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SHORT COMMUNICATION

A New Lorisid Humerus from the Early Miocene of Uganda

DANIEL L. GEBO, *Northern Illinois University*
LAURA MACLATCHY, *State University of New York*
and ROBERT KITYO, *Makerere University*

ABSTRACT. An early Miocene (18–20 mya) distal humerus from Napak, Uganda, is the only element of the forelimb to be allocated to African Lorisinae. Its loris-like features distinguish it from other East African material that more closely resembles galagids. Tracing the evolution of the lorisoid body has been a difficult task due to the lack of good fossil material. Here, we add a single specimen to this poor record. This humerus helps to document the beginning of extant lorisid locomotor specialization and function.

Key Words: Lorisidae; Miocene; Locomotion.

INTRODUCTION

Few fossils exist to document the evolution of the postcranium of Lorisoidea (cheirogaleids, but see YODER, 1994, galagids and lorisids) (WALKER, 1970, 1978; MACPHEE & JACOBS, 1986; GEBO, 1986, 1989; MCCROSSIN, 1992). This has severely hampered our understanding of the history of locomotor adaptation in these primates. In the Miocene of East Africa, the sites Chamtwara, Koru, Legetet, Moroto, Maboko, Mwafanganu, Napak, Rusinga, and Songhor have all produced fossil lorisoids but postcranial material remain rare. In 1994, we found a single primate distal humerus (MUZM 30; MUZM: Makerere University Zoology Museum) at locality V at Napak (Uganda) to add to this small list of lorisoid material.

MATERIALS AND METHODS

In this manuscript, we use the taxonomic term Lorisoidea to include both Lorisidae (e.g. *Loris, Nycticebus, Perodicticus, Arctocebus, Nycticeboides*, and *Mioeuoticus*) and Galagidae (e.g. *Galago, Galagoides, Euoticus, Otolemur*, and *Komba*), although the fossil forms may require their own families in the future. We compared MUZM 30 to a variety of extant lorisids ($n=18$ for 3 genera: *Perodicticus, Nycticebus*, and *Loris*) and galagids ($n=20$ for 3 genera: *Galago, Galagoides*, and *Otolemur*) at the Field Museum of Natural History (Chicago), as well as to casts of Miocene lorisoids. Measurements were taken on the humerus following SZALAY and DAGOSTO (1980) and GEBO et al. (1994) and are listed in Table 1. The Napak localities are dated to the early Miocene using both faunal correlations and by K/Ar (BISHOP, 1958; BISHOP et al., 1969; PICKFORD, 1981).

Table 1. Humeral measurements after SZALAY and DAGOSTO (1980) and GEBO et al. (1994).

	MUZM 30 (mm)
Biepicondylar (mediolateral) width (BW)	13.2
Capitulum (mediolateral) width (CW)	5.1
Capitulum (proximodistal) height	4.0
Anterior trochlear (mediolateral) width (TW)	3.9
Anterior trochlear (proximodistal) height (medial)	5.1
Anterior trochlear (proximodistal) height (lateral) (TH)	3.2
Posterior trochlear (mediolateral) width	4.6
Posterior trochlear (proximodistal) height (medial)	4.7
Posterior trochlear (proximodistal) height (lateral)	4.0
Articular (mediolateral) width (AW)	9.0
Trochlear-lateral epicondylar (mediolateral) width (TLE)	9.2
Trochlear (anteroposterior) length (TL)	4.8
Capitular (anteroposterior) length (CL)	4.8

RESULTS AND DISCUSSION

Description. MUZM 30 is a distal right lorisid humerus extending 18.7 mm in length (Fig. 1). The proximal shaft is broken at the site of origin of the brachial flange. Distally, the proximo-lateral edge of the capitulum is eroded and broken away, including the region of the capitular tail, as is a small piece of the medial trochlear rim. The zona conoidea is greatly reduced in MUZM 30 as it is in lorises (SZALAY & DAGOSTO, 1980; ROSE, 1993) and in contrast to galagos (Fig. 2). The distal humerus possesses an entepicondylar foramen, a reduced brachial flange, a dorsoepitrochlear pit, and a deep olecranon fossa. The medial epicondyle is prominent and faces slightly posteromedially. The capitulum is round and we are unable to discern the presense of or the shape of a capitular tail in this specimen due to damage. The radial fossa is moderately deep in MUZM 30. The trochlea has a well-defined medially sloping inferior rim which produces a conically shaped trochlea (Fig. 1), a morphological condition similar to that of lorises. Medial to lateral proximodistal trochlear heights provide a ratio of 1.6, a value which substantiates the cone shape of the MUZM 30 trochlea. Extant galagos and the fossil galagid, KNM-SO-1029 (ratio=1.1), possess values closer to 1.0 implying a more rectangular shaped trochlea (see Fig. 2). Trochlear width to capitular width shows MUZM 30 to have a value of 0.76, a value that is high for lorises but comparable to several galagos and *Cheirogaleus major* (SZALAY

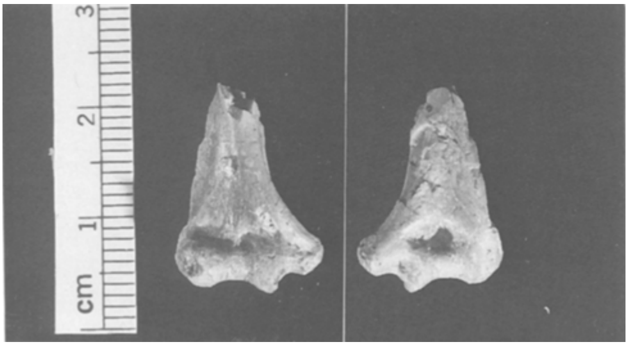

Fig. 1. Anterior (left) and posterior (right) views of MUZM 30, a distal humerus from Napak.

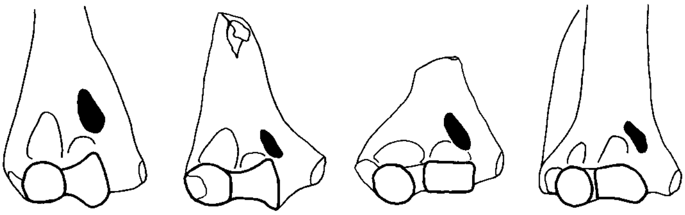

Fig. 2. Comparison of distal humeri. Left to right: *Loris*, MUZM 30, KNM-SO 1029, and *Galago*. All specimens are drawn to approximately the same mediolateral width.

& DAGOSTO, 1980). Thus, the capitulum is not expanded as in extant lorises. Trochlear width to articular width equals 0.43 for MUZM 30, a value similar to many galagos as well (SZALAY & DAGOSTO, 1980). The medial epicondyle extends 4.0 mm beyond the medial trochlear rim.

Function. The deep olecranon fossa allows greater elbow extension while the prominent medial epicondyle and brachial flange imply well-developed muscle masses associated with rotation, flexion, and extension of the forearm. The deep radial fossa suggests fully flexed elbows for MUZM 30 as well. The conically shaped trochlea with the downturned medial rim implies medial elbow stability during extension. A downturned trochlea is observed in a variety of quadrupedal primates (e.g. *Saimiri*, cercopithecines, and *Alouatta*; SZALAY & DAGOSTO, 1980; FLEAGLE & SIMONS, 1982; ROSE, 1993). We interpret these anatomical features to suggest that forelimb function resembled arboreal quadrupedal and cautious climbing primates with several functional similarities to extant lorises.

Comparisons. In overall morphology, this humerus is similar to other Miocene lorisids and to galagos in that it is robust and retains a prominent medial epicondyle, as do galagos but not extant lorises (Fig. 2). Several other primitive features are present in this humerus including an entepicondylar foramen, a brachial flange, and a dorsoepitrochlear pit, which is not usually found in living strepsirhines but is present in adapids like *Adapis* (DAGOSTO, 1983). MUZM 30 is very distinctive in two features. First, the trochlea is cone-shaped with the medial trochlear rim being prominently downturned. A prominent downturned trochlea is particularly characteristic of Asian lorises. Second, the olecranon fossa is very deep in MUZM 30. This feature is also found in lorisid humeri, including the late Miocene and Asian *Nycticeboides* (MACPHEE & JACOBS, 1986), but not in galagids where the olecranon fossa is very shallow (HILL, 1953). Further, both the cone-shaped and downturned trochlea and the deep olecranon fossa are features unlike other distal humeri attributed to Miocene galagids (i.e. KNM-SO 1029; Fig. 2). Although MUZM 30 represents a humerus more primitive than the humeri of extant lorises, the humeral features suggest an allocation with Lorisidae rather than Galagidae.

The distal humerus is the size of *Hapalemur griseus* (880 g: FLEAGLE, 1988) and is similar in its distal width to *Nycticebus coucang* (920 g: FLEAGLE, 1988), although *Nycticebus* has much larger joint surfaces than does MUZM 30. We therefore estimate a body size approximating 900 g to be associated with this humerus. In terms of species allocation, *Progalago dorae, Mioeuoticus bishopi, Komba robustus*, and *Komba minor* are the only known Miocene lorisoids from Napak. Only *Progalago* and *Mioeuoticus* are large enough to be associated with this humerus (WALKER, 1978; MCCROSSIN, 1992).

Until recently, we would simply have allocated this humerus to *Mioeuoticus*, a Miocene lorisid, on the basis of morphology. Unfortunately, there are several complications with this straight forward allocation. First, McCROSSIN (1992) transfered *Progalago* to the lorisid clade allowing this humerus to be reasonably attributed to both *Progalago* and *Mioeuoticus*. Second, the KNM-SO 1029 humerus, which had been previously allocated to *Progalago songhorensis* (WALKER, 1970; GEBO, 1989) on the basis of size, does not share the loris-like features of the MUZM 30 humerus. For example, the KNM-SO 1029 distal humerus displays a very different trochlear and olecranon fossa morphology compared to MUZM 30. In fact, the humeral morphology of KNM-SO 1029 is similar to that of other Miocene lorisoid distal humeri, which have all been attributed to *Komba*, a Miocene galagid (WALKER, 1970, 1978; GEBO, 1989; McCROSSIN, 1992). We therefore suggest that KNM-SO 1029 should be allocated to the Miocene galagids as well since MUZM 30 represents the only known humerus documenting loris-like characteristics in the Miocene of East Africa. Unfortunately, no 500 g species of *Komba* are presently known to exist. Even McCROSSIN's (1992) weight estimations (95% confidence limits) barely overlap between *Komba robustus* (279 – 433 g) and *Progalago songhorensis* (433 – 639 g) leaving the suggestion of reallocating KNM-SO 1029 to *Komba robustus* unlikely on the basis of size. Given these problems, we simply point out the loris-like affinities of the MUZM 30 humerus and prefer not to allocate this specimen to a particular taxon.

CONCLUSION

Galagos come from an ancestry of vertical clinging and leaping and the bodies of living bushbabies, whether large or small, reflect this ancestry. In a highly divergent path of locomotor evolution, lorises have forsaken leaping and have emphasized climbing, clambering, and suspensory movements, movements that shaped lorisid bodies very differently from their evolutionarily close relatives, the galagos. Tracing the evolutionary path of lorisoid body changes over time has been a difficult task due to the paucity of postcranial material. Here, we add a single specimen to this poor historical record. The MUZM 30 humerus helps to show that in the early Miocene, some postcranial elements were beginning to diverge from the common ancestral lorisoid pattern and beginning to resemble extant lorisids. This is true for a few other hindlimb elements as well (GEBO, 1986; McCROSSIN, 1992). Morphological divergence and specification in the early Miocene is also true for the galagid material (especially the proximal femur; see WALKER, 1970) while other postcranial elements present a more mosaic pattern. Thus, the many shifts and changes of body adaptation and evolution within Lorisoidea remain largely unknown at present. Although many more fossils will be needed to fully understand the timing and morphological changes associated with lorisoid postcranial evolution, MUZM 30 adds a significant element to this puzzle and helps to document the beginning of lorisid locomotor adaptation and evolution in the forelimb.

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Authors' Names and Addresses: Daniel L. Gebo, *Department of Anthropology, Northern Illinois University, DeKalb, Illinois 60115-2854, U. S. A.*; Laura MacLatchy, *Department of Anatomical Sciences, State University of New York, Stony Brook, New York 11794, U. S. A.*; Robert Kityo, *Department of Zoology, Makerere University, Kampala, Uganda.*