bordy et al. (2004) lacks the pertinent macro- and micro-morphological analyses and comparisons with modern nests that would allow their attribution to termites. It also lacks any analysis about the age of the structures in comparison with the host rocks. Moreover, the described features do not indicate termitic origin, as summarized below:

- (1) Eolian dunes, such as those described from the Clarens Formation, are inhabited only by a few termites, which construct subterranean nests and not mounds. In addition, this environment is poorly vegetated or lacks any vegetation at all, which would not support large colonies of termites.
- (2) The features and size of the interconnecting bioturbated cylinders are not compatible with any known termite gallery.
- (3) The orientation of the structures is not diagnostic of termite nests, especially given that the pillars, buttresses, and bioturbated cylinders show the same orientation.
- (4) The purported buttresses are almost unknown for termite nests and show a close resemblance to structural joints.
- (5) Type 1 burrows lack a detailed description and interpretation. For this reason, it is impossible to attribute them to social or solitary organisms, much less to termites, when branching is rare.
- (6) Attribution of type 2 burrows to ants is unsupported. Besides, this aspect is not critical to the identification of termite nests.
- (7) Type 3 burrows display characteristics that occur in a wide array of sedimentary deposits and are not diagnostic of termite nests.
- (8) The wall of the purported termite nests is an order of magnitude thinner than the same structure in modern termite nests.
- (9) The absence of clay in the structures is contradictory with the inferred fungus-growing termites because the clay content of soil is critical for the construction of subaerial nests by this particular group.
- (10) The presence of advanced fungus-growing termites as purported producers of the Tuli structures is unlikely from the early Jurassic because the oldest termites come from the Cretaceous, and there is no record of grasslands and gilled fungus until the Tertiary.

REFERENCES

- ABE, T., 1987, Evolution of life types in termites: *in* Kawano, S., Connell, J.H., and Hidaka, T., eds., *Evolution and Co-adaptation in Biotic Communities*: University of Tokyo Press, Tokyo, p. 125–148.
- BORDY, E.M., BUMBY, A.J., CATUNEANU, O., and ERIKSSON, P.G., 2004, Advanced early Jurassic termite (Insecta: Isoptera) nests: evidence from the Clarens Formation in the Tuli Basin, Southern Africa: *PALAIOS*, v. 19, p. 68–78.
- BORDY, E.M., and CATUNEANU, O., 2002, Sedimentology and paleontology of upper Karoo aeolian strata (Early Jurassic) in the Tuli Basin, South Africa: *Journal of African Earth Sciences*, v. 35, p. 301–314.

- BOWN, T.M., and LAZA, J.H., 1990, A Miocene fossil termite nest from southern Argentina and its paleoclimatological implications: *Ichnos*, v. 1, p. 73–79.
- BOYER, P., 1975, Etude particuliere de trois termitieres de *Bellicositermes* et de leur action sur les sols tropicaux: *Annales des Sciences Naturelles, Zoologie*, 12 Série, v. 17, p. 273–446.
- BROCHU, C.A., SUMRALL, C.D., and THEODOR, J.M., 2004, When clocks (and communities) collide: estimating divergence time from molecules and the fossil record: *Journal of Paleontology*, v. 78, p. 1–6.
- BROMLEY, R.G., 1990, *Trace Fossils: Unwin Hyman*, London, 280 p.
- CLOUD, P., GUSTAFSON, L.B., and WATSON, J.A., 1980, The works of living social insects as pseudofossils and the age of the oldest known Metazoa: *Science*, v. 210, p. 1013–1015.
- COATON, W.G., 1947, The Pienaars River complex of wood-eating termites: *Journal of the Entomological Society of South Africa*, v. 9, p. 130–177.
- COATON, W.G., 1981, Fossilised nests of Hodotermitidae (Isoptera) from the Clanwilliam district, Cape Province: *Journal of the Entomological Society of South Africa*, v. 44, p. 79–81.
- COLLINS, M.S., 1969, Water relations in termites: in Krishna, K., and Weesner, F. M., eds., *Biology of Termites, Volume I: Academic Press*, New York, p. 433–458.
- COSARINSKY, M., GENISE, J.F., and BELLOSI, E.S., 2004, Micromorphology of modern epigeal termite nests and possible termite ichnofossils: a comparative analysis: *Abstract Book, First International Congress on Ichnology*, p. 26.
- EKDALE, A.A., BROMLEY, R.G., and PEMBERTON, S.G., 1984, Ichnology: the Use of Trace Fossils in Sedimentology and Stratigraphy: *Society of Economic Paleontologists and Mineralogists*, Tulsa, 316 p.
- ELLIOTT, D.K., and NATIONS, J.D., 1998, Bee burrows in the Late Cretaceous (Late Cenomanian) Dakota Formation, northeastern Arizona: *Ichnos*, v. 5, p. 243–253.
- EMERSON, A.E., 1949, Termites studies in the Belgian Congo: *Deuxieme Rapport Annuel del Institut pour la Recherche Scientifique en Afrique Centrale*, v. 1949, p. 149–159.
- ENGEL, M.S., 2000, A new interpretation of the oldest fossil bee (Hymenoptera: Apidae): *American Museum Novitates*, v. 3296, p. 1–11.
- ENGEL, M.S., 2001, A monograph of the Baltic bees and evolution of the Apoidea (Hymenoptera): *Bulletin of the American Museum of Natural History*, v. 259, p. 1–192.
- FONTES, L.R., 1998, Cupins nas pastagens do Brasil: algumas indicações de controle: in Fontes, L.R., and Filho, E.B., eds., *Cupins: O Desafio do Conhecimento, Fundacao de Estudos Agrarios Luiz de Queiroz—FEALQ*, Sao Paulo, p. 211–225.
- GENISE, J.F., 1997, A fossil termite nest from the Marplatense stage (late Pliocene) of Buenos Aires Province, Argentina, as paleoclimatic indicator: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 136, p. 139–144.
- GENISE, J.F., 2000, The ichnofamily Celliformidae for *Celliforma* and allied ichnogenera: *Ichnos*, v. 7, p. 267–284.
- GENISE, J.F., 2004, Ichnotaxonomy and ichnostratigraphy of chambered trace fossils in palaeosols attributed to coleopterans, termites and ants: *Special Publications of the Geological Society of London*, v. 228, p. 419–453.
- GENISE, J.F. and BOWN, T.M., 1994, New trace fossils of termites (Insecta: Isoptera) from the Late Eocene–Early Miocene of Egypt, and the reconstruction of ancient isopteran social behavior: *Ichnos*, v. 3, p. 155–183.
- GRASSÉ, P., 1937, Recherches sur la systématique et la biologie des termites de l'Afrique Occidentale Française: *Annales de la Société Entomologique de France*, v. 106, p. 1–99.
- GRASSÉ, P., 1944, Recherches sur la biologie des termites champignonnistes (Macrotermitinae): *Annales des Sciences Naturelles, Zoologie*, 11 série, v. 6, p. 97–171.
- GRASSÉ, P., 1982, *Termitologia, Tome I: Masson*, Paris, 676 p.
- GRASSÉ, P., 1984, *Termitologia, Tome II: Masson*, Paris, 613 p.
- GRASSÉ, P., 1986, *Termitologia, Tome III: Masson*, Paris, 713 p.
- GRASSÉ, P. and NOIROT, C., 1948a, La "climatisation" de la termitiere par ses habitants et le transport de l'eau: *Comptes Rendus de l'Academie des Sciences*, v. 227, p. 869–871.
- GRASSÉ, P., and NOIROT, C., 1948b, Sur le nid et la biologie du *Sphaeroterme sphaerotherax* (Sjöstedt): *Annales des Sciences Naturelles, Zoologie*, 11 série, v. 10, p. 149–165.
- GRASSÉ, P., and NOIROT, C., 1951, Nouvelles recherches sur la biologie de divers termites champignonnistes (Macrotermitinae): *Annales des Sciences Naturelles, Zoologie*, 11 série, v. 13, p. 291–342.
- GRIMALDI, D., 1999, The co-radiations of pollinating insects and angiosperms in the Cretaceous: *Annals of the Missouri Botanical Garden*, v. 86, p. 373–406.
- HILL, G.F., 1915, Northern Territory Termitidae, Part 1: *Proceedings of the Linnean Society of New South Wales*, v. 40, p. 83–113.
- JARZEMBOWSKI, E.A., 1981, An early Cretaceous termite from southern England (Isoptera: Hodotermitidae): *Systematic Entomology*, v. 6, p. 91–96.
- JARZEMBOWSKI, E.A., 2003, Palaeoentomology: towards the big picture: *Acta Zoologica Cracoviensia*, v. 46, p. 25–36.
- LABANDEIRA, C.C., 1998, The role of insects in the late Jurassic to middle Cretaceous ecosystems: in Lucas, S.G., Kirkland, J.I., and Estep, J.W., eds., *Lower and Middle Cretaceous Terrestrial Ecosystems: New Mexico Museum of Natural History and Science Bulletin*, v. 14, p. 105–124.
- LEE, K., and WOOD, T., 1971, *Termites and Soils: Academic Press*, London, 251 p.
- MACHADO, A. DE B., 1983, The contribution of Termites to the formation of laterites: *Proceedings of the II Seminar on Lateritisation Process*, Sao Paulo, p. 261–270.
- MACPHAIL, M.K., and HILL, R.S., 2002, Paleobotany of the Poaceae: in Mallett K., and Orchard, A., eds., *Flora of Australia*, 43, Poaceae 1: *Australian Biological Resources Study*, Canberra, p. 37–70.
- MARTÍNEZ-DELCLÓS, X., and MARTINELL, J., 1995, The oldest known record of social insects: *Journal of Paleontology*, v. 69, p. 594–599.
- MATHEWS, A.G., 1977, *Studies on Termites from the Mato Grosso State, Brazil: Academia Brasileira de Ciencias*, Rio de Janeiro, 267 p.
- MERMUT, A.R., ARSHAD, M.A., and ST-ARNAUD, R.J., 1984, Micropeological study of termite mounds of three species of *Macrotermes* in Kenya: *American Journal of the Soil Science Society*, v. 48, p. 613–620.
- MENAMARA, K. 1995, *Pinnacles: Western Australia Museum Press*, Perth, 27 p.
- MICHENER, C.D., 1974, *The Social Behavior of Bees: The Belknap Press of Harvard University*, Cambridge, Massachusetts, 404 p.
- NEL, A., PERRAULT, G., PERRICHOT, V., and NERAUDEAU, D., 2004, The oldest ant in the Lower Cretaceous amber of Charente-Maritime (SW France)(Insecta: Hymenoptera: Formicidae): *Geologica Acta*, v. 2, p. 23–29.
- NOIROT, C., 1970, The nests of termites: in Krishna, K., and Weesner, F.M., eds., *Biology of Termites, Volume II: Academic Press*, New York, p. 73–126.
- NOIROT, C., 1977, Nest construction and phylogeny in termites: *Proceedings of the VIII International Congress of the International Union for Studies on Social Insects*, p. 177–180.
- RATCLIFFE, F.N., and GREAVES, T., 1940, The subterranean foraging galleries of *Coptotermes lacteus* (Frogg.): *Journal of the Council for Scientific and Industrial Research*, v. 13, p. 150–160.
- RETALLACK, G.J., 1990, *Soils of the Past: Unwin Hyman*, Boston, 520 p.
- RETALLACK, G.J., 2004, Late Oligocene bunch grassland and early Miocene sod grassland paleosols from central Oregon, USA: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 207, p. 203–237.
- RUELLE, J.F., 1964, L'architecture de nid de *Macrotermes natalensis* et son sens fonctionnel: in Bouillon, A., ed., *Etudes sur les Termites Africains: Lepoldville University, Leopoldville*, p. 327–362.
- SANDS, W.A., 1969, The association of termites and fungi: in Krishna, K., and Weesner, F.M., eds., *Biology of Termites, Volume 1: Academic Press*, New York, p. 495–524.
- SANDS, W.A., 1987, Ichnocoenoses of probable termite origin from Laetoli: in Leakey, D.M., and Harris, J.M., eds., *Laetoli, a Pliocene Site in Northern Tanzania: Oxford University Press*, Oxford, p. 409–433.
- SCHAEFER, C.E., 2001, Brazilian latosols and their B horizon as long-term biotic constructs: *Australian Journal of Soil Research*, v. 39, p. 909–926.
- SCHUSTER, M., DURINGER, P., NEL, A., BRUNET, M., VIGNAUD, P., and

- MACKAYE, H.T., 2000, Découverte de termitières fossiles dans les sites à Vertébrés du Pliocène tchadien: description, identification et implications paléocéologiques: *Comptes Rendus Académie des Sciences de Paris (Sciences de la Terre et des Planètes)*, v. 331, p. 15–20.
- STOOPS, G., 1964, Application of some pedological methods to the analysis of termite mounds: *in* Bouillon, A., ed., *Etudes sur les Termites Africains*: Lepoldville University, Leopoldville, p. 379–398.
- TAYLOR, T.N., and TAYLOR, E., 1993, *The Biology and Evolution of Fossil Plants*: Prentice Hall, New Jersey, 982 p.

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Reply

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“I know perfectly well that you will not at all agree with the lengths which I go. . . I may, of course, be egregiously wrong; but I cannot persuade myself that a theory which explains (as I think it certainly does) several large classes of facts, can be wholly wrong. . .” (Charles Darwin’s letter to L. Jenyns, 13/11/1859—Darwin, 1887)

We would like, first of all, to thank Genise et al. (2005) for the opportunity to elaborate on our work, to clarify their misperceptions of our work and motivate us to continue the search for a deeper understanding of continental ichnology. We also thank the editor for allowing us to advance and improve our research through this interaction. Even though we believe that theories develop through the stimulus of argument and counterargument, most of the criticism presented by Genise et al. (2005) is rejected for the reasons outlined below.

This correspondence originates from the fundamental conceptual difference between Genise et al. (2005) and the authors of this reply regarding the interpretations of the Tuli trace fossils as termite-made structures (Bordy et al., 2004). Genise et al. (2005) argue that a certain degree of correspondence with the fossil record must be present in order to recognize such complex traces as termitic in origin, and since the body fossils of termites have not yet been found in rocks older than Late Cretaceous, these Early Jurassic traces could not have been made by ter-

mites. Effectively, thus, Genise et al. (2005) deny the possibility that any pre-Late Cretaceous termite nests will be found and use their published viewpoint as an adequate-enough reason to deny the credibility of any alternative hypotheses and any data used to support such alternative ideas. Even when Genise et al. (2005) explicitly dismiss the temporal gap as a main criticism of our work, the issue of age permeates their comment several times.

First of all, this argument somewhat limits progress because it implies that all that was to be discovered in Earth’s rock record already has been done, and there is no possibility anywhere in the world to fill the age gap between these traces and their body fossils. In addition, many trace fossils are accepted as realistic paleontological occurrences in the absence of any known genetic body fossil. In our view, however, there can indeed be undiscovered fossils that could fill this gap—the long-overlooked Tuli trace fossils being an ideal example. By publishing our findings and putting forward challenging ideas with regard to the evolution of social insects, it is hoped that further research will be fostered which could indeed test the correctness of both the present hypotheses (i.e., Early versus Late Mesozoic origin of termites). Therefore the work by the authors of this reply is perceived as being in line with the desired “exploration of Triassic and Jurassic strata” as suggested by Martínez-Delclòs and Martinell (1995, p. 588), who also stated, *inter alia*, that “termite sociality evolved prior to the breakup of Gondwana” and possibly “before the Jurassic.” This Early Mesozoic origin of social insects (including ants) has been hypothesized by many researchers (Emerson, 1955; Bouillon, 1970; Emerson and Krishna, 1975; Carpenter and Burnham, 1985; Labandeira and Sepkoski, 1993; Hasiotis and Dubiel, 1995; Hasiotis, 1998, 2002, 2004; Eggleton, 2000). In addition, Wray et al. (1996) not only suggested a much earlier evolution of animal groups than that of their body-fossil record, but also discussed how molecular clocks (regarded by Genise et al. (2005) as objective measures) vary with time, and therefore cannot be taken as independent measures of geologic time.

Secondly, Genise and co-workers also suggest that temporal gaps of 25 million years are expected, but anything longer than that is dubious. Genise et al. (2005) fail to provide reasons and references for this arbitrary benchmark of 25 million years. To highlight the fallacy in Genise et al.’s (2005) argument, the reader is referred to recent developments in the recovery of crayfish body and trace fossils (Hasiotis and Mitchell, 1993; Hasiotis et al., 1994)—discoveries that extended the fossil record of crayfish by about 170 million years in North America and 100 million years in Eurasia. Interestingly, the description of the Triassic crayfish trace fossils predated the discovery of the Triassic crayfish body fossils, and thus the ichnological research can be perceived to have prompted the recovery of the previously unknown Triassic crayfish body fossils. Another example outside the canons of Genise et al.’s (2005) expected gap is a recent eutherian fossil discovery by Ji et al. (2002) that extends the eutherian record by about 40–50 Myr.

According to Kuhn (1970), reaching scientific consensus between two competing scientific theories is not possible unless participants adopt some values that in the process of persuasion can be shared. With regard to the complexi-

ties of trace fossils, it is suggested that these shared values should be the complexity criteria for social insect nests that were determined by Genise (2004), requiring a complex system of distinct tunnels, shafts, and galleries (e.g., burrows), as well as chambers, which are the larger cavities usually connected by the smaller burrows. Most certainly, these criteria are met in the case of the disputed Tuli traces since they are an assemblage of chambers of diverse sizes interconnected by an intricate burrow system of different diameters and orientations. This also clearly indicates that the Tuli trace fossils can be considered to have high morphological complexity, which probably resulted from the cooperative work of multiple individuals, and therefore the behavioral homology between the ancient trace makers and their modern counterparts (i.e., termites) easily could be inferred, unlike in the case of very simple trace-fossil morphologies (e.g., bird-like footprints; Melchor et al., 2002) where a higher degree of caution had to be exercised.

One of the major criticisms leveled by Genise et al. (2005) is that the descriptions in Bordy et al. (2004) are not detailed enough. Firstly, the intention was to provide information for the interested geoscientific community in the form of a holistic description and interpretation of the Tuli trace fossils, and therefore a detailed ichnotaxonomic analysis of these features was not provided. However, the importance of such endeavors is recognized, especially in light of the fact that since publication of this article in *PALAIOS*, several new sites and new forms of trace fossils have been discovered in the same Clarens Formation throughout southern Africa.

Moreover, when arguing about the importance of detailed descriptions, Genise et al. (2005) refer to work done by Machado (1983) and Sands (1987). It is perhaps of interest to note that, while the first work only includes detailed micromorphological analysis, and the latter contains only elaborations on macro-scale morphologies of some African trace fossils, Genise (2004) contests the termitic affinity suggested by the above authors as well. The same criticism, (i.e. the lack of detailed micromorphological analysis) also is directed by Genise (2004) at several other termite trace-fossil descriptions (e.g., Bown, 1984; Genise and Bown, 1994; Hasiotis and Dubiel, 1995; Genise, 1997), but the most criticized account is on the works done by Hasiotis and co-workers. Acknowledging the notion that quantity is not quality, the sheer number of peer-reviewed publications by Hasiotis and co-workers are at odds with Genise's (2004, p. 447) claims that "conclusions are based largely on poorly supported interpretations of Triassic and Jurassic trace fossils. . ." and are based on "inadequate documentation" (for a comprehensive reference list of this author, see Hasiotis, 2004). While it is not intended here to hold a brief for Hasiotis and co-workers, the fundamental differences are thus emphasized between our and Genise et al.'s (2005) viewpoints on what is considered a sound description and a plausible explanation regarding the origin of continental trace fossils.

Micromorphological studies (e.g., thin-section analysis under polarizing microscope, examination of polished slabs) were indeed undertaken on the Tuli trace fossil samples, but because of the very limited lithological differences between the burrows (i.e., passive burrow-fills) and host rock, these studies did not result in any outcomes

worthy of publication. On the other hand, it is important to recognize that in addition to its rather inconsistent nomenclature on macromorphological descriptions, the current ichnological literature essentially lacks a systematic approach (i.e., methodology) to the highly acclaimed micromorphological studies. This chaotic state of the "emerging ichnotaxonomic framework" (Genise, 2004, p. 444) is rather worrying, especially in light of the above-mentioned large number of southern African discoveries of Early Jurassic age, and it prompts us to wonder when the interested potential audience will be given a chance to hear about the outcomes if the recent mode of presentation is not permitted.

Paleoichnology is indeed a young discipline, and its laboratory—the contemporary environment—is well equipped but underutilized, which is manifested in the virtual lack of modern systematic and quantitative analyses of the internal and external architecture of recent termite nests. The scarcity of well-described modern analogues has hampered sound comparison of the disputed traces to modern nests. The literature in this regard was investigated very carefully, and is monitored on an ongoing basis; thus, it was noted with pleasure that somewhat relevant descriptions have been published recently (e.g., work by Uys, 2002 and Korb, 2003). It is hoped that this status quo will remain only until more modern traces are rigorously described both at micro- and macroscopic scales to allow sound comparisons between modern and ancient termite trace fossils.

Fossils of living organisms and the products of their activity (i.e., trace fossils), together with other geological phenomena, are incomplete in the rock record largely due to variable preservation potentials, and the missing parts are often deduced or even speculated upon. It is clear that levels of tolerance towards speculation vary from discipline to discipline, and is obviously higher in those that are mainly descriptive, historical subjects (e.g., paleoichnology) and in which many of the concepts and features would be difficult to describe quantitatively. While detailed descriptions (both for modern and ancient traces) are crucial, there always will be some limitations to the interpretations, and some will indeed be speculative.

In summary, three out of the four reliability criteria set by Genise et al. (2005) [i.e., (1) the complexity of the described trace fossils; (2) the methodology applied for their study; (3) the existence of a sound ichnotaxonomy; (4) the control by the body-fossil record] are partly acceptable. Firstly, criterion (1) is fulfilled in the case of the Tuli termites, which in our view were described in sufficient depth. Secondly, because of the status quo regarding micro- and macromorphological descriptions in paleoichnology (see Genise, 2004, p. 444), (2) cannot be met and this therefore invalidates (3) [(i.e., (3) cannot be carried out without (2)]. Finally, regarding criterion (4), it defies one of the basic principles of science, which requires all of us to look out for new findings, critically analyze them, and, if acceptable, modify previous views and concepts accordingly. Considering 4, it also seems that Genise et al. (2005) consider the fossil record as a frozen field that allows variation only if it occurs within an arbitrarily determined expected gap in the record of fossil organisms.

PALEOENVIRONMENT

It is rather unfortunate that Genise et al. (2005) misquoted and misinterpreted our previous work, by suggesting that descriptions of the locality of the disputed traces within the associated sedimentary structures are inconsistent. A direct quote regarding the occurrence of these structures within the Clarens Formation of the Tuli Basin is provided for the reader to judge whether there are inconsistencies: "Within the basal lithosomes, rare horizontal lamination (Sh) is observed in 0.2–1 m thick, lens-shaped sandstones alternating with also lens-shaped, massive sandstones. Very rarely, the massive beds contain scattered, angular silcrete fragments (Sc). Some of these basal beds are slightly coarser grained (fine to medium sand) than the majority of the Clarens Formation. These beds commonly display bioturbation features (see Palaeontological findings section). Wind ripple forms or ripple-foreset cross-lamination are not detected." (Bordy and Catuenanu, 2002, p. 307). In the "Paleontological findings" section of the same paper (p. 309), before the actual description of the disputed structures, it is clearly indicated "Several trace fossils are present in the lower and middle part of the Clarens Formation." It is important to point out the above-mentioned basal lithosomes (i.e., deposits of non-channelized, intermittent, rapid shallow flows in interdune areas, p. 308, 309) together with the channelized, ephemeral-stream deposits (p. 308) of the lower part of the formation were interpreted exclusively on sedimentological data (Bordy and Catuenanu, 2002). These independent sedimentological criteria, in conjunction with the paleontological evidence gathered from dinosaur footprints and the seasonal growth-rings of large petrified wood logs (i.e., relatively high biodiversity with definite vegetation present), led to the interpretation of a wetter phase within the overall sand-sea environment of the Clarens Formation. Bordy and Catuenanu (2002, p. 312) clearly spell out that these interpretations are independent from the ichnological findings (emphasis added herein): "Therefore the bioturbation features described are interpreted here as additional, *although indirect, evidence* of a wet aeolian system." It is hoped that this clarifies that there is no circular reasoning in our work, and that the disputed traces were not utilized to reconstruct a semi-arid environment, rather, other lines of evidence (e.g., sedimentary structures, tree rings) were used.

Genise et al. (2005) state that termites could not have occurred in semi-arid environments similar to those interpreted for the wet interlude(s) in the Clarens Formation. This is at odds with observations of a high abundance of termite nests in various semi-arid regions of present-day sub-Saharan Africa (Uys, 2002). In addition, similar trace fossils interpreted as termite nests were described and used, in conjunction with other climate indicators, as structures indicative of changing climatic (i.e., seasonally wet), as well as hydrologic conditions in an otherwise arid environment from the Upper Jurassic Morrison Formation (Hasiotis, 2004) and from the Late Pleistocene record of the Central Namib Desert (Smith et al., 1993). It is, however, a fact that Genise (2004) disregarded most of the work by above-mentioned authors, together with work by other South Africans who have described termites in early to middle Mesozoic units (i.e., Smith and Kitching, 1997).

Genise et al. (2005) also mention that termites could occur in seasonally inundated areas, which is in full agreement with our interpretations of the position of the disputed structures within the Clarens semi-arid environment.

INTERCONNECTING BIOTURBATED CYLINDERS

In this section, Genise et al. (2005) argue that horizontal cylinders in the Tuli traces are incomparable with any known termite galleries, yet highlight the fact that similar features are present in polycalic nests. Since the interpretation of these features was worded carefully to show that the described features are not identical but rather show resemblance to interconnecting galleries in polycalic nests ("tunnels *might* be explained in terms of polycalism;" emphasis added; Bordy et al., 2004, p. 74), the criticism presented in this section is dismissed. Considering the various sizes of nests present, investigating the idea presented by Fontes (1998; referenced in the Comment by Genise et al., 2005) is intriguing, because it is possible that the Tuli sites preserved not only several generations of nests, but also nests in different stages of development (i.e., ontogenetic stages of Hasiotis, 2002) in one locality. With regard to the large size difference of the preserved horizontal cylinders (average size 20 cm, not 20–30 cm as misquoted by Genise et al., 2005) and modern termite galleries, it is unclear why one needs to take the principle of uniformitarianism to such an extreme that even if overall characteristics of ancient and modern features are similar, their relationship would be rejected based on the lack of absolute identical characteristics. This seems to defy the principle of evolution, and ignores the most important dimension of any geological investigation—geologic time—which is a crucial factor allowing for nest-alteration processes such as paleo-weathering, taphonomy, pedogenesis, diagenesis, and the possibility of repeated reoccupation and modification by subsequent generations of termite colonies (Hasiotis, 2004).

ORIENTATION OF STRUCTURES

The "low consistency in nest orientation" (Bordy et al., 2004, p. 73) was meant to refer to Figure 5B only and not to Figure 5A, since the data are of low consistency only at Site 2. This was a typographical error, which in turn is clearly indicated by the consistency ratio of 0.80 measured for the Site 1 features. We thank Genise et al. (2005) for bringing this error to our attention, and hope that this correction will reinforce the striking similarity between the orientation data of these ancient features and those noted for some modern Australian termite nests. This shows that in some cases, orientation of the structures produced by termites is certainly diagnostic.

The buttresses shown in Figure 6A are not in contact, and the picture shows two nests set apart from each other by at least 1.5 m, with the two separate buttresses both tapering towards the north (towards the viewer). Buttresses do penetrate deeply into nests, which gave us the idea that they might have been used not only as windbreakers but also as support structures (hence the name).

The possible reason given by Genise et al. (2005) for the strong similarity in the orientation of the various features was considered, but it is not applicable. There are struc-

tural joints and dykes in the area, but their orientation is roughly ENE–SSW, and they have no effect on the described features except for intersecting them passively, thus showing that joint-formation and Early Jurassic dyke emplacement postdate the formation of the ichnological features.

TYPE 1 BURROWS

It is not possible to answer the question whether these networks are the result of random crossing of burrows made by solitary organisms or not. As Genise et al. (2005) point out, such complex-looking networks can be constructed by a multitude of solitary organisms, and perhaps this is why a truly complex network of burrows cannot be taken as an indicator of social behavior. We have not assumed so either, but rather presented other features from the same locality that collectively point to the explanation that these trace fossils are a result of eusocial activities. This approach is applied widely in sedimentology where individual sedimentary structures have limited value, but when used in association, they are powerful tools in reconstructing ancient sedimentary processes.

Genise et al. (2005) overlook the evidence of typical central structures of fungus-growing termite nests in the Tuli structures, even though larger cavities in the central part of the features (clearly shown in Figure 9A) are common, especially in the second pillar-type (see also the last sentence of the Major Pillar Types; Bordy et al., 2004, p. 71).

OTHER INTERNAL CHARACTERS

The interpretation of the type two burrows again was worded carefully to show that these features, which seem to be common in similarly-aged aeolian strata throughout southern Africa, are enigmatic, hence the tentative interpretation. Any suggestions for possible trace makers apart from ants would be highly appreciated.

The wall thicknesses given were average data (from a number of nests) collected mainly from smaller and better-exposed pillars. The taller pillars are invariably buttress-supported and the size of the pillar is proportional to that of the buttress associated with it. While it is possible that the tall pillars had thicker walls (now eroded away), it is suspected that they were not necessarily supported by the thicker walls, but rather by the buttresses. This would obviate the need for thicker external walls as presented by Genise et al. (2005). Perhaps such buttresses represent an earlier form of nest architecture; again, the unflinching application of uniformitarianism to the n^{th} degree by Genise et al. (2005) is questionable.

Regarding the building material of modern fungus-growing termites and that of the Tuli trace fossils, it is puzzling as to why such behavior should be deemed to have remained frozen for 200 million years. Similarities, including seeking out modern termites that utilize sand to build their nests, such as *Cortaritermes fulviceps*, which uses sand mixed with organic matter (L.R. Fontes, pers. comm., 2004) are important, but to match every single detail surely is impossible and is, in fact, rather questionable. With such astringent criteria, it is quite possible that one would find the geological record devoid of any termite fossil nest. To set the record straight, the massive facies

Sm in the Clarens Formation cannot be taken as “consistent with the proposed aeolian dune origin of the deposits” (Genise et al., 2005, p. 305), since this lithofacies has many possible interpretations, ranging from primary (e.g., rapid deposition from sediment-laden currents, several mass-movement processes) to secondary (e.g., original bedding disruption by rain splash and subsequent liquefaction; complete bioturbation) processes.

CO-EVOLUTIONARY ASPECTS

Macrotermitinae has never been proposed as possible producers of the Tuli structures. However, it has been said that based on close resemblance to modern nests and discussions with entomologists, the Tuli structures resemble constructions by modern fungus-growing termites. It is unfortunate that Genise et al. (2005) suggest that we went as far as to identify 200-million-year-old trace makers at the subfamily level. That level of precision was not claimed in the paper. Supposedly, because the only modern termites with elaborate nests and fungus-growing habit are the *Macrotermitinae*, a connection was implied unintentionally. It is clear, however, based on current phylogenetic evidence that the more recently evolved *Macrotermitinae* are unlikely to have originated in pre-Cretaceous times even though they are now placed in a basal position within so-called higher termites (Kambhampati and Eggleton, 2000; P. Eggleton, D. Bignell, pers. comm., 2005), therefore, the Tuli structures could not have been made by them. If fungus growing truly is a character of termites that appeared only one time (i.e., in *Macrotermitinae*) in the evolution of termites, then the Tuli structures were not made by fungus-growing termite taxa. This does not eliminate termites as possible trace-makers, however, because elaborate nest building is not exclusive to *Macrotermitinae*, but is common, for instance, in the more ancient *Hodotermitidae* (one of the earliest branching termite families; P. Eggleton, pers. comm., 2005) as well. It is perhaps interesting to note here that similarities between some of the more recently discovered southern African trace fossils and nests of the modern South African *Hodotermitidae* (Uys, 2002) are rather prominent.

CONCLUSIONS

Consideration of the Tuli trace fossils as root traces was ruled out originally in Bordy (2000), and repeated in Bordy and Catuneanu (2002, p. 311). These reports also concluded (undeniably on few, but relevant observations) that the traces were made by termites, and the Bordy et al. (2004) paper was meant to gather further information and present a better case for this hypothesis.

Genise et al. (2005, p. 306) state, “It seems that Tuli structures have never been found included in the overlying deposit, but always as emergent structures from exposed rocks.” The photographs clearly show that the traces and host rocks are identical. Indeed, a number of these structures are half-emergent and some are still engulfed within the rock (often clearly visible in cliffs). Therefore, there is no reason whatsoever to suspect that these features are not contemporaneous with the host Lower Jurassic Clarens Formation. In this section, it is notable that Genise et al. (2005) seem to consider the Tuli structures to

have been made by termites provided they are on, and not in, the ancient rocks of the Clarens Formation.

It is hoped that many of the concerns aired by Genise et al. (2005) already have been addressed in Bordy and Catuneanu (2002) and Bordy et al. (2004), as well as being clarified in this reply. In the light of the fact that Genise et al. (2005) fail to propose a plausible alternative explanation for the disputed features, and in the absence of any other possible group of organisms as potential trace makers, our original proposal is not modified: the Tuli trace fossils, with their very complex morphologies, which, in many cases strongly resemble modern termite structures, were products of either some unknown eusocial organisms, or species of ancient termites now extinct.

REFERENCES

- BORDY, E.M., BUMBY, A.J., CATUNEANU, O., and ERIKSSON, P.G., 2004, Advanced early Jurassic termite (Insecta: Isoptera) nests: evidence from the Clarens Formation in the Tuli Basin, Southern Africa: *PALAIOS*, v. 19, p. 68–78.
- BORDY, E.M., and CATUNEANU, O., 2002, Sedimentology and paleontology of upper Karoo aeolian strata (Early Jurassic) in the Tuli Basin, South Africa: *Journal of African Earth Sciences*, v. 35, p. 301–314.
- BOULLION, A., 1970, Termites of the Ethiopian region: in Krishna, K., and Weesner, F.M., eds., *Biology of Termites*, Vol. 2: Academic Press, New York, p. 154–279.
- CARPENTER, F.M., and BURNHAM, L., 1985, The geological record of insects: *Annual Review of Earth and Planetary Sciences*, v. 13, p. 297–314.
- DARWIN, F., ed., 1887, *The Life and Letters of Charles Darwin: Vol. II*: John Murray, London, p. 348.
- EGGLETON, P., 2000, Global patterns of termite diversity: in Abe, T., Bignell, D.E., and Higashi, M., eds., *Termites: Evolution, Sociality, Symbioses, Ecology*: Kluwer Academic Publishers, Dordrecht, p. 25–51.
- EMERSON, A.E., 1955, Geographic origins and dispersions of termite genera: *Fieldiana Zoology*, v. 37, p. 465–521.
- EMERSON, A.E., and KRISHNA, K., 1975, The termite family Serritermitidae (Isoptera): *American Museum Novitates*, v. 2570, p. 1–31.
- GENISE, J.F., 2004, Ichnotaxonomy and ichnostratigraphy of chambered trace fossils in palaeosols attributed to coleopterans, termites and ants: *Special Publications of the Geological Society of London*, v. 228, p. 419–453.
- GENISE, J.F., BELLOSI, E.S., and GONZALEZ, M.G., 2004, An approach to the description and interpretation of ichnofabrics in palaeosols: *Special Publications of the Geological Society of London*, v. 228, p. 355–382.
- GENISE, J.F., BELLOSI, E.S., MELCHOR, R.M., and 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*, v. 20, p. 303–308.
- HASIOTIS, S.T., 1998, Continental trace fossils as the key to understanding Jurassic terrestrial and freshwater ecosystems: *Modern Geology*, v. 22, p. 451–459.
- HASIOTIS, S.T., 2002, Complex ichnofossils of solitary and social soil organisms: understanding their evolution and roles in terrestrial paleoecosystems: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 192, p. 259–320.
- HASIOTIS, S.T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain region, USA: environmental, stratigraphic, and climatic significance of terrestrial and freshwater ichnocoenoses: *Sedimentary Geology*, v. 167, p. 277–368.
- HASIOTIS, S.T., and DUBIEL, R.F., 1995, Termite (Insecta: Isoptera) nest ichnofossils from the Triassic Chinle Formation, Petrified Forest National Park, Arizona: *Ichnos*, v. 4, p. 119–130.
- Ji, Q., LUO, Z.-X., YUAN, C.-X., WIBLE, J.R., ZHANG, J.-P., and GEORGI, J.A., 2002, The earliest known eutherian mammal: *Nature*, v. 416, p. 816–822.
- KAMBHAMPATI, S., and EGGLETON, P., 2000, Taxonomy and phylogeny of termites: in Abe, T., Bignell, D.E., and Higashi, M., eds., *Termites: Evolution, Sociality, Symbioses, Ecology*: Kluwer Academic Publishers, Dordrecht, p. 1–24.
- KORB, J., 2003, Thermoregulation and ventilation of termite mounds: *Naturwissenschaften*, v. 90, p. 212–219.
- KUHN, T.S., 1970, *The Structure of Scientific Revolutions*, Second Edition: The University of Chicago Press, Chicago, 210 p.
- LABANDEIRA, C.C., and SEPKOSKI, J.J., JR., 1993, Insect diversity in the fossil record: *Science*, v. 261, p. 310–315.
- MACHADO, A. DE B., 1983, The contribution of termites to the formation of laterites: in Melfi, A.J., and Carvalho, A., eds., *Proceedings of the II Seminar on Lateritisation Process*, Sao Paulo, University de Sao Paulo, p. 261–270.
- MELCHOR, R.N., DE VALAIS, S. and GENISE, J.F., 2002, Bird-like fossil footprints from the Late Triassic: *Nature*, v. 417, p. 936–938.
- SANDS, W.A., 1987, Ichnocoenoses of probable termite origin from Laetoli: in Leakey, D.M., and Harris, J.M., eds., *Laetoli, a Pliocene Site in Northern Tanzania*: Oxford University Press, Oxford, p. 409–433.
- SMITH, R.M.H., and KITCHING, J., 1997, Sedimentology and vertebrate taphonomy of the Tritylodon Acme Zone: a reworked palaeosol in the Lower Jurassic Elliot Formation, Karoo Supergroup, South Africa: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 131, p. 29–50.
- SMITH, R.M.H., MASON T.R., and WARD, J.D., 1993, Flash-flood sediments and ichnofacies of the Late Pleistocene Homeb Silts, Kuiseb River, Namibia: *Sedimentary Geology*, v. 85, p. 579–599.
- UYS, V., 2002, A guide to the termite genera of southern Africa: Pretoria, Plant Protection Research Institute Handbook 15, 116 p.
- WRAY, G.A., LEVINTON, J.S., and SHAPIRO, L.H., 1996, Molecular evidence for deep Precambrian divergences among metazoan phyla: *Science*, v. 274, p. 568–573.

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