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Fossil bird eggs from the Pliocene of Laetoli, Tanzania: Their taxonomic and paleoecological relationships

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Abstract

Recent paleontological investigations at the Pliocene site of Laetoli and at neighboring localities on the Eyasi Plateau of northern Tanzania have led to the recovery of a sizable collection of fossil bird eggs. The material comes from the Upper Laetolil Beds, dated at ~3.6–3.8 Ma, and the Lower Laetolil Beds, dated at 3.8 Ma to older than 4.3 Ma. The preservation of relatively complete eggs (other than those of ratites) is an extremely rare occurrence in the fossil record, and Laetoli is the only locality in Africa that has produced such well-preserved eggs. Deposition of carbonatite air-fall tuffs led to the rapid burial of the eggs sub-aerially, and they were then preserved in paleosols that were geochemically conducive to their preservation.

The collection of fossil eggs from Laetoli can be assigned to at least five different species of ground-nesting birds, including two or three species of francolins, a species of guineafowl, and a larger bird of uncertain taxonomic status about the size of a bustard. Most of the eggs can be assigned to a large species of *Francolinus*, similar in size to the extant *F. afer* and *F. leucoscepus*. A smaller species of francolin, about the size of *Francolinus coqui* or *F. sephaena*, is also represented, but is less common. A single egg may represent an even smaller species of francolin, about the size of *Francolinus lathami* or *F. nahani*, but its attribution to *Francolinus* is less certain. The evidence of at least two species of *Francolinus* at Laetoli indicates that francolins were already taxonomically diverse in East Africa by the mid-Pliocene. Three eggs are similar in their overall dimensions and morphology to the living *Numida meleagris*, the helmeted guineafowl.

An avian community including at least one small species of francolin, a larger francolin, and a guineafowl (as well as ostriches and a vulture) implies that the paleoecology at Laetoli was likely to have been open woodland, bushland, savanna or grassland. However, francolins and guineafowl generally require low brush and thickets for refuge, as well as trees to roost in at night, so they tend to prefer mosaic ecotonal habitats offering open feeding areas with good visibility, but with dense vegetation cover and patches of woodland nearby.
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1. Introduction

Laetoli in northern Tanzania represents one of the most important Pliocene localities in sub-Saharan Africa (Leakey and Harris, 1987; Leakey, 1987a). It is particularly renowned for the discoveries of skeletal remains and footprint trails of the early fossil hominin, *Australopithecus afarensis* (Leakey and Hay, 1979; Hay and Leakey, 1982; Leakey, 1987b,c; Robbins, 1987; Tuttle, 1987). However, paleontological collections at Laetoli have also yielded a diverse associated fauna of fossil vertebrates, including over one hundred species of mammals, reptiles, and birds (Harris, 1987a). The previously published bird remains consist of 32 post-cranial elements (Watson, 1987) and two eggs of ground-nesting birds (Cunningham-van Someren, 1987), as well as eggshell

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fragments of *Struthio* spp. (Harrison and Msuya, 2005). Fossil footprints of ostriches, guineafowl, and other smaller birds have also been recorded (Leakey, 1987d). By comparison with the mammalian fauna, the avifauna is quite small, and comprises *Torgos* sp., *Francolinus* spp., *Numida* sp., *Streptopelia* spp., *Bubo* sp., and *Struthio* spp. (Watson, 1987; Harrison and Msuya, 2005).

Since 1998, the author has conducted renewed investigation at Laetoli, and this has led to the recovery of additional bird fossils. The collection now comprises over two hundred skeletal specimens, over eight hundred ostrich egg shell fragments, and more than twenty eggs. The skeletal material and ostrich eggshells are the subject of separate contributions to be published elsewhere (Harrison and Msuya, 2005), while the current study focuses on the fossil eggs.

A detailed description of the stratigraphy and geochronology of the Laetoli region has already been published (Hay, 1976, 1978, 1987; Hay and Reeder, 1978; Hay and Leakey, 1982; Drake and Curtis, 1979, 1987; Manega, 1993), so only the essential details are given below (Fig. 1). The Laetolil Beds are divisible into two major lithological units. The lower unit consists mainly of aeolian tuffs interbedded with airfall and water-worked tuffs. K–Ar dating of the lower unit indicates an age from ~3.8 Ma to more than 4.3 Ma (Drake and Curtis, 1987). The upper unit consists of a series of aeolian and airfall tuffs (Hay, 1987). The top of the unit is delimited by the Yellow Marker Tuff, with other tuffs throughout the sequence designated as marker tuffs (Tuffs 1–8). Radiometric dates provide a reliable age estimate for the Upper Laetolil Beds of 3.5–3.8 Ma. Overlying the Laetolil Beds is a series of tuffs and calcretes comprising the Upper and Lower Ndolanya Beds (Hay, 1987). Radiometric dates of 2.58 and 2.66 Ma for the Upper Ndolanya Beds (Ndessokia, 1990; Manega, 1993) are consistent with an earlier estimated age of ~2.5–2.7 Ma based on faunal correlations (Maglio, 1973; Harris and White, 1979; Beden, 1987; Gentry, 1987; Harris, 1987a,b; Hooijer, 1987).

A total of 21 eggs is now known from Laetoli and the nearby locality of Emboremony 1 (located about 20 km southwest of Laetoli) (Fig. 2). Of these, two eggs from Laetoli previously described by Cunningham-van Someren (1987), are referred to here, but the location of the specimens is unknown, and the originals have not been re-examined. The Laetoli eggs were collected during the course of three different expeditions; three eggs were found by Louis and Mary Leakey in 1959, eight were recovered by Mary Leakey from 1974–1978, and ten specimens have been collected by the author since 1998. Most of the fossil eggs (76%) are from Laetoli localities 9S, 10 and 10W, and derive from horizons situated stratigraphically between Tuff 3 and the base of the Upper Laetolil Beds, with an estimated age of ~3.6–3.8 Ma (Drake and Curtis, 1987). Three of the remaining specimens were recovered at Laetoli localities 9, 10E and 13, and are probably slightly younger, since most fossil vertebrates from these localities are from

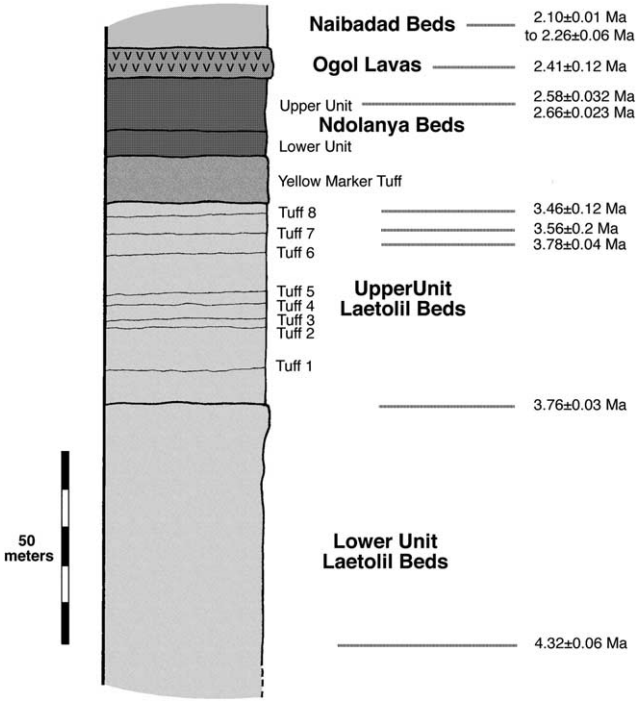

Fig. 1. Generalized stratigraphic section and radiometric dates for the sequence at Laetoli (after Hay, 1987; Drake and Curtis, 1987; Ndessokia, 1990; Manega, 1993).

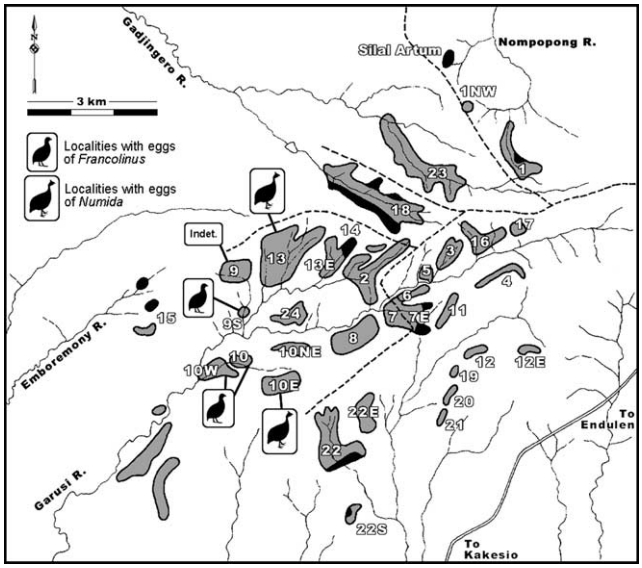

Fig. 2. Map of Laetoli, showing exposures of Upper Laetolil Beds (grey shading) and Ndolanya Beds (black shading), with white numbers and names referring to individual collecting localities. Localities that have yielded fossil bird eggs are indicated by the pictograms. Note the different distributions of eggs referred to *Francolinus* and *Numida*. Emboremony 1 is located about 15 km to the southwest of the Laetoli area.

between Tuffs 5 and 7, estimated to be ~3.5–3.6 Ma in age (Drake and Curtis, 1987). Finally, two eggs were recovered from the Lower Laetolil Beds at Emboremony 1, dating from 3.8 Ma to older than 4.3 Ma.

The preservation of relatively complete bird eggs (other than those of ratites) is an extremely rare occurrence in the fossil record, and Laetoli is the only locality in Africa that has produced such well-preserved eggs. The unusual sedimentary setting at Laetoli, characterized by sub-aerial deposition of carbonatite tuffaceous sediments, is undoubtedly an important factor contributing to this exceptional preservation. All of the taxonomically identifiable eggs can be attributed to ground-nesting galliform birds belonging to the families Phasianidae (quails and francolins) and Numididae (guineafowl). Descriptions of these specimens are presented below, and their significance for understanding the taphonomy, taxonomic diversity, and paleoecology of the Laetoli avifauna is discussed.

2. Description of fossil bird eggs from Laetoli

EP 652/01 (Laetoli Loc. 10, Upper Laetolil Beds between Tuffs 1 and 3) (Fig. 3). A pair of eggs derived from a single clutch, still partially preserved in a block of tuffaceous sediment. One egg (B) is entire, undeformed and well-preserved, except for a series of minor cracks on the exposed surface. The apex is still embedded in the matrix, so its length can only be estimated at ~44 mm. Its maximum diameter is 30.4 mm. The other egg (A) is broken, comprising slightly more than half of the egg. The equatorial circumference is incomplete, so it is not possible to measure the maximum diameter, but it can be estimated to have been ~30 mm. The broken margin is fairly fresh, indicating that the damage occurred as it eroded out of the sediment. The internal cavity is partially refilled with unconsolidated and reworked sediment. The internal surface of the shell is otherwise coated with a thin layer of calcite. The shell is relatively thick, with an average thickness at the broken margin of 0.7 mm. The eggs are uniformly cream colored with no evidence of pigmentation. The external surface is finely rugose, with numerous microscopic pinprick pores perforating the surface. The latter are irregularly distributed with a density in the equatorial region of ~60/cm^2. The equator in both eggs is situated closer to the blunt pole, about two-thirds of the distance from the apical pole, giving the egg an oval shape. The diameter/length index[1] is 69.1, indicative of a moderately long egg.

[1] The diameter/length index = maximum diameter at equator × 100/maximum length. This index is developed here to facilitate comparisons of the relative proportions of modern and fossil bird eggs. Based on this index, the following descriptive scheme is adopted: long, 55–65; moderately long, 65–75; short, 75–85; sub-spherical 85–95.

The original orientation of the eggs is still preserved. Egg A was lying horizontally in the sediment, whereas egg B had a long axis ~50° to the horizontal, with the apex of the egg directed inferiorly. The broken end of the egg is the more rounded pole. Its oblique orientation in the sediment meant that this pole was exposed and weathered first as the egg eroded out of the sediment. The two eggs were situated in close proximity, being separated by only 2.5 mm. The long axes of the two eggs in the horizontal plane diverged at ~65°. It is reasonable to infer, given the fragility of the eggs and their remarkable preservation, that they were not transported prior to deposition, and that they were buried where they were laid. There is no evidence that vegetation or pebbles lined a nest; rather it appears that the eggs were laid on bare ground in a shallow scrape.

The eggs are similar in size to extant medium-sized ground-nesting birds, such as the larger species of francolins (*Francolinus*), lapwings (*Vanellus*), and sandgrouse (*Pterocles*). In terms of diameter/length proportions and shape, the fossil eggs are most similar to those of francolins. Lapwing and sandgrouse eggs are similar to the fossils in being moderately long, although those of the former differ in being more pyriform in shape, while those of the latter are typically elliptical in shape, rather than oval. The eggs of *Francolinus* are generally relatively shorter than the fossils, ranging from moderately long to short, but they are similar in shape. Overall, the shape, proportions and size of the fossil eggs are most consistent with them belonging to *Francolinus*. The eggs of the crested francolin (*Francolinus sephaena*) are the most similar in shape, although they tend to be smaller in size and less elongated. In terms of overall size, the eggs approach those of the larger species of francolins from East Africa, such as *F. afer*, *F. rufopictus*, and *F. leucoscepus*. In support of this generic attribution is the relatively thickened and rugose eggshell, which is a characteristic feature of francolin eggs.

It cannot be determined that the pair of eggs preserved represents the full complement of the clutch, but the evidence is certainly consistent with a small clutch size. Francolins tend to have relatively large clutches (averaging 4–7 eggs) compared with lapwings and sandgrouse, which usually only have 3 eggs (less often 2 eggs), although it is not uncommon for extant species of francolins to have clutches containing as few as 3 eggs (Maclean, 1993; Tarboton, 2001; Madge and McGowan, 2002).

These eggs can be attributed to a large species of *Francolinus*, similar in size to the living East African spurfowl, *F. afer* (red-necked spurfowl), *F. rufopictus* (grey-breasted spurfowl), and *F. leucoscepus* (yellow-necked spurfowl).

EP 707/01 (Laetoli Loc. 10W, Upper Laetolil Beds between Tuffs 1 and 3) (Fig. 4a). An almost entire, but slightly crushed egg. Portions of the shell have been

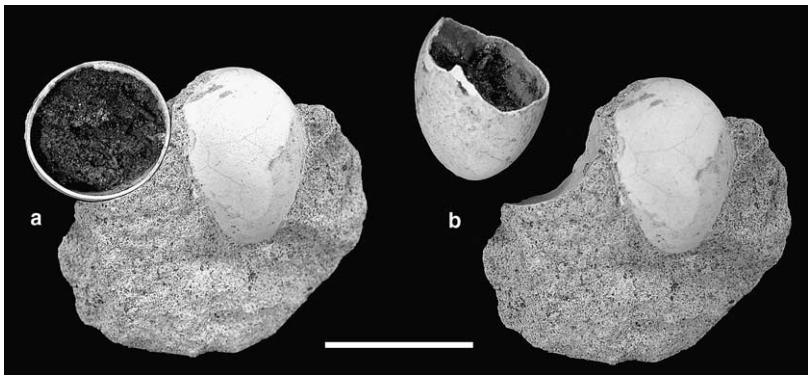

Fig. 3. Fossil bird eggs, EP 652/01, from Laetoli referred to *Francolinus* sp., large species. Block of sediment in which (a) the two eggs (A and B) are shown in the position in which they were preserved, and (b) with one egg (A) removed. Scale bar = 30 mm.

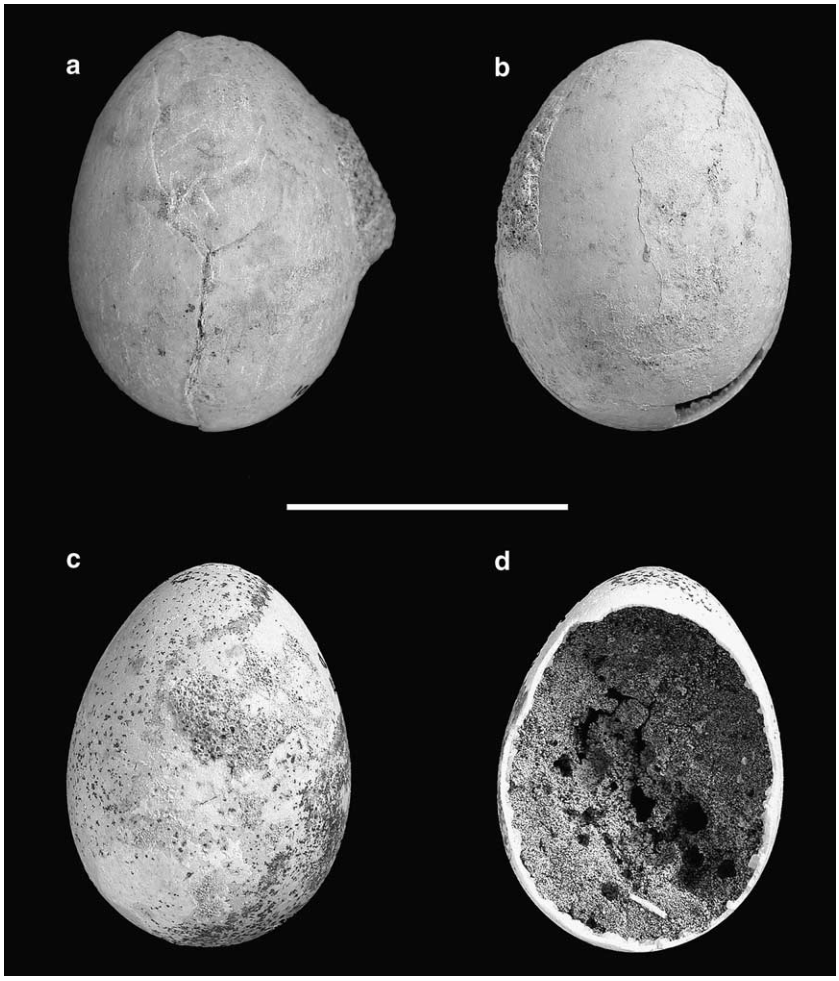

Fig. 4. Fossil bird eggs from Laetoli referred to *Francolinus* sp., large species. (a) EP 707/01; (b) EP 1000/03; (c) EP 1107/03; (d) EP 1107/03, showing infilling sediment in internal cavity that has been bioturbated by insects. Scale bar = 30 mm.

lost through erosion and pre-depositional breakage. The apex of the egg is missing and a pronounced longitudinal crack extends the length of the egg with slight displacement (~1 mm) of the two halves of the egg, as well as slight telescoping of the broken edges of the shell at the blunt pole of the egg. A further fragment of shell is missing from the equatorial region. Sediment is exposed at both locations where shell is missing, indicating that the interior cavity was entirely filled with consolidated fine-grained tuffaceous sediments. This implies

that the egg was damaged prior to deposition, and that wind-borne volcanic ash was blown into the exposed apertures (by contrast, eggs that were buried entire, such as EP 652/01, retain hollow interiors lined with a thin layer of calcite crystals that formed subsequent to burial).

The egg is 43.2 mm long (but since the tip of the egg is missing, it was probably ~44 mm when entire). The maximum diameter is 30.7 mm. These measurements provide a diameter/length index of 69.8, indicating a moderately long egg. The egg is oval, with the equator positioned about two-thirds along the length of the egg towards the rounded pole.

The egg is cream colored and of uniform coloration, with no indication of pigmentation. The eggshell is relatively smooth, but examination under a low-powered microscope reveals the presence of irregularly distributed pinprick pores. The pores are elongated, with their long axis generally aligned with the long axis of the egg. The pores have a density of ~80/cm^2.

The size and morphology of the egg are closely similar to those of EP 652/01, and there is little doubt that it belongs to the same taxon, *Francolinus* sp.

EP 1000/03 (Laetoli Loc. 10, Upper Laetolil Beds between Tuffs 1 and 3) (Fig. 4b). An almost entire, but slightly crushed egg. Sub-parallel cracks pass longitudinally and slightly obliquely around the egg, and this has resulted in the loss of thin slivers of shell in three locations. This damage was acquired post-depositionally, as indicated by the fresh breaks, and it is clear that the egg was buried and preserved entire and undistorted. The exposed internal surface of the egg was not infilled with sediment, but has a thin lining of calcite. Shell thickness cannot be measured directly, but estimates based on the broken margins suggest an average thickness of ~0.6 mm. The shell is uniformly cream colored with no pigmentation. The surface of the shell is relatively smooth, with numerous pinprick pores arranged in irregular fashion. Pores are barely visible with the naked eye, and their density in the equatorial region is 66/cm^2. The egg is oval in shape, with the equator located one-third of the length from the rounded pole. The maximum length of the egg is 40.8 mm and the maximum diameter is 32.1 mm, with a diameter/length index of 76.5 (i.e., short). The egg is close in size and identical in morphology to EP 652/01 and EP 707/01. It can be attributed to a large species of *Francolinus*.

EP 1107/03 (Laetoli Loc. 10W, Upper Laetoli Between Tuffs 1 and 3) (Fig. 4c and d). A partial egg, broken longitudinally, but preserving slightly more than half the egg, so that both poles are present. The broken margin has relatively fresh breaks, indicating that the egg was more complete when initially buried. The internal cavity is slightly less than half filled with fine-grained tuffaceous sediment that had settled inside the egg prior to burial. A small fragment of eggshell, 4.4 mm long, is preserved in the infilling matrix. These observations indicate that that the egg was broken before being buried, and that that the egg was laying on its side at the time (since the surface of the infill is aligned with the long axis of the egg). In addition, in the center of the egg, the infilling sediment has been disrupted by bioturbation by small insects. There is evidence of tunneling by larvae, as well as external smooth-walled casts of at least five pupal cases, of a species of dipteran. The dimension of the most complete pupal cast is 5.0×2.6 mm. Presumably a female insect entered the egg at a break in the shell prior to burial and laid its eggs in or on the surface of the unconsolidated wind-borne sediments, and the larvae pupated inside. The exposed internal surface of the shell is lined with a thin layer of calcite. The external surface has patches of adhering calcite and dark manganese staining. Otherwise, the egg is smooth and uniformly pale yellow–brown (somewhat darker than the other eggs from Localities 10W, 10 and 9S).

The length of the egg is 41.3 mm and its maximum diameter is 30.5 mm. The diameter/length index is 73.8 (i.e., short). It is oval in shape, with its equator situated about one-third from the blunt pole of the egg. The pore distribution and disposition cannot be determined. The egg is consistent in size and morphology with EP 652/01, EP 707/01 and EP 1000/03, and can also be assigned to *Francolinus* sp.

EP 2078/03 (Emboremony 1, Lower Laetolil Beds) (Fig. 5a and b). Entire, but crushed egg, with slight compression in the transverse plane. One side of the egg has lost shell fragments from about one-third of its area, and a series of large cracks radiate out from this damaged area. The internal surface is completely filled with primary air-fall tuff. Most of the sediment exposed in the internal cavity has a smooth surface that was evidently covered with shell at the time of burial, but a central area of roughened matrix marks the area of pre-burial damage to the shell through which volcanic ash was accumulated. The original break formed a sub-rectangular aperture less than 200 mm^2 in area. Once buried, the weight of the sediment deformed the egg so that the equatorial diameter is only 87% of its original dimension.

The egg is oval, with the equator located about one-third from the bluntly rounded pole. The length of the egg is 42.9 mm, the diameter at the equator is 32.7 mm, and the diameter/length index is 76.2 (i.e., short). The egg shell is thin, with an average thickness of only 0.4 mm. The egg ranges in color from cream to pale yellow–brown. Pores are not visible over most of the external surface due to adhering matrix and calcite, but a few areas have a pore density of ~80/cm^2. This specimen is similar in size and morphology to the eggs described above, and can be referred to the same species of *Francolinus*.

LIT 59-269 (Laetoli, probably Laetoli Loc. 10 or 10W, Upper Laetolil Beds) (Fig. 5c and d). A partial

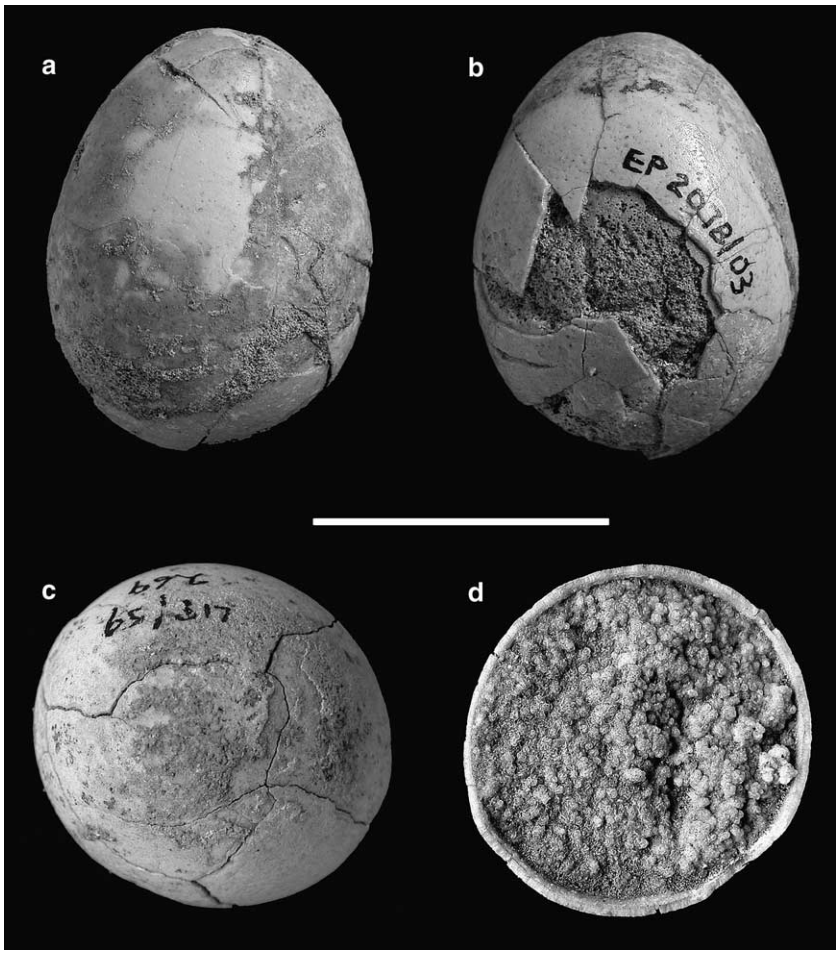

Fig. 5. Fossil bird eggs from Laetoli and Emboremony referred to *Francolinus* sp., large species. (a) EP 2078/03, best-preserved surface; (b) EP 2078/03, damaged surface; (c) LIT 59-269, oblique view of blunt pole of partial egg; (d) LIT 59-269, view of internal cavity of egg with thick layer of calcite crystals. Scale bar = 30 mm.

egg preserving an obliquely fractured section of the blunt pole, comprising about one-third of the original egg. The external surface is slightly weathered and exhibits a number of radial and longitudinal fractures. No pores are visible. The internal surface is filled with secondarily deposited calcite crystals, which indicate that the egg was buried intact. The shell is relatively thick, with an average thickness of ~1.1–1.2 mm. It is consistent in size and shape with EP 652/01, EP 707/01, and EP 1000/03.

The provenience of LIT 59-268 and LIT 59-269 is not recorded, but it is known that Louis and Mary Leakey worked primarily at Localities 10, 10E and 10W during their short field season at Laetoli in 1959 (Leakey, 1987a). Such a provenience can also be inferred from the fact that most of the specimens of certain provenience recovered subsequently from the Upper Laetolil Beds have come from Localities 10 and 10W.

This specimen is morphologically and metrically comparable to the eggs of *Francolinus* sp.

LIT 59-268 (Laetoli, probably Laetoli Loc. 10 or 10W, Upper Laetolil Beds) (Fig. 6). An almost entire egg, cracked and slightly deformed, with a small triangular piece of shell missing from the apical end. The internal cavity of the egg appears to be entirely infilled with sediment, which must have entered through the tiny perforation at the apex. A large crack transects the egg longitudinally. The egg is oval in outline, with the equator situated closest to the blunt pole, about one-third along the length of the shell. The maximum length and diameter of the egg is 39.4 and 30.7 mm, respectively, which yields a diameter/length index of 77.9 (i.e., short). The shell is uniformly cream colored. Small elliptical pinprick pores, with their long axes aligned with the long axis of the egg, have a density estimated at 80–100/cm^2. The specimen is comparable in size and morphology to EP 652/01, EP 707/01, and EP 1000/03, all attributable to *Francolinus* sp.

EP 535/98 (Laetoli Loc. 10, Upper Laetolil Beds between Tuffs 1 and 3). This specimen consists of a fragment of eggshell measuring 20.8 × 18.2 mm. The outer surface of the shell is weathered, accentuating the size of the pores, which are now visible with the naked eye. The pore density is ~60/cm^2, comparable to that of

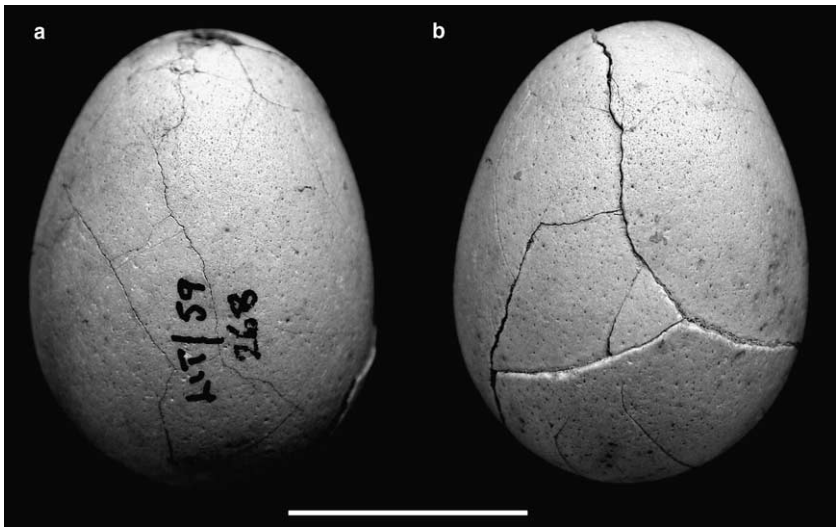

Fig. 6. Fossil bird egg, LIT 59-268, from Laetoli referred to *Francolinus* sp., large species. (a) and (b) two different views. Scale bar = 20 mm.

EP 652/01. Shell thickness is only ~0.4 mm, thinner than in EP 652/01 and 707/01, but this may have been affected by weathering. The internal surface is encrusted with calcite crystals, suggesting that the egg was buried whole. Since the shell curvature matches that of the specimens described above, and the general morphology is consistent, it is reasonable to infer that it belongs to the same taxon, *Francolinus* sp.

EP 708/01 (Laetoli Loc. 10W, Upper Laetolil Beds between Tuffs 1 and 3). Another fragment of eggshell measuring 20.8 × 18.9 mm. The external surface of the shell is well-preserved, with irregularly arranged elliptical pores. Pore density is ~60/cm^2. Shell thickness is 0.6 mm, only slightly thinner than that of EP 652/01. The internal surface has a thick layer of calcite crystals suggesting that the egg was entire when initially buried. Based on its size and morphological attributes it can be referred to *Francolinus* sp.

EP 1275/01 (Laetoli Loc. 9S, Upper Laetolil Beds below Tuff 2). A fragment of an egg comprising the apical pole. The surface is weathered and cracked, and it was evidently exposed to weathering for some time after fossilization. The internal surface is thickly encrusted with calcite crystals, which suggest that it was buried as an entire egg. The pore density is ~80/cm^2, and shell thickness is ~0.5 mm. The curvature, general morphology, and shell thickness are all closely comparable to *Francolinus* sp.

EP 1276/01 (Laetoli Loc. 9S, Upper Laetolil Beds below Tuff 2). Three fragments of eggshell collapsed together and cemented by thin layers of adhering sediment. These were apparently broken fragments of a single egg lying on the land surface at the time of the eruptive event that buried them. The middle piece is the largest, with an area of ~200 mm^2, and this is closely overlain by a small piece of shell. The remaining eggshell piece is convex in the opposite plane. Shell thickness is 0.7 mm. The pores are small and inconspicuous, oval to circular in outline, with a pore density in the ~60–80/cm^2 range. The curvature of the shell fragments, the surface morphology, and the shell thickness are comparable to those of *Francolinus* sp.

LAET 75-532A (Laetoli Loc. 10, Upper Laetolil Beds). Fragment of egg consisting of the pointed apical pole only. The fragment measures 21.1 × 20.6 mm. The shell is relatively thick, with an average thickness of 0.7 mm. Pore density is ~100/cm^2. The shell is uniformly cream-colored. The contour of the apical pole suggests that the egg may have been similar in shape to those described above, although it does appear to have been slightly larger in size. Overall, the morphology suggests that LAET 75-532A can be assigned to *Francolinus* sp.

LAET 75-532B (Laetoli Loc. 10, Upper Laetolil Beds). A fragmentary specimen consisting of slightly more than half of an egg, still embedded in a block of sediment. The block shows that the egg was isolated, with no other eggs from the clutch in close association. The internal cavity of the shell is hollow, except for a lining of calcite of variable thickness. It is evident that the specimen was buried as an entire egg. The shell is relatively thick, with an average thickness of 0.8 mm. The maximum diameter of the egg is 32.1 mm. It is not possible to estimate the overall length of the egg or to reconstruct its original shape. Judging from the diameter, it was slightly larger than EP 652/01 and EP 707/01, but probably belongs to the same taxon, *Francolinus* sp.

LAET 78-5371 (Laetoli Loc. 10, Upper Laetolil Beds). A fragment of shell with an area in excess of 600 mm^2. The surface of the shell is weathered, and the circular to elliptical pores have been accentuated so that they are now clearly visible with the naked eye.

Shell thickness averages 0.7 mm. The internal surface of the shell preserves adhering sediment that indicates that the egg was broken at the time of deposition. Given its overall similarity to the eggs described above, it is also referred to *Francolinus* sp.

LAET 76-3965 (Laetoli Loc. 9S, Upper Laetolil Beds below Tuff 2) (Fig. 7a). This specimen consists of a crushed and fragmentary egg in a block of sediment that also preserves a smooth depression representing the external mold of a second egg (not preserved) of similar size and shape. The two eggs were separated by a minimum distance of 16.7 mm, and their long axes are aligned at 130° relative to each other in the horizontal plane. In addition, fragments of eggshell are preserved in the intervening space. This suggests that the clutch was scattered and the eggs fragmented prior to burial. The estimated length of the egg is 35 mm. The length and diameter of the depression (which provides minimum dimensions only) is 32×28 mm. The egg appears to have been elliptical to sub-spherical in shape. It is smaller than EP 652/01 and EP 707/01 (which are about 25% longer), but matches the dimensions of LAET 75-1438 (see below) described by Cunningham-van Someren (1987). These smaller eggs from Laetoli are similar in size to small species of francolins (*Francolinus*), lapwings (*Vanellus*) and sandgrouse (*Pterocles*) among extant ground-nesting birds. In terms of its shape, however, LAET 76-3965 best matches those of *Francolinus*, being most similar in overall size to the living *Francolinus coqui* or *F. sephaena*.

LAET 75-1438 (Laetoli Loc. 9S, Upper Laetolil Beds below Tuff 2). This specimen was briefly described by Cunningham-van Someren (1987). The present author has not had the opportunity to study the original specimen. The egg measures 35.5×28.5 mm, and according to Cunningham-van Someren (1987) it provides an almost perfect match in size and shape for eggs of *F. sephaena*.

LIT (no accession number) (Laetoli, probably Loc. 10 or 10W, Upper Laetolil Beds) (Fig. 7b). A relatively complete egg, missing only a portion of the blunt pole. This specimen is of uncertain provenience, but most likely comes from Laetoli Locality 10 or 10W (see LIT 59-269 above for a fuller explanation). The shell is well-preserved with just a few superficial cracks. The internal cavity contains fine-grained primary tuff that presumably filled the broken egg at the time of deposition (and confirms its Laetoli provenience). Pores are generally not visible, except in a few places where slight weathering has eroded the surface to expose small, evenly dispersed pinprick pores. It is not possible to estimate pore density. The shell is very thin, with an average thickness of only 0.1 mm. The egg is uniformly cream colored, except for small spots and patches of dark grey manganese staining. The egg is oval in shape, with a bluntly rounded apex and an equator that is situated approximately mid-way along its length. The length of the egg can be estimated to be ~29 mm, while its maximum diameter is 21.1 mm. This provides a diameter/length index of 72.8 (i.e., short). This egg is estimated

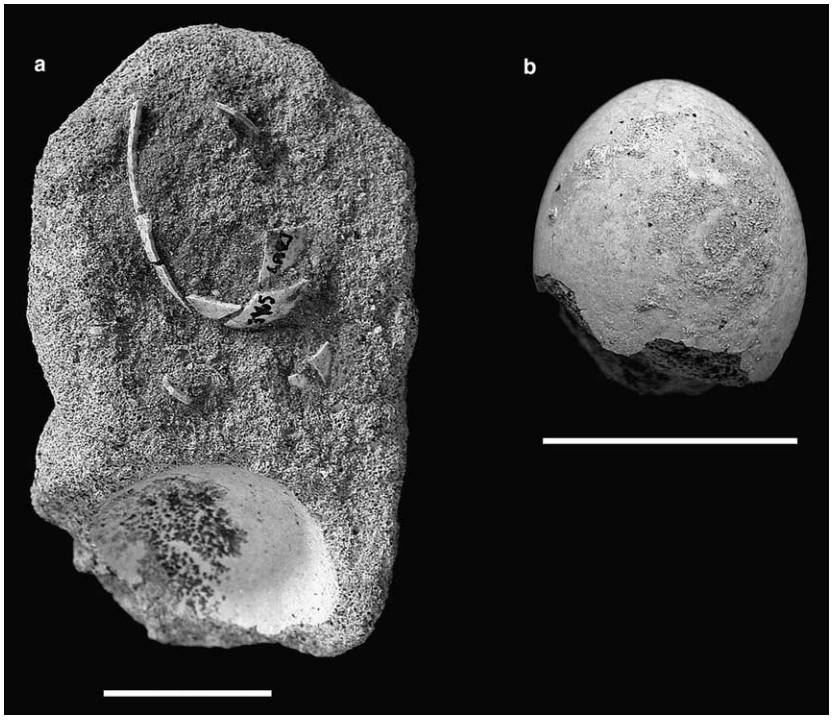

Fig. 7. Fossil bird eggs from Laetoli referred to *Francolinus*. (a) LAET 75-3965, block of sediment containing a broken egg and a natural cast of a second egg, *Francolinus* sp., small species. (b) LIT (no accession number), partial egg, cf. *Francolinus*. Scale bars = 20 mm.

to be somewhat smaller (more than 20% shorter overall) than LAET 76-3965 and LAET 75-1438, and differs in having a relatively narrower diameter and the equator situated closer to the apical pole.

The fossil egg is similar in size to those of small species of francolins (*Francolinus*), quails (*Corturnix*), coursers (*Cursorius*), plovers (*Charadrius*), and pratincoles (*Glareola*) among extant ground-nesting birds. The oval shape and blunt apex of the fossil egg distinguishes it from those of plovers and quails, which tend to have pyriform eggs with more pointed apices. It differs from those of coursers in being relatively longer in relation to its diameter. Overall, the fossil is most similar in shape and proportions to eggs of *Francolinus* and *Glareola*. If it belongs to a francolin then it would be attributable to a different, somewhat smaller, species from that represented by LAET 76-3965. The smallest species of *Francolinus* found in East Africa today, with eggs comparable in size to the fossil, are *F. lathami* and *F. nahani*, presently restricted to forested regions of Uganda and northwestern Tanzania (Stevenson and Fanshaw, 2002). The most common pratincole found today in East Africa is the collared pratincole (*Glareola pratincola*), which usually nests colonially on lakeshores and riverine flats (Zimmerman et al., 1996), and seems an unlikely attribution for the fossil given what we know about the Pliocene bird fauna and paleoenvironment at Laetoli. Given the evidence, *Francolinus* seems to be the most likely taxonomic assignment for the fossil, but its attribution should be considered provisional only.

EP 1358/01 (Emboremony 1, Lower Laetolil Beds) (Fig. 8a). A fragmentary specimen, comprising slightly more than half of an egg broken along its long axis and lacking its apical pole. The length of the preserved portion is 41.9 mm, but its original length can be estimated to be 53 ± 1 mm. The maximum diameter is 36.3. The shape of the egg is oval, with a diameter/length index of 68.5 ± 1.3 (i.e., moderately long). This specimen differs from EP 652/01, EP 707/01, and EP 1000/03 (assigned to *Francolinus* sp.) in being somewhat larger in size (~20% longer) and having a more strongly tapering pointed pole and more rounded blunt pole. The shell is also much thinner (0.3 mm), especially given the larger overall size of the egg. The surface of the shell is finely crenulated, and no pores are visible. The egg is infilled with pale grey tuffaceous sediment that represents primary airfall tuff or aeolian tuff deposited directly in the internal cavity at the time of or shortly after the volcanic eruptive event.

This specimen is comparable in size to eggs of extant species of helmeted and crested guineafowl (*Numida* and *Guttera*) and smaller bustards or korhaan (*Eupodotis*) among dry country ground-nesting birds. It differs in shape from those of *Eupodotis*, which are elliptical to spherical in shape, rather than oval. The fossil egg matches closely the size and shape of those of helmeted guineafowl (*Numida meleagris*), although the latter do tend to have a slightly greater diameter relative to their length (extant helmeted guineafowl eggs average 52.7×42.3 mm, index = 80.3, Ogawa et al., 2002; 52.6×40.2 mm, index = 76.4, Maclean, 1993). In addition, measurements of eggshell thickness in captive guineafowl indicate that the eggs are almost twice as thick as those of the fossil eggs (Ogawa et al., 2002). Nevertheless, despite these differences, the overall morphology of EP 1358/01 does indicate that it can be assigned with some confidence to Numididae, and most probably to *Numida* (Fig. 8).

LAET 76-3840 (Laetoli Loc. 13, Upper Laetolil Beds) (Fig. 8b). A large fragment of egg measuring 41.8×39.3 mm. The distribution of the associated sediment indicates that the egg was fragmentary at the time

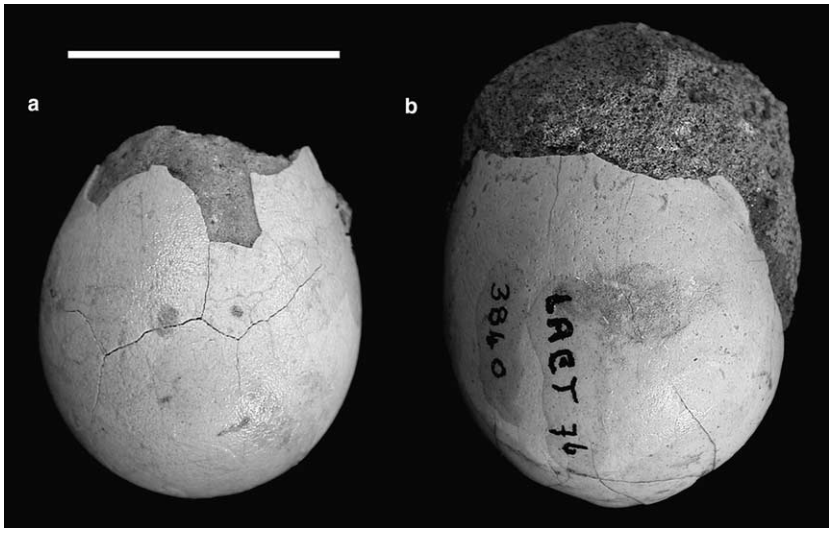

Fig. 8. Fossil bird eggs from Laetoli and Emboremony referred to *Numida* sp. (a) EP 1358/01; (b) LAET 76-3840. Scale bar = 30 mm.

of deposition of the tuff. The minimum diameter of the egg is 38.7 mm, but the original maximum diameter is estimated to have been 40–42 mm. The shell is relatively thin (0.3 mm) as in EP 1358/01. The pores are barely visible to the naked eye, circular to elliptical in shape, with a density of $\sim$80/cm^2, and their long axis is arranged parallel to the long axis of the egg. LAET 76-3840 is similar in shape and general size to EP 1358/01, although it has a slightly greater maximum diameter. It can be assigned to *Numida* sp.

LAET 75-2003 (Laetoli Loc. 10E, Upper Laetolil Beds). This specimen was briefly described by Cunningham-van Someren (1987). The present author has not seen the original specimen. According to Cunningham-van Someren (1987), the egg measures 51 × 39 mm, has a relatively thick shell, and is closest in size and morphology to eggs of *N. meleagris*.

LAET 74-268 (Laetoli Loc. 9, Upper Laetolil Beds). An eggshell fragment, approximately 450 mm^2 in area. The fragment has a low convexity, suggesting that it was derived from an egg that was perhaps slightly larger than EP 1358/01. Shell thickness is 0.8 mm. Unfortunately, the shell surface has been finely coated with sediment, so microscopic details are not discernable. The internal surface was infilled with sediment. This may belong to a species somewhat larger than the helmeted guineafowl, and is best left unattributed until more complete material is available.

3. Discussion

The well-preserved bird eggs from the Pliocene of Laetoli (dating from $\sim$3.5 Ma to older than $\sim$4.3 Ma) are a unique occurrence in the fossil record of Africa. Their exceptional preservation is related to the unusual depositional and taphonomic setting at Laetoli. Comparisons of the preservation of the eggs allow some inferences to be made about the different conditions under which the eggs were buried and fossilized. In addition, from a paleobiological perspective, the collection of fossil eggs allows some preliminary conclusions to be made concerning the taxonomic diversity, evolutionary history, and paleoecology of the avifauna at Laetoli.

3.1. Preservation and taphonomy

The unique sedimentary context at Laetoli, characterized by sub-aerial deposition of carbonatite tuffaceous sediments, undoubtedly contributed to the exceptional preservation of the eggs. Entire and broken (or hatched) eggs, originally laid on the ground surface in shallow scrapes, were buried by successive inundations of air-fall tuffs. Once buried, the geochemistry and alkalinity of the soils favored preservation of the eggshell. Of the eggs that are well enough preserved, seven were apparently buried entire, while ten were broken or damaged prior to burial. The amount of time that eggs were exposed on the surface is difficult to estimate. None of the eggs shows any marked degree of weathering, and their fragile nature would suggest that they were buried relatively rapidly. Evidence that small dipterans pupated inside the internal cavity of EP 1107/03 may indicate that some damaged eggs were exposed on the surface. Hayward et al. (1989) have reported finding a single dipteran larva in a broken egg buried by ashfall in a modern setting. However, given the number and small size of the larvae in EP 1107/03 the most likely scenario is that the insect eggs were laid on the internal surface of the broken bird egg prior to its burial, rather than the alternative possibility that the larvae or adult insect burrowed down through the sediment to reach the buried egg.

The reason that the majority of eggs have been found in the Upper Laetolil Beds below Tuff 3 at Localities 9S, 10, and 10W, is probably due to the fact that these tuffs are generally more weathered, with a richer clay content, than corresponding sediments from other Laetoli localities (Hay, 1987). It is also noteworthy that the eggs of *Francolinus* were collected from the Upper Laetolil Beds below Tuffs 3 at Localities 9S, 10, and 10W, while those referred to *Numida* were recovered from Localities10E and 13 (at which the main fossiliferous horizons are Upper Laetolil Beds between Tuffs 5 and 7). This could imply taphonomic differences in the preservation of eggs of different species, deposition of tuffs during different nesting seasons (for example, *N. meleagris* generally breeds during the early part of the rainy season, while the larger species of *Francolinus* breed during the end of the rainy season; Madge and McGowan, 2002), or ecological differences that result in species with different nesting preferences being represented.

3.2. Taxonomy and evolution

The collection of fossil eggs from Laetoli can be assigned to at least five different species of ground-nesting birds, including two or three species of francolins, differentiated mainly by size, a species of guineafowl, and a larger species of uncertain affinities. A summary of the taxonomic attribution of the eggs, as well a list of specimens, is presented in Table 1.

Most of the eggs from the Upper Laetolil Beds can be assigned to a large species of *Francolinus*, similar in size to the living spurfowl, *F. afer* (red-necked spurfowl), *F. rufopictus* (grey-breasted spurfowl), and *F. leucoscepus* (yellow-necked spurfowl). The best-preserved specimens are EP 652/01, EP 707/01, EP 1000/03, EP 1107/03, and LIT 59-268. Several more fragmentary specimens are provisionally attributed to the same taxon based on size and general morphological characteristics (Table 1). In addition, a relatively complete egg, EP 2078/03, from the Lower Laetolil Beds at Emboremony

Table 1
Classification of the bird eggs from the Laetolil Beds, Laetoli, Tanzania

Taxon	Assigned specimens[a]
Order Galliformes	
Family Phasianidae	
Francolinus sp., large species	EP 535/98, EP 652/01, EP 707/01, EP 708/01, EP 1275/01, EP 1276/01, EP 1000/03, EP 1107/03; EP 2078/03, LAET 75-532A, LAET 75-532B, LAET 78-5371, LIT 59-268, LIT 59-269
Francolinus sp., small species	LAET 75-1438[b], LAET 76-3965
cf. *Francolinus*	LIT (no accession number)
Family Numididae	
Numida sp.	EP 1358/01, LAET 75-2003[b], LAET 76-3840
Aves indeterminate	LAET 74-268

[a] Accession prefix abbreviations: EP—collections made by expeditions led by the author at Laetoli and neighboring localities on the Eyasi Plateau from 1998–2003 (material housed in the National Museum of Tanzania, Dar es Salaam); LAET—collections recovered by Mary Leakey from 1974–1981 (material housed in the National Museum of Tanzania, Dar es Salaam); LIT—collections made by Louis and Mary Leakey at Laetoli in 1935 and 1959 (material housed in the National Museums of Kenya, Nairobi).
[b] Specimens briefly described by Cunningham-van Someren (1987), but not seen by the author.

1 can be assigned to the same taxon. No fossil birds (other than ostrich eggshell fragments; Harrison and Msuya, 2005) have previously been recognized from the Lower Laetolil Beds, so EP 2078/03 (and EP 1358/01 below) represents the first record (Table 2).

In addition, a smaller species of francolin, about the size of the extant *F. coqui* (coqui francolin) or *F. sephaena* (crested francolin), is represented by LAET 76-3965 and LAET 75-1438. A single specimen, collected by Louis and Mary Leakey in 1959, might represent an even smaller species of francolin, about the size of *F. lathami* or *F. nahani*, but at present, its attribution to *Francolinus* is considered provisional.

A small collection of fossil bird bones has been described from Laetoli (Watson, 1987), and the most common taxon (more than 50% of specimens) in the Upper Laetolil Beds is a large species of *Francolinus*, about the size of *F. leucoscepus*. The tarsometarsus of this taxon bears a well-developed spur, as in most extant species of francolins (Watson, 1987). These skeletal remains are a good match in size for the larger francolin eggs described here. Watson (1987) also described two postcranial specimens of a smaller francolin, about the size of *F. coqui*, from the Upper Laetolil and Ndolanya Beds. These are consistent in size with the small francolin eggs.

Fossil francolins are known from several other Pliocene localities in Africa (i.e., Langebaanweg, Duinefontein, and Kromdraai in South Africa) dating back to ~5 Ma (Pocock, 1970; Rich, 1974, 1980; Olson, 1985; Crowe, 1992). Possible records of francolins at Arrisdrift, Namibia and Rusinga Island, Kenya may extend the record of the group back to the early Miocene (Harrison, 1980; Crowe, 1992). Genetic data imply that African francolins diverged from their sister taxon by at least the late Miocene (Crowe et al., 1992; Bloomer and Crowe, 1998). The evidence of two species of *Francolinus* at Laetoli, and possibly three, indicates that francolins were already taxonomically diverse in East Africa by the mid-Pliocene.

Three fossil eggs, EP 1358/01, LAET 76-3840, and LAET 75-2003, are attributed to *Numida* sp. EP 1358/01 is from the Lower Laetolil Beds at Emboremony 1, while the remaining two specimens were recovered from the Upper Laetolil Beds. Based on their overall dimensions and morphology, they are most similar to the living *N. meleagris*, the helmeted guineafowl, which is extremely common in the Laetoli area today. Watson (1987) has described fossil bones assignable to *Numida* sp. from the Upper Laetolil Beds, and these represent about one-third of the fossil birds collected from this stratigraphic unit. In addition, footprints of guineafowl are numerous in the Upper Laetolil Beds (Leakey, 1987d). Fossil guineafowl have not been identified at other Plio-Pleistocene localities in Africa, but they are known from late Pleistocene sites in central Europe (see Brodkorb, 1964).

Table 2
Summary of dimensions of bird eggs from the Laetolil Beds[a]

Taxon	Maximum length		Maximum diameter		Index[b]		Thickness of eggshell	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Francolinus sp., large	42.1	39.4–44.0	31.2	30.4–32.7	73.9	69.1–77.9	0.7	0.4–1.2
Francolinus sp., small	35.3	35.0–35.5	28.5	–	80.3	–	–	–
cf. *Francolinus*	29.0	–	21.1	–	72.8	–	0.1	–
Numida sp.	52.0	51.0–53.0	37.7	36.3–39.0	72.5	68.5–76.5	0.3	0.3

[a] All measurements in mm.
[b] Diameter/length index = maximum diameter at equator × 100/maximum length.

One specimen, LAET 74-268, cannot be readily attributed to a particular taxon. This egg is estimated to be slightly larger than those of *Numida* sp., and is distinguished morphologically in having thicker eggshell. It may correspond better is size with the somewhat larger vulturine guineafowl (*Acryllium vulturinum*). Among extant birds, there are few ground-nesting, non-wetland species that have eggs larger than those of guineafowl. Excluding ostriches, the largest eggs are produced by members of the Otididae (bustards), which have average egg lengths ranging from 49–83 mm (Maclean, 1993; Tarboton, 2001). It is possible that the fossil egg belongs to one of the smaller species of bustards. No skeletal remains of this taxon have been reported from Laetoli, but a single undescribed fossil footprint of a bird about the size of a kori bustard (*Ardeotis kori*) was identified in Tuff 7 at Laetoli Loc. 4 in 1998.

3.3. Paleoecology

There has been some debate about the inferred paleoecology at Laetoli during the time of the deposition of the Upper Laetolil Beds. Earlier interpretations of the faunal, paleobotanical, and geological evidence (Bonnefille and Riollet, 1987; Denys, 1987; Gentry, 1987; Harris, 1987a,b; Hay, 1987; Leakey, 1987a; Verdcourt, 1987; Walker, 1987; Watson, 1987) suggested that Laetoli was an arid to semi-arid grassland with scattered bush and tree cover, and possibly patches of acacia woodland. In contrast, Andrews (1989) has argued that the structure of the mammalian community indicates a more heavily wooded environment than that acknowledged by most previous researchers. Additional support for this contention comes from the isotopic and faunal analyses of Cerling (1992), Reed (1997), and Musiba (1999). Eggs of ground-nesting birds are especially useful in paleoecological reconstruction because of the certainty that they have not been transported far from their original locations and that they were preserved in habitats that were conducive for those species to breed (unlike carcasses and skeletal elements, which may end up far removed from that species' preferred habitats, due to transportation and translocation).

Francolins are well-represented in East Africa today, with 19 species currently recognized (Stevenson and Fanshaw, 2002). They are found in a diversity of habitats, ranging from tropical forest to montane forest, open woodland, grassland, and moorland. However, the majority of species occur in areas of open woodland, savanna, bush, and grassland (Hall, 1963; Sinclair et al., 1993; Zimmerman et al., 1996; Stevenson and Fanshaw, 2002; Madge and McGowan, 2002). Most species are relatively shy, and prefer areas with adequate grass or bush cover in which to flee if disturbed, as well as trees to roost in at night. Typically, francolins lay their eggs on the ground in shallow scrapes, about 10–20 cm in diameter, that are unlined or sparsely lined with dry grass blades (Tarboton, 2001; Madge and McGowan, 2002).

In the southern Serengeti today, the following species of francolins occur: the small-size quail-francolins *F. coqui* (coqui francolin) and *F. sephaena* (crested francolin), and the somewhat larger spurfowls, *F. leucoscepis* (yellow-necked spurfowl), *F. rufopictus* (grey-breasted spurfowl) and *F. afer* (red-necked spurfowl) (Zimmerman et al., 1996; Stevenson and Fanshaw, 2002; Madge and McGowan, 2002; see Crowe et al., 1992 for taxonomy). However, these do not have overlapping distributions, and, as noted by Hall (1963), it is rare for more than one large species and one small species of francolin to be sympatric. A similar association appears to have been the case in the Pliocene, with a large spurfowl, similar in size to *F. leucoscepis* or *F. afer*, occurring with a smaller francolin about the size of *F. coqui* or *F. sephaena*.

N. meleagris (helmeted guineafowl) is widespread in eastern Africa today, being found in woodland, bush, savanna and shrubby grassland (Zimmerman et al., 1996; Stevenson and Fanshaw, 2002; Madge and McGowan, 2002). It is very common in the Laetoli area, where large flocks numbering several hundred individuals are encountered. Guineafowl require trees in which to roost at night. At Laetoli they congregate communally in wooded areas at sundown, especially in the trees fringing the Garusi River. Guineafowl lay their eggs in grassland or lightly wooded areas, and commonly locate their nests under bushes or other dense cover. The nest consists of a shallow scrape in the ground, 20–32 cm in diameter, lined with blades and stems of grass and other herbaceous plants (Tarboton, 2001).

An avian community including at least one small species of francolin, a larger francolin, and a guineafowl (as well as ostriches and a vulture) implies that the paleoecology at Laetoli was most likely open woodland, bushland, savanna or grassland. However, in habitats where grassland predominates, francolins and guineafowl require low brush and thickets for escape and refuge, as well as trees to roost in at night. As a result, they prefer mosaic ecotonal habitats offering open feeding areas with good visibility, but with dense vegetation cover and patches of woodland nearby (Dörgeloh, 2000). Combining these data with evidence from skeletal remains should eventually permit a more comprehensive assessment of the paleoecology of the Laetoli avifauna.

4. Summary and conclusions

Recent paleontological investigation at the Pliocene site of Laetoli and at neighboring localities on the Eyasi Plateau of northern Tanzania have succeeded in recovering a sizable collection of bird fossils. Among these are a number of eggs of ground-nesting galliform birds belonging to the families Phasianidae (quails and

francolins) and Numididae (guineafowl). The collection of fossil eggs from Laetoli now includes 21 specimens. Two of the eggs have been briefly described previously (Cunningham-van Someren, 1987), but the present study provides the first detailed description of the entire collection. The material comes from the Upper Laetolil Beds (dated at ~3.5–3.8 Ma) and the Lower Laetolil Beds (dated at 3.8 Ma to older than 4.3 Ma). The latter specimens, from the locality of Emboremony 1, are the first fossil birds (except for ostrich eggshell fragments) reported from the Lower Laetolil Beds.

The preservation of relatively complete eggs (other than those of ostriches) is an extremely rare occurrence in the fossil record, and Laetoli is the only locality in Africa that has produced such well-preserved fossilized eggs. Deposition of carbonatite air-fall tuffs led to the rapid burial of the eggs, and they were then preserved in paleosols that were geochemically favorable for the preservation of eggshell.

The fossil eggs from Laetoli can be assigned to at least five different species of ground-nesting birds, including two or three species of francolins, a species of guineafowl, and a slightly larger bird of indeterminate taxonomic status (Table 1). Most of the eggs can be assigned to a large species of *Francolinus*, similar in size to *F. afer* and *F. leucoscepus*. A smaller species of francolin, about the size of the extant *F. coqui* or *F. sephaena*, is also represented, but is less common. A single egg may represent an even smaller species of francolin, about the size of *F. lathami* or *F. nahani*, but its attribution to *Francolinus* is less certain. Fossil francolins are known from other Pliocene localities in Africa, and their fossil record may extend back to the early Miocene (Harrison, 1980). The evidence of at least two species of *Francolinus* at Laetoli indicates that francolins were already taxonomically diverse in East Africa by the mid-Pliocene. Three fossil eggs from Laetoli are similar in their overall dimensions and morphology to the living *N. meleagris*, the helmeted guineafowl, which is common in the Laetoli area today.

An avian community including at least one small species of francolin, a larger francolin, and a guineafowl (as well as ostriches and a vulture) implies that the paleoecology at Laetoli was likely to have been open woodland, bushland, savanna or grassland. However, in predominantly grassland habitats, francolins and guineafowl require low brush and thickets for escape and refuge, as well as trees to roost in at night. As a result, they generally prefer mosaic ecotonal habitats offering open feeding areas with good visibility, but with dense vegetation cover and patches of woodland nearby.

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