LATEST PLIOCENE MOUSEBIRDS (AVES, COLIIDAE) FROM OLDUVAI GORGE, TANZANIA

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(With 8 figures and 4 tables)

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ABSTRACT

Two mousebird species, *Colius* cf. *C. striatus* and *Urocolius* sp., have been recognized amongst the fossil bird remains of Olduvai. This is the first fossil record of the genus *Urocolius*. The only other African fossil record of the order Coliiformes is *Colius hendeyi* from Langebaanweg, south-western Cape. Several other fossil species are known from Europe. The extant Coliiformes now occur only in Africa.

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INTRODUCTION

The mousebird remains from Olduvai Gorge in Tanzania form a minor part of the entire avian assemblage from that area. Out of a total of some 30 000 bird bones belonging to about 46 different taxa (D. Matthiesen pers. comm.), only 57 bones have been assigned to the family Coliidae. These are none the less important because the fossil record of this family is poor. The only other fossil mousebird recorded from Africa is the extinct species *Colius hendeyi* Rich & Haarhoff, 1985, from the Early Pliocene site of Langebaanweg in South Africa. Two extinct species occurred in Europe during the Late Eocene and at least a further six species (requiring revision) in the Miocene (Ballmann 1969; Olson 1985; Mourer-Chauviré 1988) (Table 1).

Today, four species of mousebirds in the genus *Colius* and two species in the genus *Urocolius* occur in sub-Saharan Africa (Schifter 1985; Fry *et al.* 1988). Comparisons between the fossils and five of the six living species (skeletons of *Colius castanotus* were unobtainable) indicate that most of the Olduvai specimens are readily distinguishable from the genus *Urocolius*. Morphological differences at the species level were more difficult to ascertain. However, it appears that all but three of the specimens belong to a single species that is closely related to the extant speckled mousebird, *Colius striatus*, which inhabits the vicinity of Olduvai Gorge today, along

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TABLE 1

Age and distribution of fossil and living mousebirds examined.

		GERMANY	FRANCE	EAST AFRICA	CENTRAL & SOUTHERN AFRICA
HISTORIC				*Colius leucocephalus* *Colius striatus* *Urocolius macrourus*	*Colius colius* *Colius striatus* *Urocolius indicus*
PLIOCENE	LATE			*Colius* cf. *C. striatus* *Urocolius* sp.	
	EARLY				*Colius hendeyi*
MIOCENE	LATE		*Colius* cf. *C. palustris*		
	MIDDLE	*Colius* sp.	*Colius palustris* *Colius* cf. *C. palustris*		
	EARLY		*Colius paludicolus* *Colius consobrinus* *Colius archiaci*		
EOCENE	LATE		*Primocolius sigei* *Primocolius minor*		

with the white-headed mousebird, *C. leucocephalus*, and the blue-naped mousebird, *Urocolius macrourus*. One proximal end of an ulna, OLD FLK NI 19721, one distal end of an ulna, OLD FLK NI 19765, and the incomplete sternal end of one coracoid, OLD FLK NI 26010, are somewhat larger than the other fossil specimens and are morphologically more similar to *Urocolius*, the genus to which they have been referred in this report. With such a small sample size, the species determination is uncertain.

The most commonly preserved elements for the genus *Colius* are the ulna, tarsometatarsus, femur and humerus. Bones that are almost complete include one humerus, two ulnae, three carpometacarpi, one phalanx I of digit II and one femur.

Reports on other fossil birds from Olduvai Gorge include those of Brodkorb & Mourer-Chauviré (1982, 1984*a*, 1984*b*) and of Harrison & Walker (1976, 1979).

The specimen numbers are catalogue numbers of the Olduvai fossil birds, and the data are kept at the Department of Zoology, University of Florida, Gainesville. The fossils belong to the Tanzanian Ministry of Antiquities, Dar es Salaam. They were collected by Mary Leakey in 1960–1962.

The following abbreviations are used in this paper:

FLK	Frida Leakey Korongo (Leakey 1965)
L	Langebaanweg
M	University of Miami
NMB	National Museum, Bloemfontein
OLD	Olduvai
PB	Osteological collection of Pierce Brodkorb
SAM	South African Museum
YPM	Peabody Museum, Yale University

Anatomical abbreviations are:

c	complete
d	distal
l	left
p	proximal
r	right

COMPARATIVE MATERIAL

Recent

Colius leucocephalus: 1 unsexed; *C. colius*: 10 males, 5 females, 6 unsexed; *C. striatus*: 15 males, 11 females, 30 unsexed; *Urocolius macrourus*: 3 males, 3 females, 1 unsexed; *U. indicus*: 11 males, 11 females, 11 unsexed.

Fossil

Colius hendeyi Rich & Haarhoff, 1985. The entire assemblage of 124 bones from Langebaanweg, South Africa, was available. Data for the other described fossil mousebirds including *Colius paludicolus*, *C. consobrinus*, *C. archiaci*, *C. palustris*, *Colius* cf. *C. palustris*, *Colius* sp., *Primocolius sigei* and *P. minor* were obtained from the literature (Milne Edwards 1871; Ballmann 1969; Brodkorb 1971; Olson 1985; Mourer-Chauviré 1988).

DESCRIPTION

Order COLIIFORMES Murie, 1872

Family **Coliidae** Swainson, 1837

Genus *Colius* Brisson, 1760

For ordinal, family and generic diagnoses, see Ballmann (1969) and Rich & Haarhoff (1985). For additional differences between the genera *Urocolius* Bonaparte, 1854, and *Colius*, see Table 2. Species of *Urocolius* generally have more strongly sculptured features than species of *Colius* in all the elements examined.

The fossils from Olduvai were also compared with, and found to be different from, the extinct genus *Primocolius* Mourer-Chauviré, 1988, from the Upper Eocene Phosphorites du Quercy in France.

Colius cf. *C. striatus*

Figs 1A–B, K, 2A, E, J, 3A, F, G, 4A, F, G

Material

Olduvai. Coracoids: FLK NI 12567 (lp with some shaft); FLK NNI 2007 (rp with shaft).

Humeri: FLK NI 10195 (lc deltoid crest slightly damaged); FLK NI 29627 (lp broken at base of bicipital crest); FLK NNI 3136 (ld); FLK NI 12875 (rp); FLK NI 12401 (rp); FLK NI 28439 (rp small fragment with head and bicipital crest missing); FLK NI 27534 (rd); FLK NNI 2482 (rd with most of shaft); FLK I 3643 (rd).

Ulnae: FLK NI 18301 (rc); FLK NI 27330 (rc); FLK NNI 20669 (lp); FLK NI 19721 (lp); FLK NI 29531 (lp, olecranon damaged); FLK NI 24547 (lp, olecranon missing); FLK NI 22756 (ld); FLK NI 25063 (ld); FLK NI 28923 (ld); FLK NI 18295 (rp, olecranon missing); FLK NI 22660 (rp); FLK NI 29532 (rp); FLK NI 13895, FLK I 5003 (rp, olecranon damaged); FLK I 5004 (rp, lacking olecranon); FLK NI 18269 (rp slightly damaged); FLK NI 19766 (rd); FLK NI 19765 (rd); FLK NI 13895 (rd internal condyle damaged).

Radius: FLK NI 21182 (lp).

Carpometacarpi: FLK NI 10373 (l lacking metacarpal III); FLK NI 7985 (l lacking metacarpal III and posterior carpal trochlea); FLK NNI 15514 (ld incomplete); FLK NI 8031 (r lacking metacarpal III, metacarpal I and posterior carpal trochlea).

Phalanx I of digit II: FLK NNI 15886 (rc).

Femora: FLK NNI 15356 (rc); FLK NI 18520 (rp); FLK NI 29596 (rp); FLK NI 19949 (rd); FLK NI 19950 (rd); FLK NI 21843 (rd); FLK NI 19973 (lp); FLK NI 23510 (lp).

Tibiotarsi: FLK I 4906 (lp rotular crest damaged); FLK NI 18432 (rp rotular crest and inner cnemial crest damaged); FLK NNI 16690 (ld); FLK NI 1356 (rd); FLK NNI 2035 (rd external condyle missing).

Tarsometatarsi: FLK NI 12867 (lp); FLK NI 18425 (lp hypotarsus damaged); FLK NI 1128 (lp hypotarsus damaged); FLK NI 7421 (ld); FLK NI 1034 (ld); FLK I 11274 (rd); FLK NI 12866 (rd); FLK NI 7499 (rd internal trochlea missing).

TABLE 2

Osteological differences between *Colius* and *Urocolius* additional to Ballmann (1969) and Rich & Haarhoff (1985).

ELEMENT	*COLIUS*	*UROCOLIUS*
CORACOID	Coracohumeral surface and furcular facet relatively compressed and slightly sloping	Coracohumeral surface and furcular facet erect and elongated
	Furcular facet circular	Furcular facet more linear
	Sternal end slightly expanded	Sternal end greatly expanded
	Sternal facet regularly shaped and relatively broad	Sternal facet irregularly shaped and narrow
	Shaft relatively straight	Shaft more curved
	Scapular facet relatively small	Scapular facet relatively large
ULNA	No scar present on surface external to humero-ulnar depression	Scar present on surface external to humero-ulnar depression
	Olecranon relatively rounded	Olecranon relatively pointed
	Fossa under external cotyla, palmar view, absent or poorly developed	Fossa under external cotyla, palmar view, generally well developed
	External condyle rounded at base of shaft, internal view	External condyle tapers to a point at base of shaft, internal view
	Carpal tuberosity relatively rounded	Carpal tuberosity relatively pointed
	Internal condyle relatively small in relation to external condyle	Internal condyle relatively large in relation to external condyle
RADIUS	Ridges on either side of distal tendinal groove not very pronounced	Ridges on either side of distal tendinal groove are more pronounced
CARPOMETACARPUS	Metacarpal I relatively short and not very recurved proximally	Metacarpal I elongated and pointed proximally
PHALANX I of DIGIT II	Metacarpal facet rounded in shape	Metacarpal facet horseshoe-shaped
	Anterior internal edge not noticeably flattened on to shaft	Anterior internal edge flattened on to shaft
FEMUR	Relatively robust	Relatively gracile
	Internal condyle relatively expanded	Internal condyle not as expanded
	Angle between head and trochanter on anterior side relatively wide	Angle between head and trochanter on anterior side more acute

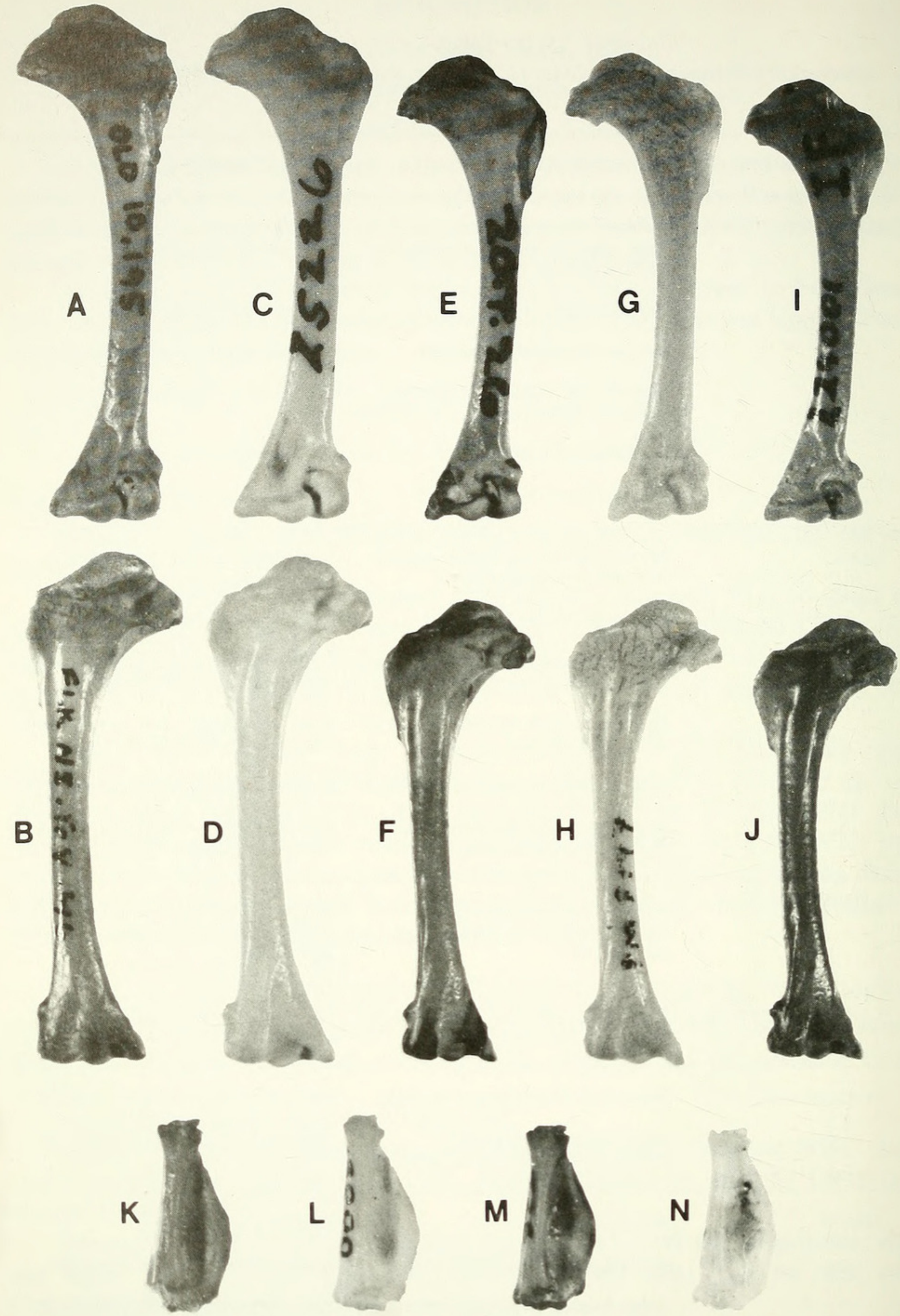

Fig. 1. A–J. Humeri. A, B. *Colius* cf. *C. striatus*, OLD FLK NI 10195. C, D. *C. striatus*, PB25226. E, F. *C. colius*, SAM–ZOT.26. G, H. *C. leucocephalus*, YPM5797. I, J. *C. hendeyi*, L24001 IF. ×3. K–N. Phalanx I of digit II. K. *Colius* cf. *C. striatus*, OLD FLK NNI 15886. L. *C. striatus*, PB19300. M. *C. colius*, SAM–ZOT.26. N. *C. leucocephalus*, YPM5797. ×4.

Age and distribution

Late Pliocene, about 1,72 to 1,83 m.y. (Curtis & Hay 1972; Haq *et al.* 1977; Savage & Russell 1983; Kappelman 1986). This species is known only from sites FLK, FLK NN and FLK N in Bed I at Olduvai Gorge, north-western Tanzania. Dating methods used include potassium-argon and geomagnetic time scales. The accuracy of the dates given have an average co-efficient of variation of between one and two per cent (Curtis & Hay 1972). A Plio–Pleistocene boundary of 1,64 m.y. is taken from Harland *et al.* (1990).

Measurements

See Rich & Haarhoff (1985) and Table 3 for measurements of species of *Colius*. Skeletons of *Colius castanotus* were unavailable for comparison.

Description

The following description differentiates the Olduvai material, here assigned to *Colius* cf. *C. striatus*, from the extant species *C. colius* and *C. leucocephalus*, and from the extinct species *C. hendeyi*, *C. paludicolus*, *C. consobrinus*, *C. archiaci*, *C. palustris* and *Colius* cf. *C. palustris*.

Most preserved elements show the characteristic features of the species *Colius striatus* and most are within the size range of that species.

Coracoid (Fig. 2J). (1) Area between furcular facet and glenoid facet, in internal view, is wide, not narrow; (2) coracohumeral surface not medially constricted; (3) coracohumeral surface rises gradually from glenoid facet in external view; (4) shaft robust; (5) external margin of dorsal surface between glenoid facet and coracohumeral surface deeply indented, forming acute angle. Characters 1–4 separate *Colius striatus* (Fig. 2K) and *Colius* cf. *C. striatus* (Fig. 2J) from *C. colius* (Fig. 2L) and *C. leucocephalus* (Fig. 2M); character 5 is unique to *Colius* cf. *C. striatus*. The coracoid is unknown for other fossil species.

Humerus (Fig. 1A, B). (1) Relatively robust proximal end; (2) head globular in anconal view; (3) deltoid crest curves relatively abruptly palmarly in anconal view; (4) median crest slightly notched; (5) entepicondyle rounded in anconal view and does not project beyond internal condyle; (6) internal condyle well rounded in palmar view and not obviously directed toward external condyle. Characters 1–3 separate *Colius striatus* (Fig. 1C, D) and *Colius* cf. *C. striatus* (Fig. 1A, B) from *C. colius* (Fig. 1E, F), *C. leucocephalus* (Fig. 1G, H), *C. hendeyi* (Fig. 1I, J) and *C. paludicolus*. Character 4 separates *C. striatus* (Fig. 1C, D) and *Colius* cf. *C. striatus* (Fig. 1A, B) from *C. hendeyi* (Fig. 1I, J), *C. leucocephalus* (Fig. 1G, H) and *C. colius* (Fig. 1E, F). Character 5 separates *Colius striatus* (Fig. 1C, D) and *Colius* cf. *C. striatus* (Fig. 1A, B) from *C. colius* (Fig. 1E, F), *C. leucocephalus* (Fig. 1G, H), *C. hendeyi* (Fig. 1I, J), *Colius* cf. *C. palustris* and *C. paludicolus*. Character 6 separates *C. striatus* (Fig. 1C, D) and *Colius* cf. *C. striatus* (Fig. 1A, B) from *C. colius* (Fig. 1E, F), *C. leucocephalus* (Fig. 1G, H) and *C. hendeyi* (Fig. 1I, J).

Ulna (Fig. 3A). (1) Proximal end, robust in internal view; (2) carpal tuberosity erect in distal view, not orientated over internal condyle. Both characters separate

TABLE 3

Measurements (mm) of living and fossil species of *Colius*.

Measurement no.	*Colius* cf. *C. striatus* range	n	mean	*C. striatus* range	n	mean	*C. colius* range	n	mean	*C. leucocephalus* n	mean
CORACOID											
2	2,8-2,9	2	2,85	2,2-3,9	51	3,26	3,0-3,5	20	3,28	1	3,2
4	1,0-1,1	2	1,05	0,7-1,2	52	0,90	0,7-1,0	20	0,90	1	1,1
5	1,3-1,4	2	1,35	0,9-1,3	52	1,10	0,8-1,3	20	1,08	1	1,2
HUMERUS											
1		1	23,70	20,9-24,6	52	22,45	21,1-22,7	20	21,94	1	21,4
2	7,0-7,3	2	7,15	6,7-8,1	54	7,35	6,5-7,3	21	6,92	1	7,0
8	1,9-2,0	2	1,95	1,7-2,5	54	1,99	1,7-2,0	21	1,87	1	2,1
4	1,6-2,0	4	1,87	1,5-2,0	50	1,72	1,5-1,8	19	1,63	1	1,7
6	4,8-5,2	6	5,10	4,6-5,5	52	4,99	4,4-4,9	21	4,62	1	4,6
7	2,4-3,0	6	2,68	2,4-3,0	52	2,72	2,5-2,9	21	2,62	1	2,4
ULNA											
1	20,3-20,6	2	20,45	18,7-22,5	53	20,26	18,8-20,3	21	19,62	1	19,8
2	3,0-3,4	10	3,23	3,0-3,7	54	3,34	2,8-3,5	21	3,10	1	3,3
4	1,2-1,2	6	1,20	1,1-1,7	51	1,28	1,0-1,3	18	1,14	1	1,3
6	2,7-2,9	6	2,78	2,6-3,2	53	2,87	2,5-2,9	21	2,67	1	2,9
RADIUS											
2		1	2,00	1,5-2,1	53	1,92	1,5-1,9	21	1,77	1	1,8
CMC											
1	13,1-13,2	3	13,16	12,6-14,7	52	13,45	12,2-13,6	21	13,0	1	12,8
2		1	3,90	3,5-4,2	52	3,85	3,3-3,9	21	3,64	1	3,5
6	1,8-2,1	3	1,90	1,5-2,0	51	1,70	1,4-1,7	21	1,59	1	1,5
7	2,9-3,1	3	2,96	2,1-3,1	50	2,76	2,6-3,1	21	2,92	1	2,5

PHI DIGII											
1		1	6,7	5,8-7,2	50	6,44	6,0-6,8	20	6,48	1	6,6
2		1	1,8	1,4-1,8	50	1,59	1,4-1,7	20	1,59	1	1,5
9		1	2,7	2,2-3,0	50	2,59	2,4-2,8	20	2,59	1	2,5
FEMUR											
1		1	21,70	20,3-23,6	50	21,82	18,9-21,7	20	20,24	1	20,7
2	4,4-4,8	5	4,54	4,2-5,0	53	4,57	4,0-4,6	21	4,29	1	4,3
3	2,7-3,1	4	2,90	2,8-3,6	53	3,18	2,6-3,3	21	2,83	1	2,9
6	4,0-4,2	4	4,10	4,0-4,6	53	4,27	3,7-4,4	21	4,03	1	3,7
7	2,7-3,2	4	3,07	2,9-3,5	53	3,19	2,6-3,2	21	2,93	1	2,9
TIB											
2		1	4,90	4,5-5,5	53	5,03	4,5-5,2	20	4,85	1	4,8
3		1	3,20	3,5-4,6	52	4,18	3,5-4,5	20	3,91	1	3,8
6	3,4-3,5	2	3,45	3,3-3,7	54	3,46	2,9-3,6	20	3,24	1	3,2
7	3,0-3,1	2	3,05	2,7-3,4	54	3,09	2,7-3,2	20	2,90	1	3,0
TMT											
2	3,0-3,5	2	3,25	3,3-3,8	51	3,51	3,2-3,7	21	3,39	1	3,3
3	3,2-3,3	2	3,25	2,9-3,6	51	3,33	2,9-3,5	21	3,14	1	3,3
6	3,5-3,6	3	3,56	3,2-3,8	49	3,43	3,0-3,6	21	3,25	1	3,3
7	1,7-1,9	4	1,80	1,6-2,2	48	1,86	1,6-2,0	21	1,76	1	1,8

Measurements are: 1 = greatest length; 2 = maximum proximal width; 3 = maximum proximal depth; 4 = minimum shaft width; 5 = minimum shaft depth; 6 = maximum distal width; 7 = maximum distal depth; 8 = maximum head depth; 9 = maximum middle depth; CMC = carpometacarpus; PHI DIGII = phalanx I of digit II; TIB = tibiotarsus; TMT = tarsometatarsus.

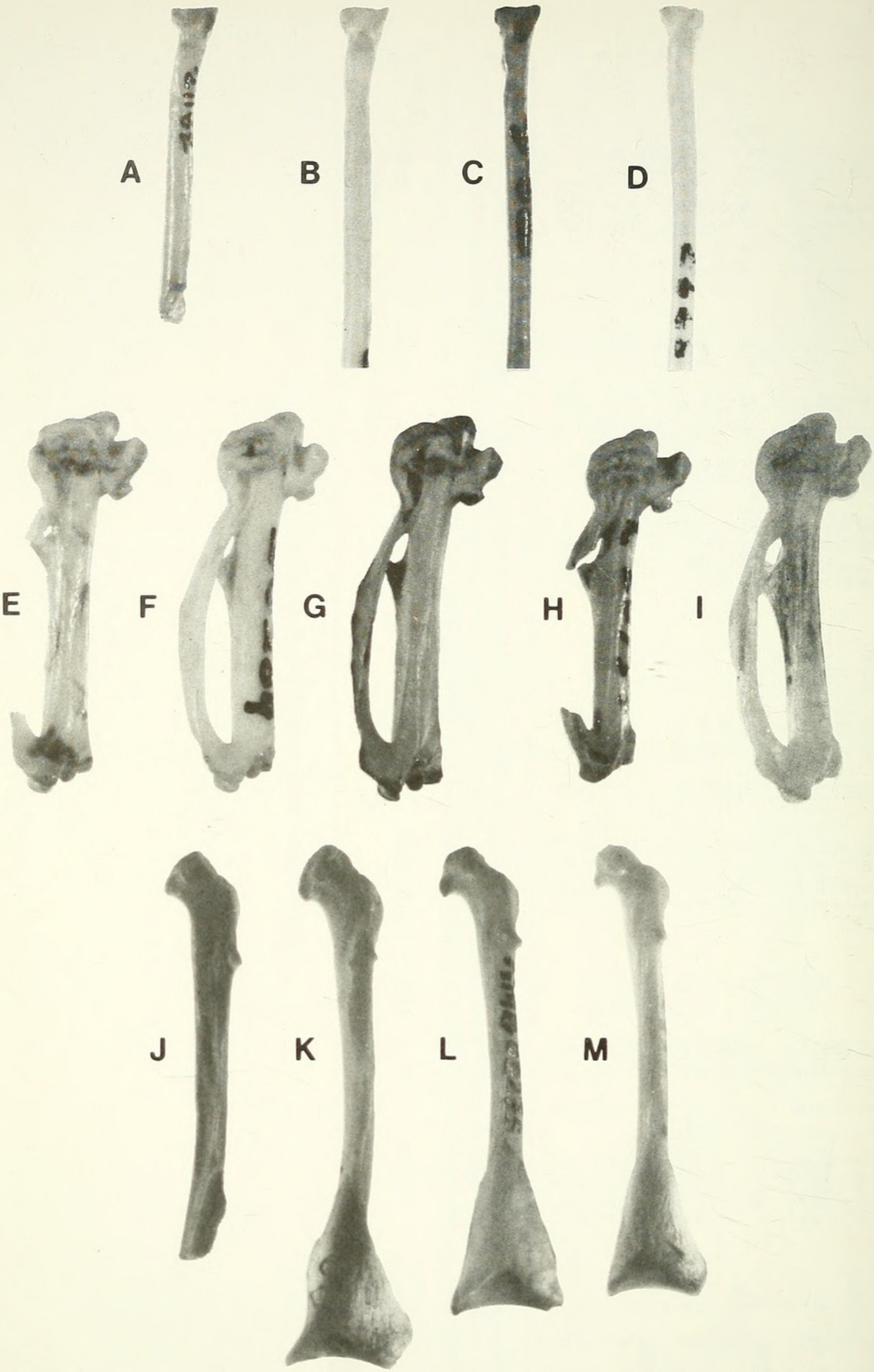

Fig. 2. A–D. Radii. A. *Colius* cf. *C. striatus*, OLD FLK NI 21182. B. *C. striatus*, PB36207. C. *C. colius*, SAM–ZOT.26. D. *C. leucocephalus*, YPM5797. ×4. E–I. Carpometacarpi. E. *Colius* cf. *C. striatus*, OLD FLK NI 10373. F. *C. striatus*, PB36209. G. *C. colius*, SAM–ZO57160. H. *C. hendeyi*, L20733. I. *C. leucocephalus*, YPM5797 (transposed). ×4. J–M. Coracoids. J. *Colius* cf. *C. striatus*, OLD FLK NNI 2007. K. *C. striatus*, PB19300. L. *C. colius*, NMB03275. M. *C. leucocephalus*, YPM5797. ×3.

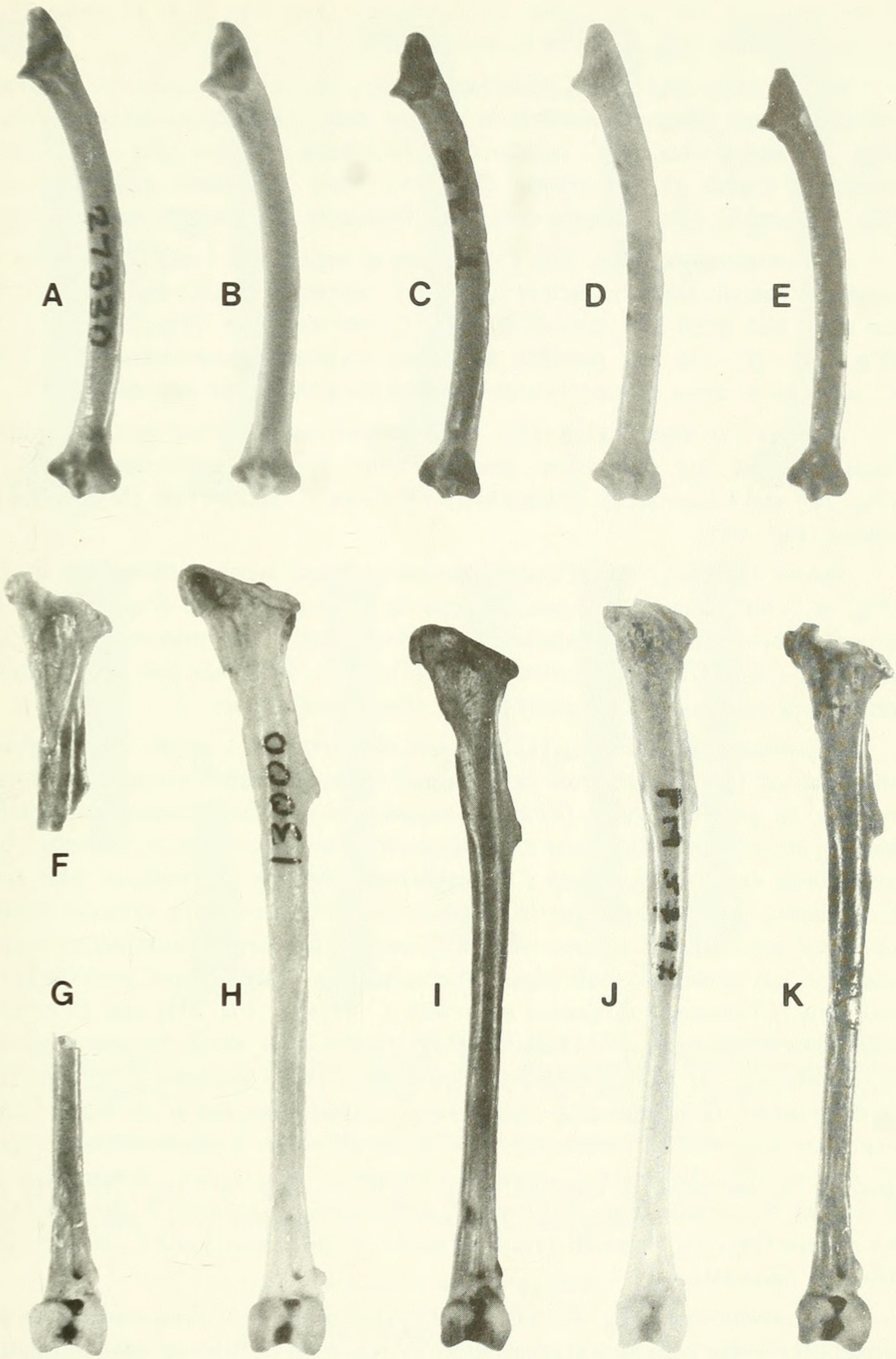

Fig. 3. A–E. Ulnae. A. *Colius* cf. *C. striatus*, OLD FLK NI 27330. B. *C. striatus*, PB36207. C. *C. colius*, SAM–ZOT.26. D. *C. leucocephalus*, YPM5797. E. *C. hendeyi*, L23163. ×3. F–K. Tibiotarsi. F. *Colius* cf. *C. striatus*, OLD FLK I 4906. G. *Colius* cf. *C. striatus*, OLD FLK NNI 16690. H. *C. striatus*, PB19300. I. *C. colius*, SAM–ZO57160. J. *C. leucocephalus*, YPM5797. K. *C. hendeyi*, L17139. ×3.

C. striatus (Fig. 3B) and *Colius* cf. *C. striatus* (Fig. 3A) from *C. colius* (Fig. 3C), *C. leucocephalus* (Fig. 3D) and *C. hendeyi* (Fig. 3E).

Radius (Fig. 2A). (1) Capital tuberosity, medially situated in anconal view; (2) ulnar facet relatively shallow in palmar view. Character 1 separates *C. striatus* (Fig. 2B) and *Colius* cf. *C. striatus* (Fig. 2A) from *C. colius* (Fig. 2C). Character 2 separates *Colius* cf. *C. striatus* (Fig. 2A) from *C. striatus* (Fig. 2B), *C. colius* (Fig. 2C) and *C. leucocephalus* (Fig. 2D). Radius of other extinct species is unknown.

Carpometacarpus (Fig. 2E). (1) Process of metacarpal I and (2) facet for digit III relatively robust. Both characters separate *C. striatus* (Fig. 2F) and *Colius* cf. *C. striatus* (Fig. 2E) from *C. colius* (Fig. 2G), *C. leucocephalus* (Fig. 2I) and *C. hendeyi* (Fig. 2H). (It was not possible to make adequate comparisons with *Colius* cf. *C. palustris* in these characters without examining the actual specimen.)

Phalanx I of digit II (Fig. 1K). (1) Proximal view, internal margin of metacarpal facet rounded, not pointed at posterior end. This character separates *C. striatus* (Fig. 1L) and *Colius* cf. *C. striatus* (Fig. 1K) from *C. colius* (Fig. 1M) and *C. leucocephalus* (Fig. 1N).

Femur (Fig. 4A). (1) Fibular condyle not as deeply notched as in *C. colius* (Fig. 4C), but more deeply notched than in *C. leucocephalus* (Fig. 4E); (2) tubercle above external condyle, posterior view, more raised and prominent than in either *C. colius* (Fig. 4C) or *C. leucocephalus* (Fig. 4E). Proximal end not diagnostic, no distal ends known for *C. hendeyi* or any other fossil species.

Tibiotarsus (Fig. 3F, G). (1) Interarticular area has a single, deep depression at the base of the rotular crest in proximal view; (2) inner cnemial crest relatively reduced in proximal view; (3) outer cnemial crest much reduced; (4) rotular crest lacking indentation; (5) rotular crest not as erect as in *Colius* cf. *C. palustris*, but more erect than in *C. archiaci* and *C. consobrinus* (difficult to compare with *Colius* cf. *C. palustris*, for same reason as above); (6) distal end with external condyle not deflected externally in anterior view; (7) internal ligamental prominence aligned with anterior, not posterior, shaft edge; (8) condyles not well rounded posteriorly in external view. Character 1 is shared only with *C. striatus* (Fig. 3H) and *C. consobrinus*. Character 2 separates *C. striatus* (Fig. 3H) and *Colius* cf. *C. striatus* (Fig. 3F) from *C. colius* (Fig. 3I) and *C. archiaci*. Characters 3 and 4 separate *C. striatus* (Fig. 3H) and *Colius* cf. *C. striatus* (Fig. 3F) from *C. consobrinus* and *C. archiaci*. Character 6 separates *Colius* cf. *C. striatus* (Fig. 3G) and all extant mousebirds (this report) and *C. hendeyi* (Fig. 3K) from *C. archiaci*. Character 7 separates *C. striatus* (Fig. 3H) and *Colius* cf. *C. striatus* (Fig. 3G) from *C. consobrinus*. Character 8 separates *Colius* cf. *C. striatus* (Fig. 3G) from all extant mousebirds (this report) and *C. hendeyi* (Fig. 3K) from *C. palustris*.

Tarsometatarsus (Fig. 4F, G). (1) Cotylae more oval than circular in proximal view; (2) cotylae with lateral edges more or less even or internal edge not more raised than external edge in anterior view; (3) external cotyla projects farther anteriad and dips slightly toward the distal end (most marked in *C. striatus* (Fig. 4H)); (4) internal trochlea almost same length as internal ridge of middle trochlea, and also relatively larger and not as close to medial trochlea. Characters 1–4 separate *C. striatus* (Fig. 4H) and *Colius* cf. *C. striatus* (Fig. 4F, G) from *C. colius* (Fig. 4I), *C. leuco-*

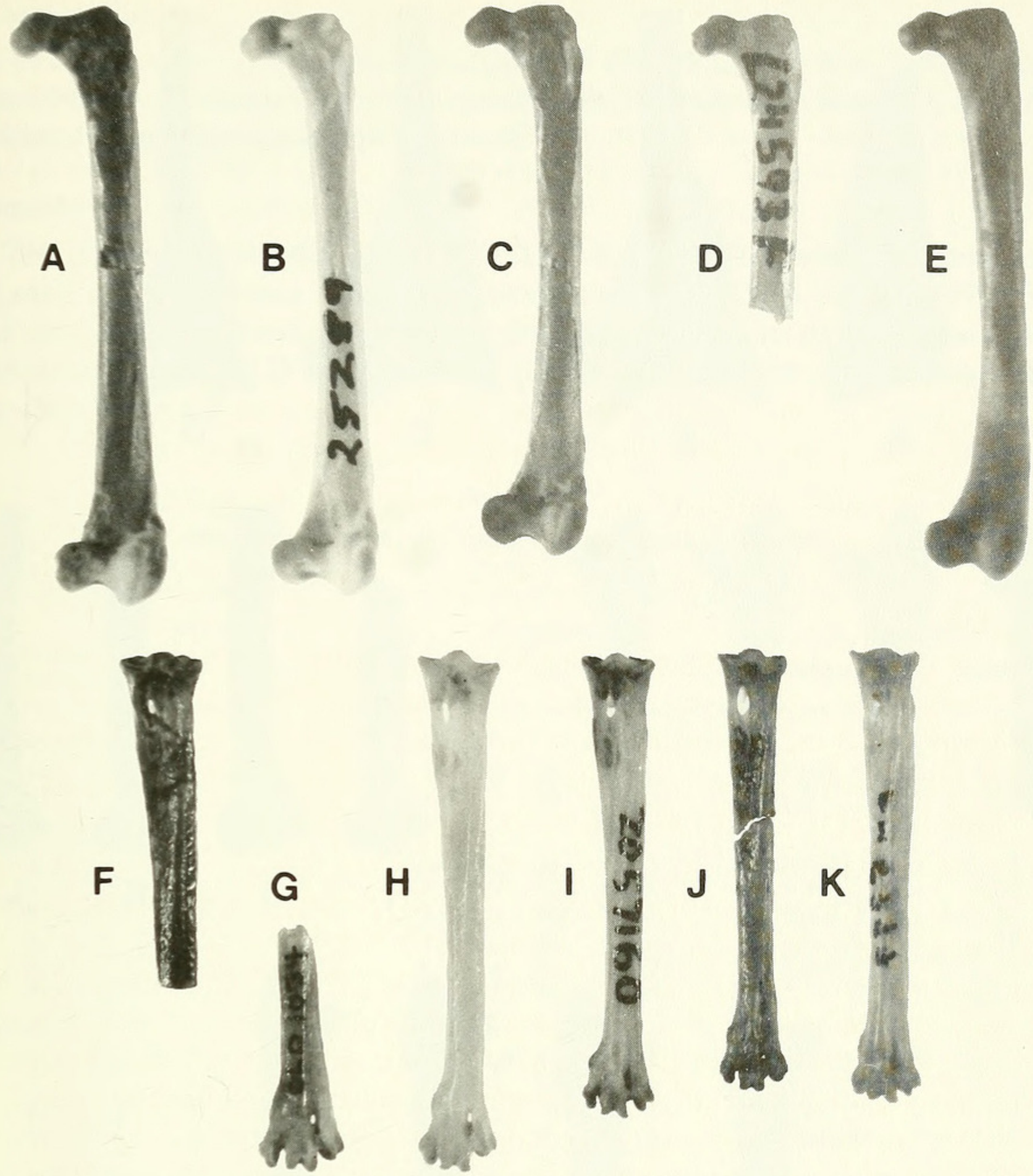

Fig. 4. A–E. Femora. A. *Colius* cf. *C. striatus*, OLD FLK NNI 15356. B. *C. striatus*, PB25289. C. *C. colius*, SAM–ZOT.26. D. *C. hendeyi*, L24593F. E. *C. leucocephalus*, YPM5797 (transposed). ×3. F–K. Tarsometatarsi. F. *Colius* cf. *C. striatus*, OLD FLK NI 12867. G. *Colius* cf. *C. striatus*, OLD FLK NI 1034. H. *C. striatus*, PB25226. I. *C. colius*, SAM–ZO57160. J. *C. hendeyi*, L28423FZ. K. *C. leucocephalus*, YPM5797 (transposed). ×2.56.

cephalus (Fig. 4K) and *C. hendeyi* (Fig. 4J). Character 4 separates *C. striatus* (Fig. 4H) and *Colius* cf. *C. striatus* (Fig. 4G) from *C. palustris*.

Genus *Urocolius* Bonaparte, 1854

Urocolius sp.

Fig. 5A, E, I, M

Material

Olduvai. Coracoid: FLK NI 26010 (r, sternal end missing sterno-coracoidal process and internal distal angle). Ulna: FLK NI 19721 (lp, with part of shaft); FLK NI 19765 (rd, with part of shaft).

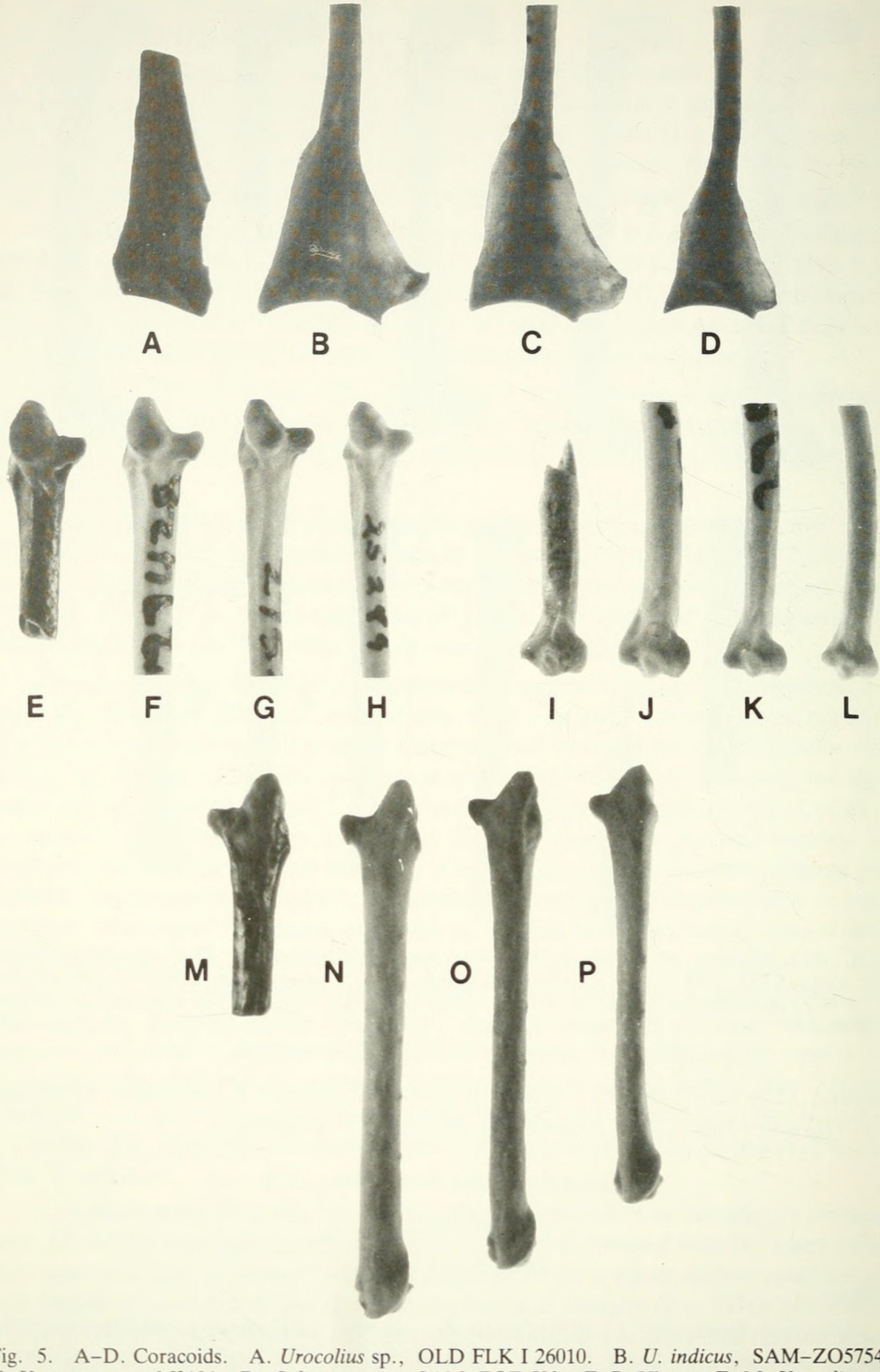

Fig. 5. A–D. Coracoids. A. *Urocolius* sp., OLD FLK I 26010. B. *U. indicus*, SAM–ZO57546. C. *U. macrourus*, M3184. D. *Colius striatus*, SAM–ZOT.592. E–P. Ulnae. E, M. *Urocolius* sp., OLD FLK NI 19721. F, N. *U. indicus*, PB27428. G, O. *U. macrourus*, PB27520. H, P. *Colius striatus*, PB25289. I. *Urocolius* sp., OLD FLK NI 19765. J. *U. indicus*, PB27428. K. *U. macrourus*, PB27519. L. *Colius striatus*, PB25289. All figures ×3.

Age and distribution

Late Pliocene, about 1,72 to 1,83 m.y. (Curtis & Hay 1972; Haq *et al.* 1977; Savage & Russell 1983; Kappelman 1986). This species is known only from sites FLK N in Bed I at Olduvai Gorge, north-western Tanzania.

Measurements

The maximum proximal width of OLD FLK NI 19721 (ulna) is 3,9 mm and its least shaft width is 1,6 mm. The maximum distal width of OLD FLK NI 19765 (ulna) is 3,3 mm. The width and depth of the shaft just anterior to the attachment of the coraco-brachialis of OLD FLK NI 26010 (coracoid) is 1,7 mm and 1,2 mm respectively. (See Table 4.)

TABLE 4

Measurements (mm) of living and fossil species of *Urocolius*.

Measure-ment no.	*Urocolius* sp.		*U. indicus*			*U. macrourus*		
	n	mean	range	n	mean	range	n	mean
CORACOID								
10	1	1,7	1,1-1,6	26	1,41	1,0-1,3	5	1,22
11	1	1,2	1,0-1,3	26	1,15	1,0-1,2	5	1,08
HUMERUS								
1			22,1-24,2	33	23,13	21,7-22,6	6	22,13
2			7,7-8,7	33	8,28	7,7-8,5	6	7,90
8			2,0-2,5	33	2,18	2,0-2,3	7	2,10
4			1,7-2,2	33	1,96	1,6-1,9	5	1,74
6			4,7-5,4	33	5,12	4,8-5,2	7	2,10
7			2,9-3,3	33	3,06	2,7-3,0	7	2,87
ULNA								
1			22,4-24,8	33	23,80	22,2-23,3	6	22,75
2	1	3,9	3,3-3,7	33	3,54	3,3-3,6	7	3,51
4	1	1,6	1,2-1,6	33	1,42	1,2-1,5	6	1,30
6	1	3,3	3,0-3,5	33	3,16	3,0-3,3	7	3,15

Measurements are: 1 = greatest length; 2 = maximum proximal width; 4 = minimum shaft width; 6 = maximum distal width; 7 = maximum distal depth; 8 = maximum head depth; 10 = shaft width sternal end just proximal to expansion point; 11 = shaft depth sternal end just proximal to expansion point.

Remarks

These specimens are larger and more robust than the modern species of mousebirds, except for *Urocolius indicus*. Unfortunately, the sterno-coracoidal process, which is missing on the fossil specimen (Fig. 5A), is one of the most diagnostic features of the coracoid at the generic level in the family Coliidae. However, the pronounced attachment of the coraco-brachialis and the presence of a small nutrient foramen close to this attachment (dorsal view) on the fossil specimen are more characteristic of the genus *Urocolius* (Fig. 5B, C) than the genus *Colius* (Fig. 5D). These features, in addition to the overall robust nature of this specimen, favour its placement in the genus *Urocolius*. It is not possible to assign it to a species.

The slightly more pointed olecranon, the well-developed fossa under the external cotyla (palmar view) and the scar on the surface external to the humero-ulnar depression on specimen OLD FLK NI 19721 (proximal ulna) (Fig. 5E, M) are features it shares with the genus *Urocolius* (Fig. 5F, G, N, O) rather than with the genus *Colius* (Fig. 5H, P). Likewise, the external condyle tapering to a point, rather than being rounded, at the base of the shaft in internal view and the pointed rather than rounded carpal tuberosity and the slightly larger internal condyle, are features that specimen OLD FLK NI 19765 (distal ulna) (Fig. 5I) has in common with the genus *Urocolius* (Fig. 5J, K) rather than with the genus *Colius* (Fig. 5L). The depth of the fossa under the external cotyla is greatest in the fossil specimen (Fig. 5E) and rather variable in the extant species of *Urocolius* (Fig. 5F, G). However, it is generally better developed in the genus *Urocolius* than in the genus *Colius* (Fig. 5H) and is therefore considered to be diagnostic at this level.

These specimens fit better within the size range of *Urocolius indicus* than that of *U. macrourus* but morphologically they share features with both species. Consequently, without a larger sample, it is not possible to assign them to a species. They provide the first Tertiary record of the genus *Urocolius*.

BIOMETRICAL ANALYSIS

METHODS

The mensural data were analysed using the co-variance biplot technique, which is one of a family of data analytic techniques that displays the rows and columns of a data matrix as points in a low-dimensional space, usually consisting of two or three axes (Greenacre & Underhill 1982). The analysis can be reduced to three steps:

1. Defining two clouds of points on their corresponding two multidimensional spaces; here the points of each cloud represent the specimens and the skeletal measurements respectively.
2. Defining a metric structure on each cloud of points that refers to how distances between specimens and between measurements are defined.
3. Defining the fit of each cloud of points to a low-dimensional space on to which the points are projected for subsequent display. These two or three dimensions represent, as accurately as possible, the points' true high-dimensional positions. A full description of the analysis can be found in Greenacre & Underhill (1982), Greenacre (1984) and Underhill (1990). Prior to analysis, the data were standardized by subtracting from each measurement its corresponding column mean. This renders all column means equal to zero but keeps the respective variances unchanged.

RESULTS

Using the above method, Figures 6, 7 and 8 help to demonstrate similarities between the fossil and living species of mousebirds studied for this report.

Figure 6 depicts the results using six measurements of the humeri (greatest length, GLE; maximum proximal width, MPW; depth of head, HD; maximum distal width, MDW; maximum distal depth, MDD; minimum shaft width, MSW) of 114 specimens representing seven species of mousebirds. Axis 1 accounts for 85 per cent of the variance of the data matrix. It is defined by variables GLE and MPW.

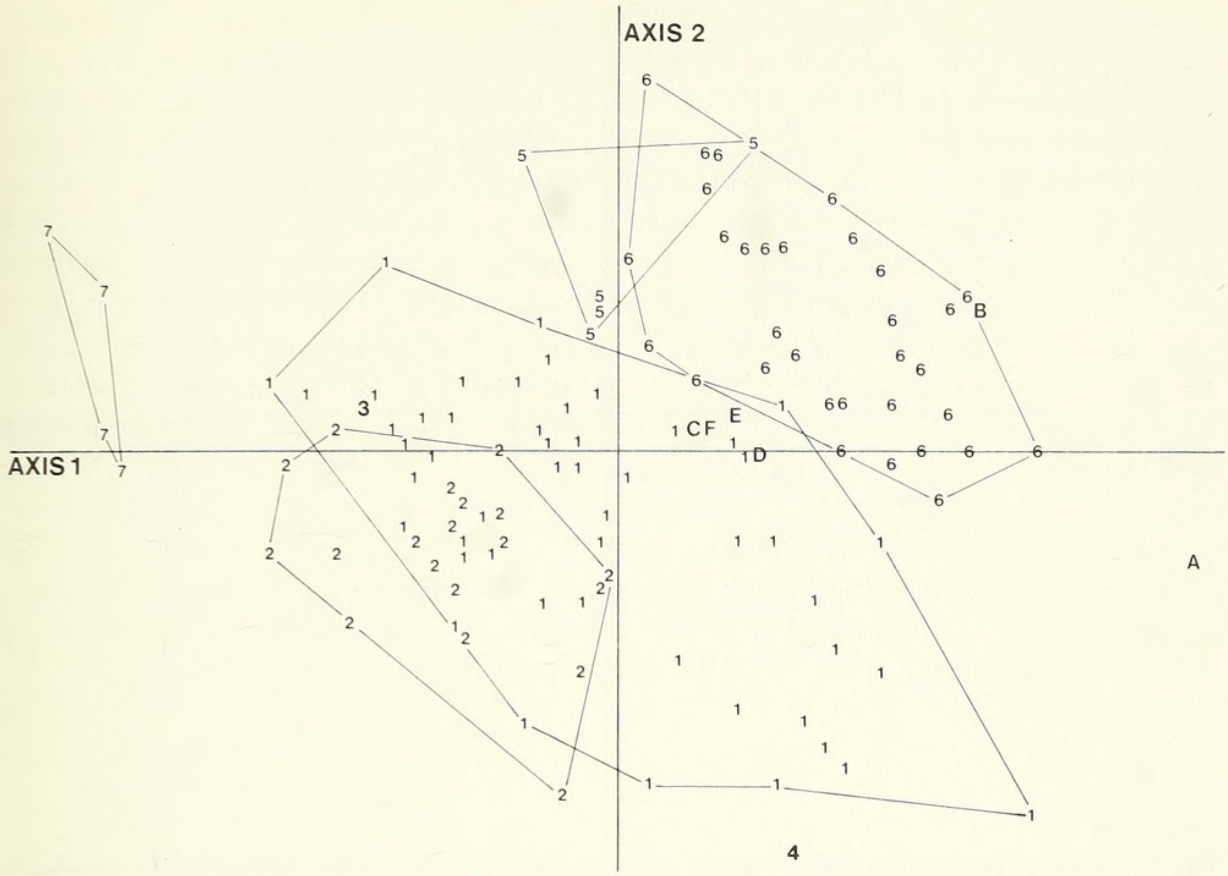

Fig. 6. Result of co-variance biplot analysis based on mensural data of the humeri of seven species of living and fossil mousebirds. 1 = *Colius striatus* (n = 51); 2 = *C. colius* (n = 19); 3 = *C. leucocephalus* (n = 1); 4 = *Colius* cf. *C. striatus* (n = 1); 5 = *Urocolius macrourus* (n = 5); 6 = *U. indicus* (n = 33); 7 = *Colius hendeyi* (n = 4). A = greatest length (GLE); B = maximum proximal width (MPW); C = maximum head depth (MHD); D = maximum distal width (MDW); E = maximum distal depth (MDD); F = minimum shaft width (MSW).

Specimens with large values for these two variables are pulled towards them, e.g. group 4 (*Colius* cf. *C. striatus*), group 6 (*Urocolius indicus*), and some specimens of group 1 (*Colius striatus*). Conversely, those specimens with small GLE and MPW are plotted on the opposite side, e.g. group 7 (*Colius hendeyi*), group 2 (*C. colius*), and part of group 1 (*C. striatus*). Axis 2, which accounts for 19 per cent of the variance, is defined by MPW and GLE. Specimens with large MPW are plotted in the same direction of that variable (B), e.g. groups 5 and 6 (*Urocolius macrourus* and *U. indicus*). Specimens with small MPW and large GLE are on the lower half of the plot, e.g. group 2 (*Colius colius*), group 1 (*C. striatus*), and group 4 (*Colius* cf. *C. striatus*). The extinct species *Colius hendeyi* (group 7) is very clearly separated from all the other species on account of it having both small GLE and MPW.

Figure 7 shows the results using three measurements (GLE, MPW and MDW) of the ulnae of 118 specimens representing seven species of living and fossil mousebirds. Axis 1 accounts for 98,8 per cent of the variance. It is defined by the variable GLE. Axis 2 is defined by variables MPW and MDW. The seven species are separated similarly as in Figure 1, with a certain amount of overlap between group 1 (*Colius striatus*) and group 2 (*C. colius*). The fossil species group 4 (*Colius* cf. *C. striatus*) falls well within the distribution of *C. striatus*. The extinct species *C. hendeyi* (group 7) is again clearly separated from all the other species.

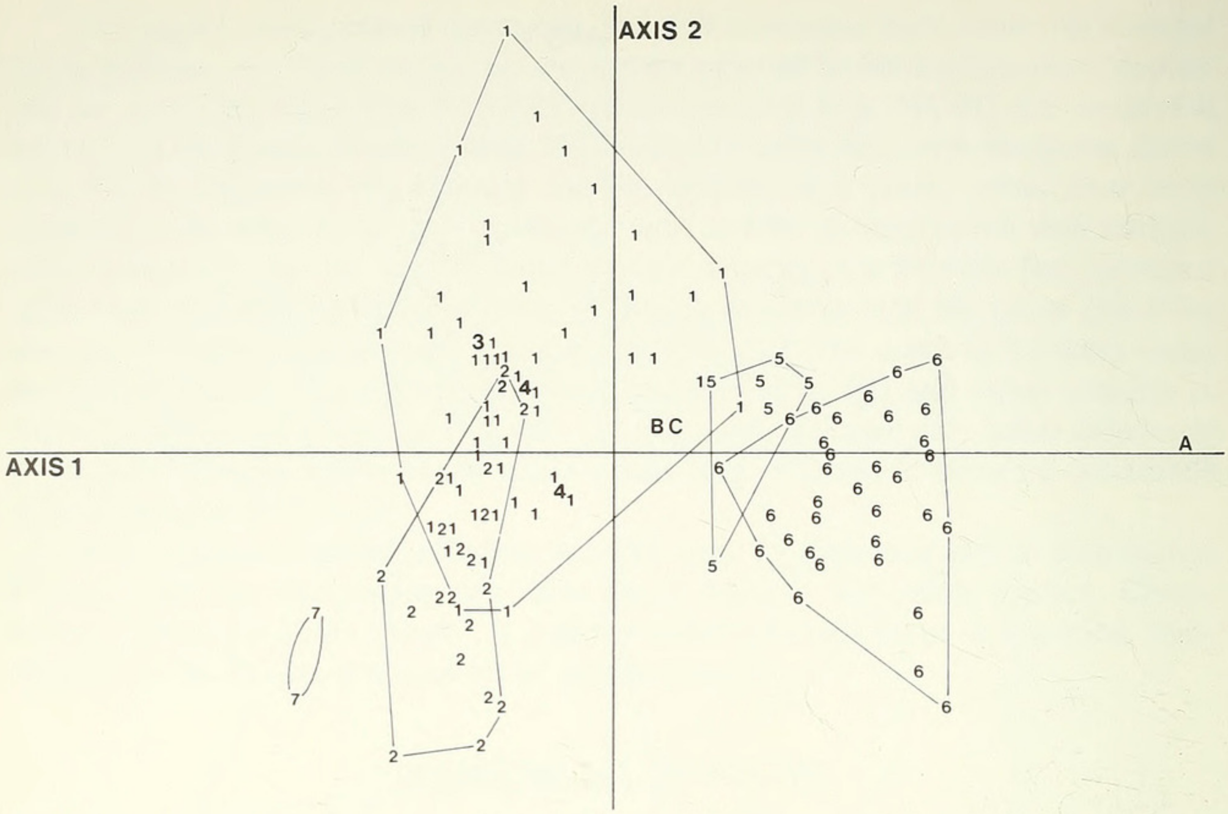

Fig. 7. Result of co-variance biplot analysis based on mensural data of the ulnae of seven species of living and fossil mousebirds. 1 = *Colius striatus* (n = 53); 2 = *C. colius* (n = 21); 3 = *C. leucocephalus* (n = 1); 4 = *Colius* cf. *C. striatus* (n = 2); 5 = *Urocolius macrourus* (n = 6); 6 = *U. indicus* (n = 33); 7 = *Colius hendeyi* (n = 2). A = greatest length (GLE); B = maximum proximal width (MPW); C = maximum distal width (MDW).

Figure 8 displays the results using three different measurements (MPW, MDD, MSW) of the ulnae of 117 specimens representing eight species of living and fossil mousebirds. Axis 1 accounts for 82 per cent of the variance. It is defined by variables MDW and MPW. Axis 2 is also defined by variables MDW and MPW. Although the species are plotted in associations similar to those in Figures 6 and 7, there is considerably more overlap. However, group 4 (*Colius* cf. *C. striatus*) still falls within the range of group 1 (*C. striatus*). Group 8, which represents *Urocolius* sp. from Olduvai, is indeed placed closest to the *Urocolius* species complex (groups 6 and 5). It must be emphasized that the measurements for *Urocolius* sp. were combined from two different specimens for the purpose of this analysis.

DISCUSSION

Most of the questions raised by Rich & Haarhoff (1985) with regard to the origin and systematics of the Coliiformes remain unanswered. Although the oldest mousebird fossils have been found in the Upper Eocene of France (Mourer-Chauviré 1988), it cannot be said that Europe is the place of origin for the Coliidae, because the fossil record for the early and mid-Tertiary of Africa and Asia is still so poorly known. The Miocene specimens from Europe still require revision. Material referred to the genus *Colius* by Ballmann (1969) may represent another extinct genus, whereas some other

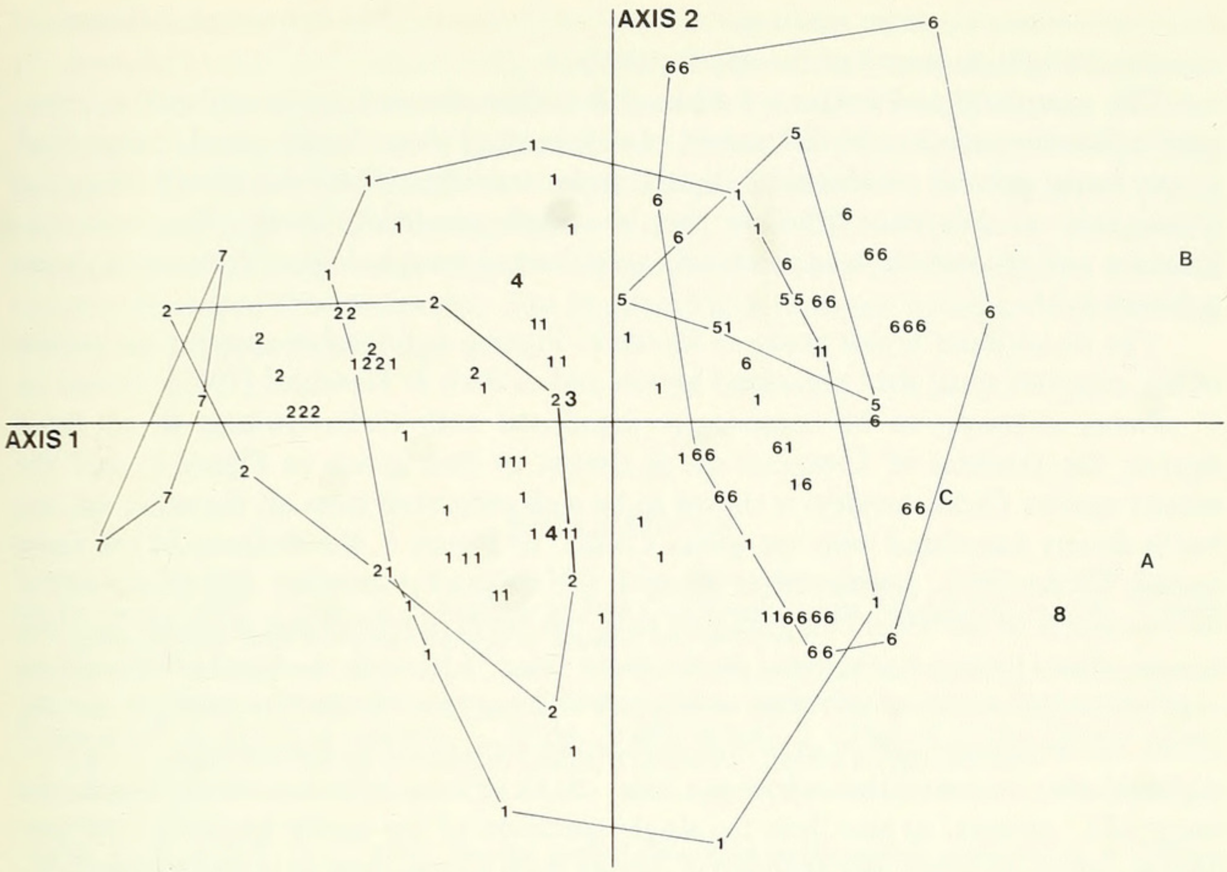

Fig. 8. Result of co-variance biplot analysis based on mensural data of the ulnae of eight species of fossil and living mousebirds. 1 = *Colius striatus* (n = 52); 2 = *C. colius*; (n = 18); 3 = *C. leucocephalus* (n = 1); 4 = *Colius* cf. *C. striatus* (n = 2); 5 = *Urocolius macrourus* (n = 6); 6 = *U. indicus* (n = 33); 7 = *Colius hendeyi* (n = 4); 8 = *Urocolius* sp. (n = 1). A = maximum proximal width (MPW); B = maximum distal width (MDW); C = minimum shaft width (MSW).

material from Europe, examined by Ballmann (pers. comm.), may belong to the genus *Urocolius*. How the living and the fossil species are related to each other is not understood. This, and the fact that only skeletal material can be studied, precludes a more definitive statement other than that the Olduvai species *Colius* cf. *C. striatus* might be ancestral to the living *Colius striatus*. More fossil material of the other Olduvai species, *Urocolius* sp., would probably help to clarify its taxonomic status. Some of the remaining questions therefore pertain to the phylogenetics of the Coliiformes, when and why they became restricted to Africa, and what limits their present distribution.

The five extant species of mousebirds studied in this report show that there is some overlap in terms of size but, generally, *Colius striatus* has the largest and most robust skeleton of that genus. The wing, tarsus and weight measurements given in Fry *et al.* (1988) suggest, however, that, of the four living species of *Colius*, the skeleton of *C. castanotus* should, in fact, be the most robust. Because of a lack of comparative specimens of this species, it was not possible to confirm this. In the genus *Urocolius*, the skeleton of the red-faced mousebird, *U. indicus*, tends to be more robust than that of the blue-naped mousebird, *U. macrourus*. A comparison between the measurements given in Rich & Haarhoff (1985) and in this paper shows that the considerably larger sample of specimens used herein has produced a wider range of variation in the elements measured; more sexed specimens were available, but there is no evidence of sexual dimorphism in any of the species studied.

The morphological features used to differentiate the species are difficult to interpret in that they tend to be differences of degree (e.g. shape, angle, etc.), rather than simply being present or absent. A better understanding of their functional relevance would help to determine whether they are phylogenetically useful. The coracoid, humerus and tibiotarsus have the most easily defined morphological differences at the species level.

The co-variance biplot analyses shown in Figures 6–8 tend to support the results of the morphological data presented herein and in Rich & Haarhoff (1985). *Colius* cf. *C. striatus* is shown to be consistently associated with *Colius striatus* in all three figures; the position of *Urocolius* sp. is closest to that genus in Figure 8; and the extinct species *Colius hendeyi* is shown to be well separated from all the other species but is clearly associated with the genus *Colius*. In Figure 6, the distance of the fossil species *Colius* cf. *C. striatus* from group 1 (*C. striatus*) is possibly due to the MPW measurement of the fossil being smaller than the norm in proportion to its GLE. This, in turn, could be due to the wear on the fossil bone. Although the fossil sample size is very small, the results of this type of analysis indicate that similarities between the different groups/species can be demonstrated in the form of loose associations. However, it should also be noted that whereas *Colius* cf. *C. striatus* falls consistently within the range of *C. striatus*, so also does the single specimen of the extant species *C. leucocephalus* (group 3). Thus, the problem of having such a small sample is also highlighted.

It is evident that the species are separated more clearly when the data used are a combination of both small and large measurements, for example, when GLE, MPW and MDW are used, as in Figure 7. Where only small measurements (MPW, MSW, MDW) have been analysed, as in Figure 8, the overlap between the different species is noticeably greater. Unfortunately, when fossil bones form part of the data base, the most useful measurements cannot always be taken, due to the incomplete nature of some of the specimens.

The fossil mousebirds from Olduvai add one more small piece to the puzzle of the history and biogeography of this curious avian order.

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