

Fossil struthionid eggshells from Laetoli, Tanzania: Taxonomic and biostratigraphic significance

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This paper is dedicated to our late friend and colleague, Christine Kiyembe, for her contributions to Tanzanian vertebrate paleontology

Abstract

Recent paleontological investigations at Laetoli and neighboring localities in northern Tanzania have produced a large collection of fossil ostrich eggshells from the Pliocene-aged Laetolil Beds (~3.5–4.5 Ma) and Ndolanya Beds (~2.6–2.7 Ma). A detailed analysis of the morphology of the eggshells and their taxonomic affinities indicates that two different species of *Struthio* are represented. In the Lower Laetolil Beds and in the Upper Laetolil Beds below Tuff 3 a new species is recognized—*Struthio kakesiensis*. This is replaced in the Upper Laetolil Beds by *Struthio camelus*, the modern species of ostrich. Since radiometric age determinations are available for the stratigraphic sequence at Laetoli, it is possible to precisely date the first appearance of *S. camelus* at ~3.6–3.8 Ma. Comparisons of the Laetoli material with specimens from the well-dated sequences at Lothagam and Kanapoi in northern Kenya, allow the taxonomic and biochronological analysis to be extended back in time to the late Miocene.

At about 6.5 Ma, *Diamantornis* and elephant birds were replaced in East Africa by ostriches belonging to the genus *Struthio*. Three time-successive species of ostriches are identified in the fossil record of East Africa, beginning with *Struthio. cf. karingarabensis* (~6.5–4.2 Ma), followed by *S. kakesiensis* (~4.5–3.6 Ma) and then *S. camelus* (~3.8 Ma onwards). A similar sequence of taxa has previously been recorded from localities in Namibia, but at these sites there is no possibility to precisely calibrate the ages of the different species using radiometric dating. Nevertheless, the broadly similar evolutionary sequence and the close correspondence in inferred ages for the succession of species in East Africa and Namibia suggest that ostrich eggshells are a very useful tool for biochronological correlation of paleontological sites in sub-Saharan Africa.

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1. Introduction

The remains of fossil struthionids are recorded from a number of Miocene and Plio–Pleistocene localities in North Africa and sub-Saharan Africa (Stromer, 1902; Andrews, 1911; Lowe, 1933; Arambourg, 1959, 1979; Brodkorb, 1963; Coppens, 1971; Rich, 1974, 1980; Sauer and Sauer, 1978; Geraads, 1995; Manlius, 2001;

Stidham, 2004), but these are generally fragmentary, often poorly dated, and badly in need of detailed description and systematic revision. However, Senut, Pickford and their colleagues have recently published a series of contributions describing fossil eggshells and skeletal remains of struthioniform ratites from Namibia, from the early Miocene onwards, that have greatly clarified the origins and phylogeny of the group (Pickford and Dauphin, 1993; Senut et al., 1994, 1995, 1998; Senut and Pickford, 1995; Pickford et al., 1995; Dauphin et al., 1996; Mourer-Chauviré et al., 1996a,b; Senut, 2000;

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Segalen et al., 2002). These authors have proposed a phyletic series linking *Namornis* (early middle Miocene), *Diamantornis* (middle Miocene) and *Struthio* (late Miocene–Present).¹ The genus *Struthio* is represented in the fossil record of Namibia by three time-successive species—*Struthio karingarabensis* (late Miocene), *Struthio daberasensis* (Pliocene), and *Struthio camelus* (early Pleistocene–Present) (Senut and Pickford, 1995; Senut et al., 1998; Senut, 2000). In addition to providing support for the inference that struthionids originated in Africa, the ubiquitous occurrence of distinct types of eggshells in the sedimentary sequence in Namibia has proved useful for establishing a biostratigraphic framework. Unfortunately, however, age estimations for the biostratigraphic units in Namibia are not calibrated with radiometric dates, only indirectly through faunal correlations of their associated micromammals. This results in a rather imprecise temporal subdivision of the biozones. Senut (2000) and Segalen et al. (2002), for example, have proposed the following timescale for the *Struthio* lineage—*S. karingarabensis* (5–8 Ma), *S. daberasensis* (2–5 Ma), and *S. camelus* (2 Ma—present).

Although the occurrence of fossil ostrich eggshells in the Pliocene sediments at Laetoli has been reported previously, no detailed accounts of the material have been published. Mary Leakey's expeditions to Laetoli in the late 1970s recorded 57 struthionid eggshell fragments from the Laetolil Beds, but all of the material was left at the site (Leakey, 1987a). A single eggshell fragment in the Natural History Museum in London (LIT A.S. 10 VI 35), recovered by Louis and Mary Leakey from Laetoli in 1935, has been suggested to belong to *S. daberasensis* (Senut, 2000). Leakey and Hay (1979) and Leakey (1987b) recorded fossilized footprints of ostriches in Tuff 7 (the Footprint Tuff), at Localities 4 and 7, but no skeletal remains attributable to *Struthio* have been recovered.

Paleontological investigations at Laetoli since 1998, directed by the senior author, have attempted to sample more systematically the temporal and spatial distribution of struthionid eggshells at the site. A relatively large sample of eggshell fragments ($n = 588$ from the Laetolil Beds; $n = 264$ from the Ndolanya Beds) is now available, and housed in the National Museum of Tanzania in Dar es Salaam. No complete or partial eggs of ostriches have been found, although individual eggs and clutches of smaller ground-nesting birds, such as *Numida* and *Francolinus*, have been collected (Cunning-

ham-van Someren, 1987; Harrison, 2005). Struthionid eggshell fragments, however, are common at Laetoli and are known from most localities (Table 1). Eggshell fragments included in the analysis were unweathered and generally well preserved, with no evidence to indicate that preservational or taphonomic factors might have contributed to the morphological or metrical differences noted below.

Struthionid remains have been recorded from several other late Miocene and Pliocene localities in East Africa (i.e., Lothagam and Kanapoi, Kenya, Harris and Leakey, 2003; Chiwondo Beds, Malawi, Stidham, 2004), but the current study is the first to present a detailed account of the fossil material. Given that radiometric age determinations are available for the stratigraphic sequence at Laetoli, evidence from the site offers the opportunity to precisely date the occurrence of the taxa represented, and thereby refine the utility of struthionid eggshells as a biostratigraphic tool.

2. Materials and methods

Today, ostriches (*S. camelus*)² are widely distributed throughout sub-Saharan Africa, although they do not occur in the tropical forest belt of equatorial west and central Africa, the miombo woodlands of south Tanzania, Zambia, Mozambique and northern Angola, and the southeastern tip of Africa (Brown et al., 1982; Zimmerman et al., 1996; Stevenson and Fanshaw, 2002). In the vicinity of Laetoli, they occur commonly in the short grassland and savanna of the southern Serengeti Plains. The local population belongs to *Struthio camelus massaicus*, a subspecies that ranges throughout most of Tanzania and eastern Kenya. Broken eggshells of ostriches are occasionally encountered in the Laetoli region, and the authors have made a small collection of fragments for comparative purposes. Details of the microstructure, pore morphology, and eggshell thickness of extant ostriches have been described previously (Nathusius, 1885; Tyler and Simkiss, 1959; Sauer, 1972; Board and Scott, 1980). Although there is variability in eggshell structure among modern ostriches, due to populational and ecological differences (see Sauer, 1968), these features have proven to be useful in discriminating between taxa of struthioniform birds in the fossil record.

¹ It should be noted that Mourer-Chauviré et al. (1996a,b) do not consider *Namornis* and *Diamantornis* to be valid genera. The description of *Struthio coppensi*, based on fossil hindlimb bones of a primitive didactyl ratite from the early Miocene (~20 Ma), and associated with primitive aepyornithoid eggshells (Mourer-Chauviré et al., 1996a), implies that these authors consider the entire lineage to belong to a single genus, *Struthio*.

² Some authorities (Freitag and Robinson, 1993; Zimmerman et al., 1996; Stevenson and Fanshaw, 2002) have suggested that the Somali ostrich, *Struthio molybdophanes*, should be recognized as a separate species. This population, from Ethiopia, Somalia and Kenya, is certainly the most distinct morphologically, and the molecular evidence indicates that it is the oldest separate lineage, with an estimated divergence date of 3.6–4.1 Ma (Freitag and Robinson, 1993). However, successful interbreeding between *S. molybdophanes* and *S. camelus* in Nairobi National Park (Zimmerman et al., 1996) suggests that a separate species may not be warranted.

Table 1

Locality and stratigraphic provenience of samples of ostrich eggshell fragments from Laetoli used in this study

Stratigraphic provenience	Localities (sample size)
Upper Ndolanya Beds (~2.6–2.7 Ma)	Loc. 7E (3); Loc. 15 (193), Loc. 18 (43), Loc. 22S (12), Silal Artum (13) (total $n = 264$)
Upper Laetolil Beds (~3.4–3.8 Ma)	Loc. 1 (9), Loc. 1NW (3), Loc. 2 (10), Loc. 3 (9), Loc. 4 (6), Loc. 5 (11), Loc. 6 (3), Loc. 7 (9), Loc. 8 (28), Loc. 9 (1), Loc. 9S (26), Loc. 10 (25), Loc. 10W (40), Loc. 10E (2), Loc. 13 (12), Loc. 15 (13), Loc. 16 (3), Loc. 17 (2), Loc. 19 (1), Loc. 20 (2), Loc. 21 (2), Loc. 22 (8) ^a , Loc. 22E (4) ^a (total $n = 229$)
Lower Laetolil Beds (~3.8– > 4.3 Ma)	Emboremony (144), Kakesio (212), Lobileita (3) (total $n = 359$)

^a The samples from Loc. 22 and Loc. 22E are excluded from the analysis because their precise stratigraphic provenience within the Upper Laetolil Beds is uncertain.

The present study makes reference to the following morphological characteristics and qualitative data: (1) shell thickness, (2) shape and size of the pore pits on the outer surface of the eggshell, and (3) density and distribution of the pore pits. A single measurement of shell thickness was taken on each eggshell fragment using digital calipers and recorded to the nearest 0.1 mm. Surface morphological features were examined using a 10× hand lens. Student's *t*-tests were employed to assess the significance of differences in shell thickness and pore density between samples (Sokal and Rohlf, 2001).

The stratigraphy and geochronology of the sedimentary sequence at Laetoli is well-documented (Kent, 1941; Pickering, 1964; Hay, 1976, 1978, 1987; Hay and Reeder, 1978; Hay and Leakey, 1982; Drake and Curtis, 1979, 1987; Ndessokia, 1990) (see Fig. 1). The Laetolil Beds are more than 123 m thick and are divisible into two lithological units. The lower unit (more than 64 m thick) consists mainly of aeolian tuffs interbedded with airfall and water-worked tuffs. K–Ar dating of the Lower Laetolil Beds indicates an age from 3.8 Ma to more than 4.3 Ma (Drake and Curtis, 1987). The upper

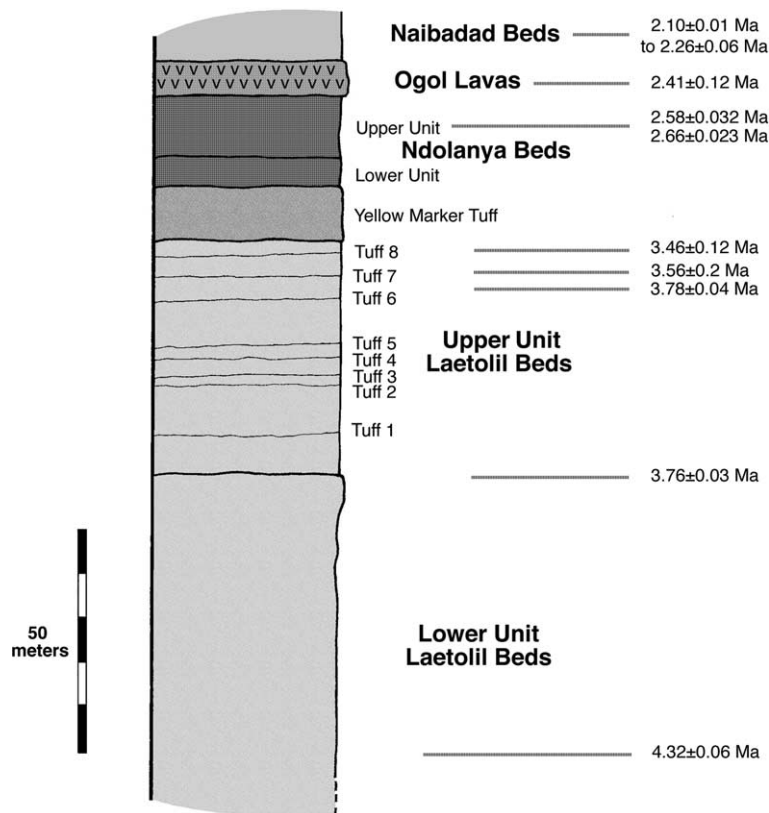


Fig. 1. Generalized stratigraphic section and radiometric dates for the sequence at Laetoli (after Hay, 1987; Drake and Curtis, 1987; Ndessokia, 1990; Manega, 1993).

unit (44–59 m thick) 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). K–Ar dates on biotites from Tuff 8, near the top of the unit, have yielded an average age of 3.46 Ma (Drake and Curtis, 1987). Disconformably overlying the Laetoli Beds are a series of tuffs and calcretes comprising the Ndolanya Beds (15–20 m thick) (Hay, 1987). These are subdivided into upper and lower units separated by a disconformity. Radiometric dates of 2.58–2.66 Ma

(Ndessokia, 1990; Manega, 1993) for the fossiliferous Upper Ndolanya Beds are consistent with faunal correlations (Maglio, 1973; Harris and White, 1979; Beden, 1987; Hooijer, 1987; Harris, 1987; Gentry, 1987). The Ndolanya Beds are overlain by the Ogol Lavas with an average K–Ar date of 2.41 Ma (Hay, 1987; Drake and Curtis, 1987).

The fossil eggshell fragments from Laetoli are derived from a number of sites and stratigraphic units (see Table 1). The relatively large sample ($n = 359$) from the Lower Laetoli Beds comes from three localities, Kakesio,

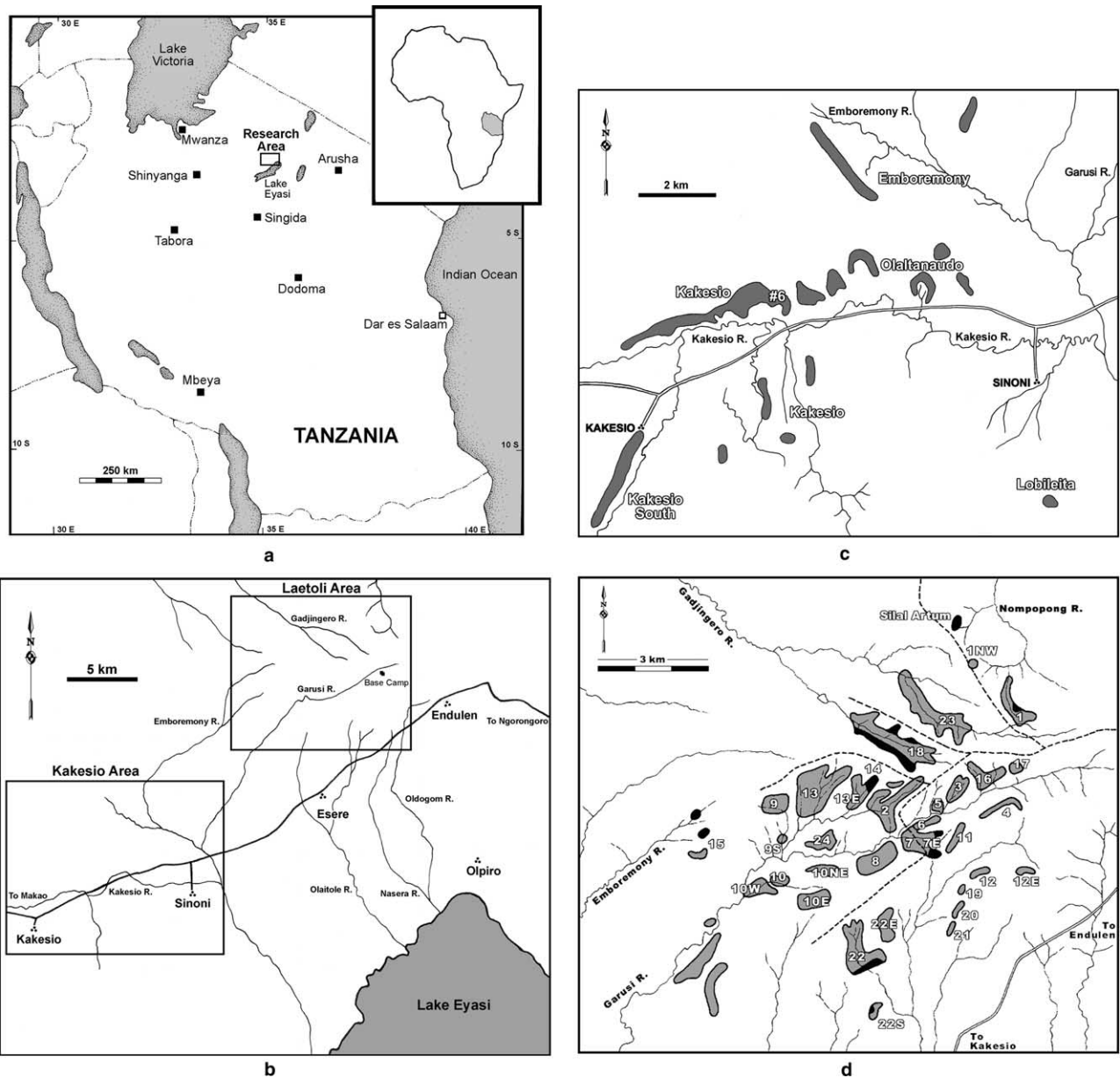


Fig. 2. Maps showing the location of the fossiliferous sites in the Laetoli region of northern Tanzania. (a) Location of research area in northern Tanzania (see (b) for detail). (b) Map of the Eyasi Plateau showing the location of the Kakesio and Laetoli areas (see (c) and (d) for detail). (c) Detail of Kakesio area showing locations of fossiliferous exposures (in grey shading) of Lower Laetoli Beds at Kakesio, Emboremony, and Lobileita. (d) Detail of Laetoli area showing exposures of Upper Laetoli Beds (grey shading) and Ndolanya Beds (black shading), with white numbers and names referring to individual collecting localities.

Emboremony and Lobileita, situated 15–20 km southwest of the main Laetoli area (Fig. 2). The eggshell samples from the Upper Laetolil Beds ($n = 217$) are from 23 different localities at Laetoli. Compared with the Lower Laetolil Beds, eggshell fragments are not so common in the Upper Unit, but they do appear to be just as widespread geographically. The only collecting localities at which eggshells have not been recovered are Locs. 11 and 12 (Fig. 2). The distinctive marker tuffs in the Upper Laetolil Beds also allow the fossil eggshells to be assigned to more precise stratigraphic sub-units. Fossil eggshells from the Upper Ndolanya Beds ($n = 264$) come from five localities (Table 1), but the majority (i.e., 73%) is derived from Loc. 15 (Fig. 2).

3. Results

3.1. Modern ostrich eggshell

The modern ostrich eggshell fragments collected in the Laetoli area, belonging to *Struthio c. massaicus*, are characterized by the following features: eggshells are relatively thin with an average thickness of only 2.1 mm (range 1.9–2.3 mm). Small pore pits are distributed in irregular fashion over the entire surface of the shell. Each pore pit contains multiple openings derived from a branching network of individual pores (Nathusius, 1885; Tyler and Simkiss, 1959). Pore pits are small, forming circular to oval pinprick depressions, with a maximal diameter of 1.0 mm. The density of pore pits is high, averaging 10.8/cm² (range 7–16/cm²) (Table 2; Fig. 3(a)).

These data are comparable to those previously presented on other modern ostrich populations (Nathusius, 1885; Schalow, 1913; Lowe, 1933; Tyler and Simkiss, 1959; Sauer, 1968, 1972). Reported eggshell thickness in extant ostriches ranges from 1.6 mm to 2.2 mm, with a mean value of 2.0. Pore size and density varies according to subspecies, with *Struthio c. camelus* having tiny individual pores (0.02–0.03 mm) that are densely scattered (100/cm²), while *S. c. massaicus* and *S. c. molybdophanes* have few (8/cm² and 10/cm² respectively), rel-

atively large pore pits (with a maximum diameter of 0.8 mm and 1.0 mm, respectively) (Schönwetter, 1927; Sauer, 1972).

3.2. Fossil struthionid eggshells from the Ndolanya Beds

The eggshell fragments from the Ndolanya Beds have the following characteristics:

Eggshells have an average thickness of 2.4 mm (range 1.8–3.0 mm). The pore pits are distributed irregularly over the shell surface. The latter are small, forming oval to circular pinprick depressions, with a maximum diameter of 1.1 mm. The density of pore pits is relatively high, averaging 11.4/cm² (Table 2; Fig. 3(b)).

Structurally these eggshell fragments are very similar to those of modern ostriches. The key differences are that the shell is slightly thicker (14.3% thicker on average; the difference is significant, $P < 0.001$) and the pore density is somewhat higher (but not significant). Given that the total variation in eggshell thickness is relatively greater in the sample from the Ndolanya Beds than is seen in extant ostriches (the coefficient of variation for the Ndolanya sample is 10.83% compared with 5.71% for the modern sample), it is conceivable that more than one taxon is represented. However, the unimodal distribution of eggshell thickness and the uniformity in other structural features suggests that a single species interpretation is the most parsimonious. In this case, the tendency for greater eggshell thickness in the Ndolanya Beds sample might be explained as a consequence of populational or ecological variation. For example, it could imply that the overall size of eggs was larger in the Ndolanya Beds compared with modern ostriches. Unfortunately, the shell pieces from the Ndolanya Beds are too incomplete to calculate curvature and estimate the original egg size. Alternatively, it is known that modern ostrich populations with better quality food or those living in areas of higher rainfall produce eggs with relatively thicker shells (Sauer, 1968). Evidence from the community structure of the mammalian fauna from the Ndolanya Beds indicates that the vegetation was semi-arid bushland, similar to that found in the area today (Kovarovic et al., 2002). In contrast, however, the

Table 2

Comparison of eggshell thickness and pore density in extant ostriches and in fossil struthionids from Laetoli^a

Stratigraphic unit—Taxon	Eggshell thickness (mm)				Pore density (per cm ²)			
	<i>n</i>	Mean	Range	SD	<i>n</i>	Mean	Range	SD
Modern— <i>Struthio camelus</i> ^b	39	2.1	1.9–2.3	0.12	30	10.8	7–16	2.80
Upper Ndolanya Beds— <i>Struthio</i> cf. <i>camelus</i>	264	2.4	1.8–3.0	0.26	52	11.4	5–30	4.63
Upper Laetolil Beds, above Tuff 3— <i>Struthio camelus</i>	126	2.1	1.5–2.8	0.21	89	10.5	5–21	3.01
Upper Laetolil Beds, below Tuff 3— <i>Struthio camelus</i>	11	2.1	1.8–2.2	0.10	8	9.1	6–13	2.32
Upper Laetolil Beds, below Tuff 3— <i>Struthio</i> sp. nov.	80	3.1	2.7–3.6	0.19	32	5.5	3–11	1.90
Lower Laetolil Beds— <i>Struthio</i> sp. nov.	359	3.2	2.5–4.4	0.32	182	4.4	1–10	1.86

^a Pore density = number of pores per cm²; *n* = sample size; SD = standard deviation.

^b Sample of *Struthio camelus massaicus* eggshell fragments collected by the authors in the vicinity of Laetoli.

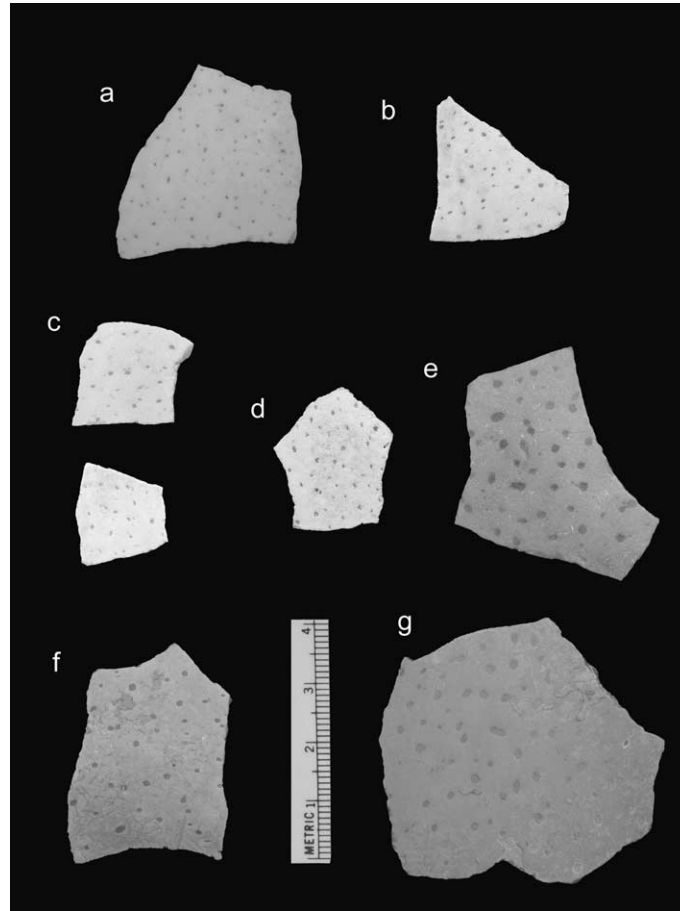


Fig. 3. Fragments of ostrich eggshells from Laetoli, Kakesio and Emboremony. (a) *Struthio camelus*, modern, Garusi Valley, Laetoli. (b) *Struthio* cf. *camelus*, EP 1070-01a, Locality 15, Upper Ndolanya Beds, Laetoli. (c) *Struthio camelus*, EP 3369-00a,b, Locality 15, Upper Laetolil Beds between Tuffs 6 and 7, Laetoli. (d) *Struthio camelus*, EP 1165-01a, Locality 1, Upper Laetolil Beds between Tuff 7 and the Yellow Marker Tuff, Laetoli. (e) *Struthio kakesiensis*, holotype, EP 019-99, Lower Laetolil Beds, Kakesio #6. (f) *Struthio kakesiensis*, EP 052-98, Lower Laetolil Beds, Kakesio #4. (g) *Struthio kakesiensis*, EP 1357-01a, Lower Laetolil Beds, Emboremony. Scale, major divisions in centimeters.

terrestrial gastropod fauna points to more mesic conditions during deposition of the Ndolanya Beds, with woodland and possibly forested habitats occurring locally. It is possible, therefore, that the fossil ostriches could have exploited a wider range of plant foods than they do at Laetoli today. Regardless, the overall structure of the eggshell fragments from the Ndolanya Beds is closely similar to that of the modern ostrich, and, as a consequence, the material is attributed here to *Struthio* cf. *camelus*.

3.3. Fossil struthionid eggshells from the Upper Laetolil Beds

Comparisons of the fossil eggshell fragments from the Upper Laetolil Beds demonstrate that two distinct types are represented. All of the samples from stratigraphic horizons above Tuff 3 ($n = 126$) and a few of the eggshells below Tuff 3 ($n = 11$) are uniform in structure, and are morphologically indistinguishable from those of modern *S. camelus*. They have the following charac-

teristics: The eggshell is relatively thin, with an average thickness of 2.1 mm (range 1.5–2.8 mm). The pore pits are identical in morphology to those described above for *Struthio c. massaicus*, with a maximal diameter of 1.0 mm. The density of pore pits averages $10.4/\text{cm}^2$ (range $7\text{--}16/\text{cm}^2$). Comparisons of the metric data presented in Table 2 show that these fossil samples are closely comparable in eggshell thickness and pore size and density to modern ostriches (differences were not statistically significant), and they are accordingly assigned to *S. camelus* (Fig. 3(c) and (d)).

However, most ($n = 80$) of the eggshell fragments from the Upper Laetolil Beds below Tuff 3 are distinctive in their morphology. They are characterized by the following features: The shell is relatively thick, with an average thickness of 3.1 mm (range 2.7–3.6). Pore pits are shallow, circular to oval in shape, with a maximum diameter of 2.0 mm. Pore pit density is relatively low, with an average of $5.5/\text{cm}^2$ (range 3–11). The shell thickness and pore density of these samples are significantly different ($P < 0.001$) from those collected above

Tuff 3. Based on our present understanding of the polarity of evolutionary change in eggshell structure in struthionids (Senut et al., 1998; Senut, 2000), we can infer that the common eggshell type found below Tuff 3, with thicker shells and larger more widely distributed pore pits, represents a more primitive species than *S. camelus* (Fig. 4). In terms of density and distribution of pore pits, these eggshell fragments are similar to those of *S. daberasensis* from the Pliocene of Namibia described and illustrated by Pickford et al. (1995), Senut (2000). In this latter species, pore pits have a maximal diameter of 2.2 mm, with a density of 4–5/cm². However, the eggshells of *S. daberasensis* are considerably thinner (with a modal thickness of 2.3 mm, and a range of 1.7–2.6 mm) than those from the Laetolil Beds, with no overlap in their ranges. *S. karingarabensis* from the late Miocene of Namibia, a more primitive species than *S. daberasensis*, has a shell thickness (range 2.9–3.2 mm) more comparable to the Laetoli sample. However, *S. karingarabensis* differs from the eggshells from Laetoli in having relatively larger and much more widely spaced pore pits (maximum pore pit diameter, 2.7 mm, pore pit density, 2.2/cm²). This combination of characteristics indicates

that the Laetoli eggshells are morphologically (and possibly phylogenetically) intermediate between those of *S. karingarabensis* and *S. daberasensis* (Fig. 4).

The evidence clearly indicates that two different species of struthionids are represented in the Upper Laetolil Beds below Tuff 3, although it is not possible to determine whether the two taxa were synchronous for a brief period or were time successive.

3.4. Fossil struthionid eggshells from the Lower Laetolil Beds

Eggshell fragments from the Lower Laetolil Beds are indistinguishable in morphology from the predominant type found in the lower part of the Upper Laetolil Beds below Tuff 3. They have the following structural characteristics: The shell is thick, with an average thickness of 3.2 mm (range 2.5–4.4 mm). The pore pits are shallow, circular to elliptical in shape, and have a maximum diameter of 2.0–2.5 mm. Pore pit density is low with an average of 4.4/cm² (range 1–10) (Table 2; Fig. 3(e)–(g)). This large sample of eggshell fragments from the Lower Laetolil Beds (*n* = 359) confirms that there are two distinct types of eggshells represented in the Laetolil Beds. Eggshells derived from the Lower Laetolil Beds and Upper Laetolil Beds below Tuff 3 are more primitive than those of *S. camelus* in being thicker and in having larger and more widely dispersed pore pits. As noted above, some of these distinctive features are shared with *S. karingarabensis* and *S. daberasensis*, but the eggshells from the Lower Laetolil Beds are unique in their combination of features. We consider these differences to be of sufficient importance to merit the recognition of a separate species.

Order Struthioniformes

Family Struthionidae

Genus *Struthio* Linnaeus, 1758

Struthio kakesiensis nov. sp.

Holotype: EP 019-99—Eggshell fragment (Fig. 3(e)). Collections of the National Museum of Tanzania, Dar es Salaam, Tanzania.

Type locality and horizon: Kakesio #6 (Coordinates: 3°21' 37S, 35°00' 47E), 27 km SW of the village of Endulen, North of the Kakesio River. Lower Unit, Laetolil Beds (Fig. 2).

Etymology: named after the type locality, Kakesio.

Diagnosis: A struthionid with struthionid eggshell type (see Tyler and Simkiss, 1959; Sauer, 1972) in which eggshell thickness averages 3.2 mm (range 2.5–4.4 mm), pore pits are shallow, circular to oval in shape, with a maximum diameter of 2.5 mm, and pore pit density averages 4.6/cm² (range 1–11). *Struthio kakesiensis* differs from extant *S. camelus* in having much thicker eggshells with larger and more dispersed pore pits (shell

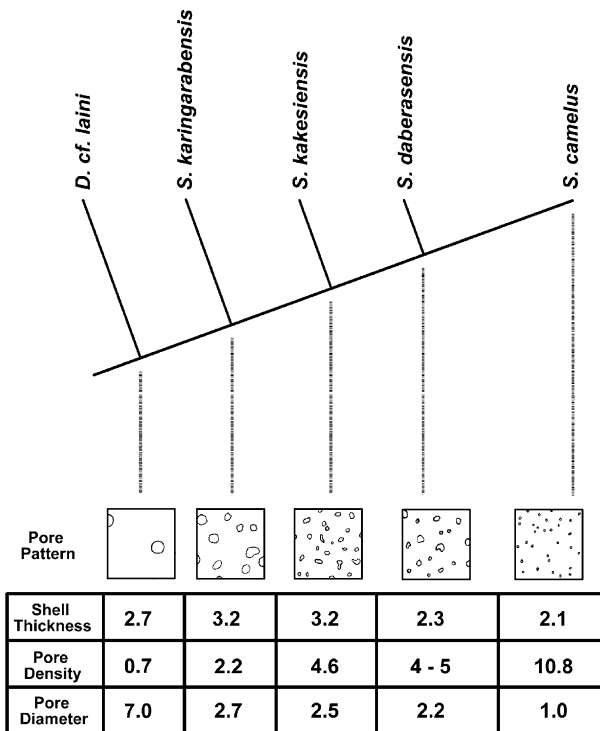


Fig. 4. Cladogram illustrating the inferred relationships between *Diamantornis cf. laini* and species of *Struthio* from the late Miocene and Pliocene of East Africa and Namibia. The differences in pore pattern, shell thickness, pore density and pore diameter are shown at the bottom of the figure. The pore pattern shows the size and distribution of pore pits seen in a 2 × 2 cm square. Shell thickness, pore density and pore diameter are average values for the species. Note that there is a progressive decrease in shell thickness and pore pit diameter, and an increase in pore pit density through the evolutionary series.

thickness and pore density are both significantly different, $P < 0.001$). The average eggshell thickness of *S. kakesiensis* is 52.4% thicker than that of *S. camelus*, with no overlap in their ranges (see Table 2). The density of pore pits in *S. kakesiensis* only 4.6/cm² compared with 10.8/cm² in *S. camelus*. Maximum pore pit diameter is 2.5 mm in *S. kakesiensis* compared with only 1.0 mm in *S. camelus*. *S. kakesiensis* resembles *S. daberansensis* from the Pliocene of Namibia in density and distribution of pore pits, but the eggshells of *S. kakesiensis* are absolutely thicker (the average shell thickness is 39.1% thicker than that of *S. daberansensis*) with no overlap in their ranges (Pickford et al., 1995; see Table 2). *S. kakesiensis* resembles *S. karingarabensis* from the late Miocene of Namibia in having eggshells of similar thickness, but the former differs in having relatively smaller and less widely dispersed pore pits. The maximum pore pit diameter in *S. kakesiensis* is 2.5 mm compared with 2.7 mm in *S. karingarabensis*, and pore pit density is 4.6/cm² compared to 2.2/cm² (Senut et al., 1998) (see Fig. 4 for comparisons). Unfortunately, it is not possible to make direct comparisons with *S. coppensi* and *S. oldowayi* because these two taxa are based on postcranial material only. Nevertheless, *S. coppensi* from the early Miocene locality of Elizabethfeld in Namibia is associated with eggshell fragments, almost certainly belonging to the same species, which retain a typical aepyornithoid pattern (Mourer-Chauviré et al., 1996a,b). They differ from those of *S. kakesiensis* in being much thicker and in having pores arranged in elongated sub-parallel grooves, rather than in oval to circular pits (Senut et al., 1995; Senut, 2000). No eggshell fragments have been described from the early Pleistocene of Olduvai Bed I that might be associated with the type material of *S. oldowayi* (Lowe, 1933).

Pickford (cited in Senut, 2000) suggests that eggshell fragments from MNK at Olduvai (Bed II, dated at ~1.5–1.6 Ma) may belong to *S. daberansensis*, but we are unable to locate the specimens on which this observation is based. The postcranials (i.e., the innominate, synsacrum and several lumbar and caudal vertebrae) of *S. oldowayi* are morphologically indistinguishable from those of extant *S. camelus*, but are apparently slightly larger in overall size (Lowe, 1933). On this basis alone, there seems to be inadequate justification to recognize the Olduvai material as a distinct species, and we therefore consider *S. oldowayi* as a subjective junior synonym of *S. camelus* (see also Harrison, 1980).

Lastly, Andrews (1911) described two eggshell fragments of uncertain age from near Touggourt in southern Algeria as belonging to *Psammornis rothschildi*. Sauer (1969) presented a detailed review of the structure and taxonomic affinities of these specimens, and suggested a close relationship to extant *S. camelus*. According to Andrews (1911), the shell is apparently much thicker (3.2–3.4 mm) than in modern ostriches (Sauer, 1969)

estimates that it may have been as thick as 4.0 mm in the unweathered state), being comparable to that of *S. kakesiensis* and *S. karingarabensis*. It is conceivable, therefore, that *P. rothschildi* may represent a senior synonym of either *S. kakesiensis* or *S. karingarabensis*. However, the eggshell fragments from Algeria appear to be similar in pore pit morphology and distribution to *S. camelus*. Sauer (1969, p. 305) has described the pore canals as “opening singly or in loose groups of two and three in an irregular pattern of distribution, hardly noticeable to the naked eye because of their small size”. This pattern is quite different from that seen in either *S. kakesiensis* or *S. karingarabensis*, and indicates a more derived eggshell morphology in *P. rothschildi*, confirming its taxonomic distinctiveness from *S. kakesiensis*.

4. Comparisons with material from other Pliocene localities in East Africa

Recent paleontological expeditions to Kanapoi and Lothagam in northern Kenya, directed by Meave Leakey, have yielded small samples of eggshells of several species of aepyornithoid and struthionid ratites (Harris and Leakey, 2003; Stidham, 2004) derived from stratigraphic horizons dated from 7.4 Ma to at least 4.1 Ma (Leakey et al., 1995, 1998; McDougall and Feibel, 2003). Since these samples are older than or contemporary with the oldest eggshells from Laetoli, they provide a valuable source of data for a broader understanding of struthionid taxonomy and biochronology in East Africa during the late Miocene and Pliocene.

Fossil eggshells from Lothagam are known from the Lower and Upper Members of the Nawata Formation (dated at 7.4 to 6.5 Ma and 6.5 to ~5.0 Ma, respectively), the Apak Member (dated at ~5.0–4.2 Ma) and Kaiyumung Member (with an estimated age of ~3.5 Ma) of the Nachukui Formation (McDougall and Feibel, 2003; Leakey and Walker, 2003). Harris and Leakey (2003) referred the ratite eggshells from Lothagam to two taxa: Aepyornithidae, genus and species indet. (from the Lower Nawata Member) and cf. *Struthio* sp. indet. (from the Lower and Upper Nawata Members, the Apak Member, and the Kaiyumung Member). Based on published descriptions and illustrations, Stidham (2004) recognized *S. daberansensis*, *Diamantornis laini*, and *D. wardi* at Lothagam. The fossiliferous horizons at Kanapoi are dated to 4.1–4.2 Ma (Leakey et al., 1998) (Fig. 5). The material, comprising more than one hundred shell fragments, has not been subject to detailed study.

Recent comparisons of the collections from Lothagam and Kanapoi by the senior author allow a revised interpretation of the taxonomy. The following taxa are recognized at Lothagam: (1) Aepyornithidae indet.

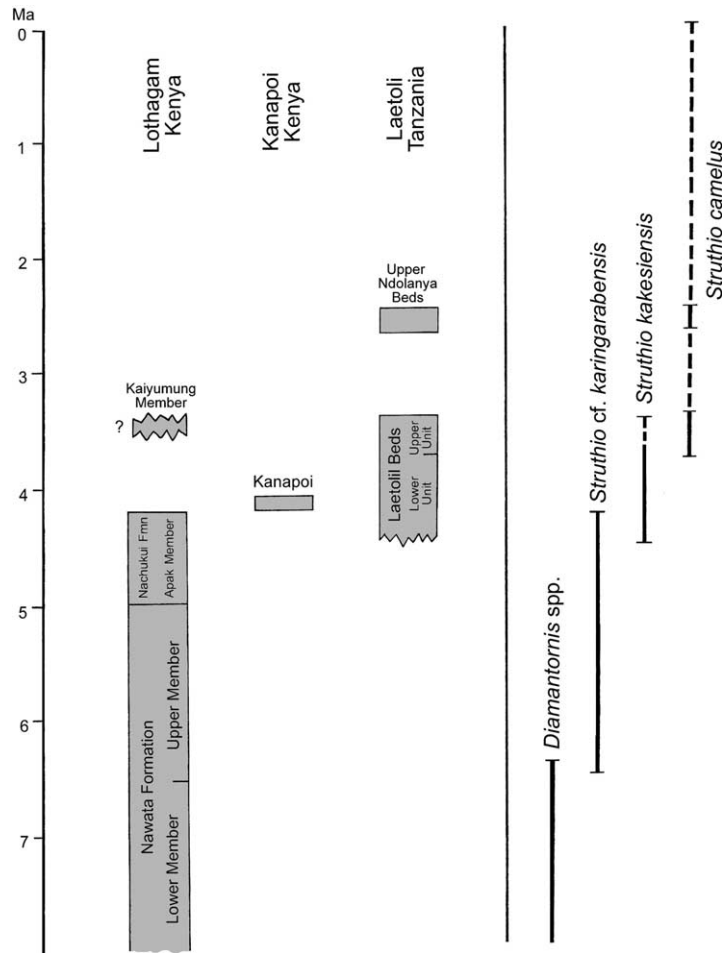


Fig. 5. Temporal ranges of the stratigraphic sequences and associated struthionid taxa at Lothagam, Kanapoi and Laetoli in East Africa.

(Lower Nawata Member)—a single egg broken into many fragments, with typical aepyornithoid pore pattern and relatively thin shell (average thickness, 1.9 mm); (2) *Diamantornis* cf. *laini* (Lower Nawata Member)—a struthionid characterized by relatively thick shell (average thickness, 2.7 mm; range, 2.2–3.4 mm), very large pore pits (maximum diameter 6.6 mm), and a low pore density (average, 0.7/cm²). This compares favorably with *D. laini* from the late Miocene of Namibia, in which modal thickness is 2.4 mm (range 2.1–2.9 mm), maximal pore pit diameter is 9.5 mm, and pore density is 0–1/cm² (Pickford et al., 1995). (3) *Diamantornis* sp. (Upper Nawata Member on the Marker Tuff dividing the Upper and Lower Members)—a single sample (KNM-LT 24973) that differs from other species of *Diamantornis* in having smaller (maximum diameter 4.0 mm) and more numerous pore pits (1.8/cm²) (see Harris and Leakey, 2003, Fig. 4.33). (4) *Struthio* cf. *karingarabensis* (Upper Nawata and Apak Members)—specimens are characterized by relatively thick shell (average thickness, 2.6 mm; range, 2.1–3.1 mm), maximal pore size of 2.4 mm, and average pore density of 2.0 cm² (Fig. 4). The morphology of these

eggshell fragments is closely comparable to that of *S. karingarabensis* from Namibia (Senut et al., 1998) (see Table 3 for comparative data), and the material is provisionally referred to this taxon. Although the shell fragments from the Apak Member are slightly thicker on average than those from the older Upper Nawata Member (i.e., 2.7 mm versus 2.5 mm), this difference is not statistically significant, and given the overall morphological similarity of the samples the material from both members can reasonably be assigned to a single taxon. They are distinguished from *S. daberensis* in having a relatively thicker shell, with slightly larger pore pits and a lower pore pit density (see Table 3). They differ from *S. kakesiensis* in having a thinner shell (23% thinner on average) and a lower pore pit density (see Table 3). (5) *Struthio* cf. *kakesiensis* (Kaiyumung Member)—the few shell fragments known from the Kaiyumung Member are thicker than those of *Struthio* cf. *karingarabensis*, and are morphologically very similar to material from the Lower Laetoli Beds assigned to *S. kakesiensis*.

The relatively large sample of eggshell fragments from Kanapoi are morphologically and metrically

Table 3

Summary of eggshell thickness, pore density and maximum pore diameter in extant ostriches and in Pliocene struthionids from East Africa

Stratigraphic unit—Taxon	Eggshell thickness (mm)		Pore density (per cm ²)		Maximum pore diameter (mm)
	Mean	Range	Mean	Range	
<i>Modern, Tanzania</i>					
<i>S. camelus</i>	2.1	1.9–2.3	10.8	7–16	1.0
<i>Laetoli, Tanzania</i>					
Ndolanya Beds— <i>S. cf. camelus</i>	2.4	1.8–3.0	11.4	5–30	1.1
Laetolil Beds— <i>S. camelus</i>	2.1	1.5–2.8	10.4	5–21	1.0
Laetolil Beds— <i>S. kakesiensis</i>	3.2	2.5–4.4	4.6	1–11	2.5
<i>Namibia</i>					
<i>S. daberensis</i> ^a	2.3	1.7–2.6	4–5	–	2.2
<i>S. karingarabensis</i> ^a	–	2.9–3.2	2.2	–	2.7
<i>Lothagam, Kenya</i>					
Upper Nawata Fm & Apak Mb— <i>S. cf. karingarabensis</i>	2.6	2.1–3.0	2.0	1–4	2.4
Kaiyumung Mb— <i>S. cf. kakesiensis</i>	3.2	3.1–3.3	2.5	2–3	–
<i>Kanapoi, Kenya</i>					
<i>S. kakesiensis</i>	3.1	2.9–3.3	4.0	3–7	1.4

^a Data derived from Pickford et al. (1995), Senut et al. (1998) and Senut (2000).

indistinguishable from those from the Lower Laetolil Beds (i.e., shell thickness and pore density are not significantly different), and can be assigned to *S. kakesiensis*.

5. Discussion

This is the first detailed study to be undertaken of struthionid eggshells from the late Miocene and Pliocene of East Africa. The large collection of eggshells now available from Laetoli and from neighboring localities, such as Kakesio and Emboremony, have helped to establish the taxonomic affinities and chronology of Pliocene East African ostriches.

The earliest species of ostrich in the Laetoli sequence is *S. kakesiensis*, a newly recognized taxon, which occurs in the Lower Laetolil Beds and the Upper Laetolil Beds below Tuff 3. This is replaced, during the brief time interval between Tuffs 1 and 3 of the Upper Laetolil Beds, by the modern species, *S. camelus*. The latter species is inferred to be more derived than *S. kakesiensis* in having a thinner eggshell, much smaller pore pits, and a higher pore density (see Table 3). We can, therefore, estimate the date of the first appearance of *S. camelus*, at least locally, with some degree of precision. The base of the Upper Laetolil beds has been dated radiometrically to 3.76 ± 0.03 Ma (Drake and Curtis, 1987). Tuff 3 has not been dated, but Hay (1987) calculated an average depositional rate of 1.7 m per 10,000 years using the K–Ar dates for the entire sequence, and this gives a satisfactory age estimate for Tuff 3 of ~ 3.6 Ma. This implies that *S. camelus* appears in the local sequence during the mid-Pliocene at ~ 3.6 – 3.8 Ma, replacing the more primitive *S. kakesiensis* (Fig. 5). This is much

earlier than the estimated appearance of *S. camelus* in Namibia reported by Senut and Pickford (1995) and Senut (2000). This may possibly imply regional differences in the modes and timing of replacement of ostrich taxa. However, the small morphological gaps between transitional species in both the Namibian and East African phyletic series suggests that speciation events were followed by rapid geographic dispersal of new forms. If this inference is correct, then the ages of the Namibian biozones might need to be reconsidered. This revised chronology for the earliest appearance of *S. camelus* also fits well with mtDNA studies that indicate that the common ancestor of modern ostrich populations diverged at 3.6–4.1 Ma (with *Struthio c. molybdophanes* being the most divergent population) (Freitag and Robinson, 1993).

The occurrence of *S. kakesiensis* at Kanapoi at 4.1–4.2 Ma, contemporary in age with the material from the Lower Laetolil Beds, shows that the taxon was widely distributed in East Africa during the mid-Pliocene. A few specimens belonging to this species have also been identified from the Kaiyumung Member at Lothagam, which has been roughly estimated to be about 3.5 Ma (Leakey and Walker, 2003). However, its last appearance at Laetoli at ~ 3.6 – 3.8 Ma may imply a slightly older estimate for the date for the Kaiyumung Member (Fig. 5). *S. kakesiensis* differs from the ostrich typically found at Pliocene localities in Namibia, *S. daberensis* (see Senut, 2000), in having significantly thicker eggshell, and in this respect is less derived.

The lower part of the Lothagam sequence provides evidence of a more primitive species of ostrich not represented at Laetoli. Specimens referred to *Struthio cf. karingarabensis* are known from the Apak Member

and the Upper Nawata Member, dating from 4.2 Ma to 6.5 Ma (Fig. 5). This species is inferred to be less derived than *S. kakesiensis* in having a lower pore density and larger maximum pore pit diameter (Table 3). *S. karingarabensis* was initially described from localities in southern Namibia (Senut et al., 1998), and was suggested to be of late Miocene age (~5–8 Ma) (Senut, 2000; Segalen et al., 2002). The material from Lothagam, therefore, allows us to refine the age of this taxon.

Finally, eggshell fragments from the Lower Nawata Member (dating from 6.5–7.5 Ma) document the occurrence of two quite different struthioniform taxa (Harris and Leakey, 2003). Most of the eggshells recovered are very similar in their overall morphology to *D. laini* from the late Miocene of Namibia (Pickford et al., 1995; Senut, 2000), and can be provisionally referred to this taxon. The material from Lothagam has the following characteristics: moderately thick shell, with an average thickness of 2.7 mm (range 2.2–3.4 mm), large pores, with a maximal diameter of 7.0 mm, and an average pore pit density of 0.7/cm². The eggshell of *Diamantornis* is more primitive than those of *Struthio*, and it provides a reasonable temporal and phyletic antecedent for the *Struthio* lineage. As noted by Harris and Leakey (2003), a single sample (KNM-LT 24973) found just above the Marker Tuff separating the Lower and Upper Members of the Nawata Formation (dated at ~6.5 Ma), here referred to *Diamantornis* sp., is more derived than *D. laini* in having pore pits smaller in size and pits that occur in higher density. This provides further evidence to support the suggestion that *Diamantornis* is ancestral to *Struthio*, since later samples of *Diamantornis* show a progressive reduction in pore pit size and increase in overall density towards to the more derived condition in *Struthio* (Fig. 4).

The second type of struthioniform eggshell from the Lower Nawata Formation at Lothagam, represented by a single fragmented egg (KNM-LT 25085), belongs to an indeterminate aepyornithid (Harris and Leakey, 2003). The fragments are derived from an horizon dated to ~6.5–6.7 Ma. The shell is relatively thin (average thickness, 1.9 mm), with a typical aepyornithoid pore pattern (Sauer, 1972). This record confirms that elephant birds survived in mainland Africa until at least the late Miocene.

The eggshells from Laetoli, as well as those from Kanapoi and Lothagam, provide, for the first time, good evidence to document the taxonomic diversity, evolutionary history, and biochronology of fossil struthionids from well-dated stratigraphic sequences in the late Miocene and Pliocene of East Africa (Fig. 5). During the late Miocene, up to ~6.5 Ma, *Diamantornis* cf. *laini* was the dominant struthioniform in East Africa, occurring contemporaneously with an aepyornithid of uncertain taxonomic affinities. *Struthio* makes its first appearance at ~6.5 Ma, and was probably derived from

an ancestral form that produced eggs morphologically similar to those of *Diamantornis*. The earliest and most primitive species of *Struthio*, *S. cf. karingarabensis*, is represented in the Upper Nawata Formation and Apak Member at Lothagam, dating from ~6.5–4.2 Ma. This species is replaced by the more derived *S. kakesiensis*, known from the Lower Laetolil Beds, Kanapoi, and the Kaiyumung Member, probably dating from ~4.5–3.6 Ma. Finally, at about 3.6–3.8 Ma, *S. kakesiensis* is replaced by the modern ostrich, *S. camelus*, which is known from the Upper Laetolil Beds and the Upper Ndolanya Beds at Laetoli (Fig. 5).

6. Summary and conclusions

Renewed paleontological research at Laetoli and at neighboring localities in northern Tanzania has produced the first systematically sampled collections of fossil ostrich eggshells from the Pliocene of East Africa. More than eight hundred eggshell fragments have been recovered from the Lower and Upper Laetolil Beds (~3.5–4.5 Ma) and the Upper Ndolanya Beds (~2.6–2.7 Ma). A detailed account of the morphology of the eggshells and their taxonomic affinities is presented above. Since radiometric age determinations are available for the stratigraphic sequence at Laetoli, the material offers an opportunity to precisely date the occurrence of the taxa represented, and to refine their utility as biostratigraphic indicators. Comparisons of the material with samples known from other East African localities, including those from Lothagam and Kanapoi, extend the analysis back to the late Miocene.

During the late Miocene, at about 6.5 Ma, *Diamantornis* and elephant birds are replaced in East Africa by ostriches belonging to the genus *Struthio*. Three time-successive species of ostriches are identified in the fossil record from East Africa, beginning with *S. cf. karingarabensis* (~6.5–4.2 Ma), followed by *S. kakesiensis* (~4.5–3.6 Ma) and then *S. camelus* (~3.8 Ma onwards). A similar sequence of taxa has previously been recorded from sites in Namibia, but unfortunately at these sites there is no possibility to precisely calibrate the ages of the different species using radiometric dating. In addition, there are two major differences in the fossil record between East Africa and Namibia: (1) aepyornithids apparently continue much later in East Africa (occurring in the late Miocene of East Africa, but restricted to the early Miocene of Namibia), and (2) *S. kakesiensis* represents the intermediate species between *S. karingarabensis* and *S. camelus* in East Africa, whereas the somewhat more derived species, *S. daberansensis*, fills this position in Namibia.³ Nevertheless, the

³ Stidham (2004) has recently reported the occurrence of ostrich eggshells from the mid-Pliocene (~3.0–3.5 Ma) Chiwondo Beds in Malawi, which are attributable to *S. daberansensis*.

broadly similar evolutionary sequence and the close correspondence in inferred ages for the succession of species confirms the suggestion that ostrich eggshells are a very useful biochronological tool for correlating paleontological sites throughout sub-Saharan Africa (Senut, 2000; Stidham, 2004).

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