

## DIFFUSE TERMITINAE NESTS SHED LIGHT ON THE AFFINITIES OF *LAETOLICHNUS KWEKAI* (KRAUSICHNIDAE)

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**ABSTRACT:** The insect trace fossil *Laetolichnus kwekai*, which is composed of a small chamber extending to slender cylinders at each end, was tentatively included in the ichnofamily Krausichnidae as termite nests. New evidence presented here provides information to validate these inferences. A more complex structure formed by interconnected *Laetolichnus* was recently found in the same Pliocene deposits (Laetoli, Tanzania) as the isolated specimens reported previously. Our study confirms inclusion of *Laetolichnus* in Krausichnidae and supports the inference that it represents a nest of a social insect. Neiochnological field studies in the coastal dunes of Buenos Aires Province, Argentina, were undertaken to refine further the nature of these affinities. Survey of the dune surface revealed abundant loose fragments of termite nests of a size and shape comparable to that of *L. kwekai*. The fragile nests constructed by *Onkotermes brevicorniger*, which are described here in detail for the first time, enable us to interpret the fossil structures. They consist of connected chambers similar to the interconnected *Laetolichnus*. These were frequently exposed and broken by wind action resulting in loose fragments similar to the isolated *Laetolichnus*. The *Celliforma* ichnofacies represented at Laetoli, which contains *L. kwekai*, indicates arid or semiarid shrublands and woodlands. The distribution of *O. brevicorniger* also corresponds to arid and semiarid shrublands and dry woodlands of Argentina. Although the African termite producer of *L. kwekai* and the South American *Onkotermes* would be phylogenetically unrelated, the analogous structures probably reflect convergent nesting behaviors as an adaptation to similar arid to semiarid environmental conditions.

### INTRODUCTION

*Laetolichnus kwekai* is an insect trace fossil described recently from the Upper Laetoli Beds at Laetoli, Tanzania (Genise and Harrison 2018). This unit, dated to 3.6–3.85 Ma (Deino 2011), also yields fossil plants, invertebrates, vertebrates such as the hominin *Australopithecus afarensis*, and trace fossils attributed to bees, beetles, and termites (Sands 1987; Darlington 2005, 2011; Harrison 2011a, 2011b, 2011c; Genise and Harrison 2018). *Laetolichnus kwekai*, as originally described, is composed of a small empty chamber with a straight, curved, sinuous, V-shaped, single-lobed, bilobate, multilobate, or subtriangular outline. The extremes of these chambers extend into slender cylinders that are usually aligned with the longest axis. In one specimen (EP 537/98), the distal part of one of the cylinders ends in an expansion, which was interpreted to be the remnant of an adjoining chamber (Genise and Harrison 2018, fig. 8C). On the basis that the specimens would have been originally connected to form a more complex structure, *L. kwekai* was included in the ichnofamily Krausichnidae and tentatively attributed to termite nests (Genise and Harrison 2018). However, its affinities have been unclear until now.

Here we describe small and fragile termite nests of *Onkotermes brevicorniger* (Silvestri 1901) (Isoptera: Termitidae: Termitinae). They were studied in the coastal dunes of the Reserva Natural Faro Querandí (37°24'36''S, 57°04'33''W), Buenos Aires Province, Argentina (Fig. 1A,

1B). Some authors have reported that *Onkotermes* constructs diffuse subterranean nests (Constantino et al. 2002; Cuzzo 2005; Torales and Fontes 2008), but otherwise the nest structure is unknown. A detailed description of the nests of *O. brevicorniger*, as well as new material of *Laetolichnus* recently collected at Laetoli, are presented here for the first time. This new evidence enables us to reinterpret *L. kwekai* and refine the identification of its producer and its ethological and paleoecological implications.

### RESULTS

#### *The Nest Structure of Onkotermes brevicorniger*

The epigeous part of the nests consist of 33 chimneys that emerge from the sand at an angle of up to 45° without any particular orientation with respect to either north or the direction of the prevailing wind (Fig. 1C, arrows). The chimneys have circular cross-sections, 3.6±1.2 mm in diameter ( $n = 23$ ), or elliptical ones, 3.9±1.1 mm wide and 2.9±0.7 mm high ( $n = 10$ ), and most have an open entrance ( $n = 30$ ) (Fig. 1D, 1E). The hypogeous part of the nests consist of a main long and horizontally oriented tunnel up to 29 cm long ( $n = 6$ ), which is located in the dry sand 7–9 cm below the surface (Fig. 2). This main tunnel is composed of expanded segments (chambers) with elliptical cross-sections, and cylindrical connectors (Fig. 2A). The chambers are 6.9–14.7 mm wide ( $n = 12$ ,

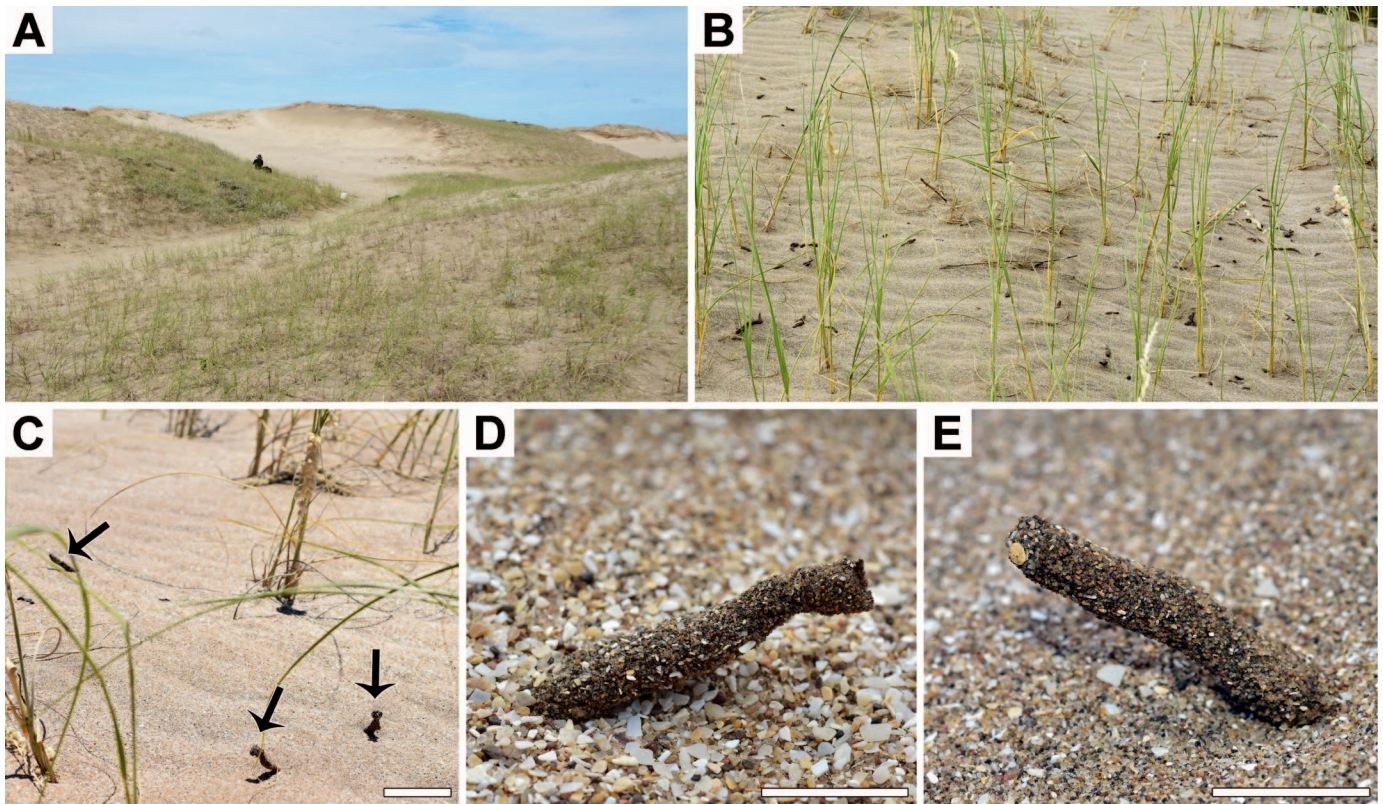


FIG. 1.—Environment and epigeous part of the nests of *O. brevicorniger* found in the Reserva Natural Faro Querandí (Buenos Aires Province, Argentina). **A**) Nesting site. **B**) Numerous loose fragments of nests found on the surface of the dunes. **C**) Epigeous chimneys without any particular orientation with respect to either north or the direction of the prevailing wind (arrows). Scale = 20 mm. **D**) Chimney with an open entrance. Scale = 10 mm. **E**) Chimney with a closed entrance. Scale = 10 mm.

3.8–4.8 mm high ( $n = 5$ ), and 19.8–54.9 mm long ( $n = 12$ ), and the connectors are 4.2–6 mm in diameter ( $n = 6$ ). Several branches extend from the main tunnel in all directions forming a boxwork (Fig. 2B–2E). Inclined branches slope upwards and usually end in the epigeous chimneys (Fig. 2B, 2C, white arrows). These branches also consist of chambers and connectors (Fig. 2E). The chambers have circular cross-sections,  $7.9 \pm 1.6$  mm in diameter and 16.8–29.6 mm long ( $n = 3$ ), or elliptical ones,  $9.6 \pm 3.1$  mm wide ( $n = 9$ ),  $6.3 \pm 2.3$  mm high ( $n = 6$ ), and 15.6–37.6 mm long ( $n = 8$ ). The connectors have circular or elliptical cross-sections,  $5.3 \pm 2.6$  mm in diameter ( $n = 30$ ), and  $7.7 \pm 1.6$  mm wide and  $5 \pm 1.1$  mm high ( $n = 5$ ), respectively. Additionally, the main tunnel shows vertically oriented cylindrical branches,  $5.3 \pm 0.6$  mm in diameter ( $n = 4$ ), penetrating 2–3 cm downwards into the wet sand located approximately 10 cm below the surface (Fig. 2D). At 9–10 cm below the surface, at the level of the dry-wet sand boundary, isolated chambers accessible through narrow individual passages with abundant termites are found (Fig. 2F). The chambers are 10.1–20 mm wide, 5.9–9.8 mm high, 21.6–31.2 mm long ( $n = 4$ ), and their individual passages are 1–1.7 mm in diameter ( $n = 4$ ). The connection of these isolated chambers to the rest of the nest cannot be traced due to the fragility and small size of the passages. Some branches are attached to dry buried grasses of *Distichlis spicata* (Poaceae) (Fig. 2B, black arrows). The termites build the entire nest using sand grains, pieces of bivalve shell, and feces as mortar (Fig. 3A–3D). The internal surface of burrows and chambers has a dark lining of fecal matter (Fig. 3E, white arrow). Workers and secondary reproductives are present in the main tunnel, the branches, and the isolated chambers; whereas alates are found only in the main tunnel and the branches due to the small size of the passages that connect the isolated chambers (Figs. 2F, 3). Neither the royal couple nor a structure resembling a royal chamber is found.

The nests of *O. brevicorniger* are so fragile that isolated fragments, probably exposed and broken by wind action, are usually found on the surface of the dunes (Fig. 1B). Some consist of a single chamber with limited remains of the connectors at both extremes. Based on their outlines, the isolated fragments are classified into: (1) straight fragments ( $n = 17$ ); (2) curved fragments ( $n = 5$ ); (3) V-shaped fragments ( $n = 5$ ); (4) single-lobed fragments with one end rounded and the other tapered ( $n = 5$ ); (5) bilobate fragments ( $n = 6$ ); and (6) subtriangular fragments ( $n = 3$ ) (Fig. 4A–4H). These fragments are 4.5–11.3 mm wide ( $n = 41$ ), 3–6.6 mm high ( $n = 35$ ), 14–41 mm long ( $n = 40$ ), and show a wall 0.4–1.1 mm thick ( $n = 26$ ).

The collected material ( $n = 106$ ), hardened with transparent matte spray varnish is deposited in the Colección Nacional de Icnología of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Autonomous City of Buenos Aires, Argentina). The collection of termites is deposited in the Colección de Entomología of the Museo Municipal de Ciencias Naturales “Lorenzo Scaglia” (Mar del Plata, Buenos Aires Province, Argentina).

#### Interconnected *Laetolichnus kwekai*

All previously described specimens were found as loose individual chambers that had varied outlines (Genise and Harrison 2018, fig. 8) (Fig. 4I–4P). Recently, four *L. kwekai* connected by their distal cylinders to form a chain, were found in a vertical section of a paleosol between Tuffs 6 and 7 in the Upper Laetolil Beds at Locality 8 ( $3^{\circ}13'33''$  S,  $35^{\circ}11'13''$  E), Laetoli, Tanzania (Fig. 5). The age of the fossil-bearing horizon is 3.66–3.7 Ma (Deino 2011). The entire structure is 72.1 mm long, and the straight chambers are (from top to bottom): 14.8 mm, 19.3 mm, 17.9 mm, and 20.1 mm long, and 4.5 mm, 5.4 mm, 6.2 mm and 5.3 mm in height. The



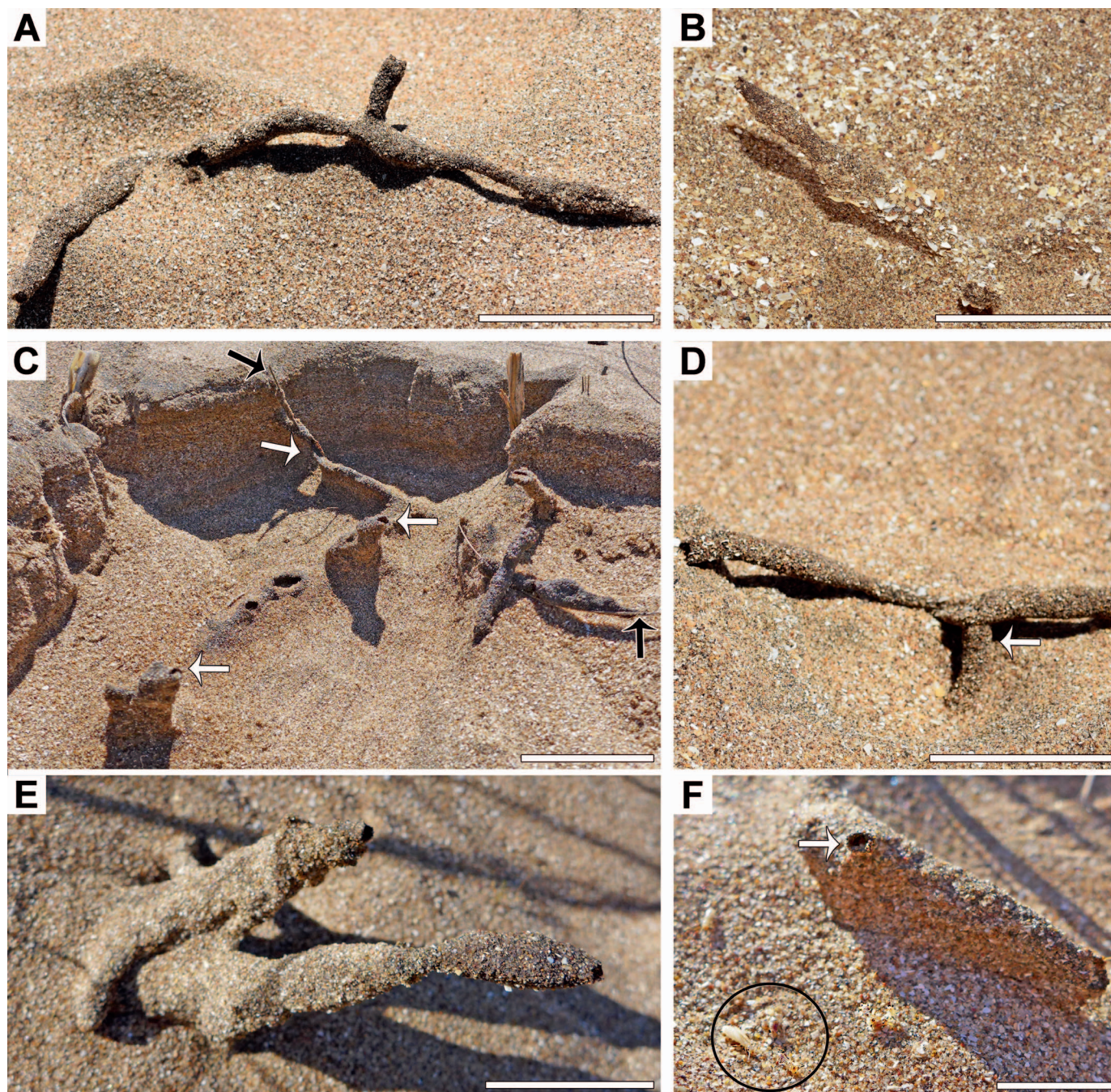


FIG. 2.—Hypogeous part of the nests of *O. brevicorniger*. **A**) A main long and horizontally oriented tunnel, composed of interconnected chambers, exposed by wind action. Scale = 5 cm. **B**) Inclined branch that ends in an epigeal chimney. Scale = 3 cm. **C**) The most complete nest showing the inclined branches (white arrows) and the branches attached to buried grass (black arrows) that extended from the main tunnel in different directions. Scale = 5 cm. **D**) A vertically oriented cylindrical branch (arrow) descending into the wet sand. Scale = 3 cm. **E**) Inclined branches showing chambers and connectors. Scale = 3 cm. **F**) An isolated chamber with numerous termites (circle) and individual passages (arrow) found at the level of the dry-wet sand boundary. Scale = 1 cm.

specimen (EP 2104/19) is deposited in the National Museum of Tanzania in Dar es Salaam.

#### DISCUSSION

The insect trace fossils included in the ichnofamily Krausichnidae are systems of interconnected chambers occurring in paleosols (Genise 2004). They are represented by 17 ichnogenera, all considered as complete or

partial nests constructed by ants or termites (Genise 2016; Genise and Harrison 2018). The newest ichnogenera *Laetolichnus*, known from fragmentary material, was tentatively included in this ichnofamily (Genise and Harrison 2018). Several possibilities were originally considered: pieces of rhizoliths preserving part of a concretion, termite galleries or oothecae surrounding twigs, and chambers of root-sucking insects constructed around roots (Genise and Harrison 2018). These hypotheses were discounted because the terminal cylinders of *Laetolichnus* do not continue



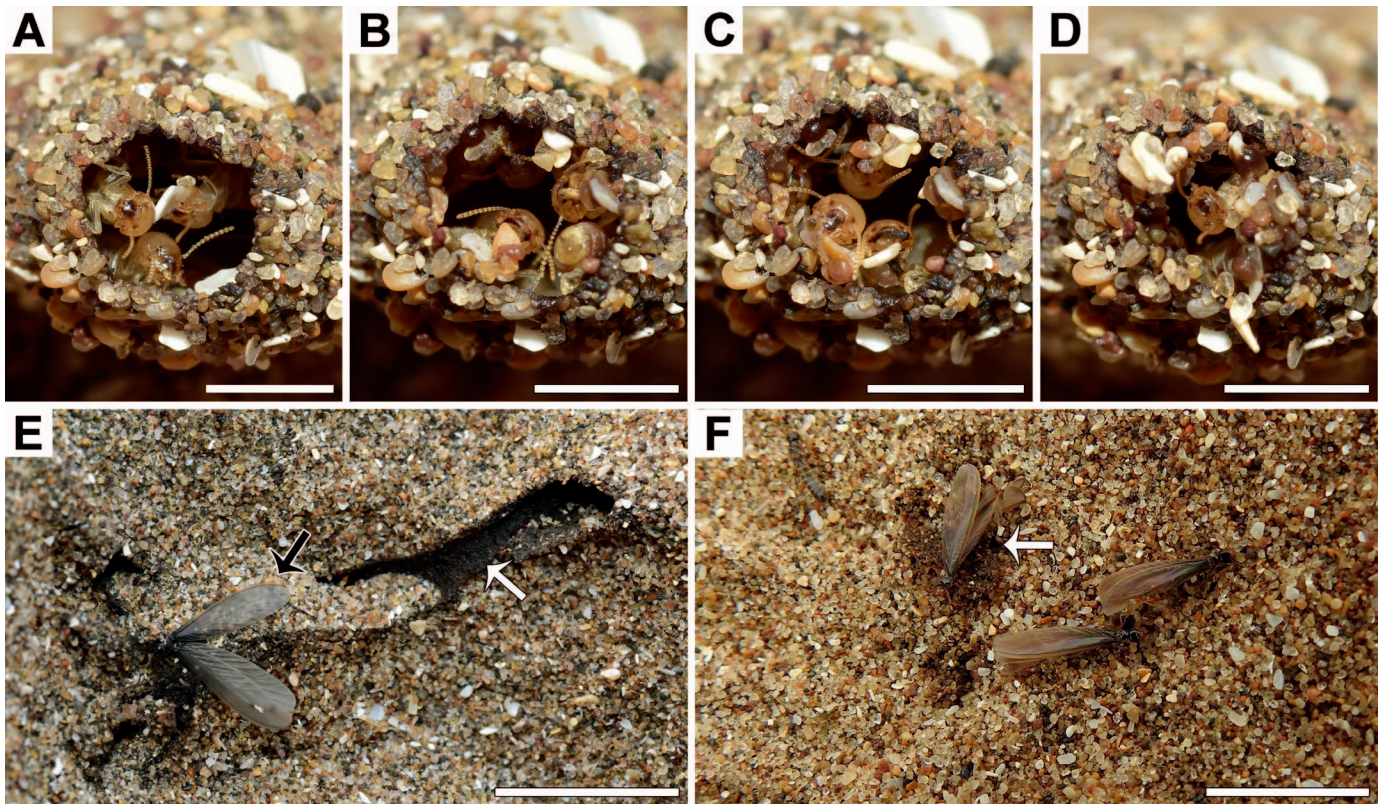


FIG. 3.—Composition of the nests of *O. brevicorniger*. A–D) Workers completing chimneys using sand grains, pieces of bivalve shell, and feces. All scales = 3 mm. E) The internal surface of a branch showing a dark lining of fecal matter (white arrow). Note the alate (black arrow). Scale = 10 mm. F) Alates that emerged from a wide hole, which is partially covered here (arrow). Scale = 10 mm.

inside the structure, thus ruling out their being roots and twigs. The presence in one specimen of a small remnant of a second adjoining chamber connected by a cylinder (Fig. 4K, arrow) suggested that the original structure was probably composed of several chambers with cylindrical connections. This led to the conclusion that *Laetolichnus* belonged to Krausichnidae and was probably constructed by termites (Genise and Harrison 2018). However, until now there has been no definitive evidence of this interconnection in the fossil record and no modern analogue structure to compare it with.

Although *L. kwekai* was originally compared with the storage pits in the foraging galleries of the nests of *Macrotermes michaelseni* (Genise and Harrison 2018), the morphology of these structures is significantly different. These storage pits, which serve to temporarily store grass pieces, are elongated depressions located along one or both sides of a flat and raised central passage floor on which the termites travel (Darlington 1982, fig. 3A). The storage pits of *M. michaelseni* are similar to those of *Baucaliotermes hainesi*, another African harvester termite (Tschinkel 2010, figs. 3, 5). In both species, the presence of the storage pits is revealed externally by the occurrence of nodular structures at the bottom of the foraging galleries (Darlington 1982, fig. 3D; Tschinkel 2010, figs. 4, 6).

The new evidence from Laetoli (Fig. 5) indicates that the described *Laetolichnus* were originally part of a larger structure formed by interconnected chambers. This provides the missing data needed to confirm that this trace fossil belongs to Krausichnidae, and provides a more complete knowledge of its morphology.

Field research at the coastal dunes of Buenos Aires Province, Argentina, provided evidence to identify the producer of *L. kwekai* and to make paleoenvironmental inferences. The survey of the dune surface showed small loose structures, mostly composed of sand grains, which were

comparable in size and shape with the isolated specimens of *L. kwekai*. Most of the categories of shape observed in *L. kwekai* were represented among these structures (Genise and Harrison 2018, fig. 8) (Fig. 4). In addition, its usual occurrence as *ex situ* fragmented structures was also compatible with *L. kwekai*. These *ex situ* surface structures were originally part of subterranean termite nests that were uncovered and fragmented by weathering.

The producer of these nests was *O. brevicorniger*, which is the southernmost termite species of South America and recorded here for the first time in Buenos Aires Province, Argentina (Constantino et al. 2002; Torales et al. 2005; Torales and Fontes 2008). An earlier study noted that *O. brevicorniger* constructed chambers interconnected by galleries (Constantino et al. 2002), but the nest structure has not been described or illustrated previously. The nests studied were composed of a main long and horizontally oriented tunnel located in the dry sand at 7–9 cm below the surface, which consisted of chambers and connectors. Several branches extended from the main tunnel in all directions: (1) inclined branches sloping upwards, which also consisted of interconnected chambers and usually ended in the epigeous chimneys, and (2) vertically oriented cylindrical branches extending deeply into the wet sand (Figs. 1, 2). In addition, isolated chambers were found at the boundary between the dry and wet sand. We postulate that the more complete nests of *L. kwekai* might show a similar structure.

The study of the nests of *O. brevicorniger* provides ethological evidence that could apply to the producer of *L. kwekai*. *Onkotermes brevicorniger* has been recorded previously inside and under herbivorous dung, in wood, and under rocks (Constantino et al. 2002; Cuzzo 2005; Torales et al. 2005). We also found this species under building remains, in an anthropic environment located 1000 meters from the dunes where they were studied.



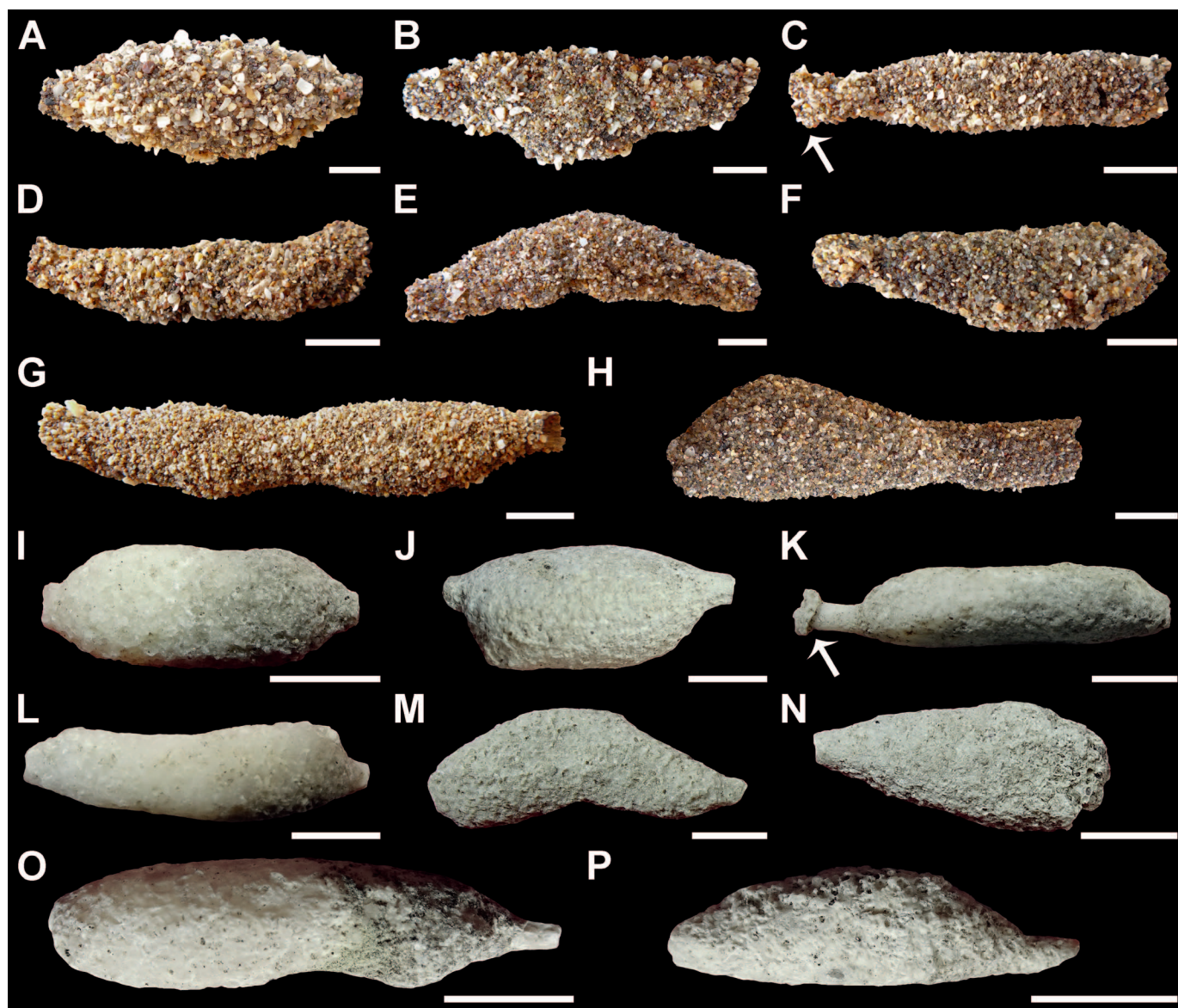


FIG. 4.—Morphological similarities between the isolated fragments of *O. brevicorniger* nests and *L. kwekai*. A–C) Straight fragments. A distal end of the fragment C with part of the adjacent chamber (arrow). D) Curved fragment. E) V-shaped fragment. F) Single lobed fragment with one end rounded and the other tapered. G) Bilobate fragment. H) Subtriangular fragment. I–K) Straight *Laetolichnus*, EP 2708c/00 (part), EP 2776a/00, and EP 537/98, respectively. Note that the distal end of K shows a similar expansion as in C (arrow). L) Curved *Laetolichnus*, EP 2708c/00. M) V-shaped *Laetolichnus*, LAET 1974–1982 (part). N) Single lobed *Laetolichnus* with one end rounded and the other tapered, LAET 1974–1982 (part). O) Bilobate *Laetolichnus*, EP 167b/00. P) Subtriangular *Laetolichnus*, LAET 1974–1982 (part). All scales = 5 mm.

Some parts of the studied nests were attached to buried grass (Fig. 2B, black arrows), suggesting that *O. brevicorniger* use the latter as food. Soil and wood have also been mentioned as food sources (Torales et al. 2009), but neither of these was available in the dunes. Grasses were the only food source, at least near the surface where the nests were situated. The small size of the colonies supports the hypothesis that these termites would not need abundant food resources, other than grasses, to survive. The same may apply to the small-sized *Laetolichnus*: small colonies feeding on limited food sources at the surface or in shallow nests just below the soil surface. The alates of *O. brevicorniger*, unknown until now, were present in December, a few days before the beginning of summer in the southern hemisphere (Fig. 3E, 3F). The open epigeous chimneys in the nests (Fig. 1D) could represent elevated takeoff runways for the dispersal flight of the alates to avoid possible complications arising due to sand slippage during

takeoff. However, some alates were also observed on one occasion emerging from a wide hole in the sand (Fig. 3F, arrow). These chimneys could also act as ventilation systems, although such structures are usually vertical and part of complex nests (Noirot and Darlington 2000). However, these small and shallow nests may not require additional ventilation mechanisms because of gas exchange through their porous structures and their proximity to the surface. The function of these chimneys is uncertain because they seem to be neither takeoff ramps for the alates nor ventilation structures. The isolated chambers located in the dry-wet sand boundary have narrow individual passages that match the small size of workers and secondary reproductives (Fig. 2F, arrow and circle) but would not allow the passage of alates.

Given the morphological similarities between the interconnected chambers of *L. kwekai* and the nests of *Onkotermes*, plus the common



FIG. 5.—Four interconnected *L. kwekai* found *in situ* at Locality 8, Laetoli, Tanzania, EP 2104/19. Scale = 15 mm.

occurrence of both as fragmentary structures *ex situ* on the soil surface, we propose that the behavior of the producer of *L. kwekai* would have been similar to that of *O. brevicorniger*, and that the latter's nests would represent the complete systems from which specimens of *Laetolichnus* were derived. *Onkotermes*, which only includes two endemic species in Argentina, is a distinct genus that could not be placed within any of the African Termitinae (Torales and Fontes 2008; Rocha et al. 2019). Therefore, *Onkotermes* and the termites that produced *Laetolichnus* would not be phylogenetically related. Thus, *Onkotermes* would not be a modern homologue but a behaviorally convergent analogue of the producer of *Laetolichnus*.

The ichnoassemblage of the Upper Laetolil Beds comprises mainly bee cells (i.e., *Celliforma ritchiei*, *C. spirifer*, *C. germanica*, *C. curvata*) and the pupation chambers of beetles (i.e., *Fictovichnus gobiensis*), typical representatives of the *Celliforma* ichnofacies (Genise 2016; Genise and Harrison 2018). Termite trace fossils, such as *Vondrichnus* and *Laetolichnus*, can be added to the list of ichnogenera comprising this ichnofacies based on the Laetoli ichnoassemblage (Genise and Harrison 2018). The development of the *Celliforma* ichnofacies in the Upper Laetolil Beds indicates that the producer of *L. kwekai* nested in shrublands and open woodlands with poor grass cover, under arid to semiarid conditions. Likewise, *O. brevicorniger* is largely distributed in Argentinian arid to semiarid shrublands and dry woodlands (Torales and Fontes 2008). Despite belonging to phylogenetically unrelated groups, the occurrence of both *Onkotermes* and the producer of *L. kwekai* in arid to semiarid environments probably necessitated similar behavioral responses, which are reflected in the structure of their nests.

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