

FOSSIL OWLS FROM EARLY MAN SITES OF OLDUVAI GORGE, TANZANIA

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SUMMARY

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Three species of owl have been recognized among the fossil bird remains of Olduvai. *Bubo leakeyae* n. sp. seems to be the immediate ancestor of the recent Spotted Eagle Owl *Bubo africanus*. The other forms are Giant Eagle Owl *Bubo cf. lacteus* and Barn Owl *Tyto alba*. These three forms indicate a landscape of lightly wooded savanna.

RÉSUMÉ

Les restes de Strigiformes d'Olduvai peuvent être attribués à trois espèces: une forme éteinte *Bubo leakeyae* n. sp., étroitement apparentée au grand-duc tacheté actuel d'Afrique *Bubo africanus* et deux formes actuelles, le grand-duc de Verreaux *Bubo cf. lacteus* et la chouette effraye *Tyto alba*. Ces trois formes correspondent à un paysage de savane légèrement boisée.

INTRODUCTION

Owls are comparatively rare among the very large number of fossil birds found in Olduvai Gorge. The remains are fragmentary and consist in large part of pedal phalanges. This can be explained by the fact that the material comes from open-air sites on the lake margin, or from lacustrine or fluvio-lacustrine sediments, and the bird remains are mainly from aquatic forms. In cave deposits the remains of owls are usually more abundant.

STRATIGRAPHIC POSITION OF THE FOSSIL MATERIAL

All the remains of Strigiformes were collected in Bed I, which is the base of the Olduvai sequence. Bed I is 60 m thick in the eastern part of the Main Gorge, and 43 m thick in the western part. Its sediments include lava flows, lake, lake-margin, alluvial fan, and alluvial plain deposits. The correlations within Bed I are made on the basis of well developed tuffs. In the lower part of Bed I the lavas have been dated at approximately 1,85 million years ago, and in the upper part of Bed I, the tuff I^F, which marks the limit between Bed I and Bed II, is dated as approximately 1,70 million years ago (Hay 1976, 1979).

SYSTEMATIC STUDY

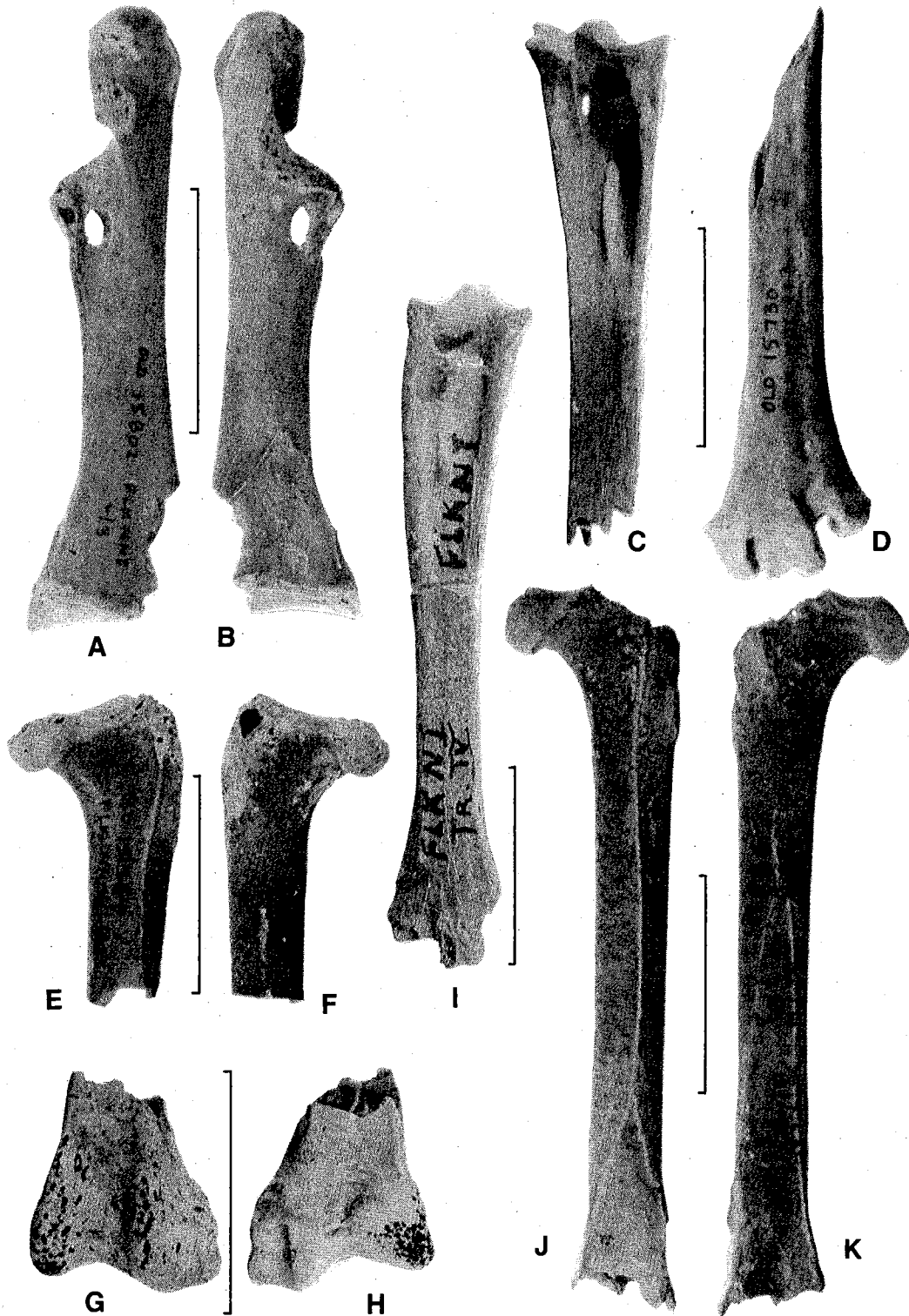
Family Strigidae Vigors Genus *Bubo* Dumeril

Bubo leakeyae n. sp. (Fig. 1)

Holotype: Left coracoid lacking the procoracoid and the external distal angle, OLD 15802, FLK NNI, Layer 3.

Paratypes: The following specimens are from layer 3 of locality FLK NNI and can be attributed to the same individual as the holotype: 15740, premaxillae; 3301, lower part of right coracoid; 15364 and 15473, proximal and distal parts of left femur; 16377, distal part of right femur; 15701, distal part of left tibiotarsus; 15776, left fibula; 16262, proximal part of right tarsometatarsus; 15730, distal part of left tarsometatarsus; 15942, 15946, 16050, 16171, 16174, 16176 to 16180, pedal phalanges.

Etymology: This species is dedicated to Mary D. Leakey who collected most of the avian fossil material of Olduvai.



Locus typicus: Olduvai Gorge, Tanzania.

Stratum typicum: Bed I, Lower Pleistocene, age between 1,85 and 1,70 million years B.P.

Diagnosis: Coracoid showing all the characteristic features of the genus *Bubo*, and differing from all the other recent genera of Strigidae. Very similar to the coracoid of the recent species *Bubo africanus* (Temminck), but larger.

Referred material

Locality FLK NNI: Holotype; paratypes; 2 pedal phalanges.

Locality DKI: 1 distal part of tibiotarsus; 2 fragments of coracoid and humerus.

Locality FLK NI: Coracoid, 2 upper and 2 lower parts; humerus, 3 distal parts; radius, 2 proximal parts; ulna, 1 distal part; carpometacarpus, 3 proximal parts; femur, 4 proximal parts and 1 distal; tibiotarsus, 3 distal parts; tarsometatarsus, 1 almost complete, 1 proximal and 1 distal parts; 1 ulnare; 20 pedal phalanges.

Minimum number of individuals

FLK NNI: Layer 3, 2 ind.

DKI: Layer 2, 1 ind.; layer 3, 1 ind.

FLK NI: Layer 1, 2 ind.; layer 2, 2 ind.; layer 3, 1 ind.; layer 4, 1 ind.; layer 5, 2 ind.

Geographic and temporal range: This species is known only from Bed I of Olduvai Gorge.

Place of conservation of the material: The fossils are currently on deposit at the University of Florida, Department of Zoology, and will later be returned to Tanzania.

Description and comparisons

Comparison with recent species

Among the recent species of the genus *Bubo*, the Olduvai fossils are closest to the Spotted Eagle Owl *Bubo africanus* (Temminck). The dimensions of fossil remains and recent comparative material are given in Tables 1 and 2.

In the recent Strigidae there is much sexual dimorphism, with females generally larger than males. However, the dimensions of the skeletal remains of *Bubo leakeyae* are generally larger than the dimensions of the largest female of *Bubo africanus* available. In the fossil population there is also some variation in size that can be explained by sexual dimorphism.

The holotype coracoid has a deep fossa under the brachial tuberosity, on the internal side of the bone, and the pneumatic foramina open in the vault of this fossa. The development of this fossa shows great variability in a recent comparative population of *B. africanus*. Some individuals have a poorly developed fossa, and some others have one very similar to that of the holotype of *B. leakeyae*. Therefore this character cannot be considered diagnostic.

In the same way the coracoidal fenestra is widely open on both anterior and posterior faces in the holotype. The opening of this fenestra is also subject to large variation in the comparative population of recent *B. africanus*.

Figure 1 (left)

Bubo leakeyae, new species, Olduvai Gorge, Tanzania (Scale = 2 cm)

- A-B Left coracoid, holotype, OLD 15802, FLK NNI, layer 3, A anterior face, B posterior face.
- C Right tarsometatarsus, proximal part, paratype, OLD 16262, FLK NNI, scree, anterior face.
- D Left tarsometatarsus, distal part, paratype, OLD 15730, FLK NNI, layer 3, anterior face.
- E-F Left femur, proximal half, paratype, OLD 15364, FLK NNI, layer 2+3, E anterior face, F posterior face.
- G-H Left femur, distal part, paratype, OLD 15473, FLK NNI, layer 3, G anterior face, H posterior face.
- I Left tarsometatarsus, almost complete, OLD 11574, FLK NI, layer 1, anterior face.
- J-K Left femur, lacking the distal part, OLD 11586, FLK NI, layer 2, J anterior face, K posterior face.

TABLE 1
MEASUREMENTS (MM) OF *Bubo leakeyae* AND RECENT OWLS.

| Measurement | <i>Bubo leakeyae</i> | | <i>Bubo africanus</i> | | <i>Bubo bubo</i> |
|------------------------------|----------------------|---|-----------------------|-----------|------------------|
| | n. sp. | | recent | | recent |
| | Range | N | ♂ n=5 | ♀ n=3 | ♂ |
| Coracoid | | | | | |
| Internal length | 51,0* | 1 | 41,1-43,7 | 41,7-46,5 | 50,5 |
| Width of head ^a | 7,6* | 1 | 5,9-6,8 | 5,8-6,3 | 7,6 |
| Upper depth | 7,8-9,2* | 2 | 6,9-7,9 | 6,8-8,0 | 8,7 |
| Width of shaft in the middle | 6,8-7,1* | 2 | 5,7-6,3 | 5,6-5,8 | 6,6 |
| Depth of shaft in the middle | 3,9-4,2* | 2 | 3,1-3,8 | 3,3-3,7 | 3,7 |
| Length sternal facet | 16,3-16,3* | 2 | 14,3-15,8 | 14,0-15,5 | 16,0 |
| Humerus | | | | | |
| Distal width | 18,2 | 1 | 17,0-17,8 | 17,3-18,6 | 21,0 |
| Distal depth | 8,9 | 1 | 8,1-9,1 | 8,6-9,0 | 9,8 |
| Depth external condyle | 8,6 | 1 | 7,7-8,7 | 8,1-8,7 | 9,9 |
| Depth internal condyle | 6,0 | 1 | 5,2-5,7 | 5,4-5,6 | 6,5 |
| Radius | | | | | |
| Proximal width | 6,9 | 1 | 5,8-6,9 | 5,6-7,2 | 6,9 |
| Proximal depth | 4,1 | 1 | 3,7-4,1 | 3,6-4,6 | 4,5 |
| Ulna | | | | | |
| Depth of external condyle | 9,2 | 1 | 8,3-9,0 | 8,6-9,3 | 10,4 |
| Width of shaft ^b | 5,0 | 1 | 4,6-5,0 | 4,8-5,2 | 5,2 |
| Depth of shaft ^b | 5,2 | 1 | 4,8-5,5 | 5,1-5,6 | 5,9 |
| Carpometacarpus | | | | | |
| Depth of shaft in the middle | 4,6 | 1 | 3,8-4,4 | 4,0-4,6 | 4,7 |
| Width of shaft in the middle | 3,3 | 1 | 3,1-3,5 | 3,2-3,5 | 3,5 |
| Femur | | | | | |
| Total length | 74± | 1 | 63,9-67,9 | 65,9-69,6 | 78,5 |
| Proximal width | 14,2-16± | 5 | 13,0-13,8 | 12,9-14,0 | 15,2 |
| Proximal depth | 8,4 | 1 | 7,4-7,8 | 7,4-8,3 | 8,2 |
| Depth of head | 5,8-6,5 | 5 | 5,1-5,6 | 5,2-5,8 | 6,0 |
| Width of shaft in the middle | 6,1-6,7 | 2 | 5,4-6,1 | 5,3-6,0 | 6,5 |
| Depth of shaft in the middle | 6,0-6,3 | 2 | 5,2-5,6 | 5,1-6,1 | 6,0 |
| Distal width | 14,7-15,1 | 3 | 12,4-13,3 | 12,5-13,7 | 14,9 |
| Depth internal condyle | 8,6-9,4 | 3 | 7,3-8,0 | 7,4-8,6 | 8,8 |
| Depth external condyle | 11,6-11,7 | 2 | 10,3-11,0 | 10,4-11,3 | 12,0 |
| Tibiotarsus | | | | | |
| Width of shaft ^c | 6,1 | 1 | 5,9-7,2 | 6,0-7,0 | 7,1 |
| Depth of shaft ^d | 3,8 | 1 | 3,6-4,0 | 3,4-4,5 | 4,2 |
| Distal width | 12,2-15,6 | 4 | 11,1-12,1 | 12,0-12,5 | 13,9 |
| Depth internal condyle | 10,7-10,7 | 2 | 9,0-10,3 | 9,7-10,7 | 11,0 |

* Measurements of the holotype

^a Width of the head on the anterior face

^b Width and depth of shaft 1 cm above the external condyle

^c Width of shaft at level of apophysis interna ligamenti obliqui (Ballmann 1969)

^d Depth of shaft just above the apophysis interna ligamenti obliqui

TABLE 2
MEASUREMENTS (MM) OF *Bubo leakeyae* AND RECENT OWLS.

| Measurement | <i>Bubo leakeyae</i> | | <i>Bubo africanus</i> | | <i>Bubo bubo bengalensis</i> |
|--|----------------------|---|-----------------------|-----------|------------------------------|
| | n. sp. | | recent | | recent |
| | Range | N | ♂ n=5 | ♀ n=3 | ♂ |
| Tarsometatarsus | | | | | |
| Total length | 67+ | 1 | 64,7-68,7 | 66,5-69,4 | 72,3 |
| Proximal width ^a | 13,2-13,7 | 2 | 10,9-12,3 | 11,5-12,8 | 13,7 |
| Proximal depth ^b | 12,8 | 1 | 10,8-11,6 | 11,0-12,2 | 13,2 |
| Width of shaft in the middle | 6,7-6,9 | 3 | 4,9-5,8 | 5,3-6,5 | 6,9 |
| Depth of shaft in the middle | 4,8-5,1 | 3 | 3,8-4,7 | 4,3-5,0 | 5,4 |
| Distal width | 15,4 | 1 | 13,1-14,0 | 13,2-14,6 | 16,7 |
| Distal depth | 11,6 | 1 | 9,3-10,0 | 9,1-10,9 | 11,0 |
| Pedal phalanges | | | | | |
| Length of Phalanx 1 D I ^c | 15,7 | 1 | 12,9-14,1 | 14,0-15,0 | 16,2 |
| Length of Phalanx 1 D II ^d | 12,5 | 1 | 10,4-11,5 | 11,3-12,4 | 12,4 |
| Length of Phalanx 2 D II ^c | 20,0-20,2 | 3 | 17,3-19,3 | 18,6-20,6 | 22,1 |
| Length of Phalanx 2 D III ^c | 13,8 | 1 | 11,9-12,3 | 12,8-14,1 | 14,1 |
| Length of Phalanx 3 D III ^c | 19,0 | 1 | 15,4-17,8 | 16,0-18,6 | 20,4 |
| Length of Phalanx 2 D IV ^c | 4,3 | 1 | 3,0-3,6 | 3,5-3,8 | 3,8 |
| Length of Phalanx 4 D IV ^c | 13,0-16,0 | 4 | 12,1-14,3 | 12,8-14,8 | 16,8 |

^a Proximal width through cotylae

^b Proximal depth from internal cotyla to internal ridge

^c Length measured on the anterior face

^d Length measured on the posterior face.

There is no morphological character distinguishing *Bubo leakeyae* from the recent species of *B. africanus*, and the only difference between these two forms is in size. *B. leakeyae* is probably the immediate ancestor of *B. africanus*.

In the widespread Palearctic Eagle Owl *Bubo bubo* which occurs in the greater part of the Old World, there is much variation in size, following Bergmann's rule. The northernmost subspecies, *B. b. bubo*, from northern and middle Europe, is very large, while the southernmost subspecies, *B. b. bengalensis*, from India, *B. b. ascalaphus* and *B. b. desertorum*, from northern Africa and eastern Asia, are much smaller.

We have compared the Olduvai fossils to a recent specimen of the small subspecies *B. b. bengalensis*, from India. This specimen is a male and thus can be considered comparatively small in relation to the entire population. Its dimensions are given in Tables 1 and 2.

In *B. b. bengalensis* the total lengths of the humerus, ulna, radius, carpometacarpus and tibiotarsus, are much greater than in *B. africanus*, but

length is only slightly greater for the coracoid, femur, and tarsometatarsus. The transverse dimensions, such as widths and depths of the ends, widths and depths of the shaft, are not very different, *B. b. bengalensis* being only slightly larger than *B. africanus*. As the dimensions of *B. leakeyae* are also slightly larger than in *B. africanus*, they come very close to the dimensions of *B. bubo bengalensis*. The question thus arises whether the Olduvai Owl could represent a small form of the species *B. bubo*. However, there are some morphological or quantitative differences between them.

In the coracoid of *B. bubo* the coraco-humeral surface extends strongly above the glenoid facet. In *B. africanus*, as in *B. leakeyae*, the coraco-humeral surface is more rounded. On the anterior face of the head of the coracoid, the furcular facet has a rather circular shape in *B. leakeyae* and *B. africanus*, and is more elongated in *B. bubo* (Fig. 2).

In the humerus of *B. bubo* the distal part is proportionally wider across than in *B. africanus* and *B. leakeyae*.

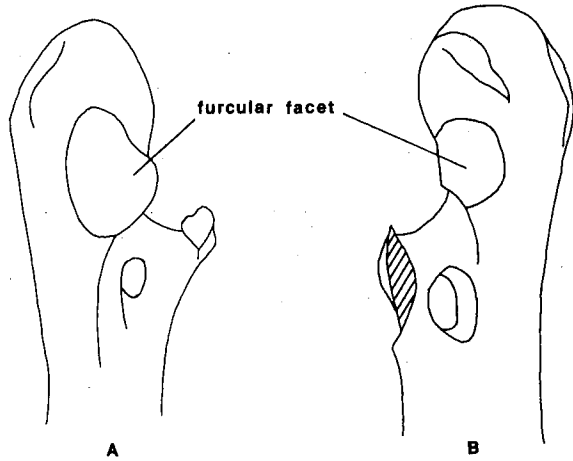


FIGURE 2

Diagram of the upper part of coracoid, anterior face, showing the shape of the furcular facet. A *Bubo bubo bengalensis*, recent, right coracoid. B *Bubo leakeyae*, n. sp. left coracoid, holotype, OLD 15802.

The carpometacarpus is distinctly longer in *B. bubo bengalensis* (71 mm) than in *B. africanus* (♂ 55,0–59,2; ♀ 57,2–60,0). We have no complete carpometacarpus for *B. leakeyae*, but on the specimen OLD 11589 it is possible to see that the length was comparable to that of *B. africanus*, and smaller than in *B. bubo bengalensis*.

The femur is also distinctly longer in *B. b. bengalensis* than in *B. leakeyae* or in *B. africanus*. In *B. bubo* the head of the femur also extends further on the internal side than in *B. leakeyae* and *B. africanus*.

In the tibiotarsus the apophysis interna ligamenti obliqui (Ballmann 1969) is more developed and situated nearer to the internal edge in *B. leakeyae* and *B. africanus* than in *B. bubo*.

The tarsometatarsus of most birds has a canalis interosseus tendinus (Baumel 1979) with its proximal opening in the distal foramen (or foramen vasculare distale (Baumel 1979)), and its distal opening is in the external intertrochlear notch. In seven of our eight comparative specimens of *B. africanus*, the canalis interosseus tendinus opens distinctly below the distal foramen. The osseous bridge which covers this canal is very narrow and is even missing on two specimens. In *B. bubo bengalensis* the canalis interosseus tendinus opens in the

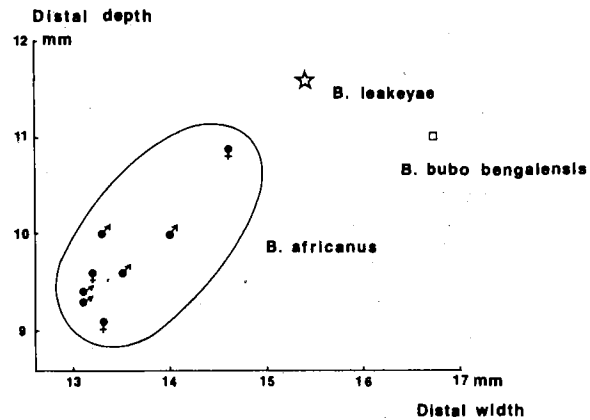


FIGURE 3

Scatter diagram of the distal part of tarsometatarsus in recent *Bubo africanus* and *B. bubo bengalensis*, and fossil *B. leakeyae*.

distal foramen and is situated closer to the external intertrochlear notch than in *B. africanus*. In the three specimens of tarsometatarsus of *B. leakeyae*, the opening of the canalis interosseus tendinus and the position of the distal foramen are the same as in *B. africanus*. Moreover, in *B. bubo bengalensis*, the internal trochlea extends more strongly on the internal side, and the trochleae are disposed on a line much less curved than in *B. africanus*. The ratios between the distal width and distal depth are as follows:

$$\text{Ratio } \frac{\text{Distal width} \times 100}{\text{Distal depth}}: \text{Bubo africanus } \sigma: 133,0-140,8 \text{ (mean } 138,8)$$

$$\text{Bubo africanus } \text{♀}: 133,9-146,2 \text{ (mean } 139,2)$$

$$\text{Bubo leakeyae}: 132,8$$

$$\text{B. Bubo bengalensis}: 151,8$$

Fig. 3 shows that the tarsometatarsus of *Bubo leakeyae* falls on the same axis as in *B. africanus*, while the tarsometatarsus of *B. bubo bengalensis* is proportionately wider in relation to its depth.

In conclusion *Bubo leakeyae* is about the same size as a small subspecies of *B. bubo*, such as *B. b. bengalensis*, but its morphological characters show

it is more closely related to the recent species *Bubo africanus*.

According to the literature on recent birds (Sharpe 1899; Roberts 1951; Mackworth-Praed & Grant 1957, 1962; Grossman & Hamlet 1964; Burton 1973; Steyn 1982) *Bubo capensis* is a much larger form than *B. africanus*. For the only bone measurement available in the literature (the tarsus length) the range of variation (62,0–82,6 mm) overlaps widely the range of *B. africanus* (64,7–69,4 mm) but the tarsometatarsus of *B. capensis* is much wider and stronger. A specimen from the South Australian Museum, Adelaide, No. B11169, sex unknown, has the following measurements for both sides: Total length, 72,3–73,0; proximal width, 18,4–18,4; distal width, 20,8–21,1; least width of shaft, 9,4–9,5 mm. The transverse measurements are much larger than in *B. africanus* and *B. leakeyae* (see Table 2).

Among the four other species of *Bubo* occurring in Africa, two are distinctly smaller, namely Akun Eagle Owl *B. leucostictus* and Fraser's Eagle Owl *B. poensis*, and two are distinctly larger, namely *B. lacteus* and Shelley's Banded Eagle Owl *B. shelleyi* (Sharpe 1875; Bannerman 1953; Burton 1973; Mackworth-Praed & Grant 1957, 1962, 1981; Grossman & Hamlet 1964).

Comparison with extinct species or subspecies

Three extinct forms of the genus *Bubo* have been described from the Old World, namely: *Bubo? floriana*e Kretzoi, from the Lower Pliocene of Hungary, *Bubo bubo davidi* Mourer-Chauviré, from the Middle Pleistocene of France, and *Bubo binagadensis* Burchak-Abramovich, from the Upper Pleistocene of Caucasus (Burchak-Abramovich 1965, 1975; Mourer-Chauviré 1975; Janossy 1978). They are very large forms, generally larger than the largest specimens of the recent European Eagle Owl (*B. b. bubo*), which is much larger than the Olduvai Owl.

In the New World L. H. Miller (1911) described *Bubo sinclairi* from the Upper Pleistocene of California, which was said to be larger than the recent North American Great Horned Owl *Bubo virginianus* (Gmelin). When compared with a larger sample of the recent form, however, *Bubo sinclairi* falls in the range of variation of the modern species. *Bubo sinclairi* should be restudied and possibly synonymized with *B. virginianus* (cf. Howard 1983).

In the Holocene of Rodriguez Island *Bubo? leaguati* Rothschild has been described. In this form, the length of the tibiotarsus is 77 mm (Lambrecht 1933), which is much smaller than the same bone in the recent African Spotted Eagle Owl *Bubo africanus*, and therefore smaller than in *Bubo leakeyae*.

Bubo cf. lacteus (Temminck)
cf. Giant Eagle Owl

Material

Locality FLK NNI: Humerus, 1 incomplete distal part; 2 pedal phalanges.

Locality FLK NI: Scapula, 1 anterior end; radius, 1 proximal part; carpometacarpus, 1 distal part; 2 fragments of tarsometatarsus; 2 pedal phalanges.

Minimum number of individuals

FLK NNI: Layer 3, 1 ind.

FLK NI: Layer 2, 1 ind.; layer 4, 1 ind.

These remains belong to a much larger owl than *Bubo leakeyae* but are very fragmentary. Most of the dimensions (Table 3) are slightly smaller than the dimensions of a recent female of Giant Eagle Owl *Bubo lacteus*, but we know that in this species the female is considerably larger than the male (Bannerman 1953; Burton 1973; Steyn 1982). We therefore designate this form as *Bubo cf. lacteus* until more material becomes available.

Family Tytonidae Ridgway Genus *Tyto* Billberg

Tyto alba cf. affinis (Blyth)
African Barn Owl

Material

Locality FLK NNI: Radius, 1 proximal and 1 distal part; ulna, 2 distal parts; carpometacarpus, 1 almost complete and 1 distal part; 1 phalanx of the wing; tarsometatarsus, 1 distal part and 2 distal fragments; 4 pedal phalanges.

Locality FLK NI: Coracoid, 2 upper parts; ulna, 1 distal part; carpometacarpus, 5 distal parts;

TABLE 3
MEASUREMENTS (MM) OF *Bubo cf. lacteus* FROM OLDUVAI

| Measurement | <i>Bubo cf. lacteus</i> Olduvai | <i>Bubo lacteus</i> ♀ recent |
|---|------------------------------------|---------------------------------|
| Humerus OLD 1920 | | |
| Length from the intercondylar furrow to the entepicondylar prominence | 17,0 | 18,2 |
| Depth of internal condyle | 7,1 | 7,7 |
| Depth of entepicondylar prominence | 9,0 | 9,2 |
| Depth of shaft at level of base of brachialis anticus scar | 6,6 | 7,6 |
| Scapula OLD 11612 | | |
| Width of glenoid facet | 8,0 | 9,2 |
| Depth of glenoid facet | 10,7 | 12,4 |
| Length from external corner of glenoid facet to acromion | 16,2 | 17,6 |
| Radius OLD 11602 | | |
| Proximal width | 6,9 | 9,4 |
| Proximal depth | 4,5 | 5,7 |
| Carpometacarpus OLD 11590 | | |
| Depth of metac. majus in the middle | 3,7 | 4,6 |
| Width of metac. majus in the middle | 4,8 | 6,5 |
| Tarsometatarsus OLD 11614 | | |
| Maximum length of internal trochlea | 10,6+ | 12,4 |
| Depth of internal trochlea | 5,8 | 7,1 |
| Posterior phalanx 2 D II OLD 11613 | | |
| Length on the anterior face | 27,3+ | 31,5 |
| Proximal width | 6,8+ | 8,8 |
| Proximal depth | 7,3 | 8,6 |
| Width of shaft in the middle | 6,3 | 7,2 |
| Depth of shaft in the middle | 4,0 | 5,3 |
| Distal depth | 6,0 | 6,8 |
| Posterior phalanx 3 D III OLD 16049 | | |
| Proximal width | 6,4 | 7,7 |
| Claw of D I OLD 11615 | | |
| Proximal width | 5,6 | 6,1 |
| Proximal depth | 7,8 | 7,9 |
| Claw of D IV OLD 16172 | | |
| Proximal width | 6,8 | 6,8 |
| Proximal depth | 8,1 | 8,1 |

tibiotarsus, 1 distal part; tarsometatarsus, 1 proximal and 2 distal parts; 21 pedal phalanges.

Locality FLK I: 3 pedal phalanges.

Minimum number of individuals

FLK NNI: Layer 2, 1 ind.; layer 2+3, 1 ind.

FLK NI: Layer 1, 1 ind.; layer 2, 1 ind.; layer 3, 1 ind.; layer 4, 3 ind.; layer 5, 2 ind.; layer 6, 1 ind.

FLK I: Main dig Zinj. level, 1 ind.

These remains show no morphological differences from the recent forms of Barn Owl *Tyto alba* Scopoli. There is a large variation of size in this

TABLE 4
MEASUREMENTS (MM) OF *Tyto alba affinis* FOSSIL AND RECENT

| Measurement | <i>Tyto alba cf. affinis</i> Olduvai | | <i>Tyto alba affinis</i> recent |
|-------------------------------|---|---|------------------------------------|
| | range | n | 2 ♂, 2 ♀ |
| Coracoid | | | |
| Width of head | 3,9 | 1 | 4,3-4,3 |
| Depth of head | 5,7-6,0 | 2 | 5,4-5,5 |
| Carpometacarpus | | | |
| Total length | 45,5 | 1 | 44,8-45,5 |
| Proximal depth | 10,0 | 1 | 9,7-9,9 |
| Width of trochlea | 5,0 | 1 | 4,6-4,8 |
| Depth of metac. majus | 2,6-2,7 | 2 | 2,3-2,5 |
| Width of metac. majus | 3,6-3,8 | 2 | 3,3-3,6 |
| Distal depth | 7,0-7,6 | 5 | 6,7-7,0 |
| Distal width | 4,0-4,7 | 6 | 3,7-4,3 |
| Ulna | | | |
| Distal depth | 6,5-7,0 | 3 | 6,4-6,6 |
| Distal width | 6,6-6,7 | 3 | 6,4-6,6 |
| Depth of shaft* | 3,8-3,9 | 3 | 3,6-4,0 |
| Width of shaft* | 4,1-4,1 | 3 | 3,8-4,2 |
| Radius | | | |
| Proximal width | 4,2 | 1 | 3,9-4,1 |
| Proximal depth | 3,0 | 1 | 2,9-3,2 |
| Distal width | 6,4 | 1 | 6,2-6,4 |
| Tibiotarsus | | | |
| Distal width | 9,5 | 1 | 9,6-9,9 |
| Depth of shaft above condyles | 3,0 | 1 | 3,1-3,4 |
| Tarsometatarsus | | | |
| Proximal width | 9,5 | 1 | 9,2-10,0 |
| Proximal depth | 6,9 | 1 | 6,5-6,7 |
| Minimum width of shaft | 4,2 | 1 | 3,5-4,4 |
| Depth at the same level | 3,5 | 1 | 3,1-3,8 |
| Distal width | 10,7-10,9 | 2 | 10,7-11,0 |
| Distal depth | 8,5 | 1 | 8,2-8,3 |
| Pedal phalanges | | | |
| Length phalanx 1 D I | 11,7 | 1 | 11,7-12,9 |
| Length phalanx 1 D II | 12,4-13,3 | 3 | 12,4-13,0 |
| Length phalanx 2 D II | 14,7-15,9 | 6 | 14,7-16,7 |
| Length phalanx 1 D III | 7,3 | 1 | 6,3-6,9 |
| Length phalanx 2 D III | 12,8 | 1 | 12,2-13,1 |
| Length phalanx 3 D III | 12,5-13,8 | 4 | 11,8-14,1 |
| Length phalanx 4 D IV | 11,3-12,8 | 2 | 12,2-13,0 |

*Depth and width of shaft 1 cm above the carpal tuberosity.

widespread species and we compared the fossil material only with the recent subspecies which lives in Africa south of the Sahara, *Tyto alba affinis* (Blyth). Our comparative material includes only four skeletons (2 males, 2 females). This sample shows no sexual dimorphism and so we give the range of variation for the males and females together. The dimensions of Olduvai and recent specimens are given in Table 4. There is no conspicuous difference in size between the fossil and recent material, and so we are unable to differentiate it from the recent subspecies *affinis*.

This is the first time that the neospecies *Tyto alba* is reported from a Lower Pleistocene level. The oldest previous records were from the Middle Pleistocene of Portugal (Harlé 1909), Israel (Tchernov 1962), and France (Mourer-Chauviré 1975). The earliest record of this species in the United States is from the last interglacial, or Sangamonian, Upper Pleistocene (Brodkorb 1971).

ECOLOGICAL CONSIDERATIONS

According to Bannerman (1953) and Burton (1973) the recent form *Bubo africanus* lives in lightly wooded savanna areas, or in forest clearings, but not in rain forest and dense woodlands. It frequents large trees (such as baobabs), small rocky hills, or steep ravines. It feeds on small rodents, snakes, lizards, insects, etc. It nests in hollow trees or on the ground (Bannerman 1953; Burton 1973). Its ancestor, *Bubo leakeyae*, probably shared the same ecological requirements.

Bubo lacteus lives in semi-arid Acacia savanna, as well as in riverine forest and dense woodlands (Burton 1973; Steyn 1982). It nests in trees. *B. africanus* and *B. lacteus* can be found in close proximity, in lightly wooded savannas. *B. lacteus* nests in trees. *Tyto alba affinis* is also found in the lightly wooded parts of Africa. These three owls therefore suggest an open landscape, of lightly wooded areas. This conclusion is in general agreement with the results of the studies of rodents (Jaeger 1979) and pollens (Bonnefille 1979).

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