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WALKING ON ASHES: INSECT TRACE FOSSILS FROM LAETOLI INDICATE POOR GRASS COVER ASSOCIATED WITH EARLY HOMININ ENVIRONMENTS

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Abstract: More than 4000 insect trace fossils collected in recent years from Pliocene deposits at Laetoli in northern Tanzania provide new insights on early hominin palaeoenvironments. These trace fossils include: *Fictovichnus gobiensis*, *Coprinisphaera murguiai*, *C. kheprii*, *Coprinisphaera* ispp., *Quirogaichnus* isp., *Teisseirei linguatus* isp. nov., *Celliforma ritchiei* isp. nov., *C. spirifer*, *C. germanica*, *C.* cfr. *curvata*, *Celliforma* ispp., *Rosellichnus* isp., *Vondrichnus planoglobus*, *Laetolichnus kwekai* igen. et isp. nov. and Krausichnidae indet. They reveal that at least one species of moth, three dung beetles and five other coleopterans, nine taxa of solitary bees, and an indeterminate number of taxa of termites inhabited the Lower Laetolil environments. The Upper Laetolil environments, which have yielded a rich diversity of vertebrate fossils, including the early hominin *Australopithecus afarensis* and its putative footprints, supported several taxa of termites, one dung beetle, five other coleopterans, and eleven taxa of bees. The Upper Ndolanya environments, which have yielded the hominin *Paranthropus aethiopicus*, record four taxa of dung beetles, four other coleopterans, and two taxa of bees. The record of larval mortality and lack of intruder activity, revealed by the absence of emergence and intruder traces, may be associated with the anoxic/hypoxic conditions caused by the instantaneous burial of soils under thick volcanic ashes. The record of the *Celliforma* Ichnofacies in the Upper Laetolil environments indicates the dominance of shrubland to woodland with limited grass cover. This is supported also by the absence of *Coprinisphaera*, which suggests a scarcity of fresh grasses and a low abundance of large mammal grazers.

Key words: insect trace fossils, Laetoli, early hominin environments, grass cover, *Celliforma* Ichnofacies.

THE study of insect trace fossils in palaeosols has experienced a profound development in recent years. More than 70 ichnotaxa, 5 ichnofamilies and 5 palaeosol ichnofacies have been recognized, dramatically improving the palaeoenvironmental analyses that can be accomplished with these trace fossils (Genise 2016). Insect trace fossils have long been used to interpret the palaeoenvironmental context at palaeontological localities in Africa related to anthropoid primate evolution, including at Laetoli (Kitching 1980; Bown 1982; Sands 1987; Ritchie 1987; Thackray 1994; Genise & Bown 1994*a*; Retallack *et al.* 1995; Duringer *et al.* 2000, 2006, 2007; Darlington 2005, 2011; Krell & Schawaller 2011; Hopley *et al.* 2013; Genise 2016; Parker *et al.* 2016). With the rapid advancements in ichnoentomology, palaeoenvironmental inferences derived from insect trace fossils require continual updating and refinement.

Recent extensive collections of insect trace fossils at Laetoli and other localities on the Eyasi Plateau in northern Tanzania (1998–2016) by one of us (TH) have resulted in the recovery of thousands of new specimens housed in the National Museum of Tanzania, Dar es Salaam, along with material previously collected by Mary Leakey (1959, 1974–1982). Specimens with the prefix EP are from the Harrison collection and those with the prefixes LAET, LIT and KK are from the Leakey collection (Genise & Harrison 2018). Specimens from the Manonga Valley in central Tanzania with the prefix WM were collected by TH in 1994.

The purpose of this contribution is to combine the current theoretical framework of ichnoentomology with evidence from new insect trace fossil data from the Laetoli area to update and augment the palaeoenvironmental interpretation. In so doing, the specific objectives are: (1) to estimate the abundance and diversity of insect trace fossils and trace makers involved; (2) to evaluate the degree of emergence and mortality of adult insects, along with the diversity of nest intruders; (3) to apply the

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ichnofacies model for inferring plant associations; and (4) to evaluate the degree of grass cover using *Coprinisphaera* as an indicator.

GEOLOGICAL SETTING

Three main stratigraphic units at Laetoli and at other sites on the Eyasi Plateau (Fig. 1A) have produced insect trace fossils (Hay 1987; Sands 1987; Ritchie 1987; Hill 1987; Kaiser 2000; Darlington 2005, 2011; Krell & Schawaller 2011). These units are the Lower Laetolil Beds (LLB), the Upper Laetolil Beds (ULB), and the Upper Ndolanya Beds (UNB) (Hay 1987; Ditchfield & Harrison 2011; Harrison & Kweka 2011). The LLB, which form the base of the local sedimentary sequence overlying the Precambrian basement, are widely exposed to the south and west of Laetoli. Radiometric dating of the LLB indicates an age of 3.85 Ma to older than 4.36 Ma (Drake & Curtis 1987; Deino 2011). The sediments consist of subaerially deposited aeolian tuffs interbedded with air-fall and water-lain tuffs. At Kakesio, 30 km to the southwest of Laetoli, the base of the LLB consists of conglomerates and sandstones, deposited in a low-energy fluvial or paludal environment. At Noiti and Esere, south of Laetoli, the LLB is dominated by fluvial, deltaic, and lacustrine deposits interbedded with air-fall tuffs and lahars. Vertebrate fossils are sparsely represented in the LLB, but terrestrial gastropods and insect traces are common.

The ULB consists of a series of aeolian, air-fall and water-lain tuffs (Hay 1987; Ditchfield & Harrison 2011). The water-worked sediments are associated with seasonal ponds and streams. Distinctive air-fall tuffs throughout the ULB are designated as marker tuffs (Tuffs 1–8) (Hay 1978, 1987; Ditchfield & Harrison 2011). Radiometric dating of the ULB provides an age of 3.6–3.85 Ma (Deino 2011). The ULB is highly fossiliferous and it has yielded a rich diversity of fossil plants, invertebrates and vertebrates, including the early hominin *Australopithecus afarensis* (Harrison 2011*a*–*c*).

Overlying the Laetolil Beds is a series of aeolian tuffs and pedogenic calcretes comprising the Ndolanya Beds (Hay 1987; Ditchfield & Harrison 2011). The UNB, dating to 2.66 Ma (Deino 2011), have yielded a rich assemblage of fossil vertebrates and invertebrates, including the hominin *Paranthropus aethiopicus* (Harrison 2011*a*–*c*, 2017). The UNB are capped by the Ogol Lavas, dated to 2.3 Ma (Drake & Curtis 1987; Deino 2011; Mollel *et al.* 2011). A composite stratigraphical section of the sediments on the Eyasi Plateau is presented in Figure 1B.

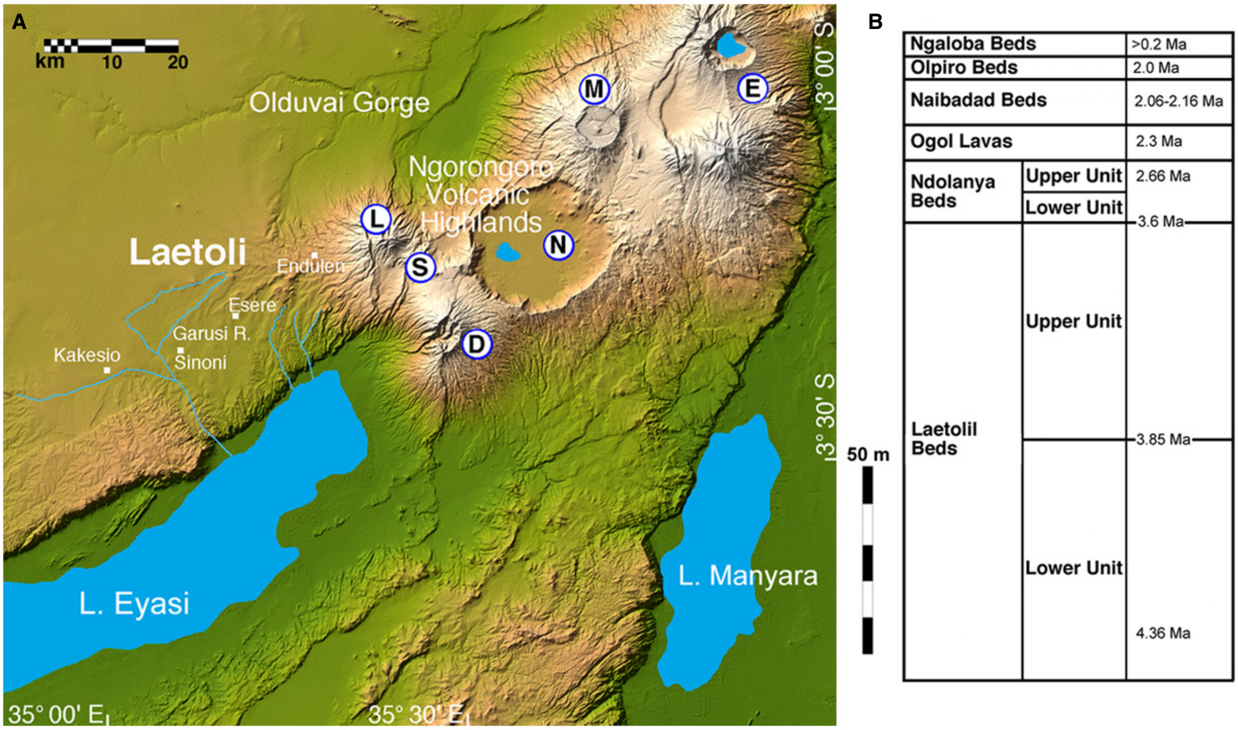


FIG. 1. A, satellite image of the Eyasi Plateau and the Ngorongoro Volcanic Highlands of northern Tanzania, showing the location of Laetoli. Volcanoes, large circles: D, Oldeani; E, Embagai; L, Lemagurut; M, Olmoti; N, Ngorongoro; S, Satiman. Villages, small white squares. Image from NASA Earth Observatory (2004). B, simplified stratigraphic scheme and geochronology of the main lithological units at Laetoli (after Harrison 2011*a*, *b*; Ditchfield & Harrison 2011; Deino 2011). Colour online.

RESULTS

Beetles

The presence of beetles is evidenced by the record of the trace fossils *Fictovichnus gobiensis*, *Coprinisphaera* ispp. and *Quirogaichnus* isp. *Fictovichnus gobiensis* includes ellipsoid to ovoid, horizontally to sub-horizontally oriented, structures that can occur as hollow cavities in palaeosols or more frequently as internal moulds with a smooth surface (Genise 2016). The Laetoli material fits with this diagnosis with one exception: it is the first time that the fossils are vertically oriented as attested by the block of matrix (LAET 81-205) collected by Mary Leakey in 1981 and illustrated by Ritchie (1987, pl. 11.14, figs 1–2) (Fig. 2A).

Laetoli specimens of *Fictovichnus gobiensis* show different outlines and sizes and probably involve a number of different trace makers. In contrast to some bee cells, most show radial symmetry (e.g. in any plane view the lateral sides are similar). Some specimens, particularly the smallest ones (3 mm in width) have a cylindrical outline, with both lateral sides running almost parallel and converging abruptly near the extremes (Fig. 2C). Other specimens, both large and small, have more arched sides converging more gently at the extremes. In these cases the maximum width is in the middle of the specimen, resulting in an ellipsoidal outline (Fig. 2D). Among these ellipsoidal specimens, some are stouter ending in more rounded extremes (Fig. 2E), whereas others are slender with more pointed extremes (Fig. 2F). Intermediate outlines between ellipsoidal and cylindrical are also present, as shown by the most abundant 5–6 mm wide, mostly translucent specimens, typical of the UNB (Fig. 2G). A minority of specimens (n = 40, 1.3%) shows a curved outline or one side straighter than the other (e.g. bilateral symmetry) (Fig. 2H). Others have a nipple-like structure at one extreme (Fig. 2I). Verde (2015) recorded similar specimens with bilateral symmetry and a pointed end, and other curved specimens, from carbonate-rich palaeosols of the Cretaceous and Palaeogene of Uruguay. In the case of the Laetoli material it is possible that some specimens were slightly deformed by carbonate overgrowth. A few other specimens (n = 36, 1.2%) are ovoid (with the maximum width displaced from the middle towards one extreme), showing one extreme slightly tapering compared with the other (Fig. 2J).

The specimens are 2–18 mm wide and 4–29 mm long (n = 2892). Most specimens (n = 1884, 65%) are 5–6 mm wide and among these the most common are 9–12 mm long (n = 1779, 61%). The abundance of the most common type increases through the stratigraphic sequence from oldest to youngest, with 293 (10%) in the LLB, 616 (20%) in the ULB, and 870 (30%) in the UNB. Some groups of specimens are remarkable because of their particular aspect ratio: the short and wide, ellipsoidal specimens (9 × 6 mm, 10–11 × 7 mm; n = 54) typical of the LLB (Fig. 2K); the small, slender, subcylindrical specimens 4 mm wide and 10–11 mm long (Fig. 2L) found in all three units; and the longest ellipsoidal ones, 23–29 mm long and 10–18 mm wide from the LLB and ULB, which probably involve different trace makers (Fig. 2M).

Ritchie (1987) claimed that what he assumed to be cocoons were not circular in cross section. However, almost all specimens of *Fictovichnus gobiensis* studied here are circular in cross section. We speculate that it is possible that he included some *Celliforma* or some of the rare bilaterally compressed *Fictovichnus* in his data. Most specimens, particularly the smaller ones, show translucent diagenetic walls composed of calcite crystals (Fig. 3A), and in some cases dark spots inside (Fig. 3B) that result from the accumulation of crystals (Fig. 3C). Ritchie (1987) believed that these were the remains of the original provisions in the bee cells. However, this cannot be the case. The specimens are casts of empty cavities lined with calcite growth, many of them becoming small geodes. The external surface of the translucent specimens is originally smooth, but in a series of specimens it is possible to observe that during later diagenetic processes a grey and rough layer may cover the surface partially or completely (Fig. 3D). In some cases root traces are present on the surface, as in other insect trace fossils from localities on the Eyasi Plateau (Fig. 3E). A few specimens (Fig. 3F) show a surface morphology composed of helical ridges, which is consistent with *Fictovichnus sciuttoi*, but they lack the diagnostic flat area and/or a scar (Genise *et al.* 2007). A few light brown specimens exhibit a surface morphology that is slightly rough and bumpy with tiny scattered holes (Fig. 3G). One of these appears to have pores similar to those of cocoons of sand wasps belonging to the Crabronidae (Fig. 3H). They are also placed tentatively in *Fictovichnus gobiensis*.

In the block of matrix with *F. gobiensis* (LAET 81–205) some specimens are preserved at the end of short vertical shafts. The filling of the shafts and the specimens are separated by a thin space, which is also present between them and the surrounding matrix (Fig. 2B). The texture of the shaft infilling is coarser than the specimen wall, which is smooth. As the specimens show no evidence of emergence, it is assumed that the shafts are not emergence tunnels, but those excavated and filled by the larvae as they penetrated the soil (Fig. 2A).

There are 27 rounded structures that can be included in the ichnogenus *Coprinisphaera* Sauer, 1955, and an additional two clustered specimens, may belong to *Quirogaichnus* Laza, 2006. The preservation of the specimens is poor, and the diagnostic characters are largely

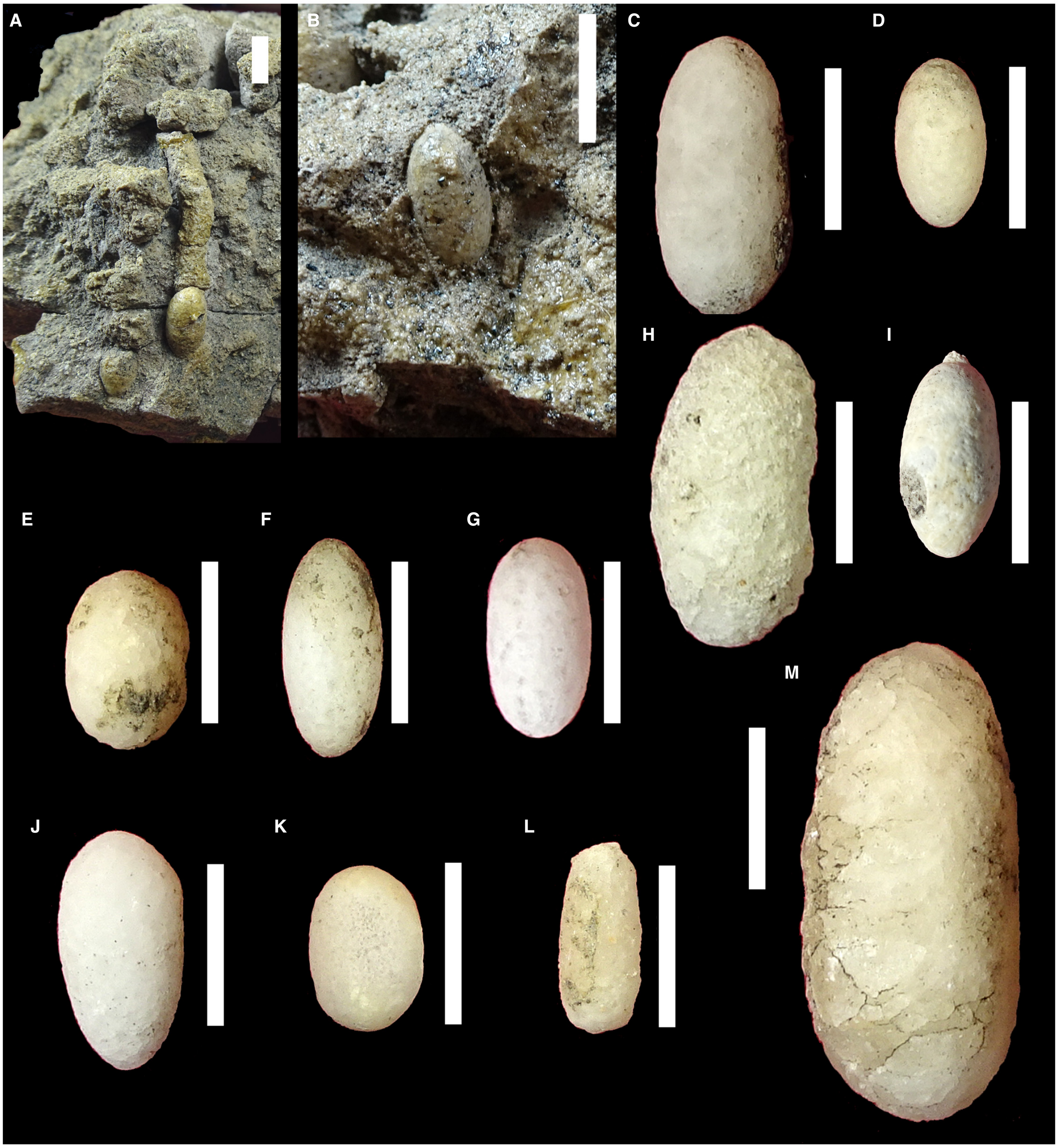


FIG. 2. *Fictovichnus gobiensis*. A, LAET 81-205, block of matrix illustrated by Ritchie (1987) showing a vertical shaft ending in a specimen of *F. gobiensis*. B, the same block showing a *Fictovichnus gobiensis* separated by a narrow space from the matrix. C, EP978/14, cylindrical outline. D, EP1006/05, ellipsoidal outline. E, EP677/12, stout specimen ending in rounded extremes. F, EP2033/16, slender with pointed extremes. G, EP289/12, intermediate outline typical of the UNB. H, EP4267/00, curved specimen. I, EP1173/01, specimen showing a nipple at one extreme. J, EP690/05, ovoid specimen. K, EP187/99, short and wide specimen typical of the LLB. L, EP1646/03, small, slender, subcylindral specimen. M, EP1215/14, long, ellipsoidal specimen. All scale bars represent 10 mm. All specimens outside the matrix are illustrated at the same scale to point out differences in size and aspect ratio. Colour online.

obscured by diagenesis or weathering. This ‘Laetoli style of preservation’ is also seen in the possible termite nests, whereas smaller trace fossils like *Fictovichnus* or *Celliforma* are well preserved. In many cases specimens are fragmentary, which adds to the uncertainty of the origin of these structures. However, they are different from rounded

FIG. 3. *Fictovichnus gobiensis*. A, EP509/14, translucent, diagenetic wall composed of calcite crystals viewed with transmitted light. B, EP339/16, dark spot in the interior of one specimen viewed with transmitted wall. C, EP690/05, accumulation of crystals in the interior, which is responsible for the dark spot; note the thin diagenetic wall. D, EP1515/00, grey and rough layer partially covering a specimen. E, EP043/00, network of rootlets covering the surface of a specimen. F, EP2708/00, surface morphology composed of helical ridges. G, EP339/16, surface morphology bumpy and with tiny holes. H, EP339/16, structures resembling equatorial pores of some wasp cocoons. I–K, putative trace makers; I, EP2156/03, Schyzonychini (Melolonthinae); J, EP2704/00, *Calcitoryctes magnificus* (Dynastinae); K, EP2777/00, Tentyriini (Tenebrionidae). L, EP437/00, pit produced by the detachment of a calcite crystal, resembling *Tombownichnus plenus*. M, EP757/12, showing remains of an equatorial tunnel probably produced by an intruder. All scale bars represent 10 mm. Colour online.

inorganic concretions that are common in the field, and they show recurrent sizes and shapes. Most of them also have a network of rootlets externally, which is a common character of insect trace fossils. Thus, these structures are considered as true *Coprinisphaera* and *Quirogaichnus*.

The holotype (EP224/04; Fig. 4A, B) and the paratype (EP1719b/03; Fig. 4C, D) of *Coprinisphaera laetoliensis* Krell *in* Krell & Schawaller, 2011 cannot be morphologically distinguished from *Coprinisphaera murguiai* (Roselli, 1939), and is thus a junior synonym. The two specimens

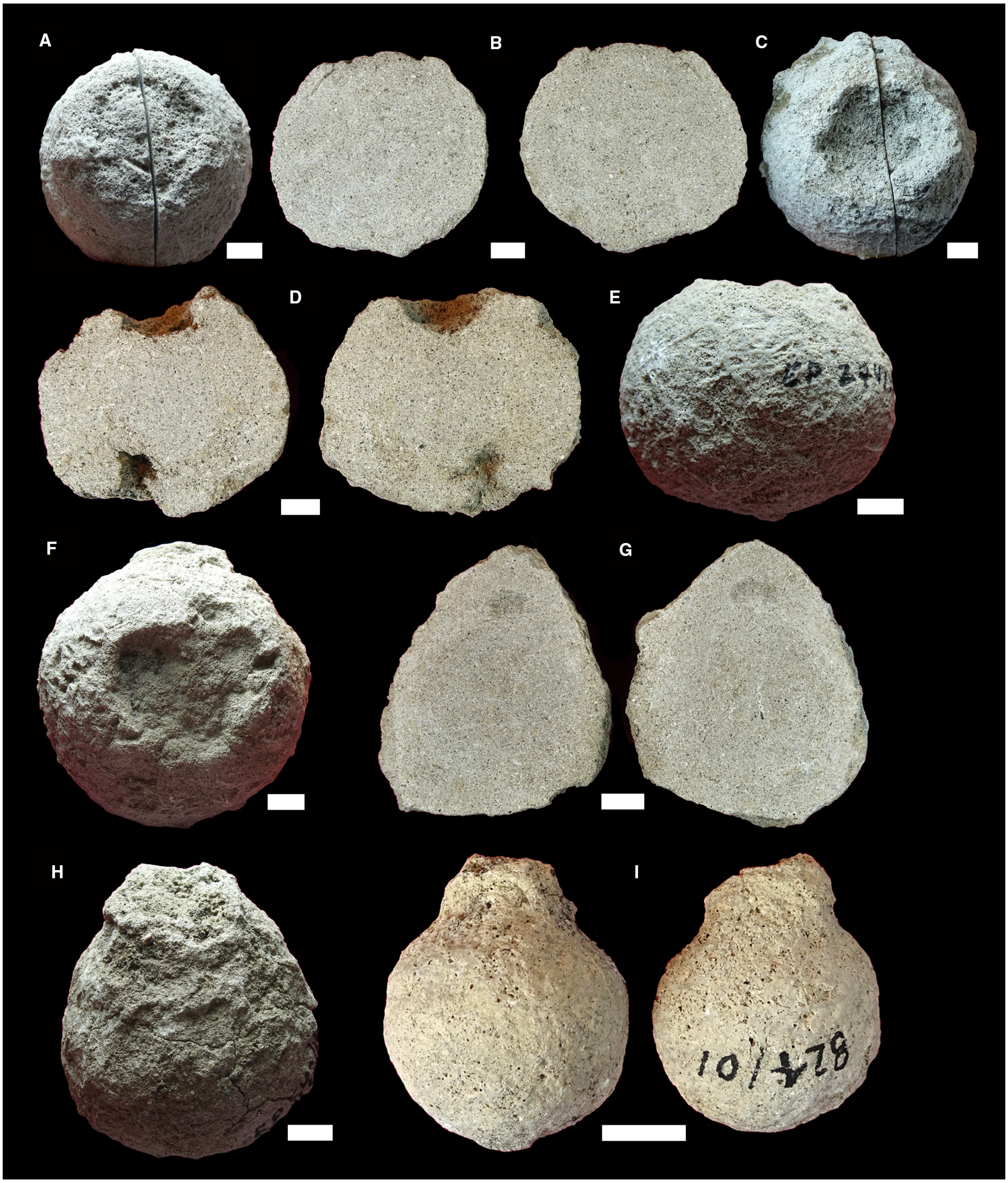


FIG. 4. *Coprinisphaera*. A–B, EP224/04, *C. murguiai*; the illustrated specimen is the holotype of *Coprinisphaera laetoliensis* Krell, which has been sectioned; A, top view showing both halves together, note the emergence hole on top; B, longitudinal section showing both halves, note the depressed outline and the wall particularly visible on the upper part around the emergence hole. C–D, EP1719b/03, a second specimen of *C. murguiai* originally designated as a paratype of *C. laetoliensis*; C, top view showing both halves together, note the emergence hole on top; D, longitudinal section showing the holotype of *Lazaichnus amplus* Krell from the base. E, EP274/14, a specimen of *C. murguiai* showing the network of rootlets on the surface. F, EP275/14, another specimen of *C. murguiai* showing the emergence hole (front) and a protuberance on top. G, EP1719a/03, *Coprinisphaera kheprii* showing the pear-shaped outline and the poorly preserved egg chamber below the upper pole; this specimen is another paratype of *C. laetoliensis* Krell. H, EP542/16, a potential second specimen of *C. kheprii*. I, EP824/01, a specimen of *Pallichnus*, which is the holotype of *Coprinisphaera ndolayana* Krell. All scale bars represent 10 mm. Colour online.

determined as *C. laetoliensis* by Krell (EP1077/01 and EP1719c/03) should also be considered to be *C. murguiai*. The large emergence hole, the main diagnostic character of the ichnospecies, is present in all these specimens (Fig. 4A–D) and in another seven specimens. The external texture of these structures is rugose, with a network of rootlets in some cases (Fig. 4E). Two specimens show lateral protuberances (22 and 55 mm in diameter) that may be a part of the trace or adherant matrix (Fig. 4F). All the specimens are slightly flattened, with a diameter greater than the height (Fig. 4B, D, E). External diameters are 53–77 mm (n = 11) and heights are 40–59 mm (n = 7). Some specimens show remains of a discrete external wall, 5 mm thick, which can be detected by subtle grooves or changes in colour (Fig. 4B). In a single exceptional case, which bears the holotype of *Lazaichnus amplus* Krell *in* Krell & Schawaller, 2011 (Lazaichnidae), the wall thickness is 15 mm (EP1719b/03) (Fig. 4D). Some specimens show depressions ranging in size from 19 mm to 55 mm, which may be interpreted as poorly preserved emergence holes (Fig. 4F).

The ichnospecies *Coprinisphaera kheprii* Laza, 2006 is represented by the specimen EP1719a/03, which is pear-shaped and sectioned in two longitudinal halves (Fig. 4G). The sections show darker areas that barely define a central chamber and in the upper pole, coincident with the external protuberance, a semicircular expansion (Fig. 4G). Such expansion, which is interpreted as the roof of the egg chamber protruding from the central chamber, is consistent with *Coprinisphaera kheprii* Laza, 2006. The diameter is 55 mm and the height 60 mm (taken in the axis that crosses the egg chamber). The wall is 8 mm thick and the egg chamber is 9 mm in diameter (Fig. 4G). The protuberance is 27 mm in diameter. The external surface is rugose with some rootlets. This is specimen A under EP1719/03, one of the paratypes of *Coprinisphaera laetoliensis* Krell; this specimen is one of the paratypes of *Coprinisphaera laetoliensis* Krell (specimen A from EP1719/03). A second possible specimen is also pear-shaped and complete, thus precluding the observation of internal diagnostic characters. It is 54 mm in diameter and 55 mm high, including the protuberance, which is 25 mm in diameter (Fig. 4H).

The other 11 specimens included here as *Coprinisphaera* ispp. are remains or complete rounded fillings, lacking an external discrete wall or other diagnostic characters. Some of them show low protuberances at a pole. The external surface is rugose and when broken, the internal texture is granulose. Two additional specimens are incomplete and lack diagnostic characters, but preserve remains of the wall. These could be included in *Pallichnus dakotensis* Retallack, 1984, an ichnotaxon for rounded trace fossils in palaeosols lacking discrete walls and showing a scar or low protuberance. However, they correspond in shape and size to the more complete *Coprinisphaera* found in the same outcrops, and so they are considered here to be fillings of *Coprinisphaera*. One of the specimens (EP824/01) is the holotype of *Coprinisphaera ndolanyana* Krell *in* Krell & Schawaller, 2011 (Fig. 4I). However, since this specimen lacks the diagnostic characters of the ichnogenus, such as the discrete wall, it is ichnotaxonomically most comparable with *Pallichnus*. It is interpreted here as a specimen of *Coprinisphaera* lacking the wall. The rounded fillings range in diameter from 21 mm to 54 mm (n = 11) and in height from 22 mm to 49 mm (n = 8). The two specimens preserving remains of the wall are 55 and 60 mm in diameter respectively and 50 and 55 mm in height. In both cases the wall is 8 mm thick.

A specimen that can be attributed to *Quirogaichnus* Laza, 2006 is composed of two small balls separated by 5 mm of matrix. Around the balls there is a cavity 2 mm thick (Fig. 5A). The balls are 18 mm in diameter and show a smooth surface; in one case covered by a network of rootlets (Fig. 5B). The only known ichnospecies, *Q. coninunctus* Laza, 2006, is represented by several small balls grouped in a common cavity and presumably without any partitions between them. The Laetoli specimen is composed of two balls separated by a thin partition of matrix and should thus be considered at least to be a different ichnospecies.

Moths

The presence of moths is evinced by the record of the new ichnospecies *Teisseirei linguatus* isp. nov. (Fig. 5C–H). The material is scarce (three complete specimens and two broken ones) but the depressed section and curvature in lateral view relate them to the only known ichnospecies, *Teisseirei barattinia* attributed to moths (Genise *et al.* 2013*a*). The extremes, one tapering and the other truncated, distinguish the latter from *T. linguatus*.

Bees

Bees are represented by several ichnospecies of *Celliforma*, and one of *Rosellichnus*. One of the most abundant is the new ichnospecies *Celliforma ritchiei* isp. nov. (Fig. 6A–C). This ichnospecies is distinguished by the presence of a cylindrical prolongation over the conical spiral closure composed of darker and coarser material.

Among the specimens of *Celliforma* bearing a spiral cap and lacking any other structure over it, identified as *C. spirifer* Brown, 1934, it is possible to distinguish several different shapes and sizes of cells corresponding to different trace makers (Fig. 6D–H). Surface morphology

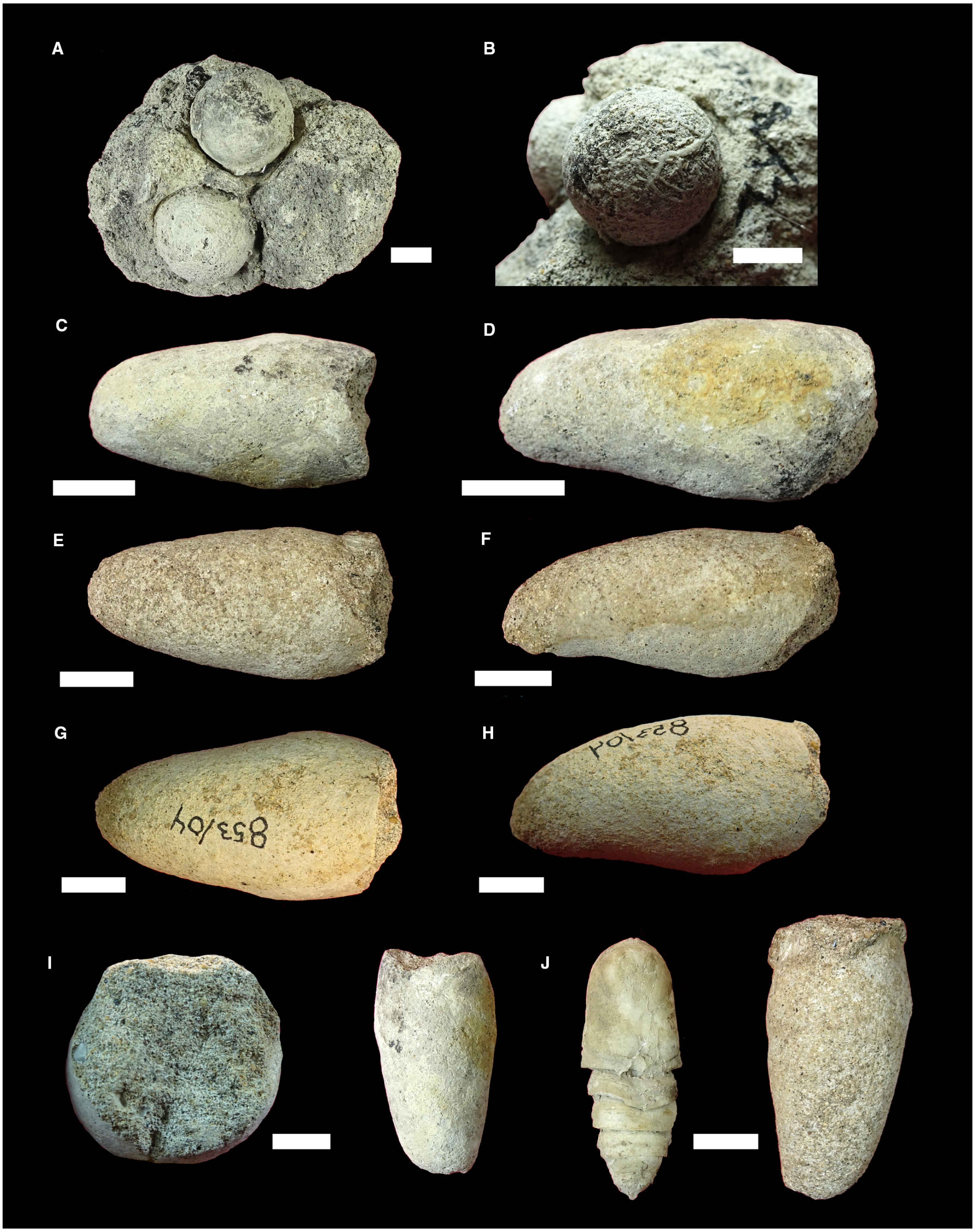


FIG. 5. *Quirogaichnus* and *Teisseirei*. A–B, EP598/12, *Quirogaichnus*; A, showing the two balls separated by a partition of matrix; B, one of the balls showing the network of rootlets on the surface. C–J, *Teisseirei linguatus* isp. nov.; C–D, EP1424/16, holotype: C, plan view; D, lateral view; E–F, EP1475/14 and G–H, EP853/04, the other two complete specimens of *Teisseirei linguatus* isp. nov., in plan and lateral view respectively; photograph in H has been reversed to fit the orientation of the others; I, cross section of one of the truncated extremes; J, comparison of two complete specimens of *Teisseirei linguatus* isp. nov. and EP352/03, the fossil pupa of a saturnid moth found at Laetoli. All scale bars represent 10 mm. Colour online.

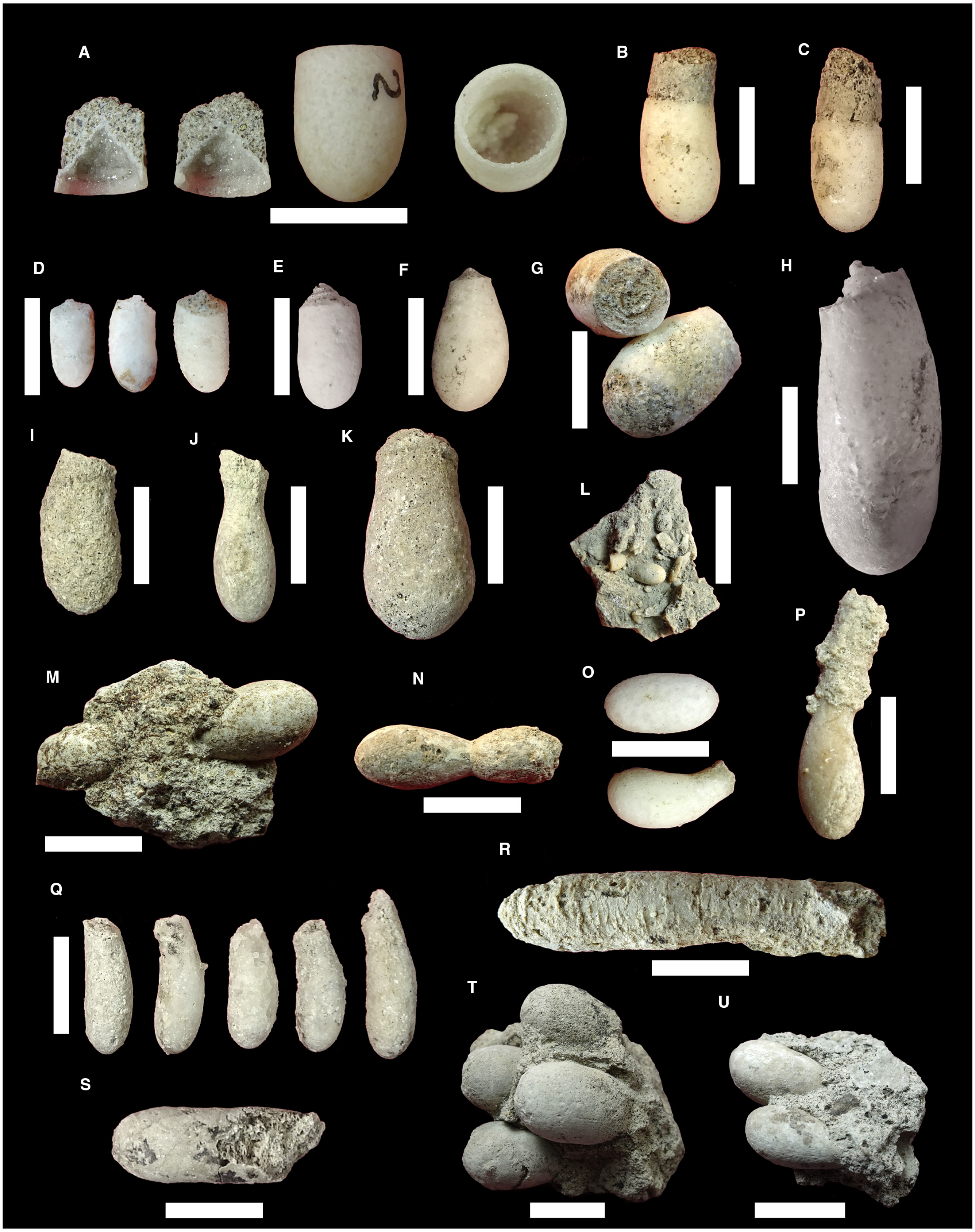
of these specimens ranges from smooth and translucent, to rough and greyish with fine rootlets. The use of dimensions or proportions as criteria to separate ichnospecies is not recommended (Bertling *et al.* 2006). Therefore, they are grouped and described informally. Type 1: very small cells, 11–12 mm long and 5–6 mm wide (n = 19), slightly curved, showing bilateral symmetry and without narrowing toward the spiral cap, which is relatively flat (Fig. 6D); the sample EP1342/16 is composed of 242 specimens, which were collected at the base of the LLB, suggesting that they come from a single nest or group of nests; a single specimen included in sample EP2023/00 comes from the ULB. Type 2: this type is the most abundant (n = 173); it is composed of sub-cylindrical, slightly curved cells, showing bilateral symmetry and no narrowing toward the spiral closure, which is conical (Fig. 6E); they are 13–20 mm long and 7–8 mm wide (n = 173); some specimens show remains of a coarser and darker material on the spiral closure; this suggests, together with other characters such as the constant width, that type 2 specimens are incomplete *Celliforma ritchiei*; most specimens come from the ULB, whereas ten of them come from the UNB, and show the same stratigraphic distribution as *C. ritchiei*; a single specimen from the LLB represents the only record of *C. ritchiei* from this unit. Type 3: four medium-sized specimens from the ULB show bilateral symmetry and a distinct narrowing towards the spiral cap, which gives a fig-shaped outline (Fig. 6F); they are 14–18 mm long and 7–8 mm wide; the spiral cap is 3–4 mm wide. Type 4: this distinctive type includes particularly wide cells with flat spiral caps (Fig. 6G); they show bilateral symmetry and no narrowing towards the spiral closure; some specimens show a central protuberance in the spiral cap; they are 16–24 mm long and the maximum width ranges from 11 mm to 17 mm (n = 32), with the most common widths being 11–13 mm (n = 27); this type is particularly common in the LLB. Type 5: four large specimens showing flat spiral cap are longer, up to 24 mm, and slender, 9–10 mm wide, than those included in type 4 (Fig. 6H); they have been recovered from the LLB and ULB, with a single specimen from the UNB.

Twelve specimens of *Celliforma* showing bilateral symmetry, no narrowing toward the top, and curved outlines (e.g. in lateral view both sides are curved) can be considered to be *C. curvata* Sarzetti *et al.*, 2014 (Fig. 6I). However, a key character of this ichnospecies is its vertical orientation and, as these specimens were collected as surface finds, this is unknown. Specimens are 13–26 mm long and 5–10 mm wide, suggesting that different trace makers were involved.

Eighteen specimens from the ULB and four specimens from the LLB show the constriction distinctive of *Celliforma germanica* Brown, 1935, even though in some cases they are poorly preserved and correct identification is doubtful (Fig. 6J–K). They are 12–25 mm long and 5–14 mm wide, and probably involve different trace makers. Medium-sized specimens 5–9 mm wide, all from the ULB, may represent one or two trace makers (Fig. 6J), whereas the larger ones, mostly from the LLB, 11–14 mm wide, may represent a third trace maker (Fig. 6K).

Specimens that do not show diagnostic characters of known ichnospecies and are not adequately represented to establish new ichnospecies are considered to be *Celliforma* ispp. In some cases, groups of specimens can be distinguished using size as a character. Another critical point is how to distinguish *Celliforma* ispp. from specimens of *Fictovichnus gobiensis* from which the adult insect emerged leaving a truncated flat top (Genise 2016). Several criteria were used: specimens with bilateral symmetry, constrictions, very elongate outlines, or necks, were discarded as truncated *Fictovichnus* and identified as *Celliforma*. Some specimens of *Fictovichnus gobiensis* show a curved outline and bilateral symmetry (Fig. 2H), but these are few and their outlines are not similar to those of *Celliforma*. Specimens with a pointed extreme were, in turn, discarded as *Celliforma*, which is characterized by a rounded extreme. In other cases, it was necessary to compare outlines. For instance, small specimens of kidney-shaped *Celliforma* with necks resemble the smallest *Fictovichnus gobiensis* preserving remains of a tunnel, but the comparison of the outlines between the latter ichnospecies and these specimens do not match (Fig. 6O). *Fictovichnus gobiensis* shows more pointed ends, whereas the *Celliforma* are more rounded at the bottom. The outline of *F. gobiensis* has both sides convex (radial symmetry), whereas the *Celliforma* has one of the sides more planar (bilateral symmetry). They also show a slight constriction toward the top, which is absent in *Fictovichnus*. Thus, they are considered to be *Celliforma* ispp. Another criterion was to consider a specimen as a truncated *Fictovichnus*, if the sample contained complete *Fictovichnus* or to consider it as a *Celliforma*, if all specimens of the sample showed flat tops. This methodology is not infallible, but it does reduce misidentifications to a negligible number that would not change significantly the conclusions reached here. Similarly, a relatively small percentage of *Fictovichnus*/*Celliforma*-like trace fossils were left undetermined because they were too incomplete, poorly preserved, or partially covered with matrix.

Among the 627 specimens of *Celliforma* ispp. it was possible to recognize morphotypes based on a combination of size, aspect ratio and morphological characters, and each type probably corresponds to a different trace maker. One type is composed of a very small single specimen, EP1373/05, 4 mm long and 2 mm wide from the ULB (Fig. 6L). Specimens of *Fictovichnus gobiensis* of similar width are few and show either cylindrical or ellipsoidal outlines, whereas this specimen is ovoid. A second type includes two cells that are probably arranged in a series (EP073/05) (Fig. 6M). However, adhering matrix precludes description and measurement of the complete structure. A second specimen, EP613/01 shows a clearer arrangement of two cells in a series (Fig. 6N). The more



complete cell is 12 mm long and 6 mm wide. Both specimens are from the ULB. Potentially two cells in a series may qualify for erecting a new ichnogenus (Verde & Genise 2007) but given that there are only two specimens partially obscured by matrix, it cannot be discounted that this arrangement arose by chance. A third type involves the smallest specimens of *Celliforma* 3 mm wide (in only three cases) to 7–8 mm (in only three cases), whereas most of the specimens are 5–6 mm wide (n = 50) (Fig. 6O). This type is composed of small, curved to kidney-shaped cells, showing in some cases a prolonged thin (3–4 mm wide) neck at one extreme, which diverge at about 130° from the longitudinal axis of the cell (Fig. 6P). They show bilateral symmetry in lateral view with both sides curved (sigmoid/convex), and lack spiral caps. Almost all of the specimens (n = 55) come from the ULB, except for a single specimen from the LLB. A fourth type, restricted to the LLB, includes thin, bilateral, curved cells, 5 mm wide and 11–14 mm long (n = 7) (Fig. 6Q). Among cells of intermediate widths (7–8 mm), those that are very elongated (19–36 mm) (n = 47) stand out as distinctive (Fig. 6R). Some broken specimens only reach 18 mm in length (n = 4). They may be somewhat curved to straight, and in lateral view they show a planar to slightly convex outline (bilateral symmetry) or a planar–planar one (radial symmetry). In many cases, it is possible to distinguish a more or less cylindrical neck at the flat end, which would represent the complete length of the structures. One specimen comes from the LLB and 46 from the ULB. This would be a fifth type.

The remaining specimens of *Celliforma* ispp. are more difficult to separate into well-defined types, although it is clear that they include different morphologies and involve different trace makers. At one extreme of the spectrum, large cells, with a diameter of 9 mm or more and 14–27 mm long, are few (n = 76) in comparison to thinner ones (n = 424). In addition, most of the larger ones (53%) come from the LLB (n = 40), which suggests different trace makers. Among the larger specimens it is possible to recognize stout cells, 11–13 mm wide and up to 25 mm long, which may correspond to incompletely preserved *Celliforma spirifer* (type 4). At the opposite end of the spectrum, the smallest specimens (n = 55), 5–6 mm wide and 9–15 mm long, are represented by nine specimens (16%) from the LLB. Apart from this, there are another nine records (2.4%) of *Celliforma* ispp. of intermediate size (7–8 mm wide) from the LLB, suggesting a change through time from small and large specimens to intermediate specimens. Specimens from the UNB are few (n = 11) and they include small, intermediate and large sizes. The remaining specimens, 5–8 mm wide and 9–20 mm long (n = 424) shows two basic morphologies, bilateral and radial, and among the latter, specimens may be curved to straight sided. Bilateral cells are horizontally oriented, in which the flatter surface is the lower surface of the cell (Michener 2007). Among the former, cells may be straight to slightly curved, which is more pronounced if there is some prolongation on top. It is difficult to decide in many cases if these necks are part of the cell or the remains of matrix. In some specimens, the neck presents a distal expansion mostly of matrix. Among the radial specimens, the sides may be parallel (i.e. they are more subcylindrical showing no narrowing toward the top), whereas in others the sides are curved or straight and convergent towards the top (i.e. they are more barrel or club-shaped specimens that narrow toward the top). Some specimens with parallel sides exhibit a shallow constriction around the equator of the cell (Fig. 6S). Radial specimens with parallel sides are compatible with *Celliforma rosellii* Genise & Bown, 1994*b*, but in the latter there is a circular rind on the top of the cell, whereas in the Laetoli material the top of the cells have a mostly irregular surface and no rind. Convergence may be strong in some specimens (e.g. the flat top of the cell becomes a small circular area as if they represent poorly preserved specimens of *Celliforma spirifer*, type 3) or gentler in others (e.g. the top is larger). However, intermediate cases occur in which it is difficult to distinguish slightly bilateral from radial symmetry and slightly convergent and curved from more straight, parallel sides. These *Celliforma*

FIG. 6. *Celliforma*. A–C, *Celliforma ritchiei* isp. nov.; A, LAET 1980-18-920 – 18-1385, holotype; specimen sectioned and illustrated by Ritchie (1987, pl. II-14, fig 11); note the hood or antechamber over the spiral conical closure and the thin diagenetic wall; B, EP492/03, paratype; C, EP3747/00, paratype; note the elongated hood. D–H, informal types of *Celliforma spirifer*; D, EP1342/16, three specimens of type 1; E, EP1466/04, type 2; F, EP1507/14, type 3; G, EP1289/04, two specimens of type 4; H, EP1263/03, type 5. I, EP1342/16, *Celliforma* cf. *curvata*. J–K, *Celliforma germanica*; J, EP2069/03, medium sized specimen; K, EP150/04, large sized specimen. L, EP1373/05, a very small specimen of *Celliforma* isp., type 1. M, EP073/05, *Celliform*a isp., type 2; two cells in a line. N, EP613/01, *Celliforma* isp., type 2; two cells in a line. O, EP044/00, *Celliforma* isp., type 3, kidney-shaped specimen compared with a specimen of *Fictovichnus gobiensis* (EP289/12) to show the differences in outline. P, EP2162/03, *Celliforma* isp., type 3; kidney-shaped specimen with a prolonged thin neck. Q, EP1342/16, *Celliforma* isp., type 4; thin, bilateral, curved cells. R, EP166/03, Celliforma isp., type 5; very elongated cell, probably preserving remains of the tunnel. S, EP1639/04, specimen of *Celliforma* isp. with a slight equatorial constriction. T, EP219/03, specimen of *Rosellichnus* isp. with five cells. U, EP073b/05, specimen of *Rosellichnus* isp. with two cells. All scale bars represent 10 mm. B–S, all specimens of *Celliforma* are illustrated at the same scale to point out differences in size and aspect ratio. Colour online.

ispp., comprising 424 specimens of intermediate size and morphologies, cannot be separated into different types, and even less into ichnospecies, but they probably correspond to a diversity of trace makers.

A cluster of five cells arranged as the spots on a die (EP219/03) may be included tentatively in *Rosellichnus* Genise & Bown, 1996, although the bottoms are at different levels and the entrances are covered with matrix (Fig. 6T). There are no indications of discrete linings and the original orientation of the cluster is unknown. Cells are 14–15 mm long and 10–12 mm wide. This specimen is from the LLB. The other specimen (EP073b/05) from the ULB shows only two cells 14 mm long and 7–8 mm wide (Fig. 6U) with similar characters to the former specimen.

Termites

Termites are represented by poorly preserved chambers attributable to *Vondrichnus planoglobus* Duringer *et al.*, 2007, the new ichnotaxon *Laetolichnus kwekai* igen. et isp. nov., and several remains of nests that can be included in Krausichnidae.

Several medium-sized chambers show a planar convex outline in section, resembling *Vondrichnus planoglobus* Duringer *et al.*, (2007), but emerging tunnels are lacking, and the poor preservation precludes further observations and identification (Fig. 7). Most show a rounded-elliptical outline in plan view, ranging in size from 4 × 5 cm to 11 × 11 cm. In some cases, the roof curves down towards the edge delimiting a peripheral rind (Fig. 7A), whereas in others the rounded-elliptical outline in planar view is interrupted by a notch (Fig. 7B). They show a thin (<1 mm), yellowish, locally cracked, and smooth external wall, with scattered tiny holes (Fig. 7C) surrounding a coarser, grey filling partially covered by root mats (Fig. 7D). In some specimens the filling seems to have alveoli ranging from 1 mm to 8 mm and the external wall has some protuberances (Fig. 7B). Another specimen (EP770/12) has eight radiating, 5 mm wide channels inside (Fig. 7E). At least two of the channels converge in a common tunnel at the base. One specimen exhibits a central spherical structure (EP470/04; Fig. 7F). Except for the latter specimen, which is unusually high (8 cm), the other structures are 3–5 cm high, 4–13 cm long and 5–8 cm wide.

Structures composed of a small chamber and remains of a second one connected by thin cylinders at both extremes are considered here to be Krausichnidae and included in the new ichnotaxon *Laetolichnus kwekai* igen. et isp. nov. (Fig. 8).

Several specimens in the Leakey collections are described and interpreted by Sands (1987) as parts of large fossil termite nests. LAET 74-252 is a flat structure showing several small circular holes and a few tunnels identified as a lower hive of *Odontotermes* (Sands 1987, pl. 11.8, fig. 46, left; Fig. 9A). LAET 74-251 is a planar convex structure, showing a granular texture externally with fine alveoli and massive interiorly, preserving some empty tunnels and protuberances. It was identified as a 'calcified ovoid', possibly representing a queen cell (Sands 1987, pl. 11.8, fig. 45; Fig. 9B). LAET 74-250 is similar to LAET 74-252, but has holes with funnels preserved on top. It was identified as a lower hive of *Macrotermes* (Sands, 1987, pl. 11.8, fig. 46, right; Fig. 9C). LAET 74-249 is a boxwork of anastomosed, flat galleries, 5 mm wide (Sands 1987, pl. 11.8, fig. 50; Fig. 9D). Along with this material there are other specimens without collection number or identification, which are mostly the remains of honeycomb-like structures or flat galleries (probably part of those illustrated by Sands (1987, pl. 11.1; Fig. 9E) or parts of ovoids, with the exception of a piece of matrix bearing part of one of Sands' 'thin-layered ovoids' and consistent with *Coatonichnus* (Duringer *et al.* 2007; Fig. 9F).

Two specimens (WM 531/94 and WM 948/94) from the Ibole Member (~5.0–5.5 Ma) from Ngofila 1 in the Manonga Valley (Harrison & Baker 1997) are similar to the calies of the Egyptian *Termitichnus simplicidens* (Genise & Bown 1994*a*; Fig. 9G, H). One of the specimens is 20 cm long, 12 cm wide, and 8 cm high, whereas the other is 20 cm long, 16 cm wide and 10 cm high. Internally, both of them show concentric arrangements of layers surrounding a central core. However, the poor preservation and lack of connecting tunnels preclude further analysis or identification.

DISCUSSION

Abundance and diversity of insect trace fossils and trace makers involved

Beetles. There were probably at least 4–5 species of dung beetles constructing the trace fossils at Laetoli. *Quirogaichnus* could be produced by a species of one of the groups that constructs several balls in a common burrow or cavity (e.g. compound nests of Halffter & Edmonds 1982). The two balls recorded here are separated by a partition of matrix, as in the case of those dung beetles that arrange brood balls linearly in a burrow separated by soil partitions (Pattern I of Halffter & Edmonds 1982). In Africa, this would be the case for some Oniticellini (Halffter & Edmonds 1982). *Coprinisphaera kheprii* was probably constructed by a distinct species of dung beetle. Finally, *Coprinisphaera murguiai* and *Coprinisphaera* ispp., the former representing balls from which the adult emerged, and the latter being fragmentary specimens, cannot be attributed to a particular group. However, the diameters involved show three modes (18–33 mm (n = 9); 50–57 mm (n = 12); and 62–77 mm

FIG. 7. *Vondrichnus planoglobus*. A, EP1290/04 showing a peripheral rind. B, EP471/04 showing a notch at the base and alveolar filling. C, EP775/16 showing a thin, cracked external wall with tiny holes. D, EP471/04 showing the external wall covered by a network of roots. E, EP770/12 exposing radiating tunnels on its surface. F, EP470/04 showing a central spherical structure. All scale bars represent 10 mm. Colour online.

(n = 5)) which may represent respectively three different species. The distribution of sizes is not related to the stratigraphic units. There are specimens of the three sizes in the LLB and the UNB. The ULB show less activity of dung beetles, represented by a single specimen of *Quirogaichnus*, whereas most of the activity is concentrated in the UNB, where 23 of the 27 specimens occur.

Ellipsoidal trace fossils in palaeosols, included in the ichnogenus *Fictovichnus*, have historically been attributed to wasp cocoons or coleopteran pupation chambers, and in some cases there are few clues to decide between these two possibilities (Genise 2016). In some instances the surface morphology is compatible with wasp cocoons, as in *Fictovichnus sciuttoi* or, in the case of *Fictovichnus aragon*,

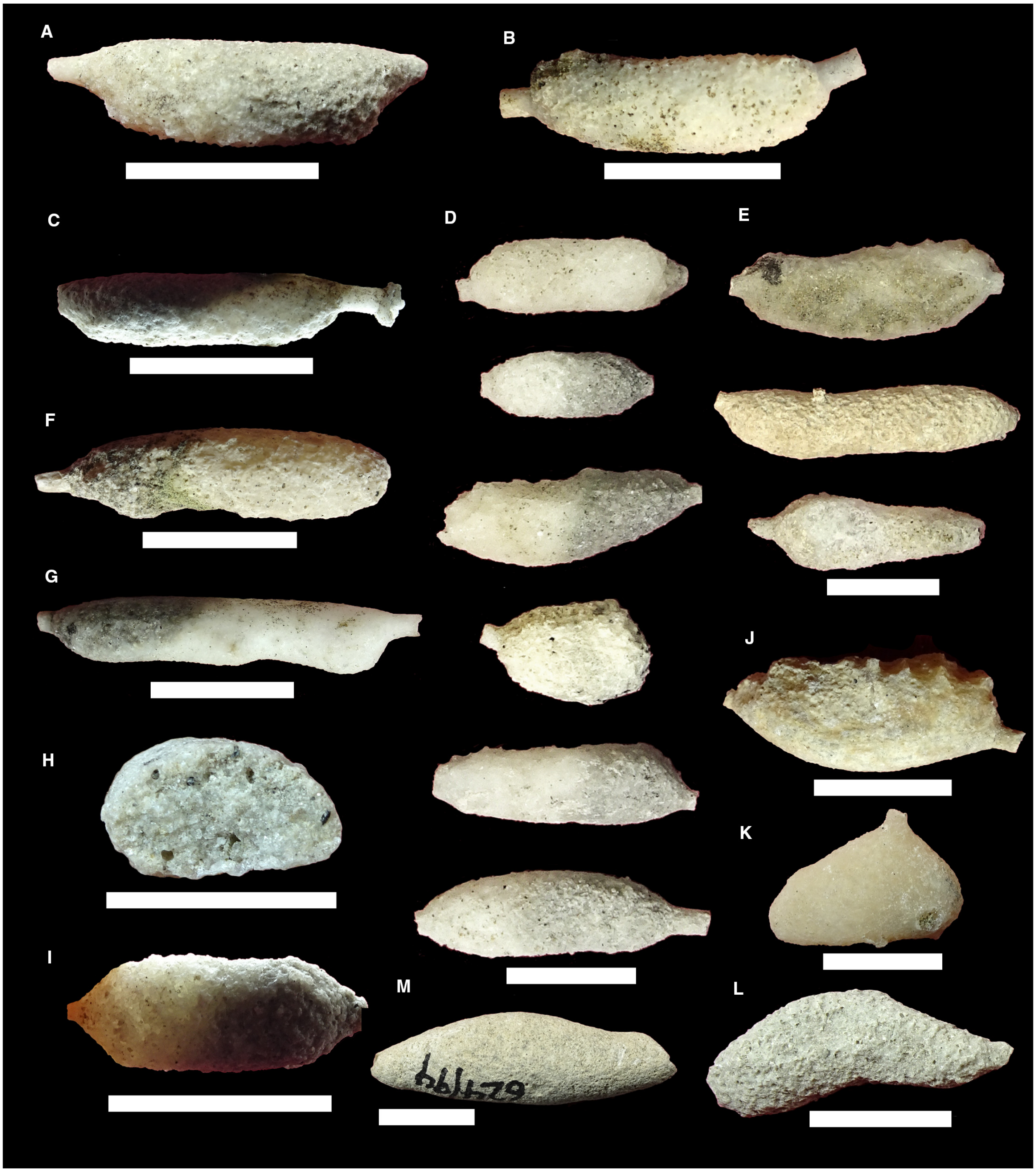


FIG. 8. *Laetolichnus kwekai*. A, EP2937/00, holotype. B, EP1394/00, paratype. C, EP537/98, paratype viewed with transmitted light, showing a dark spot and that the prolongation does not continue inside the chamber; note the prolongation with an expansion at the end. D, EP2708c/00, a sample with six specimens showing different shapes. E, EP341/00, a sample with three specimens showing different shapes. F, EP167b/00, a bilobed specimen. G, LAET 1974–1982, a multilobed specimen. H, LAET 74-129, an elliptical cross section of one specimen. I, EP2708c/00, a specimen viewed with transmitted light, showing a dark spot and that the prolongation does not continue inside the chamber. J, EP472a/00, a specimen showing an ill-defined, irregular ridge. K, EP816/00, a subtriangular specimen. L, LAET 1974–1982, V-shaped specimen. M, WM 624/94, a putative specimen of *L. kwekai* from the Tinde Member in the Manonga Valley. All scale bars represent 10 mm. Colour online.

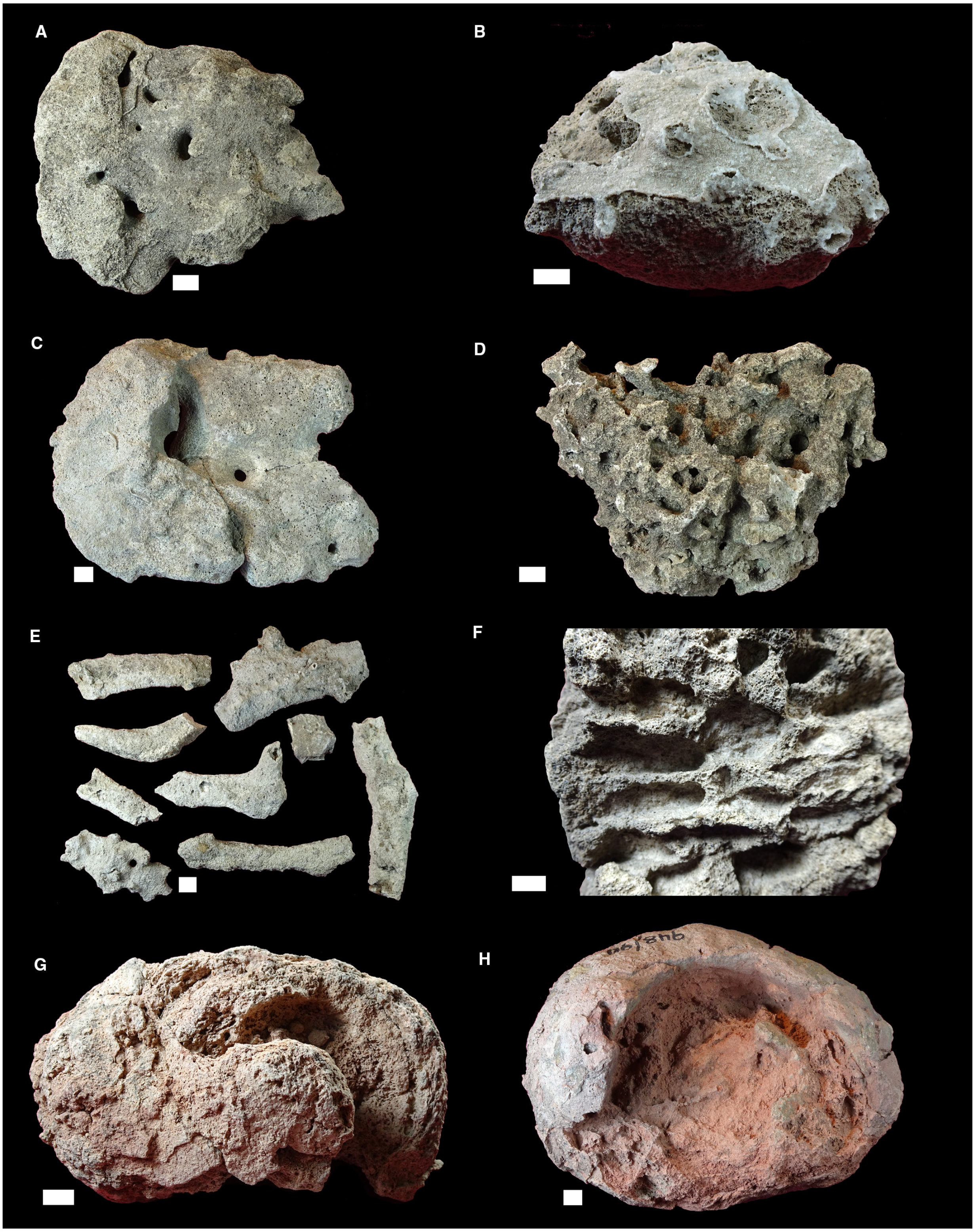


FIG. 9. Krausichnidae indet. A, LAET 74-252, flat structure showing several small circular holes identified as a lower hive of *Odontotermes* by Sands (1987). B, LAET 74-251, calcified ovoid *sensu* Sands possibly representing a queen cell. C, LAET 74-250, flat structure preserving holes with funnels identified as a lower hive of *Macrotermes* by Sands (1987). D, LAET 74-249, boxwork of anastomosed galleries. E, LAET 1974–1982, flat galleries. F, LAET 1974–1982, part of Sands' 'thin layered ovoid' consistent with *Coatonichnus*. G–H, structures similar to calies of *Termitichnus simplicidens*; G, WM 531/94; H, WM 948/94. All scale bars represent 10 mm. Colour online.

one of the extremes is tapering as in wasp cocoons (Genise *et al.* 2007; Alonso-Zarza *et al.* 2014). *Fictovichnus gobiensis* is more complex because it lacks wasp characters and has been attributed more frequently to casts of coleopteran pupation chambers, especially of beetles that construct ellipsoidal pupation chambers in soils, such as Tenebrionidae, Curculionidae and Scarabaeidae (Johnston *et al.* 1996; Genise 2016). Ritchie (1987) considered the Laetoli specimens to be infill casts of wasp cocoons without comparing them with coleopteran pupation chambers, even though he recognized that the Laetoli trace fossils were less elongated and less tapering than the cocoons of sphecid wasps. We tentatively consider them to be coleopteran pupation chambers because, despite the appearance that the calcite wall gives to them, they are just casts of empty cavities in the soil, showing no evidence of the discrete wall of wasp cocoons. The dense aggregation of coleopteran pupation chambers in a palaeosol is comparable to the case of *Rebuffoichnus guanche* in the Canary Islands (Genise *et al.* 2013*b*).

The *Fictovichnus gobiensis* specimens match the size and general outline of some of the fossil beetles from the ULB, belonging to Tenebrionidae, Melolonthinae and Dynastinae (Krell & Schawaller 2011) (Fig. 3I–K). Is it reasonable to conclude that some of these taxa were the trace makers of *Fictovichnus gobiensis* from the ULB? If one assumes that they were preserved because they were the most abundant taxa, then is it reasonable to postulate that they were related to the most common pupation chambers in the Laetoli palaeoenvironments.

Independent of the taxa involved, outline, size, surface texture and stratigraphy can be used to estimate the possible number of trace makers of *Fictovichnus gobiensis* from the different beds. The minimum number of trace makers involved would be those producing: (1) the smallest (3 mm) subcylindrical specimens mostly from the ULB; (2) ellipsoidal and stouter specimens in all units; (3) ellipsoidal and slender specimens distributed in all units; (4) the most abundant 5–6 mm wide specimens showing an intermediate outline between subcylindrical and ellipsoidal, whose number increases from the LLB to the UNB; (5) specimens somewhat curved or showing bilateral symmetry mostly from the UNB; (6) ovoid specimens distributed in all three stratigraphic units; (7) short and wide ellipsoidal specimens typical of the LLB; and (8) an undetermined number of trace makers, at least two, producing the largest specimens from the LLB and ULB. An estimated minimum number of trace makers for *Fictovichnus gobiensis* would be nine. Four are represented in all three beds, whereas another two are typical of the LLB and ULB respectively, and one more of the UNB.

Specimens with a surface morphology of helical ridges from the LLB and ULB and specimens with a bumpy surface and tiny holes from the UNB are probably produced by other beetles, but wasps cannot be discounted.

Moths. *Teisseirei* has been attributed to the pupation chambers of moths that pupate in soils, such as the Sphingidae (Genise *et al.* 2013*a*), but the latter authors left open the possibility that Saturnidae could be other possible candidates. A saturnid pupa described from the ULB (Kitching & Sadler 2011) matches the size and shape of *Teisseirei linguatus* (Fig. 5J). *Teisseirei linguatus* from the LLB is based on a few specimens and the recognition of this ichnogenus at Laetoli is tentative. It shares with the other known ichnospecies, *T. barattinia* from southern South America, the elliptical cross section, which is the most important diagnostic character and allows its attribution to moths (Genise *et al.* 2013*a*). In the new ichnospecies, the width/height ratio (1.05–1.20) is lower than in *T. barattinia* (1.5). The elliptical section is only present in half of the specimens, and they lack the multilayered wall and the internal pits of *T. barattinia*.

Bees. Ichnodiversity in combination with size indicates that Laetoli was inhabited during the Pliocene by at least 20 species of bees. The uniform width of *Celliforma ritchiei* suggests that it was probably produced by a single species. The different sizes of *Celliforma spirifer* grouped in five types would indicate the presence of at least four species, considering that one type can be attributed to poorly preserved specimens of *C. ritchiei*. Different sizes of *Celliforma germanica* indicate the presence of at least three species. Different sizes of the possible specimens of *Celliforma curvata* suggest that they were produced by at least two species. Another two species are represented respectively by specimens of *Rosellichnus* isp., and those with cells in a series, since these arrangements are distinctive of particular taxa (Michener 2007). Among the specimens included in *Celliforma* ispp., which are mostly distinguishable by size or aspect ratios, it is more difficult to estimate the number of species involved. A single specimen 4 mm long and 2 mm wide represents the smallest bee recorded, whereas the largest ones are more than 9 mm wide. Small, kidney-shaped to curved, specimens, 5–6 mm wide, would represent another species, whereas those showing the same width but more straight outlines, another one. The same is true for elongated cells, 19–36 mm long and mostly 7–8 mm wide, whereas the small, very thin (5 mm) and curved specimens from the LLB would represent another species. Among the medium and large sized specimens, showing no other distinctive characters, at least two trace makers can be distinguished based on the symmetry of cells (bilateral vs radial), but a higher diversity can be considered judging by the different sizes involved. Ichnostratigraphy of the Celliformidae is shown in Table 1. Many of the larger specimens of

TABLE 1. Ichnostratigraphy of Celliformidae at Laetoli.

Ichnotaxon	LLB	ULB	UNB
Celliforma ritchiei	Single specimen	Abundant	Scarce
Celliforma spirifer type 1	Abundant		
Celliforma spirifer type 3		Present	
Celliforma spirifer type 4	Abundant		
Celliforma spirifer type 5	Present	Present	Present
Celliforma germanica medium sized		Present	
Celliforma germanica large sized	Present		
Celliforma curvata	Present	Present	
Celliforma isp. type 1		Present	
Celliforma isp. type 2		Present	
Celliforma isp. type 3	Single specimen	Present	
Celliforma isp. type 4	Abundant		
Celliforma isp. type 5	Scarce	Abundant	Scarce
Rosellichnus isp.	Single specimen	Single specimen	

LLB, Lower Laetolil Beds; ULB, Upper Laetolil Beds; UNB, Upper Ndolanya Beds

Celliforma ispp. are from the LLB, as well as some of the smallest ones, in comparison with the ULB where most specimens are intermediate in size.

As a whole, from 1341 specimens of Celliformidae studied, 339 (25%) come from the LLB, including the 242 small cells from a single small outcrop probably belonging to a single or a few nests, 970 (73%) come from the ULB, and only 32 (2%) from the UNB. These results indicate that during deposition of the three main stratigraphic units at Laetoli the palaeoenvironments were highly suitable as nesting sites for bees. Large aggregations of nests by solitary bees (Tribe Anthophorini) are relatively common in the Laetoli area today, especially during the dry season in flat open patches with little or no grass cover that expose fine-grained, moderately consolidated, and well-drained clays (Fig. 10A).

There are few characters of the recorded fossil bee cells that are useful to identify their potential producers. Cells with bilateral symmetry are known among the Stenotritidae, Colletinae, Andrenidae, Halictidae and Melittidae. The latter two taxa are well represented in Africa (Michener 2007). Cells that narrow or show constrictions toward the entrance, such as *Celliforma germanica*, the small kidney-shaped *Celliforma* ispp. and the type 3 of *Celliforma spirifer*, are comparable to cells of Halictidae (Michener 2007). The trace maker of *Celliforma ritchiei* that accumulates coarse grains in the tunnel against the spiral cap to produce an antechamber is comparable to the bee *Ancylandrena larreae* (Andrenidae) (Rozen 1992, 1994). However, in that case the bee accumulates small pebbles and soil in the antechamber and the cell and antechamber are surrounded by a thick discrete wall. *Celliforma curvata* from North America and South America are attributed to Diphaglossinae, which are known for constructing curved cells (Sarzetti *et al.* 2014). However, the material described here is only tentatively included in this ichnospecies since the original orientation of the cells in the palaeosol is lacking. Besides, Diphaglossinae do not occur in Africa. At present, the soils of Laetoli are used for nesting by a species of *Pachymelus* (Anthophoridae) (D. Martins pers. comm. 2017), which produce dense aggregations (Fig. 10A). The meager knowledge of the nesting behaviour of soil nesting African bees, along with the few characters shown by the cells, precludes more precision in identifying the taxa involved.

Termites. There are several structures in the Leakey collection recorded as termite nests, which were presumably recognized by Sands (Fig. 9A–F). The key to identifying these structures as fossil termite nests was probably Sands' knowledge of extant termite nests of the region, without which the isolated and fragmentary specimens would be difficult to identify. Sands (1987) recognized seven types of trace fossils attributable to termites, including different parts of Macrotermitinae nests and those at different stages of development and/or constructed in different types of soil. Darlington (2005, 2011) confirmed the interpretations by Sands (1987) and described new types, such as an inverted pear-shaped chamber and small vertical shafts. In contrast to other trace fossils described here, most of the observations on termite nests come from *in situ* material that was impossible to collect due to its size. Collected specimens are therefore not reliable for estimating abundance of termites. Field observations by Sands (1987) and Darlington (2005, 2011) agree that termite activity was much higher in the ULB than in the LLB. There is no mention of the occurrence of termite activity in the UNB. The difference between the ULB and LLB is not really one of frequency but of type. The ULB has massive nests that cover several square metres and some horizons are extensively bioturbated and tunneled by termites, whereas in the LLB small ovoid termitaries with a diameter of 30–40 cm are very common, especially at Kakesio and Emboremony.

Further compelling evidence of termites is the planar convex chambers, which appear to be isolated and poorly preserved calies of *Vondrichnus planoglobus*. Some specimens have an internal alveolar pattern, as seen in *Vondrichnus planoglobus*, that preserve *Microfavichnus alveolatus* inside (Duringer *et al.* 2007) (Fig. 7B). They also resemble the 'small calcified ovoids', which were interpreted by Sands (1987) as queen cells or the basal part of hives of *Macrotermes* or *Odontotermes* nests (Fig. 9A–C). The piece of thin-layered ovoid representing

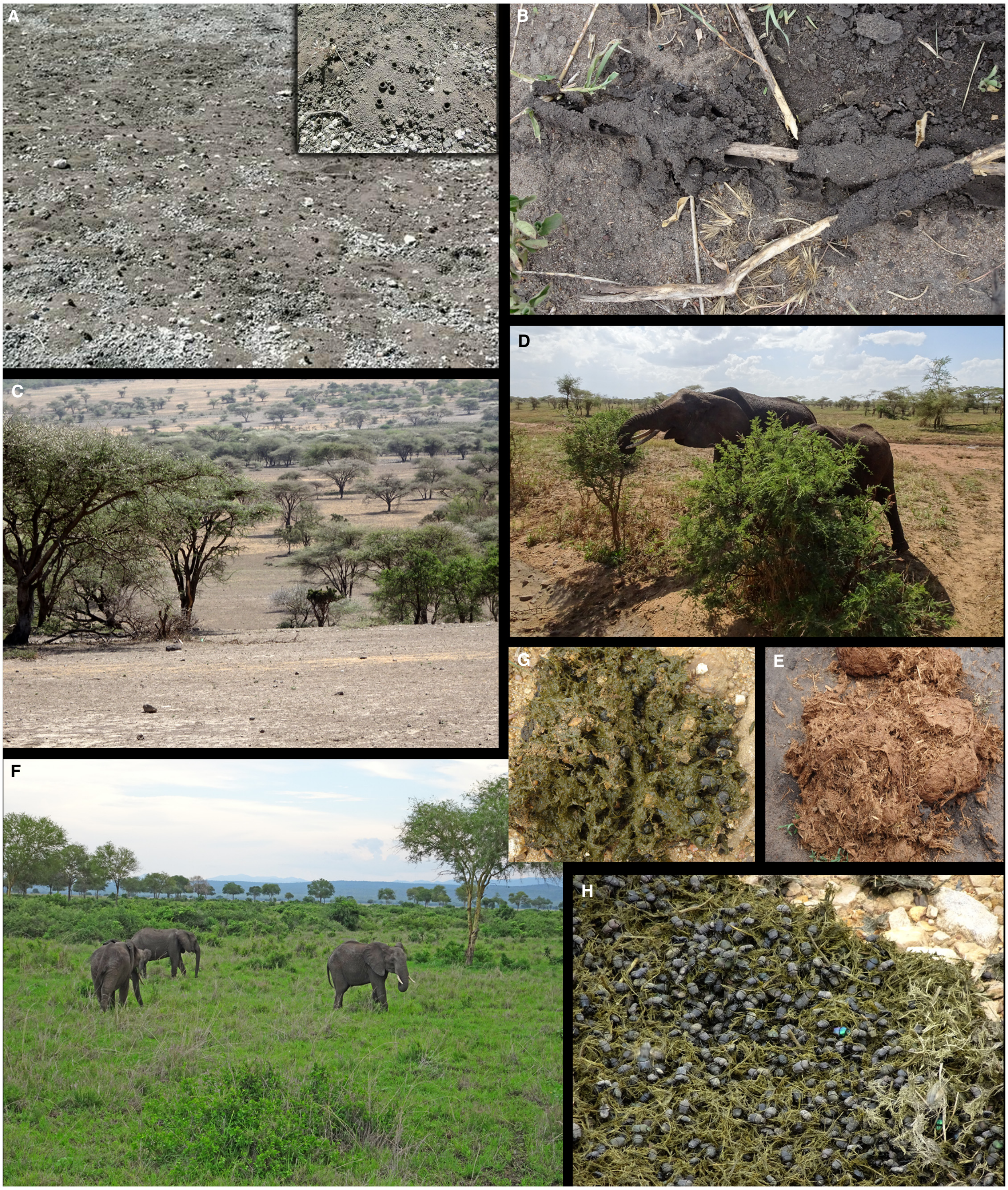


FIG. 10. Trace makers and environments. A, aggregation of Anthophorini (Apidae) nesting in the soil at Laetoli; inset shows close up of the turrets at the nest entrances. B, sticks covered by termite galleries in the Serengeti National Park (northern Tanzania). C, landscape along the road to Olduvai Gorge showing a dry woodland with poor grass cover as indicated by the *Celliforma* Ichnofacies for the palaeoenvironments of the Upper Laetoli Beds. D, elephants in the Serengeti browsing on acacias during the dry season. E, dropping of an elephant during the dry season full of coarse fibres and devoid of dung beetles. F, elephants grazing on fresh grasses after the rains at Mikumi National Park (central Tanzania). G–H, moist droppings of grazing elephants at Mikumi full of fine grass fibres and dung beetles. Colour online.

a specimen of *Coatonichnus globosus* (Duringer *et al.* 2007; Fig. 9F) and the two specimens from the Ibole Member in the Manonga Valley may represent calies of *Termitichnus simplicidens* (Fig. 9G, H).

In contrast to other trace fossils whose affinities are clear, there are several possibilities to consider when analysing the affinities of *Laetolichnus kwekai*. At first glance, it may resemble a piece of a thin rhizolith preserving part of a surrounding concretion. However broken specimens show that both prolongations are independent; they do not continue inside the structure. Also, the central part exhibits extremes too rounded to be considered a broken piece of a concretion. The lack of a central cylinder crossing the entire structure also discounts other possibilities, such as termite galleries surrounding small sticks (Fig. 10B), chambers of cicadas or other root sucking insects constructed around roots, or insect oothecae around sticks. A more likely possibility is that they represent chambers connected with the remains of tunnels at both extremes. One of the specimens shows an expansion at the end of one cylinder (Fig. 8C), suggesting the possibility that more than one chamber may have been connected. Considering the evidence, and particularly the possibility that other chambers were connected, this ichnotaxon is tentatively included in Krausichnidae. To some extent, these structures may be comparable in function with the storage chambers present in the system of underground passages of *Macrotermes michaelseni*. These are elongated depressions 2–5 mm high, 2–3.5 cm long and 1 cm or less wide occurring alongside the passages to temporarily store food (Darlington 1982).

Many of the structures recognized as fossil termite nests are more accurately parts of nests. It is therefore difficult to estimate the number of species of termites involved at Laetoli. *Vondrichnus planoglobus*, *Laetolichnus kwekai* and the boxworks of galleries, may all be a part of more complex nests. A rough estimation of the taxonomic diversity was presented by Darlington (2011): three species of *Macrotermes*, an Apicotermitinae, the producer of the flattened ovoids comparable with *Coatonichnus globosus* (Duringer *et al.* 2007), all from the ULB, and the producer of the thin-layered ovoids at Kakesio in the LLB (Sands 1987). Tentatively, *Vondrichnus planoglobus* from the LLB and ULB, *Laetolichnus kwekai* from the ULB, and the two possible specimens of *Termitichnus simplicidens* from the Ibole Member in the Manonga Valley would add further species to the list.

Mortality of larvae and absence of intruders

In classical localities, where hundreds or even thousands of insect trace fossils in palaeosols can be collected, such as at Laetoli, it is common to find a high percentage of emergence success and also a high presence of traces produced by intruders. In localities where fossil bee cells are abundant, like those from Uruguay and the Canary Islands, the percentage of traces with successful emergence of adults is very high: about 96% in Uruguay (Genise & Hazeldine 1998) and about 95% in the Canary Islands (La Roche *et al.* 2014). In the former, the presence of traces in traces (Lazaichnidae) produced by intruders is also high (Genise & Bown 1996; Genise & Hazeldine 1998; Mikuláš & Genise 2003). Similarly, the *Coprinisphaera* of Patagonia and Ecuador show an estimated emergence success of 67%, along with the presence of traces produced by intruders (Sánchez *et al.* 2010, 2013). Percentages of holes produced by intruders (*Tombownichnus plenus*) in coleopteran pupation chambers (*Rebuffoichnus guanche*) from Corralejo on Fuerteventura in the Canary Islands reach up to 71% (Genise *et al.* 2013*b*).

In contrast, of 1341 bee cells examined at Laetoli, 675 specimens included in *C. ritchiei* and *C. spirifer* preserve the spiral cap and indicate that the occupant died inside the cell. This represents 50% of the total sample. In addition, the absence of spiral cap in other cells is not indicative of emergence since representatives of different taxa of bees do not construct one. Specimens of *Celliforma* ispp. (11–13 mm wide and up to 25 mm long) may represent incomplete *C. spirifer* type 4 from which the adult emerged or in which the spiral cap is weathered or missing for other reasons. In any case, the number of incomplete specimens (n = 38) is similar to the complete ones (n = 32), indicating at least 45% of mortality. A more precise estimation can be made using *Celliforma ritchiei*. There are 401 specimens preserving the spiral cap and/or the hood, representing closed cells from which the adult never emerged, whereas none can be identified unequivocally as open.

The case of *Fictovichnus gobiensis* is easier to document because emergence produces a truncated end. Of 2976 *Fictovichnus gobiensis* measured, fewer than 200 show a truncation at one extreme that may represent emergence. The high mortality of insects inside cells and pupation chambers is paralleled at Laetoli by the dense concentrations of achatinid gastropods found buried inside their aestivation burrows by volcanic ash (Harrison & Kweka 2011).

Probably the same circunmstances that produced the high mortality of larvae and pupae in soils also preclude the activities of the many species of cleptoparasites, parasitoids and detritivores that typically invade insect traces in search of provisions, larvae, or the remains of organic matter. The 4317 specimens of bee cells and coleopteran pupation chambers show no traces of intruders. Some specimens show tiny holes resembling *Tombownichnus*, but a closer examination indicates that they are pits produced by the detachment of calcite crystals (Fig. 3L).

Also, being casts, more likely evidence of intruders would be full relief remains of tunnels, such as protuberances, attached to the walls. A dozen specimens (n = 13, 0.4%) of *Fictovichnus gobiensis* show the remains of tunnels (Fig. 3M). The only record of an intruder is a specimen of *Lazaichnus amplus* from the UNB, which represents a burrow in the wall and filling of a specimen of *Coprinisphaera* (Krell & Schawaller 2011).

One of the causes for this mortality and lack of activity of intruders may be the continued influx of volcanic ashes that cover the soils creating an anoxic/hypoxic environment that kills organisms at deeper levels. In the LLB packages of tuffs, representing air-fall events, may exceed 1 m in thickness, whereas those in the ULB do not usually exceed 30–50 cm.

The Celliforma *Ichnofacies*

Genise *et al.* (2000) proposed Laetoli as a case of the *Coprinisphaera* Ichnofacies based on data presented by Ritchie (1987) and Sands (1987). The ichnofacies model for palaeosols was just being developed at that time, and there were no ichnofacies available for associations involving mostly bee cells, pupation chambers, and rare or no *Coprinisphaera*. Also, with hundreds of trace fossils of hymenopterans and termites collected and described, it was difficult to know whether *Coprinisphaera* was actually absent or simply overlooked or confused with concretions. Previously, only a single specimen of *Coprinisphaera* from the LLB was mentioned by Sands (1987).

Recent intensive collection has increase the number of specimens from hundreds to thousands, and the creation of new ichnofacies and further development of the ichnofacies model for palaeosols (Genise *et al.* 2010, 2016) result in a new scenario. The number of insect trace fossils collected follows the same trend shown by fossil vertebrates and gastropods, in which large numbers have been recovered from the ULB and fewer specimens from the LLB and UNB (Harrison 2011*a*, *b*). Table 2 shows the number of specimens of insect trace fossils for each stratigraphic unit. In sum, 957 specimens have been collected from the LLB, 2196 from the ULB, and 1256 from the UNB. Termite nests and tunnels are most abundant in the ULB, less common in the LLB, and absent in the UNB.

TABLE 2. Number of trace fossils collected from the Laetoli stratigraphic units.

Ichnotaxon	LLB	ULB	UNB
Celliforma	339	970	32
Fictovichnus	596	1179	1201
Coprinisphaera	4		23
Quirogaichnus		1	
Teisseirei	5		
Vondrichnus	8	2	
Laetolichnus		43	
Krausichnidae indet.	5	1	

LLB, Lower Laetolil Beds; ULB, Upper Laetolil Beds; UNB, Upper Ndolanya Beds

The rarity of *Coprinisphaera* and *Quirogaichnus* in the LLB and ULB after decades of intensive collection (e.g. 5 among 3153 studied trace fossils) contrasts with the hundreds of specimens of different species of *Celliforma* and thousands of *Fictovichnus gobiensis*, and this indicates that these associations of trace fossils can be included in the *Celliforma* Ichnofacies. The *Celliforma* Ichnofacies is characterized by the presence of *Celliforma*, *Fictovichnus*, *Pallichnus* and *Teisseirei*, which are interpreted as bee, wasp, coleopteran, and moth trace fossils, respectively. The ichnodiversity is moderate, but the abundance is high. The ichnofacies develops on carbonate-rich palaeosols. The preservation of land snails (Tattersfield 2011) along with insect trace fossils is common (Genise 2016; Genise *et al.* 2016). The Laetoli ichnoassemblages match this definition. At Laetoli, the Krausichnidae are added to this ichnofacies for the first time. The *Celliforma* Ichnofacies is associated with arid to semi-arid scrub and woodlands, palustrine vegetation, or relatively bare soils due to frequent flooding. In sum, it is representative of palaeoenvironments with little or no grass cover, where bees find well insolated soils to nest, and the scarcity of grasses deters large grazers that produce the dung used by beetles to construct *Coprinisphaera*. The development of the *Celliforma* Ichnofacies particularly in the ULB, is indicative of a palaeoenvironment comprising shrubland to woodland with poor grass cover. This result is concordant with the previous inferred palaeoenvironment based on other palaeontological evidence (Harrison 2011*a*; Su & Harrison 2015). Palaeobotany, stable isotopes, mesowear, bovid postcranial ecomorphology, small and large mammal community structure, and terrestrial gastropods indicate that the palaeoecosystem of the ULB was dominated by a mosaic of closed woodland, open woodland, shrubland and grassland (Kingston & Harrison 2007; Su & Harrison 2007, 2015; Kovarovic & Andrews 2007, 2011; Peters *et al.* 2008; Bishop *et al.* 2011; Denys 2011; Kaiser 2011; Kingston 2011; Harrison 2011*a*; Rossouw & Scott 2011; Bamford 2011*a*, *b*; Su 2011; Tattersfield 2011). The *Celliforma* Ichnofacies suggests the dominance of shrublands and open woodlands, where bees found well insolated soils to nest (Fig. 10C).

The LLB show a similar association of insect trace fossils, which is compatible with the *Celliforma* Ichnofacies, but with only about one-third of its abundance (Table 2). This result agrees with previous palaeoecological inferences that the LLB was dominated by dry woodland and bushland. During the frequent ash falls (Harrison 2011*a*) nesting activities would have been interrupted until the recovery of suitable conditions, resulting in fewer traces. In addition, preservational factors cannot be discounted since other types of fossils are also less frequent than in the ULB (Harrison 2011*a*, *b*).

Evidence from the UNB poses a different problem because the insect trace fossils are less diverse (Table 2). Of the 1256 specimens collected, 1201 are *Fictovichnus gobiensis*. Most belong to a single trace maker, whereas the remaining specimens belong in equal proportions to *Coprinisphaera* and *Celliforma.* It is difficult to explain the decrease of diversity when the evidence does not point to substantial ecological changes, except for somewhat drier conditions with a greater proportion of grassland as part of the predominantly woodland ecosystem (Harrison 2011*a*, 2017). There is no evidence of termites as in older beds, and only 32 bee cells have been recovered in contrast to about 1000 in the ULB. If grass became so abundant as to cover the soil and deter bees from nesting, then, why is *Coprinisphaera* so scarce? Despite the overall scarcity, the frequency of *Coprinisphaera* increases in comparison to the ULB, which could indicate a displacement of the *Celliforma* Ichnofacies by the *Coprinisphaera* Ichnofacies, possibly associated with a shift to more grass-dominated habitats.

Dung beetles or grass beetles? The notable scarcity of Coprinisphaera *at Laetoli*

Rarely it is analysed, or worthwhile to do so, why an insect trace fossil is not recorded at a locality. However, the case of *Coprinisphaera* at Laetoli is different. There are good reasons to expect *Coprinisphaera* to occur in the deposits at Laetoli. First, tropical Africa is the region with the most genera (105) and species (2141) of dung beetles, only paralleled by the Neotropical region with 82 genera and 1381 species (Davis 2009). Moreover, in Africa large dung beetles exploit the dung of a wide diversity of native mammals, whereas in the Neotropical region the only dung available to many species is that of domestic cattle. So, Africa is an ideal habitat for extant dung beetles. Second, many African species are medium to large sized and produce brood balls that are consistent in size with *Coprinisphaera* ichnospecies (Halffter & Edmonds 1982; Hanski & Cambefort 1991; Scholtz *et al.* 2009; Mlambo *et al.* 2015). Third, by the Pliocene dung beetles were fully diversified and well established in Africa (Scholtz 2009*a*). Fourth, the pyroclastic palaeosols at Laetoli are similar to those of the Cenozoic of South America where *Coprinisphaera* is very abundant (Genise 2016) and is associated with other insect traces, such as bee cells and coleopteran and moth pupation chambers. Finally, previous inferences suggest that environmental conditions at Laetoli, such as temperature, humidity and soils, as well as the presence of large mammals (Harrison 2011*a*) were compatible with the potential presence of dung beetles.

If conditions for dung beetles were so ideal why is *Coprinisphaera* so scarce at Laetoli? Is there a missing element? First, it is important to note that *Coprinisphaera* is only made by dung beetles that produce balls of medium to large size. They mostly use dung pats or fumets of regular size with high moisture content (Scholtz 2009*a*; Mlambo *et al.* 2015). Although exceptions occur, these are much less parsimonious to assume than the general rule. For instance, the ball maker *Kheper nigroaeneus* is a large ball maker that is capable of combining small pellets of antelopes to make a brood ball (Edwards & Aschenborn 1988). Many dung beetles prefer dung pats of ruminant herbivores composed mainly of fine fibres, whereas some large ball maker species in *Heliocopris* and *Kheper* prefer coarse-fibred non-ruminant dung (Edwards 1991). With a few exceptions, the moisture content of dung is the main factor that controls its utlization by dung beetles. In experiments carried out with African herbivores it was demonstrated that dung with less than 68% of moisture content was not utilizable by dung beetles (Edwards 1991; Holter & Scholtz 2007; Scholtz 2009*b*). Accordingly, African dung beetle activity and particularly ball making is highly correlated with the wet season (Kingston & Coe 1977; Edwards 1991; Cambefort 1991; Davis & Dewhurst 1993; Scholtz 2009*b*). In Kenya, dung beetles are practically absent during the dry season (Kingston 1977 *in* Cambefort 1991). Similarly, in northern Tanzania during the dry season, the activity of dung beetles is very limited and the rolling of dung balls by large dung beetles is rarely observed (Fig. 10D, E). Rainfall is a primary factor in the seasonality of dung beetle activity by softening the soil and allowing emergence of adults (Kingston & Coe 1977), but it also increases the water content of dung: mammals are well hydrated, their droppings are less exposed to desiccation and, particularly, they contain fresh grass and browse that grow during and after the rains (Edwards 1991). Experiments conducted in Australia on native and imported African dung beetles showed that dung quality, particularly the content of green grasses after rainfall, was directly related to dung beetle activity and reproduction (Ridsdill-Smith 1986; Matthiessen *et al.* 1986; Macqueen *et al.* 1986). Dung produced from green pastures is moister, less fibrous, more homogeneous in texture, and it shows greater protein content and enzymatic and microorganism activity, and less lignin (Greenham 1972). Other experiments confirm that dung beetles prefer the dung of animals that feed on grass rather than of those that feed on hay or corn silage (Barth 1993).

Davis & Scholtz (2001) proposed a classification of dung types: (1) small, dry pellets from small and medium-sized herbivores; (2) small, odiferous droppings from omnivores and carnivores; (3) often large, fairly dry, coarse-fibred droppings from large, non-ruminant herbivores; and (4) large, moist, fine-fibred droppings from large ruminant herbivores (i.e. pats and fumets of Stuart & Stuart 2013). The first three types are present in northern Tanzania in the dry season; the fourth type is mostly lacking. This situation changes after the rains, when green grass returns (Fig. 10F). Even mixed feeders like elephants, which behave mostly as grazers, producing moist dung pats full of fine fibres of grass that attract *Coprinisphaera* makers (Fig. 10G, H). Large grazing bovids (e.g. wildebeest) produce dry pellets during the dry season, and softer fumets during the wet season (Edwards 1991; Stuart & Stuart 2013) that are also usable by *Coprinisphaera* makers.

The evidence indicates that moist dung produced by herbivores eating green grass was relatively scarce on the Laetoli palaeolandscape (see Harrison 2011*d*) and *Coprinisphaera* makers were correspondingly rare. This implies that grass cover was limited, an inference that is further supported by the massive nesting of bees discussed above. This conclusion agrees with analyses of dental mesowear and stable isotopes of ungulates (Kingston & Harrison 2007; Kingston 2011; Kaiser 2011) which show that the herbivore community in the ULB was dominated by browsers and mixed feeders, while the UNB, where most of the *Coprinisphaera* have been recovered, had a greater diversity of specialist grazers (Kaiser 2011; Harrison 2017).

CONCLUSIONS

Based on the insect trace fossils, the LLB palaeoenvironment was inhabited at least by one species of moth, three taxa of dung beetles and five other taxa of coleopterans, nine taxa of bees, and an indeterminate number of taxa of termites; the ULB palaeoenvironment supported a larger number of taxa of termites, one species of dung beetle, eleven taxa of bees, and five other taxa of coleopterans; and the UNB palaeoenvironment was occupied by four taxa of dung beetles, four other taxa of coleopterans, and two taxa of bees. Some wasps may also be represented in the three units. Apart from the higher diversity of insects, the ULB palaeoenviroments showed the greatest abundance of individuals based on the number of trace fossils recovered. The UNB show the lowest diversity and abundance.

The high percentages of insect trace fossils showing no indication of adult emergence (94% in the case of *Fictovichnus gobiensis* and greater than 50% in the case of bee cells) suggests a high mortality during their subterranean egg/larval stage. This corresponds with the few cases of traces of intruders recorded at Laetoli (0.04%), compared to other classical localities of insect trace fossils in palaeosols. The combined evidence indicates that some factor precluded the intruder activity and the full larval development in Laetoli soils. This underground mortality is also confirmed by the preservation of aestivating terrestrial gastropods in the LLB. This high mortality and lack of intruder activity may correspond to the anoxic/hypoxic conditions caused by the burial of soils under thick deposits of volcanic ashes.

The association of abundant bee cells (*Celliforma* ispp.) and coleopteran pupation chambers (*Fictovichnus gobiensis*) in carbonate-rich palaeosols, along with land snails and the absence of *Coprinisphaera* is representative of the *Celliforma* Ichnofacies. The full development of the *Celliforma* Ichnofacies in the ULB indicates the dominance of a palaeoenvironment of shrubland to woodland with limited grass cover. The LLB show a similar association of insect trace fossils that is compatible with the *Celliforma* Ichnofacies, but with only one-third of the abundance of specimens. Factors such as more frequent and heavier ash falls might account for a decrease in nesting activities. However, preservational factors need to be taken into account considering that other types of fossils are also less frequent in the LLB compared with the ULB. The UNB exhibit low diversity of insect trace fossils and the presence of a greater number of *Coprinisphaera* suggest a potential displacement from the *Celliforma* to the *Coprinisphaera* Ichnofacies indicative of habitats with more extensive grass cover.

Considering the abundance and diversity of extant African dung beetles capable of producing *Coprinisphaera*-like brood balls, the suitability for nesting in pyroclastic soils, and the availability of appropriate ecological and preservational conditions at Laetoli, the relative scarcity of *Coprinisphaera* is somewhat surprising. It is suggested that the scarcity of fresh grasses and the low incidence of large grazers were the primary causes.

SYSTEMATIC ICHNOLOGY

Ichnofamily COPRINISPHAERIDAE Genise, 2004

Teisseirei linguatus isp. nov.

Figure 5C–J

LSID. urn:lsid:zoobank.org:act:C6A10FE7-7375-4086-8730-BD0927A7BA1B

Derivation of name. After the Latin *lingua* meaning tongue.

Holotype. EP1424/16 from the Lower Laetolil Beds, Kakesio 7.

Diagnosis. Teisseirei showing a tongue-like shape. One extreme is tapering and depressed in cross section, whereas the other is wider, somewhat rounded in cross section and truncated, ending in a flat irregular surface. The widest and more depressed section corresponds to the middle of the structure. In lateral view, it is slightly curved.

Description. All specimens show smooth external surface, whereas the filling is coarser. The holotype, EP1424/16 is 32 mm long, the tapering extreme is 9 mm high and 9 mm wide, 16 mm wide and 18 mm high in the middle, and 15 mm high and 16 mm wide at the truncated extreme (Fig. 5C, D). EP1475/14 is 40 mm long, the tapering extreme is 11 mm wide (broken in the other axis) in the middle, and in the other extreme is 17 mm high and 19 mm wide (Fig. 5E, F). EP853/04 is 44 mm long, the tapering extreme is 12 mm high and 12 mm wide, in the middle, the width is 21 mm, and the other extreme is 21 mm high and 24 mm wide (depressed section) (Fig. 5G, H). EP1709/12 includes two fragmentary specimens. One of them is 33 mm long, the tapering extreme is 14 mm wide (broken in the other axis), and towards the middle it is 17 mm high and 18 mm wide. The other specimen is 43 mm long, the tapering extreme is 8 mm wide and 8 mm high and towards the middle it is 21 mm high and 25 mm wide.

Ichnofamily CELLIFORMIDAE Genise, 2000
Celliforma ritchiei isp. nov.
Figure 6A–C

LSID. urn:lsid:zoobank.org:act:89F78501-9798-4F77-AB94-AADD0B52BA8C

Derivation of name. Dedicated to J.M. Ritchie who published the first study of the hymenopteran trace fossils from Laetoli.

Holotype. LAET 1980-18-920 – 18-1385 from the Upper Ndolanya Beds, Locality 18. The specimen, illustrated by Ritchie (1987, pl. II-14, fig. 11), is sectioned in three pieces, showing the complete empty chamber and the hood bearing the spiral closure sectioned longitudinally (Fig. 6A). It is selected as holotype because it displays all the diagnostic characters.

Paratypes. EP492/03 (Fig. 6B) and EP3747/00 (Fig. 6C) from the Upper Laetolil Beds, Locality 3 and Locality 22, respectively.

Diagnosis. Celliforma showing a conical spiral closure and a cylindrical prolongation over it composed of a darker and coarser material. The complete structure is subcylindrical, slightly curved and shows bilateral symmetry (e.g. in a sagittal plane one surface is flatter than the opposite one).

Remarks. The presence of a hood composed of coarse material over the spiral cap is unknown among *Celliforma* ichnospecies. It is reminiscent of the antechambers of *Palmiraichnus*, but the ichnospecies of the latter have a thick discrete wall around the cell and antechamber, which is lacking in all ichnospecies of *Celliforma*.

Description. In most cases, specimens are smooth and translucent, composed of a thin diagenetic wall of calcite crystals, which should not be confused with an original discrete wall, and empty internal cavity (Fig. 6A). Overgrowth of crystals result in darker areas inside the specimens mostly at the bottom, when observed with transmitted light. The hood is grey, darker than the chamber and is composed of coarser material (Fig. 6A). They are 11–22 mm long (n = 231), the shorter specimens (11–15 mm, n = 30) show poor preservation or short hoods (2–5 mm, n = 22), whereas the longest ones (19–22 mm, n = 44) have the longest hoods (up to 8 mm long). Most specimens (n = 154) are 16–18 mm long. The cell maximum widths are more constant, mostly 7–8 mm (n = 226), with a few cases being 5, 6 and 9 mm respectively (n = 5). Hoods are 2–8 mm long and 5–7 mm wide (n = 189).

Ichnofamily KRAUSICHNIDAE Genise, 2004
Ichnogenus LAETOLICHNUS nov.

LSID. urn:lsid:zoobank.org:act:3AC1E85E-C248-4A6F-BE33-2F3F97EB38E5

Derivation of name. After Laetoli, the site of its occurrence.

Type ichnospecies. Laetolichnus kwekai isp. nov.

Diagnosis. As for ichnospecies, by monotypy.

Remarks. The inclusion of these structures in Krausichnidae is tentative. Some specimens show evidence that two chambers may be connected to the same common cylinder. There is no other Krausichnidae with such morphology.

Laetolichnus kwekai isp. nov.
Figure 8

LSID. urn:lsid:zoobank.org:act:85241FAE-01E9-4905-9CFD-1D5FFF0F9ED9

Derivation of name. Dedicated to Amandus Kweka for his many valuable contributions to documenting and better understanding the prehistory of Tanzania.

Holotype. EP2937/00 from the Upper Laetolil Beds, Locality 10E (Fig 8A). *Paratypes*: EP1394/00 (Fig. 8B) and EP537/98 (Fig. 8C) from the Upper Laetolil Beds, Locality 6 and Locality 10, respectively.

Diagnosis. Structure composed of a central, roughly ellipsoid, subcylindrical to subtriangular, straight to curved chamber, showing rounded to elliptical cross section and prolonged in two small thin cylinders at both extremes. The central chamber is bilobate in some specimens. The prolongations are aligned with the long axis of the chamber in some specimens, but in others they are displaced from it.

Description. In plan view, some specimens show that one of the extremes of the chamber is more rounded while the other is more tapering, whereas in others both extremes are rounded or tapering (Fig. 8D, E). In lateral view, the outline may be bilobate (Fig. 8F), multilobate (Fig. 8G), single-lobed with one extreme rounded and the other tapering (Fig. 8B, D, E), or may be somewhat flat. Many specimens show elliptical cross sections (Fig. 8H). The interior of the chamber is empty and surrounded by a diagenetic translucent wall of calcite crystals. The accumulation of crystals may produce dark spots when seen with transmitted light (Fig. 8C, I). Broken and translucent specimens show that prolongations at the extremes are not connected in the interior (Fig. 8C, I), i.e. it is not a single cylindrical structure surrounded by a central chamber. In some specimens, one side of the chamber shows an ill-defined and irregular ridge (Fig. 8J). Many specimens are straight, whereas others are curved, sinuous (Fig. 8D, E), subtriangular (Fig. 7K) or form an open V (Fig. 8L). Aligning both prolongations, the central chamber may be oriented diagonally relative to it either in planar or lateral view. One of the specimens exhibits one prolongation with an expansion at the end (Fig. 8C). This expansion may be interpreted as a remnant of a second chamber (EP537/98). Specimens are 9–26 mm long (n = 46), most of them are 12–18 mm long (n = 30), 4–10 mm wide (n = 46) and 3–7 mm high. A specimen (WM 624/94) from the Tinde Member (~4.5–5.0 Ma) at Kininginila in the Manonga Valley (Harrison & Baker 1997) is similar to those from the Eyasi Plateau, but larger (31 mm long and 9 mm in maximum diameter) and more circular (Fig. 8M).

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DATA ARCHIVING STATEMENT

A list of all examined material is available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.v8921.

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