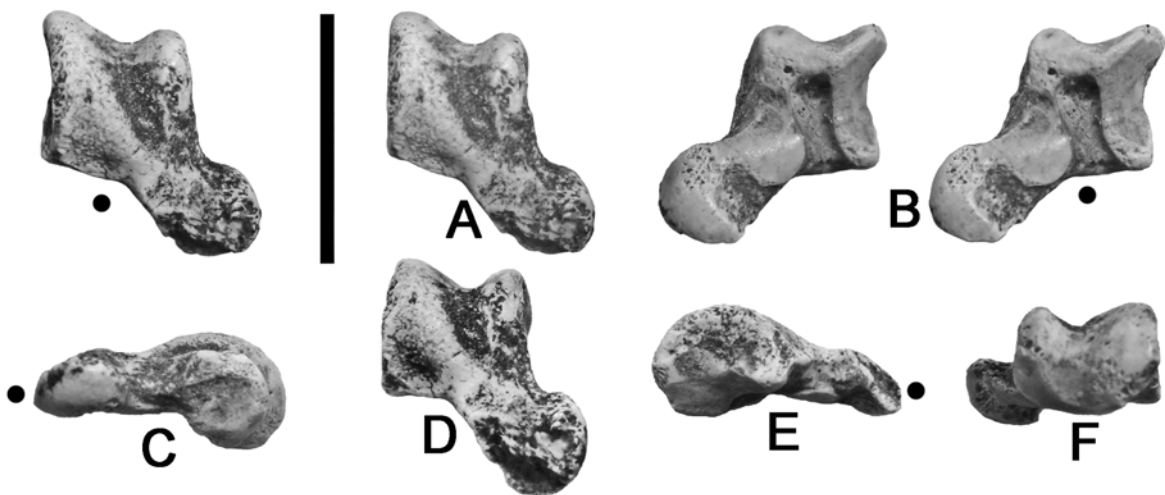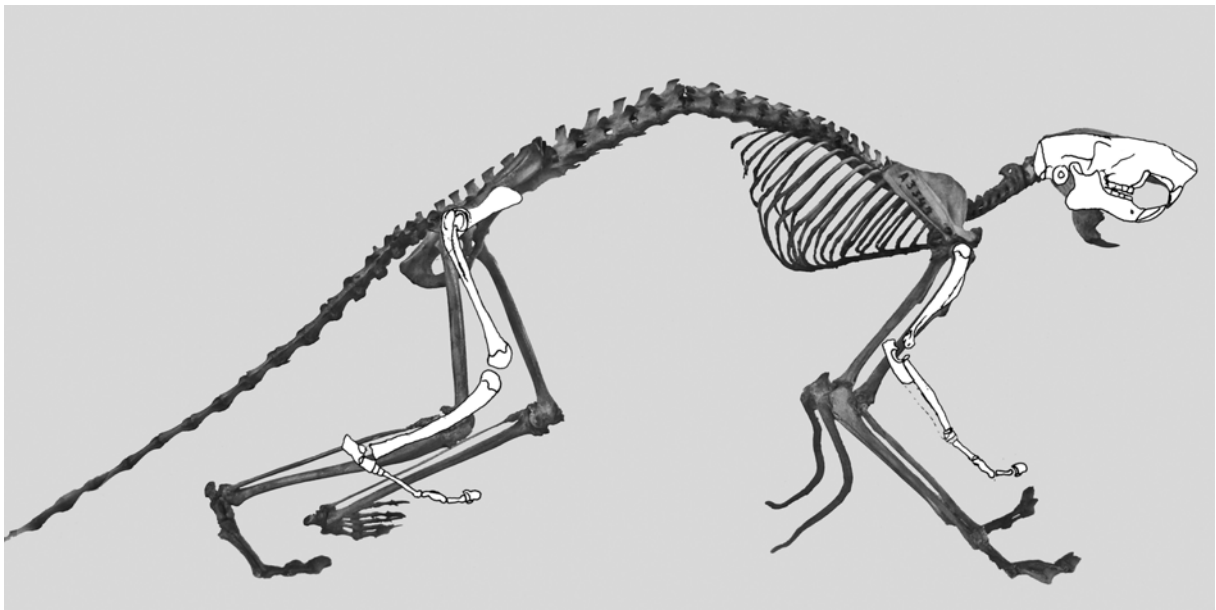# GEO-PAL UGANDA

Uganda Museum, Kampala

Geo-Pal Uganda

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Uganda Museum, P.O. Box 5718, Kampala

The osteology of *Nonanomalurus soniae*, a non-volant arboreal rodent (Mammalia) from the Early Miocene of Napak, Uganda

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ABSTRACT

Every now and then, the fossil record yields a specimen which clarifies numerous contentious issues and resolves many uncertainties. A skeleton of a medium-sized rodent found at Napak XV, Uganda, during the 2007 field survey of the Uganda Palaeontology Expedition, represents such a fossil, as it throws important light on a number of interpretations of supposed strepsirrhine evolution and on the relationships among "flying squirrels". When extracted from its matrix the fossil was identified as *Paranomalurus soniae* Lavocat, 1973. However, its skeleton is so divergent from those of Anomaluridae that the species is unlikely to belong to this family as thought by Lavocat (1973). Dentally it differs from *Paranomalurus bishopi* and *Paranomalurus walkeri* as was noted by Lavocat (1973). Its incisors are mesio-distally longer relative to the labio-lingual dimension than in the very compressed section observed in *P. bishopi*, and its cheek teeth have transverse valleys that open lingually, which contrasts with those of *P. bishopi* and *P. walkeri*, in which the lingual wall of the upper cheek teeth is continuous and unmarked by sinuses. Four proximal ulnae from Napak show expansion of the olecranon process characteristic of Anomaluridae, proving the presence of this family at the site, but the ulnae of "*P.*" *soniae* are completely different, indicating not only that it represents a genus different from *Paranomalurus*, but also that it differs from it at the family level. The aim of this paper is to discuss the taphonomy, osteology and taxonomy of this skeleton. An analysis of its functional anatomy will be presented in a separate paper.

Key Words : Nonanomaluridae, New Family, Early Miocene, Uganda, Napak, skeleton

INTRODUCTION

We here describe and illustrate an almost complete skeleton with skull and both mandibles (Nap XV 170'07) of a rodent, *Nonanomalurus soniae* (Lavocat, 1973) gen. nov. from Napak, Uganda. The skeleton is morphologically divergent from that of extant *Anomalurus* and extinct *Paranomalurus*. For an anomaluroid rodent the specimen from Napak XV shows unexpected features of the humerus and femur, some of which are related to enhanced mobility of the shoulder, elbow and hip joints, and have thus converged towards those of arboreal primates, which explains why several fossils from Uganda and Kenya previously thought to belong to primates (Walker, 1970; Gebo *et al*., 1997; MacLatchy & Kityo, 2002) belong instead to rodents.

True anomalurids occur at Napak on the basis of cranio-dental and postcranial fossils, notably four proximal ulnae which are morphologically almost identical to those of extant *Anomalurus derbyanus* and *Anomalurus peli*. On the basis of their dimensions, we attribute one of these ulnae to *Paranomalurus bishopi*, and the other three to *Paranomalurus walkeri*, but confirmation of these identifications must await the discovery of skeletal remains associated with cranial material. The co-occurrence of the two anomaluroid families in the same sedimentary formation indicates that by 18.5 Ma the Nonanomaluridae (new family) and Anomaluridae were distinct rodent lineages which may

well have separated from each other as early as the Eocene. The dental similarities between the two families noted by Lavocat (1973) are due partly to shared ancestry with primitive "anomaluroids" (a term that now needs to be used with caution) and partly due to convergence suggesting similar diets. The relationships between Nonanomaluridae and other anomaluroids such as Zegdoumyidae need further study, in particular if postcranial remains can be obtained for the Eocene forms.

Had it not been articulated to the skull, the Napak XV postcranial skeleton would have been extremely difficult to attribute to the correct family, because there are several other mammals from the Napak deposits which have approximately the same body size : Erinaceidae (*Amphechinus rusingensis*) Macroscelididae (*Miorhynchocyon*, *Myohyrax*) carnivores (small Viverridae, Mustelidae) primates (Galagidae) as well as rodents (*Paranomalurus bishopi*, *Paranomalurus walkeri*, *Diamantomys luederitzi*, *Paraphiomys pigotti*, *Afrocricetodon songhori*, *Renefossor songhorensis*). Partial postcranial skeletons of the erinaceid (Butler & Hopwood, 1957; Mein & Pickford, 2008) and some of the rodents (*Paraphiomys*, *Diamantomys*, *Renefossor*) have been recovered (Lavocat, 1973) which simplifies the task, but the combination of a superficially anomalurid-like dentition with such a skeleton was unpredictable because its postcranium is so divergent from that of *Anomalurus*. In a previous paper on lorisid evolution (Pickford, 2012) this skeleton was referred to *Paranomalurus bishopi*, but now that the dentition is visible after removal of the matrix, it is clearly not this taxon, but belongs to what used to be known as *Paranomalurus soniae* which is of similar dimensions, but has divergent dental and mandibular morphology.

MATERIALS AND METHODS

The skeleton, Nap XV 170'07, was partly extracted from its sediment matrix using a combination of mechanical (micrograveur) and acid (7% formic acid) techniques. The bones were consolidated using cyanate and plexigum. The rib cage and vertebral column were largely left in connection, so they are still partly enclosed in sediment. Digital photographs were taken at various stages of extraction in order to record the positional relationships between the bones. Further studies using micro-ct scans are envisaged, for understanding the morphology of the vertebrae in particular.

The specimen was compared with other fossil anomalurids from Kenya (Songhor, Koru) and Uganda (Napak) and with skeletons of extant anomalures housed at the MNHN, Paris, and the Africa Museum, Tervuren. Institution abbreviations are as follows:-

AMT – Africa Museum, Tervuren
KNM – Kenya National Museum, Nairobi
MNHN – Museum National d'Histoire Naturelle, Paris
NHMUK – Natural History Museum, London, United Kingdom
UM – Uganda Museum, Kampala

Osteological nomenclature is based on Greene (1935). Like this author, we do not enter into highly detailed and lengthy written descriptions, but prefer to let the images speak for themselves. As such, this article is an illustrated osteological catalogue of *Nonanomalurus soniae*, with some comments where clarification is warranted, or where peculiar morphology is observed.

GEOLOGICAL CONTEXT AND AGE

Napak XV, discovered in 2007, is a locality not far from Napak V (Musalizi *et al.*, 2009) (Fig. 1). It is within the Napak Member aged about 18.5 Ma (Pickford, 2002) on account of the presence of three species of tragulid (Table 1) typical of the upper part of the member (the lower part possesses only *Siamotragulus songhorensis*). The fossils are preserved in nephelinite-carbonatite tuffs rich in termite foraging tubes and petrified wood. These tuffs have been variably calcified, and readily react with weak acetic and formic acid, which were used to free the fossils from the matrix.
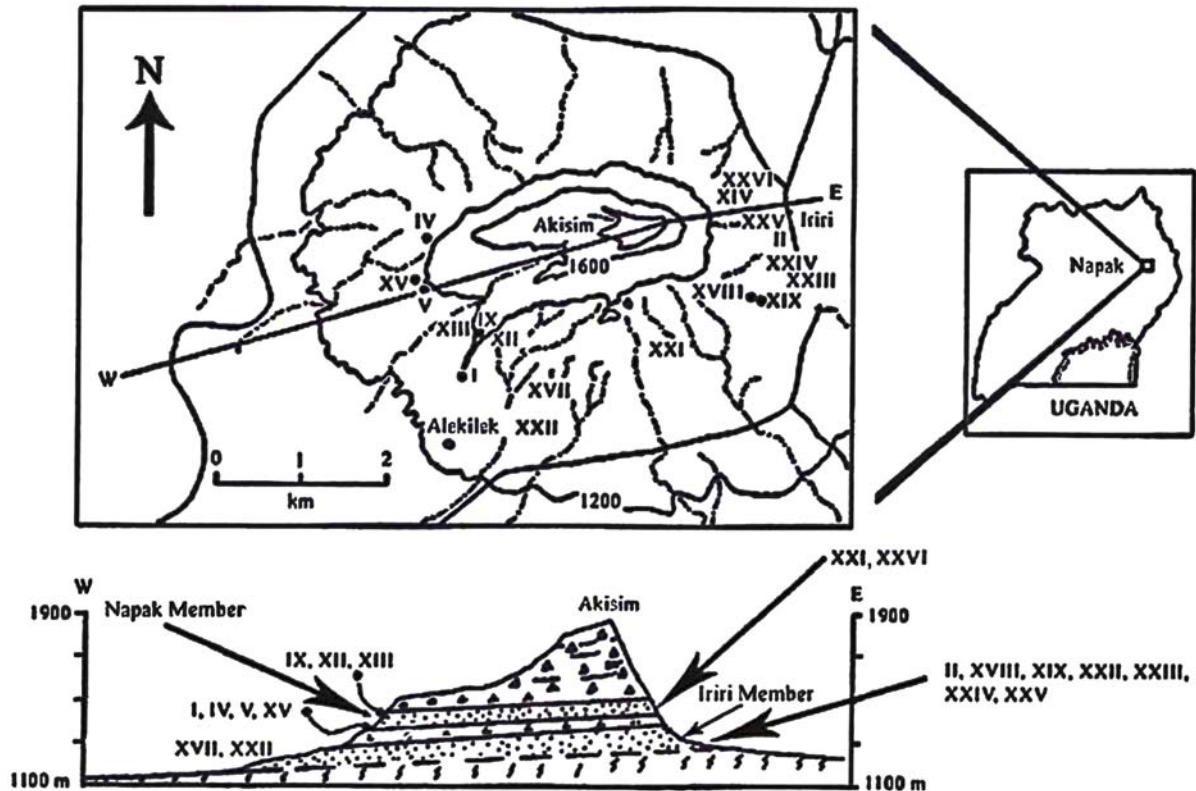
Figure 1. Locations and stratigraphic positions of fossiliferous localities in the Akisim remnant of the Napak Volcano, Uganda.

ASSOCIATED FAUNA

Nap XV is unusual for the Napak suite of localities on account of the abundance of crocodilian remains. Crocodiles have been recorded previously from Nap I and Nap V (Bishop, 1968) but at these sites their remains are rare and fragmentary. At Nap XV in contrast, there are at least four individuals, represented by abundant associated skeletal parts, mandibles, skulls, scutes and limb bones. The fossils are complete enough to indicate that they belong to a species similar to the Rusinga taxon, *Brochuchus pigotti*. Other fossils in the assemblage include a diversity of terrestrial gastropods, birds, squamates including snakes, lizards and a gymnophione (Rage & Pickford, 2011) chelonians, insectivores, macroscelideans, rodents, primates, carnivores, deinotheres, rhinocerotids, chalicotheres, anthracotheres, suids, tragulids, pecorans and primates (Table 1).

Among the plant remains found at Napak XV, the seeds of *Celtis* are quite common, and there are fragmentary leaves of dicotyledons, and stems of grasses or sedges.

Table 1. Faunal list of Napak XV.

Arthropoda	Millipede exoskeletons
	Termite fungus gardens and foraging tubules
	Lepidopteran cocoons
Gastropoda	*Maizania* sp.
	Tholachatina leakeyi
	Burtoa nilotica
	Subulinidae
	Pseudopeas sp.

3

	Edouardia sp.
	Conulinus sp.
	Trochonanina sp.
	Trochozonites sp.
	Thapsia sp.
	Tayloria sp.
	Gulella sp.
	Haplonepion naggsi
Amphibia	Gymnophione
Reptilia	Varanidae
	Chamaeleonidae
	Ophidea
	Chelonia
	Brochuchus pigotti
Aves	Indet. sp.
Insectivora	*Protenrec* sp.
	Erinaceidae
Macroscelidea	*Miorhynchocyon* sp.
Microchiroptera	Genus indet.
Rodentia	*Diamantomys luederitzi*
	Paraphiomys koruensis
	Simonimys genovefae
	Nonanomalurus soniae
	Paranomalurus bishopi
	Paranomalurus walkeri
	Afrocricetodon songhorensis
	Renefossor songhorensis
Primates	Galagidae sp.
	Ugandapithecus major
	Micropithecus clarki
	Kalepithecus songhorensis
	Iriripithecus alekileki
	Karamojapithecus akisimia
Proboscidea	*Deinotherium hobleyi*
Carnivora	*Hecubides euryodon*
Hyracoidea	*Brachyhyrax aequatorialis*
Perissodactyla	*Brachypotherium* sp.
	Butleria rusingensis
Artiodactyla	*Brachyodus aequatorialis*
	Nguruwe kijivium
	Dorcatherium parvum
	Dorcatherium iririensis
	Siamotragulus songhorensis
	Walangania africanus

TAPHONOMY

Nap XV 170'07, is an almost complete skeleton of a rodent found in several small blocks of carbonatite-nephelinite tuff that fit together (Fig. 2). The blocks contain the skull and both mandibles, the vertebral column, rib cage, both scapulae, complete left humerus and radius and parts of the ulna, broken right humerus, ulna and radius and disarticulated wrist and manual bones (which are close together) a damaged pelvis, complete left femur and tibia, broken right femur and tibia, talus, ankle and pedal bones. Several isolated vertebrae were screened from the soil surrounding the blocks of

fossiliferous tuff, and these are presumed to derive from the same individual. Intermingled with the skeleton was a shell of a subulinid gastropod (terrestrial snail) some termite foraging tubes and a piece of fossilised plant stem (grass or sedge). Inside the thoracic cage there were four incompletely ossified long bone diaphyses (two femur and two tibiae) an isolated frontal bone, and an incompletely formed otic bulla, which we take to represent the remains of a fœtus (less likely a new born infant), which indicates that the adult individual was a female.
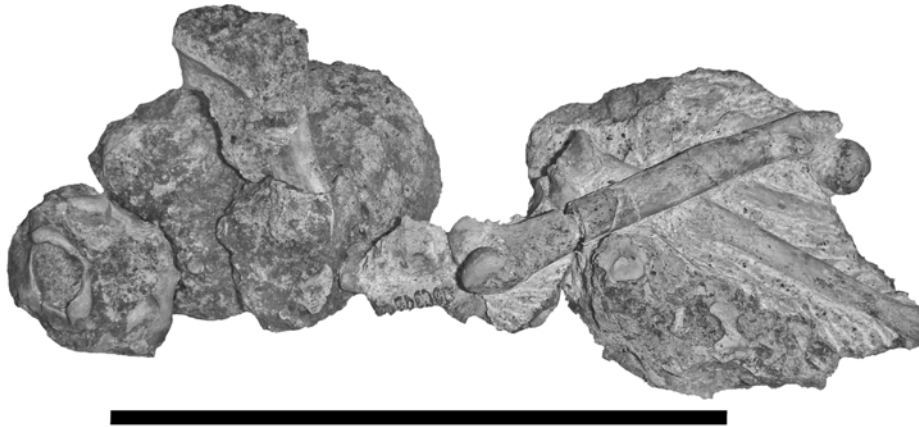

Figure 2. The skeleton of *Nonanomalurus soniae* was found in several blocks which fit together. Here the skull and right mandible (to the left of the image) are attached to a small block containing the left mandible and the distal left femur which fits onto the main block containing the thorax, and arm bones (on the obverse side) and the left femur and tibia (here partly exposed during preparation) (scale : 10 cm).

The positions of the bones in the blocks indicate that the individual was buried in a curled-up position, with the knee joint close to the head, the fore-arm fully flexed against the humerus (Fig. 3) and lying sub-parallel to the femur and tibia-fibula which were also sub-parallel to each other. Part of the vertebral column lay alongside the humerus on one edge of the block, and close to the femur on the opposite edge, confirming the curled-up configuration of the individual. Caudal vertebrae were found in various places, one in the acetabulum, another close to the skull. Some metapodials and phalanges were found inside the left orbit. The left calcaneum was intricately nested among several vertebrae and ribs (Fig. 4), not far from the distal end of the left tibia. The two patellae and some metapodials are located in the centre of the thoracic cavity (Fig. 5). The right clavicle is close to the right scapula.
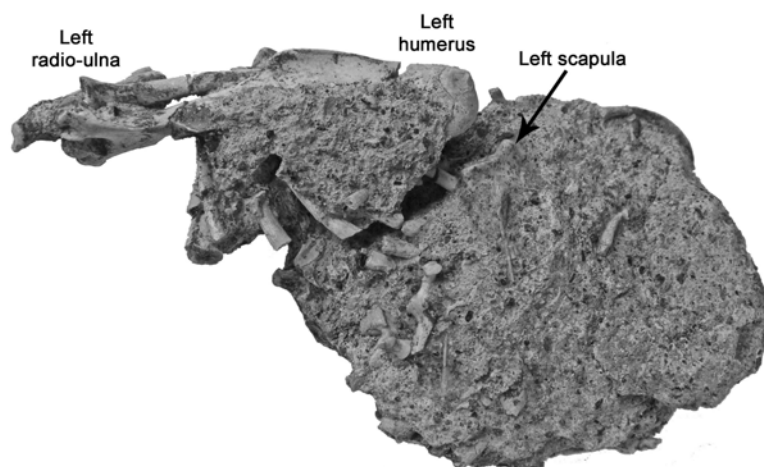

Figure 3. Dorsal view of part of the thorax, left scapula, left humerus and radio-ulna partly prepared. Note the ribs and vertebrae still largely encased in sediment (scale : 10 mm).
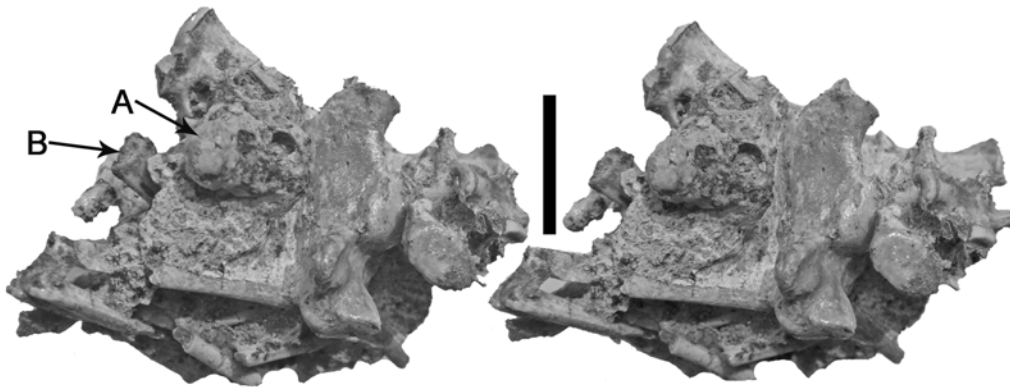
Figure 4. Calcaneum of *Nonanomalurus soniae* nested between vertebrae, ribs and parts of a foetal skull (A – otic bulla) and a foetal diaphysis (B – left tibia) (scale : 10 cm).
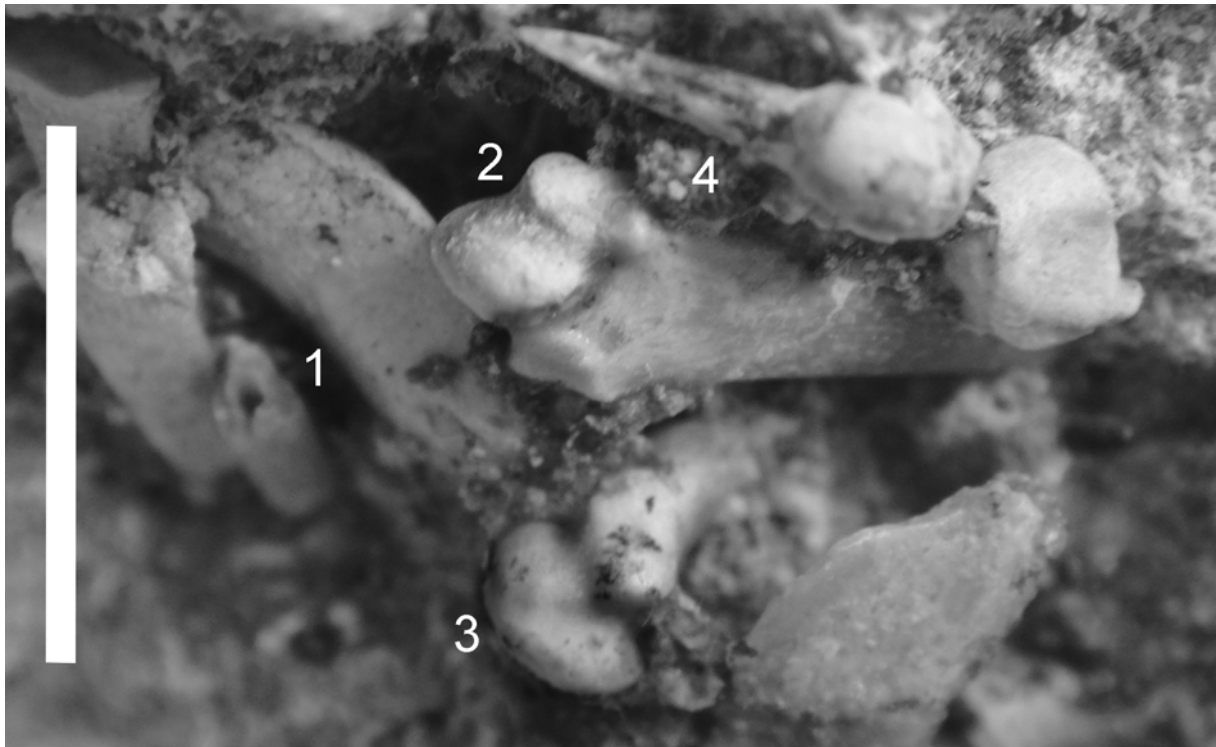

Figure 5. Inside the thoracic cage of *Nonanomalurus soniae*, Napak XV, Uganda. 1) patella, 2) distal metapodial, C) distal metapodial, D) plantar view of third phalanx (note the slit in the plantar surface of the "claw")(scale 10 : mm).

The condition of the skeleton reveals that it did not suffer significant post-mortem transportation, although it is clear that some bones have moved slightly after death, probably during putrefaction, and that sediment compaction has occurred, leading to the distortion of the splanchnocranium, and displacement of the mandibles relative to the skull. The atlas and axis were found close to the lower incisor of the right mandible about 5 cm from the occipital condyles of the skull. The right mandible was close to the distal end of the left femur. The left mandible lay flat on the ventral side of the skull but turned at right angles to it. Several phalanges were found in the left orbit. The overall aspect of the skeleton is that it lay confined within a burrow or nest which helped to keep the bones more or less in

their correct anatomical position during putrefaction until it was completely encased in sediment. This in turn suggests that the individual may have occupied a shallow burrow on the forest foor.

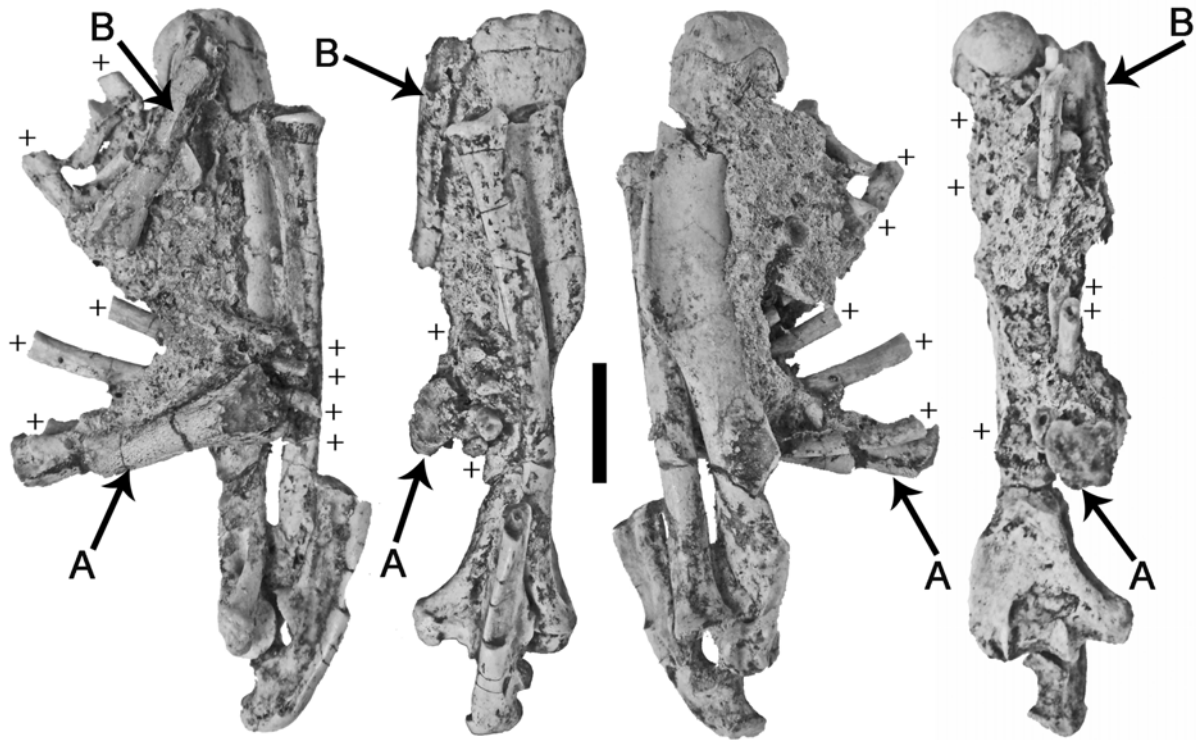The position of the foetal bones is recorded in Fig. 6, and the adult and foetal femora are compared in Fig. 7.

Figure 6. Four views (from left to right, medial, anterior, lateral and posterior) of part of the block containing the thorax of *Nonanomalurus soniae* from Napak XV, Uganda. Note the foetal diaphyses (black arrows) lying on the interior side of the thoracic cavity defined by the ribs (+ symbols), outside of which lies the articulated left humerus and radio-ulna. A) left femur, B) right tibia (scale : 10 mm).

Figure 7. Adult left femur and foetal right femur of *Nonanomalurus soniae* from Napak, Uganda. The foetal femur was extracted from the thoracic cavity of the adult individual where it was associated with three other foetal long bone diaphyses, a left frontal bone and an incompletely formed otic bulla (scale : 10 mm).

SYSTEMATIC DESCRIPTION

Order Rodentia Bowdich, 1821

Family Nonanomaluridae nov.

Genus *Nonanomalurus* nov.

Type Species *Paranomalurus soniae* Lavocat, 1973

Diagnosis : Rodent with anomaluroid cheek dentition; skull comparable in overall dimensions to that of *Paranomalurus bishopi*; incisors not highly compressed mesio-distally; second transverse valley in upper cheek teeth open to the lingual and buccal sides; crests III and V completely traversing the crown; crest IV shorter, free lingually or fused either to crest III or crest V; mandible less massive than that of *P. bishopi*; mandibular condyle posed on an elongated bony peduncle (the condyloid process); elements of the trigonid clearly discernible in lower cheek teeth; external sinus tends to be confluent with valley III; metaconid crest not reaching the protoconid but terminating at mid-breadth of the crown and its extremity often fused to the anterior cingulum in m/1, but disappearing entirely in m/2 and m/3; post-cranial skeleton with no obvious gliding adaptations; olecranon process of ulna not expanded antero-posteriorly, elbow joint constrained with well defined sigmoid cavity bordered by sharp edges; diaphyses of humerus, radius, ulna, tibia and fibula not greatly elongated. Fibula not fused to the tibia; calcaneum with short talar part and relatively elongated and robust tuber calcis, talus with an oblique ridge on the tibial surface extending from the lateral trochlea onto the neck of the talus, distal metapodial articulations solid with prominent central ridges ventrally and globular dorsal surface. First phalanges with strong, elongated flexor ridges, second phalanges with dorsally positioned almost cylindrical distal epiphysis, terminal phalanges highly medio-laterally compressed, and with ungual sheath on one side only and a slit-like longitudinal depression on the ventral side of the "claw" which is not bifid.

Species *Nonanomalurus soniae* (Lavocat, 1973)

Holotype : KNM SO 788, left maxilla containing P4/-M2/ from Songhor, Kenya.

Diagnosis : The IInd transverse valley of the upper cheek teeth reaches the lingual and buccal margins of the crowns. Upper and lower incisors not very compressed; length of P4/-M3/, 13 mm; length p/4-m/3, 14.6 mm (for original diagnosis see Lavocat, 1973, p. 187).

Material : Nap XV 170'07, almost complete skeleton associated with skull and mandibles.

Locality : Napak XV, Napak Member, near Alekilek, Uganda.

Age : Early Miocene ca 18.5 Ma.

Description :
The skull
The skull has suffered distortion such that the splanchnocranium has been pushed to the right (as viewed from the dorsal aspect) at an angle of ca 30° and has been tilted about 10° towards the ventral side (Fig. 8, Fig. 9). The palate has participated in the movement, such that the angle between the occlusal plane of the cheek teeth and that of the basicranium is too sharp, and it has shifted slightly towards the right side.
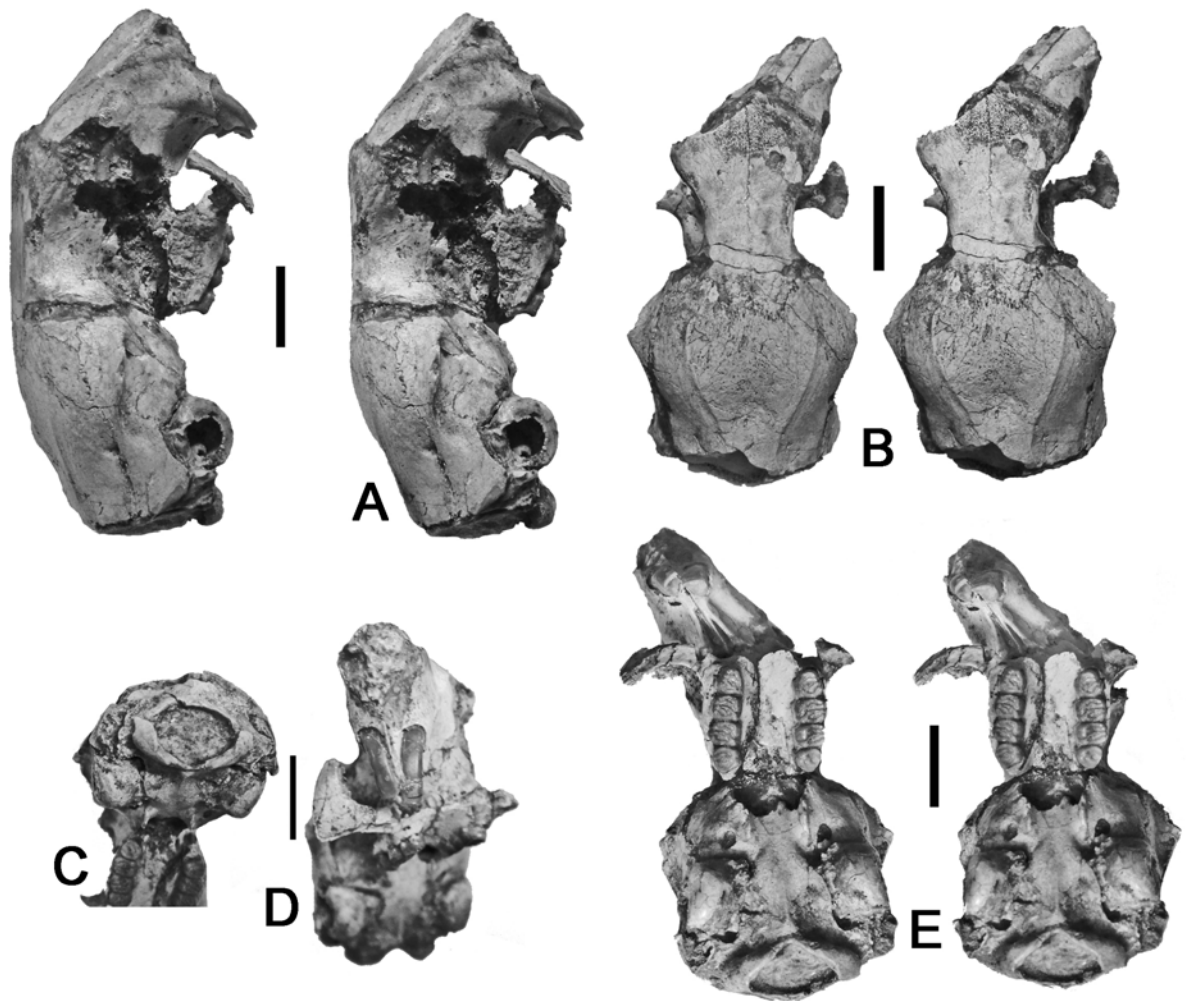
Figure 8. The skull of *Nonanomalurus soniae*, A) stereo right lateral view, B) stereo dorsal view, C) posterior, D) anterior, E) stereo occlusal view (scale : 10 mm).
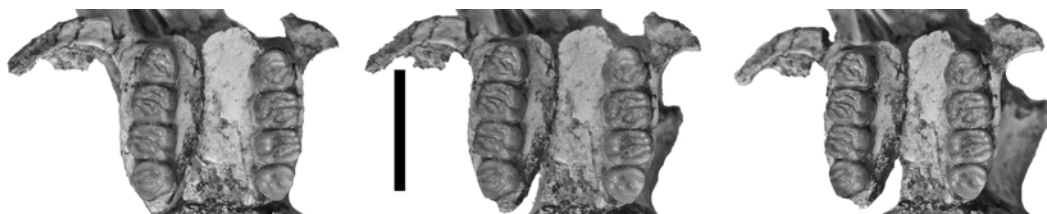

Figure 9. Stereo triplet of the palate of *Nonanomalurus soniae* (scale : 10 mm).

In dorsal aspect, the neurocranium is almost as broad as it is long. It shows two well defined curved parietal lines on its upper surface, converging anteriorly and posteriorly but not meeting each other. The space between the lines is slightly convex. Laterally the skull surface slopes more strongly towards the post-orbital crest which is at about mid-height of the neurocranium. This crest fades out distally and is absent above the level of the tympanic bullae. Above its distal termination there is a small post-glenoid foramen (Table 2).

Table 2. Measurements (in mm) of the skull and mandible of *Nonanomalurus soniae* from Napak XV, Uganda.

Measurement	mm
Skull	
Total length	72,2
Diameter of occipital foramen latero-lateral	10,7
Height of occipital foramen dorso-ventral	7,5
Orbital constriction latero-lateral	11,5
Biauricular diameter	24,5
Breadth of brain case beneath rear of zygomatic arch	25
Mandible	
Articular process to incisor alveolus	41,5
Cheek tooth row length	14,3
Height from articular process to base of angle	22
Height at diastema	9,3

The mandible (Fig. 10) is less deep than that of *Paranomalurus bishopi*, and the articular process is elongated, as was noted by Lavocat (1973). Measurements are provided in Table 2.
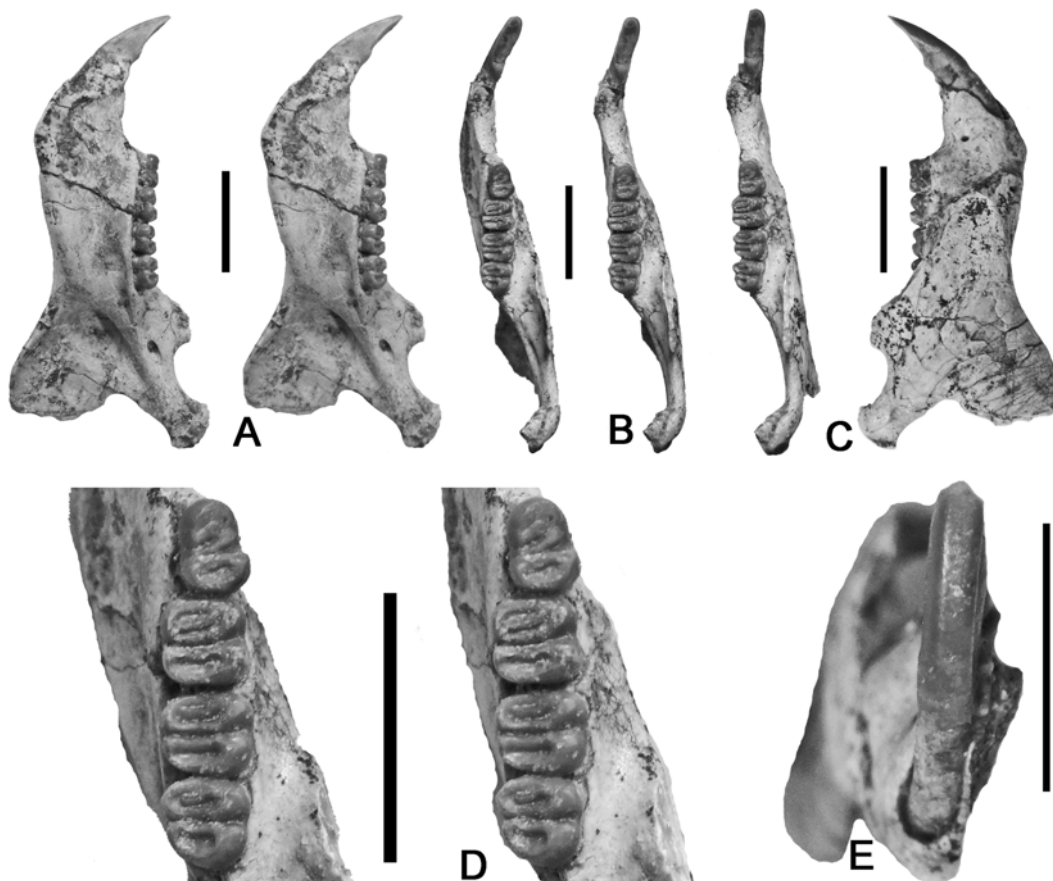

Figure 10. The right mandible of *Nonanomalurus soniae*, A) stereo lingual view, B) stereo triplet of the occlusal aspect, C) buccal view, D) stereo occlusal view of the lower cheek teeth, E) anterior view (scales : 10 mm).

The axial skeleton
The atlas (Fig. 11) has large facets for the occipital condyles, and much smaller facets for the axis vertebra.

The axis (Fig. 11) has a well developed odontoid process, and a blade like dorsal crest.

In addition to these anterior neck vertebrae, there are 5 cervical vertebrae, 19 thoracic + lumbar vertebrae, 3 sacral vertebrae and 8 caudal vertebrae preserved.
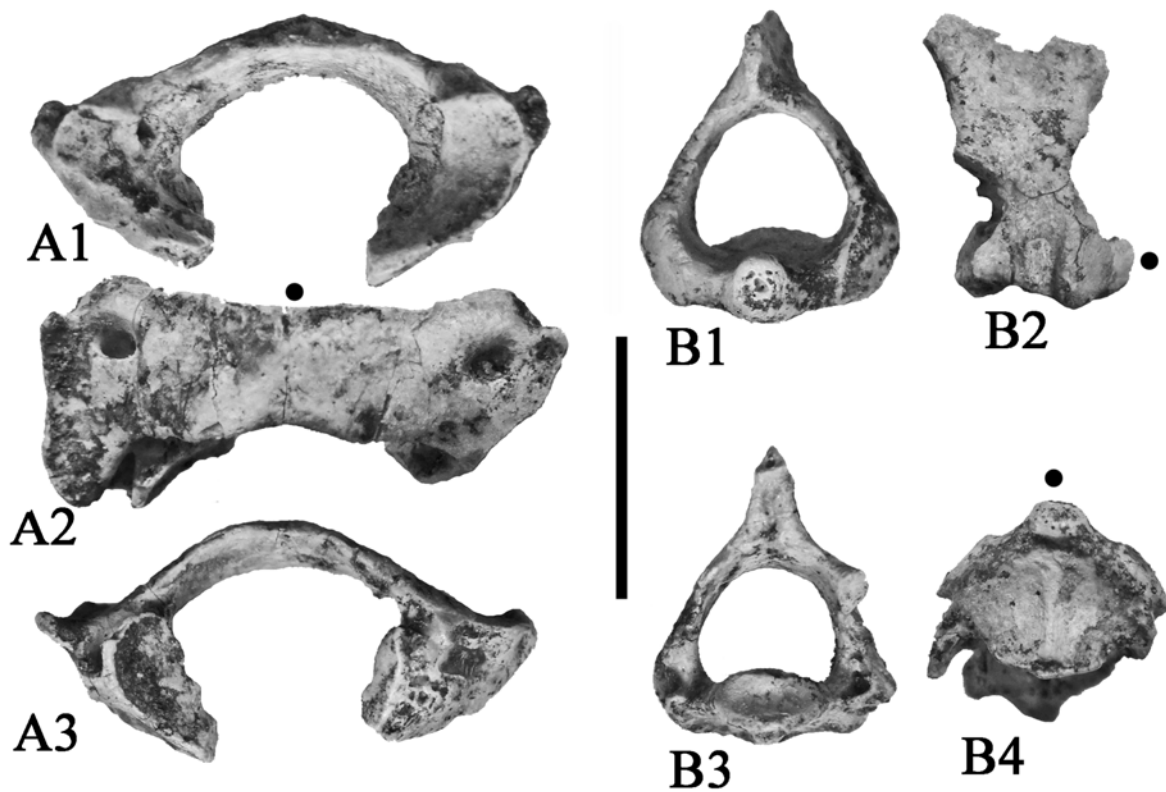

Figure 11. Atlas and axis of *Nonanomalurus soniae* from Napak XV, A) atlas, A1- anterior, A2 – dorsal, A3 – posterior views, B) axis, B1 - anterior, B2 – right lateral, B3 - posterior, B4 - ventral views (dots show the anterior side) (scale : 10 mm).

The thorax and shoulder girdle
In dorsal view the scapula is relatively short measured from the glenoid fossa to the vertebral border, and broad measured from the anterior edge to the posterior edge, when compared to the scapula of *Anomalurus* which is much longer than broad. The vertebral spine is well developed but not very tall, and only slightly overhangs the blade (Fig. 12).

The clavicle is strongly developed (at least the visible proximal part to the right of the scapula in Fig. 12, B). The two scapulae are underlain by several ribs and vertebrae (Fig. 13).

The ribs show no significant differences from those of many other rodents, with long slender bodies, and quite long necks separating the costal head from the tubercle.
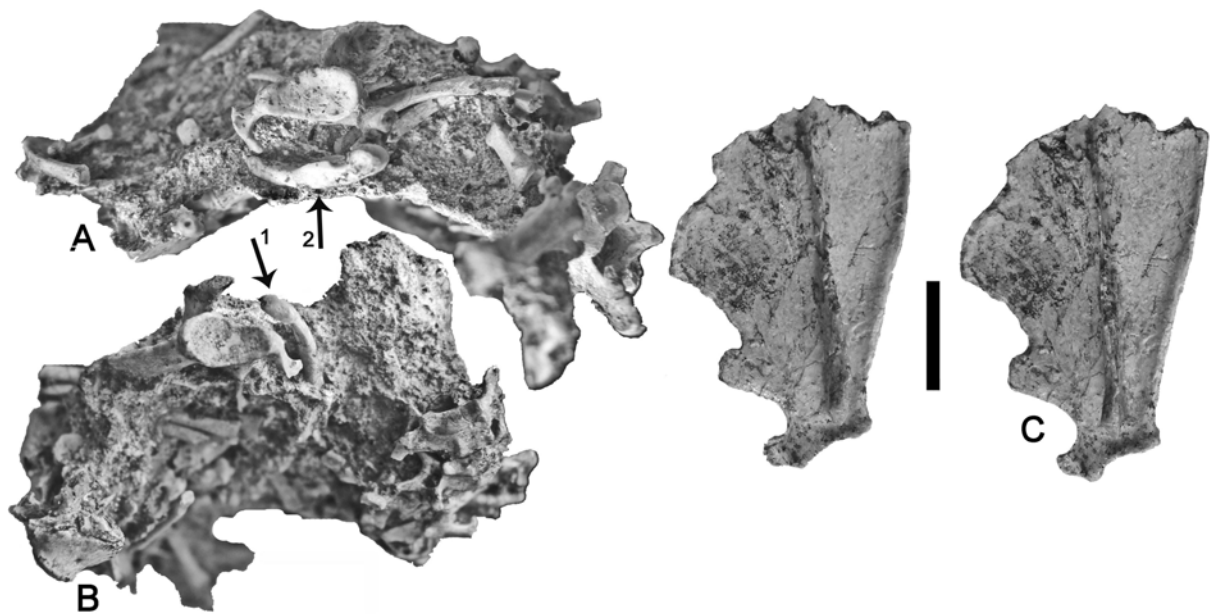
Figure 12. Scapulae of *Nonanomalurus soniae* from Napak XV, Uganda, A-B) views of the glenoid surface of A) left scapula and a first phalanx (2) beneath it, B) right scapula with clavicle (1), C) stereo superior view of left scapula (scale : 10 mm).
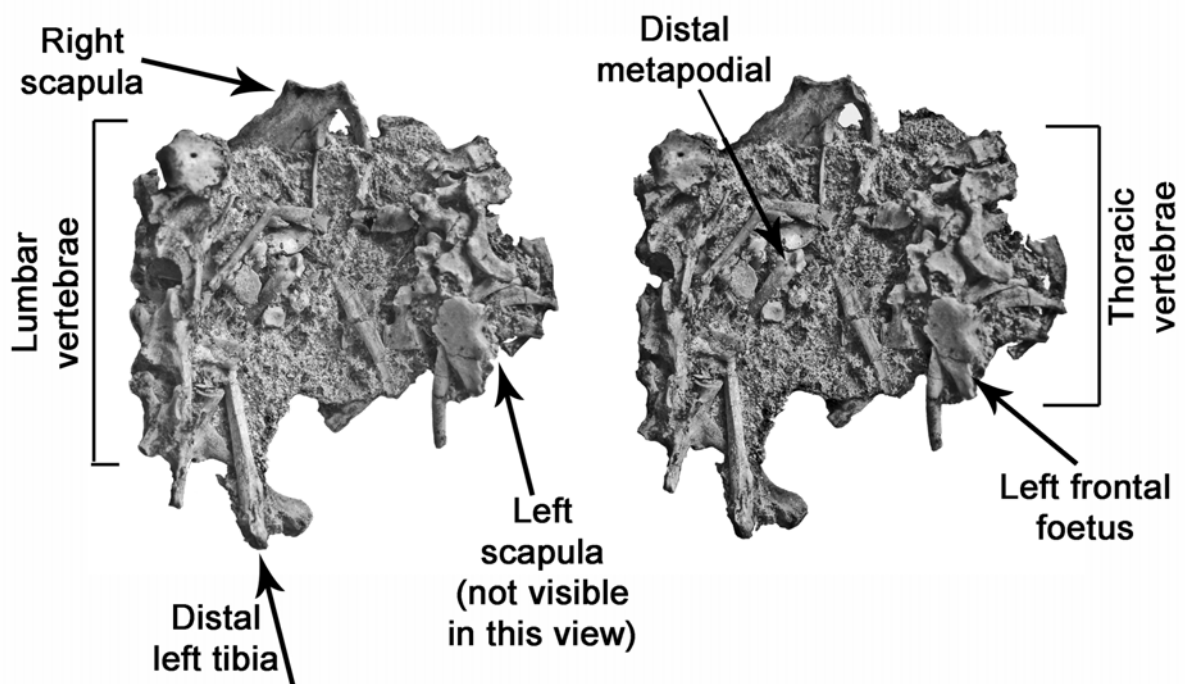

Figure 13. Stereo ventral view of part of the thorax of *Nonanomalurus soniae* from Napak XV, Uganda. In this orientation the two scapula (the left one not visible in this view) are overlain by the ribs, which are in turn overlain by the lumbar vertebrae, the left fibula and a metapodial, and by some elements of a foetus (only the left frontal of the latter is labelled) (scale : 10 mm).
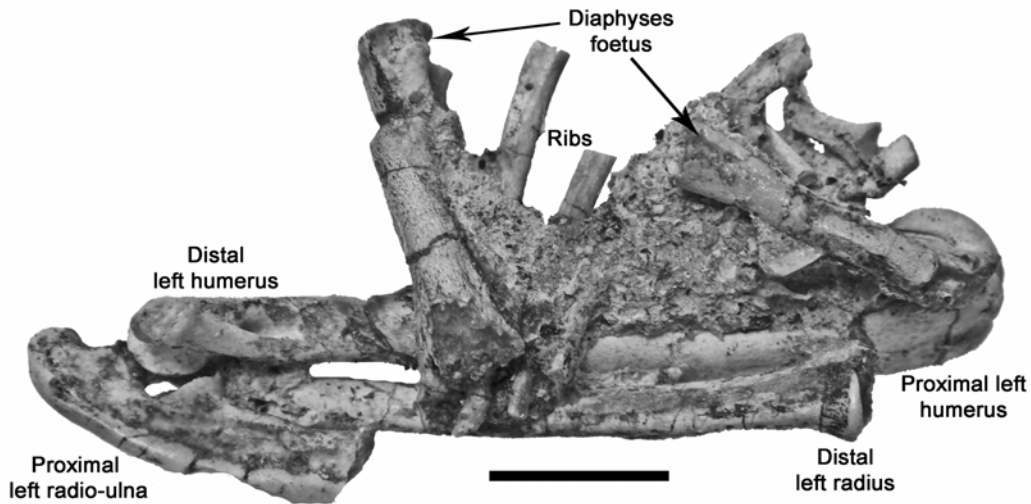
Figure 14. Left humerus and radio-ulna stuck to part of the thorax of *Nonanomalurus soniae* from Napak XV, Uganda, medial view (scale : 10 mm).

The humerus (Fig. 14, Fig. 15) has a slightly sigmoid diaphysis, with a well developed deltoid crest extending at least half the length of the bone, and strongest in its distal extremity. There is an entepicondylar foramen, the lateral distal crest is well formed, the medial epicondyle salient. The proximal epiphysis is not completely fused to the diaphysis, in contrast to the distal epiphysis which is.

Figure 15. Left humerus of *Nonanomalurus soniae* from Napak XV, Uganda. A) stereo posterior (extensor) view, B) medial, C) stereo anterior (flexor) view, D) lateral, E) distal and F) proximal views (dots show the anterior side) (scale : 10 mm).

The radius (Fig. 14, Fig. 16) is slightly curved, with ovoid proximal and distal epiphyses. There is a well developed tubercle just beneath the proximal articulation.

The ulna diaphysis is slightly curved, the proximal part has well a defined sigmoid notch with sharp edges overhanging the proximal and distal edges of the notch. There is a clear facet for the radius. In *Anomalurus* the edges of the sigmoid notch are rounded and the notch itself is wide open anteriorly, the proximal and distal lips being retracted, providing less constaint of the joint than in *Nonanomolarus*. The olecranon is about as tall as the sigmoid notch, the proximal extremity is short antero-posteriorly, and the apex is slightly concave.
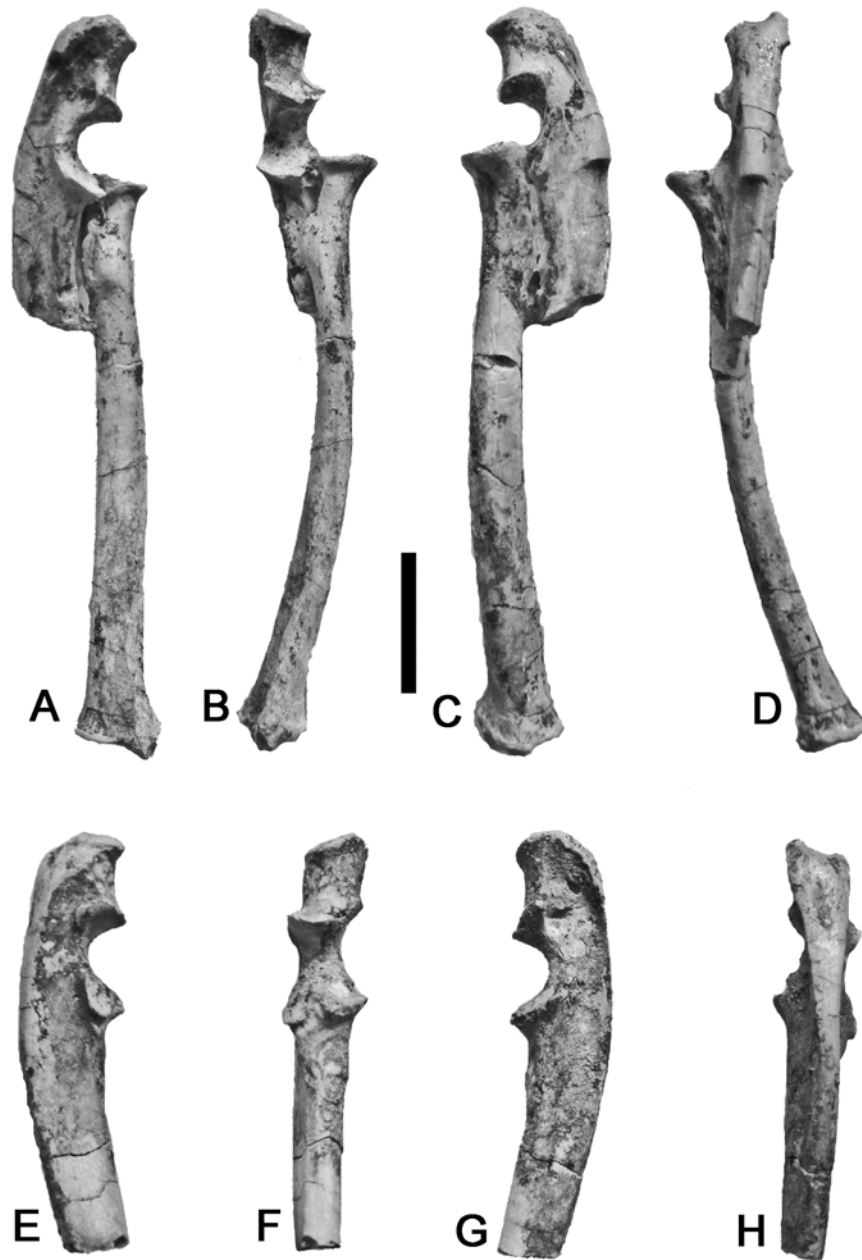

Figure 16. Radius and ulna of *Nonanomalurus soniae* from Napak XV, Uganda. A-D) left proximal ulna and complete radius, A) medial, B) anterior (flexor), C) lateral, D) posterior (extensor) views; E-H) right proximal ulna in E) lateral, F) anterior, G) medial and H) posterior views (scale : 10 mm).

Table 3. Measurements (in mm) of the bones of the pectoral girdle and forelimb of *Nonanomalurus soniae* from Napak, Uganda, *Paranomalurus bishopi* and *Paranomalurus walkeri* (dap – antero-posterior diamatar, dml – medio-lateral diamater, pd – proximo-distal).

Bone / Measurement	Specimen / mm	Specimen / mm	Specimen / mm	Specimen / mm	Specimen / mm
Scapula	*N. soniae* Nap XV 170'07				
Articular end total cranio-caudal breadth	11,9				
Glenoid facet cranio-caudal breadth	7,8				
Glenoid facet height dorso-ventral	4,6				
Total length along spine	35				
Humerus	*N. soniae* Nap XV 170'07	MUZM 30			
Total length	53,8	0			
Head dap	8,5	0			
Head dml	7	0			
Proximal end dap	10	0			
Proximal end dml	9,9	0			
Distal end dml	13,5	13			
Distal articulation anterior dml	8,6	8			
Distal end dap	5,2	4,7			
Distal articulation posterior dml	5,2	5			
Midshaft dap	5	0			
Midshaft dml	4	0			
Radius	Nap XV 170'07				
Total length	40,6				
Proximal articulation dap	3,8				
Proximal articulation dml	5				
Distal articulation dap	4,6				
Distal articulation dml	6,1				
Midshaft dap	2,6				
Midshaft dml	3,4				
Ulna	Nap XV 170'07	*P. walkeri* Nap V 51'08	*P. walkeri* Nap Sans N°	*P. walkeri* KNM SO 806	*P. bishopi* Nap IV 185'11
Total length	Ca 51		Juvenile	est. from fig.	
Top of sigmoid notch dap	6,2	10,5	9,7	10,4	13,3
Base of sigmoid notch dml	5,6	6,5	5,6	5,6	6,7
Sigmoid notch height pd	5,4	7	5,3	7,1	7,2
Olecranon process anterior height	7,1	9	6,4	6,9	8,7
Olecranon process shaft dml	3,1	3	2,7	2	2,3
Olecranon process shaft dap	5,1	10,4	9,4	10,5	14,3
Sigmoid notch dap	3,9	6,9	6,4	7,4	9,2
Sigmoid notch dml	3	3,4	2,9	3,2	3,8
Summit of olecranon process dap	4,4	15	10,3	15,4	17,8

The pelvic girdle
The sacrum (Fig. 17) is incomplete, but the proximal vertebra and part of a wing are preserved which are not fused together.
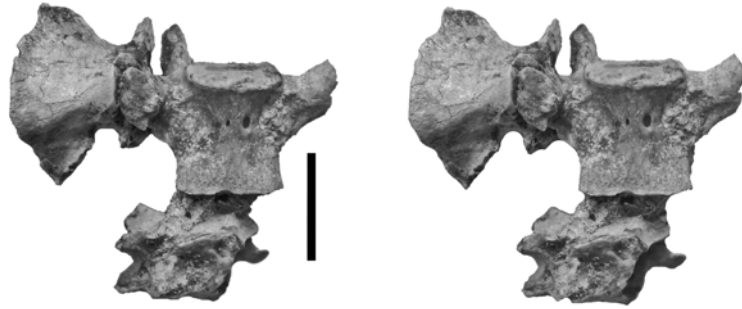
Figure 17. Sacrum of *Nonanomalurus soniae* from Napak XV, Uganda, stereo ventral view. Note that the vertebrae of the sacrum are not fused together and that the sacral wing is also unfused to the vertebrae (scale : 10 mm).

The os coxa (Fig. 18) is incomplete distally, but better preserved proximally. There is nothing remarkable about this bone, as it resembles rodent pelves in general. The rim of the acetabulum is raised into a sharp ridge on its anterior, dorsal and posterior parts.
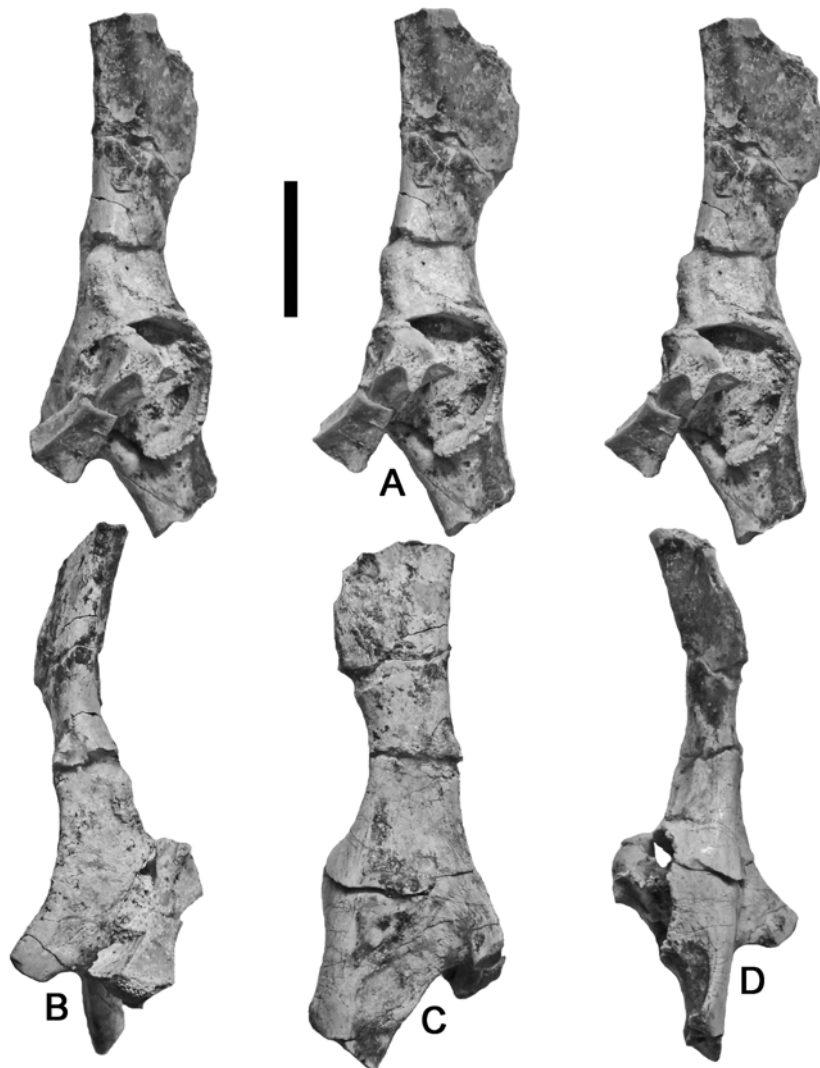

Figure 18. Left os coxa and a caudal vertebra, A) stereo triplet in lateral view, B) ventral, C) medial, and D) dorsal views (scale : 10 cm).
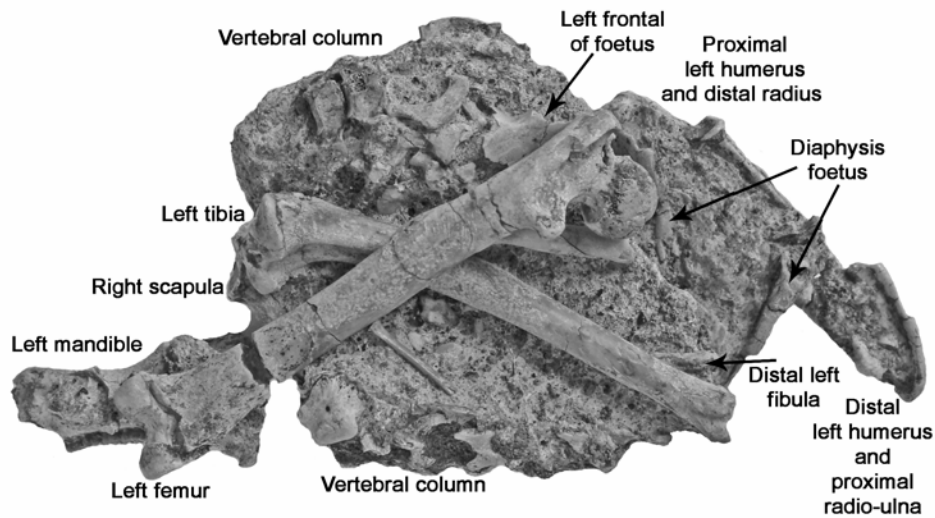
The hindlimb (Table 4)

Figure 19. Ventral view of thorax of *Nonanomalurus soniae* overlain by the left femur, tibia and fibula.

The femur (Fig. 19, Fig. 20) has an almost straight diaphysis which curves slightly anteriorly towards its proximal end. The proximal epiphysis is completely fused to the neck of the femur, but the distal epiphysis is not fused to the shaft. The greater trochanter extends very slightly above the head of the femur, the lesser trochanter is prominent, even if small, and the third trochanter is represented by a ridge on the lateral side of the bone with sharp but low crests leading proximally and distally from it. The digital fossa is deep and separates the neck from the posterior edge of the greater trochanter.

Table 4. Measurements (in mm) of the bones of the pelvis and hindlimb of *Nonanomalurus soniae* from Napak, Uganda (dap – antero-posterior diameter, dml – medio-lateral diameter).

Bone / Measurment	Specimen / mm
Os coxa	Nap XV 170'07
Acetabulum dap	10,9
Acetabulum dml	10,5
Femur	
Total length	75,5
Head dap	10
Head dml	9,5
Neck dap	4
Distal end dap	11,4
Distal end dml	13,6
Patellar groove dml	5,2
Intercondylar groove dml	4,3
Midshaft dap	5,2
Midshaft dml	7,5
Distance between ends of greater and lesser trochanters	10
Tibia	
Total length	67,2
Proximal end dap	11
Proximal end dml	13,2
Distal end dap	7,3

|	
Distal end dml	9,9
Distal articulation dap	5,3
Distal articulation dml	7,7
Midshaft dap	5,5
Midshaft dml	3,9
Calcaneum	
Total height	10
Greatest breadth across sustentaculum	10,9
Tuber calcis breadth midshaft	3
Tuber calcis dorso-planter dimension midshaft	5,5
Talus	
Breadth of tibial trochlea	5,9
Length of lateral trochlear lip	7
Length of neck and head plantar side	7
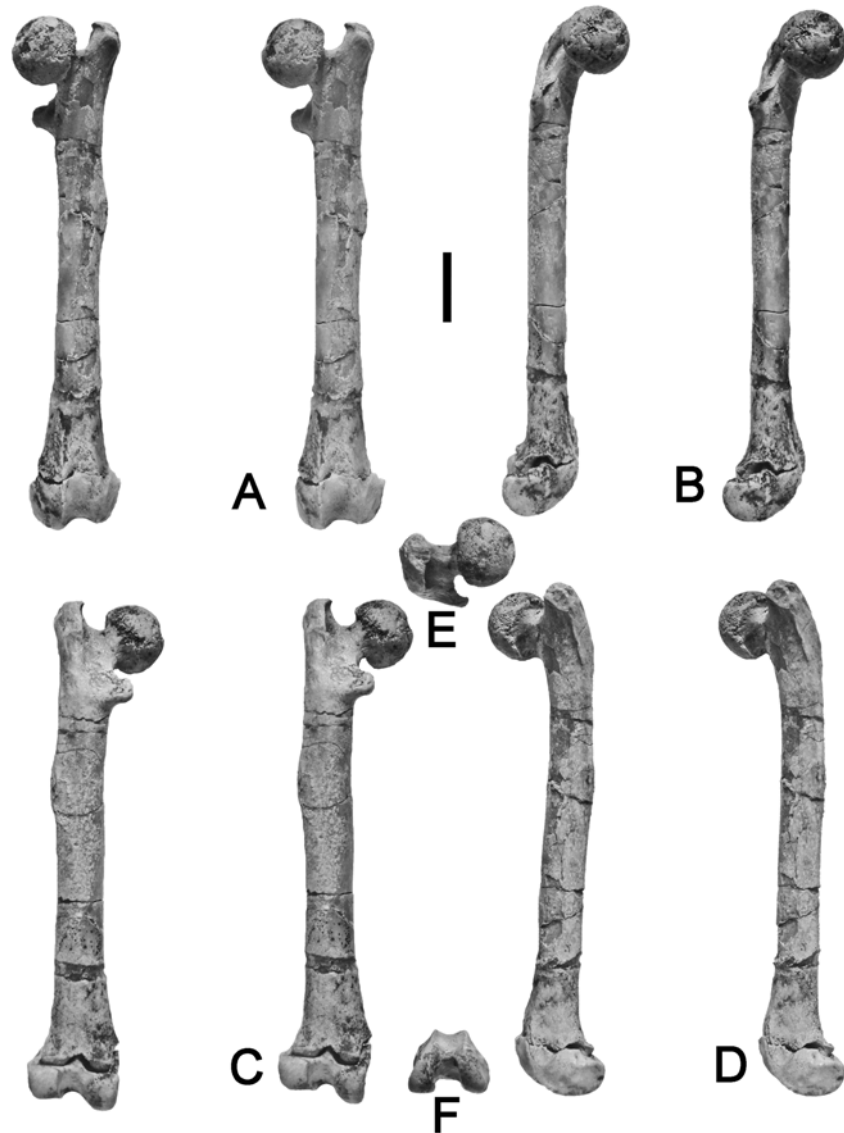
Figure 20. Left femur of *Nonanumalurus soniae* from Napak XV, Uganda. A) stereo anterior view, B) stereo medial view, C) stereo posterior view, D) stereo lateral view, E) proximal view, F) distal view (scale : 10 mm).

The tibia (Fig. 19, Fig. 21) is gently curved in its proximal half, but straight distally. The proximal epiphysis is not fused to the diaphysis, but the distal one is. The proximal articulation has weak to absent ridges between the lateral and medial articular facets for the distal condyles of the femur. The lateral depression on the proximal third of the diaphysis is weakly excavated.

The fibula is unfused to the tibia, both proximally and distally.
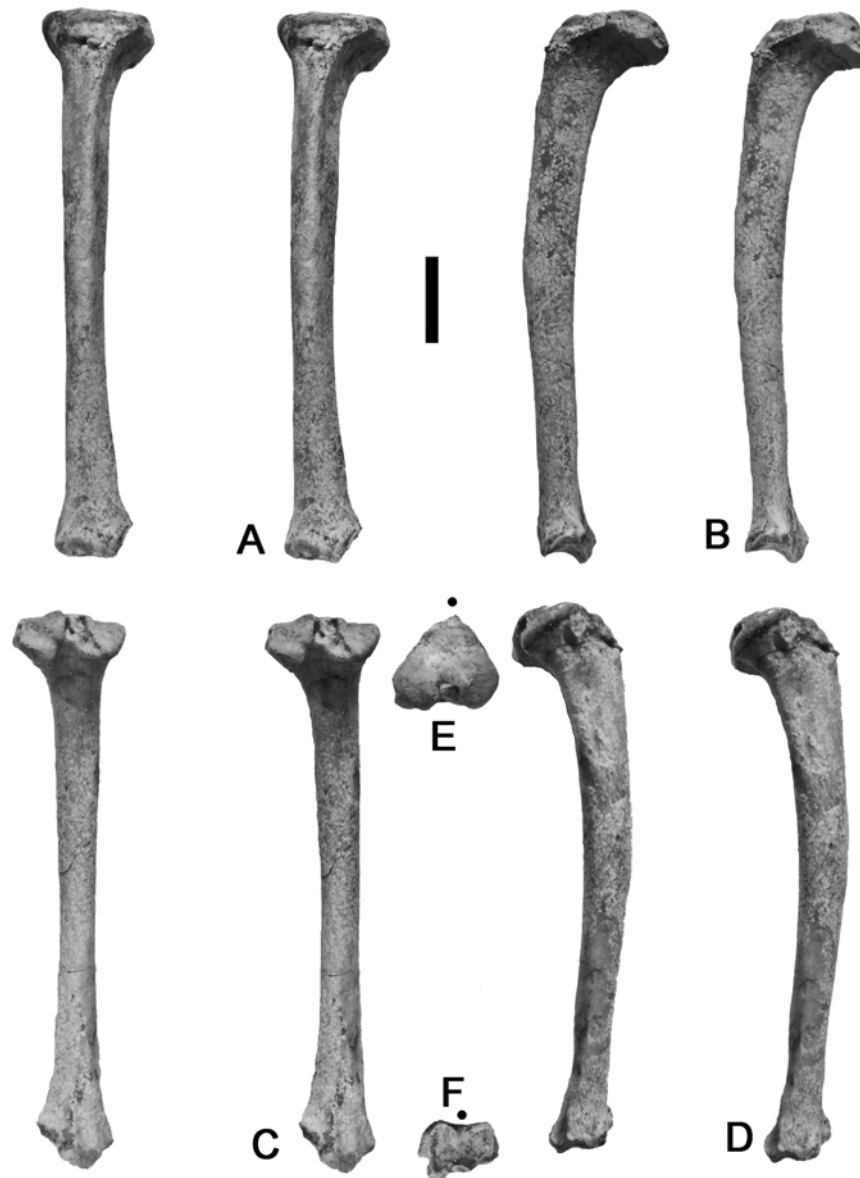
Figure 21. Left tibia of *Nonanomalurus soniae* from Napak XV, Uganda. A-D stereo views A) anterior, B) lateral, C) posterior, D) medial, E) proximal, and F) distal views (dot shows the anterior side) (scale : 10 mm)..

Calcaneum
The calcaneum (Fig. 22) has a short talar portion, and a slightly elongated tuber calcis. The summit of the tuber calcis is excavated by a wide antero-posterior depression. The sustentaculum is about one third of the breadth of the bone.
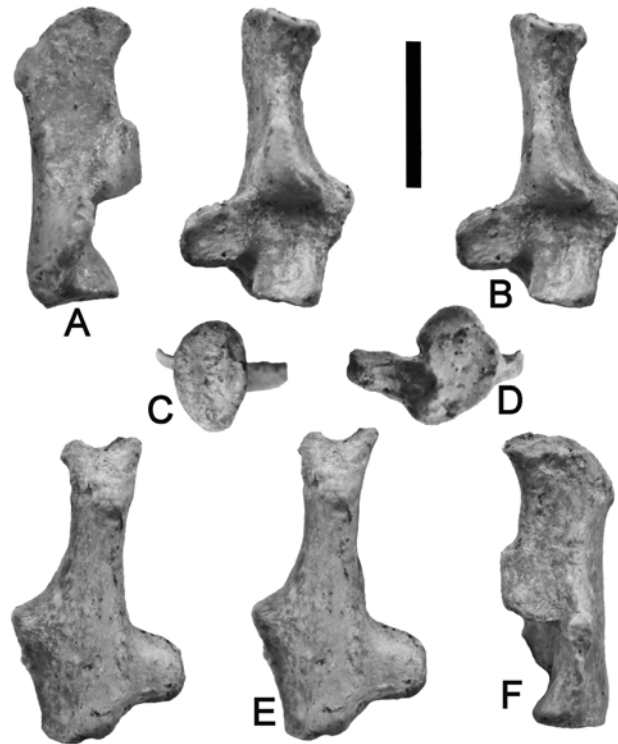
Figure 22. Left calcaneum of *Nonanomalurus soniae* from Napak XV, Uganda. A) medial view, B) stereo dorsal view, C) tuber calcis, D) navicular view, E) stereo plantar view, F) lateral view (scale : 10 mm).

Talus
The talus (Fig. 23) is remarkable for the presence of a strong rounded ridge of bone extending from the lateral lip of the trochlea onto the neck of the talus. The lateral trochlea is appreciably larger than the medial one.
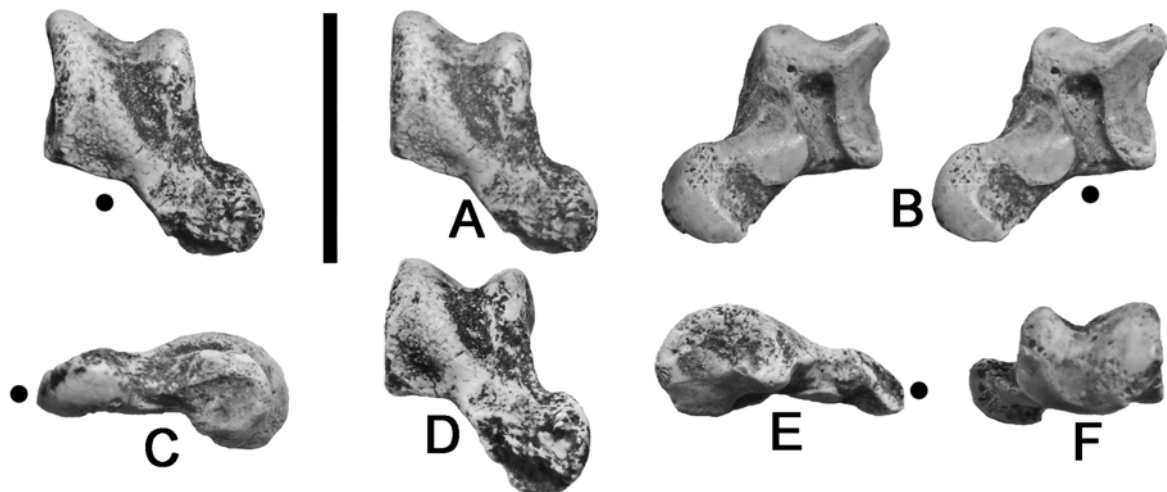

Figure 23. Right talus of *Nonanomalurus soniae* from Napak XV, Uganda. A) stereo superior view, B) stereo plantar view, C) medial view, D) oblique supero-posterior view to show strong ridge running between the lateral trochlea and the head, E) lateral view, F) posterior view (dots show the anterior side) (scale : 10 mm).

Metapodials

The distal ends of the metapodials (Fig. 24) are remarkable for their strength, the presence of well developed ridges on the flexor side which extend from the epihysis well onto the diaphysis, and of hemispherical articular facets on the dorsal or extensor side of the bones. The medial and lateral fossae for ligamentary attachments are well developed.

Figure 24. Metapodials of *Nonanomalurus soniae* from Napak XV, Uganda. A-B) distal ends probably of metacarpals A1), B1) stereo dorsal views, A2), B2), stereo flexor views, C-D) distal ends probably of metatarsals, C1) D1) stereo dorsal views, C2) D2) stereo ventral views, C3) D3) stereo inter-metapodial views D) is slightly damaged apically (scale : 10 mm).

Phalanges

The first phalanx is remarkable in three ways (Fig. 25). Firstly, the proximal articular facet is well developed and forms a distinct hollow in the proximal end, corresponding to the hemispherical articulation of the metapodial. Secondly, the shaft is quite curved (convex dorsally) with very strongly developed flexor ridges on the flexor side of the bone. Thirdly, the distal epiphysis is cylindrical.

The second phalanx (Fig. 25) has a straight diaphysis at the distal end of which is a cylindrical epiphysis raised above the level of the diaphysis. The proximal facet is a hollow cylinder.

The third phalanx (Fig. 25) is peculiar in possessing a well developed ridge for attachment of the claw, but only on one side of the bone. *Anomalurus* has very weak to absent ridges of attachment of the claw. In the fossil the basal tubercle is strongly developed, and the basal part of the claw has a clear but narrow slit running longitudinally. *Anomalurus* has a sharp basal part of the claw, with no sign of a

basal slit. In lateral view the claw is tall and short. The dorsal edge of the claw is sharp. The articular facet is a hollow cylinder.
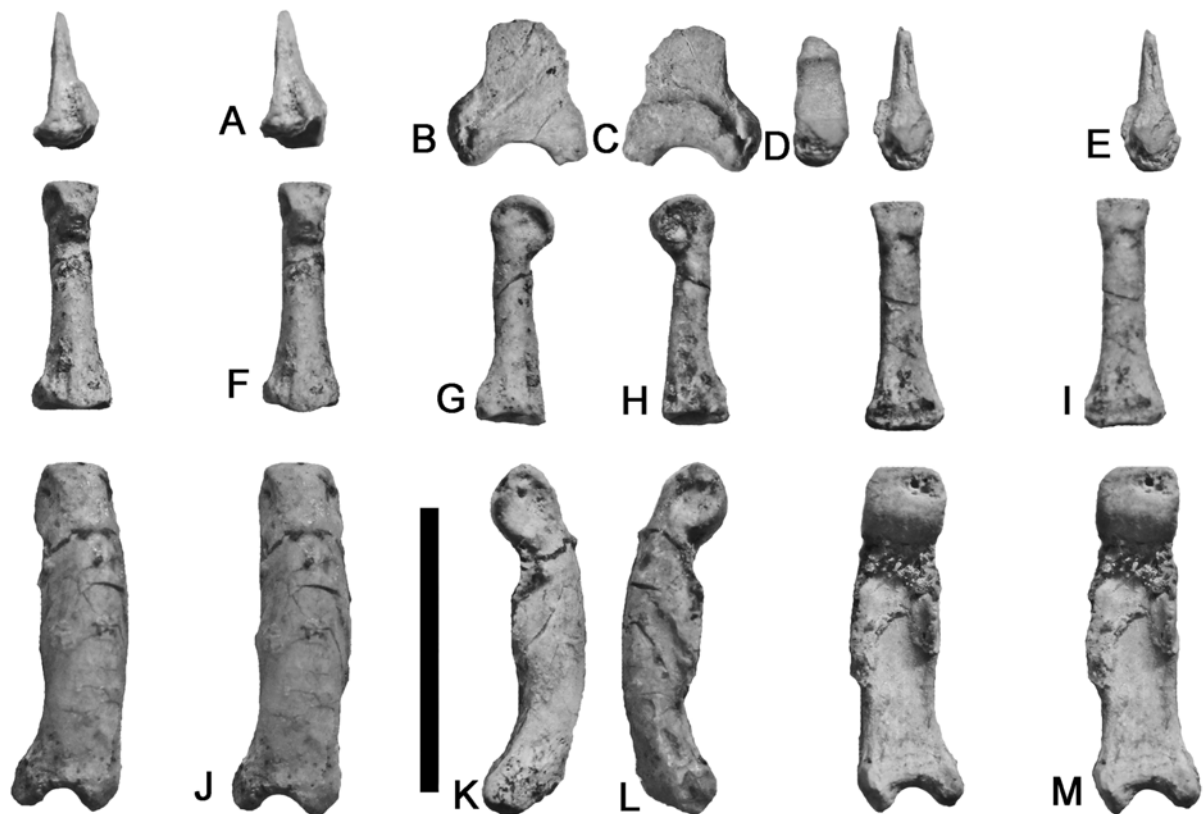

Figure 25. Phalanges of *Nonanomalurus soniae* from Napak XV, Uganda. A) Third phalanx, B) second phalanx, C) first phalanx. A, F, J) stereo dorsal view, B, G, K and C, H, L) medial and lateral views, D) proximal view, E, I, M) stereo flexor views (scale : 10 mm).

Metric comparison of the skeletons of *Nonanomalurus soniae* and *Anomalurus peli*
We compared measurements of the skull, long bones, scapula, calcaneum and phalanges of extinct *Nonanomalurus soniae* and extant *Anomalurus peli*. These two species have skulls that are closely similar in total length (Table 5) the ratio between the two being 103% (the fossil skull is marginally longer than the extant skull). In all postcranial measurements in contrast, the extant species has considerably longer bones than the fossil one. Thus the lengths of the long bones of *Nonanomalurus soniae* are between 54,9% and 79,6% of the corresponding bones in *Anomalurus peli*. The calcaneum of *N. soniae* is very short, 44,6% of that of *A. peli*, whereas the autopods of the two species are somewhat closer in dimensions – *N. soniae* having phalanges that are 60% to 88,9% of the dimensions of those of *A. peli* (Table 5).

Table 5. Measurements (in mm) of the skull and parts of the postcranial skeleton of *Anomalurus peli* and *Nonanomalurus soniae*, and the ratio between the two species.

Element/Measurement	*N. soniae*	*A. peli*	Ratio *N.s. / A.p.*
Skull	Nap XV 170'07	MNHN A 3343	
Total length	72,2	70	103
Scapula			
Length along posterior edge	33	52	63,5

22

Humerus			
Total length	53,8	98	54,9
Radio-ulna			
Total length	40,6	100	40,6
Femur			
Total length	75,5	114	66,2
Head dap	10	11,4	71,4
Tibia			
Total length	67,2	120	56
Calcaneum			
Total length	10	22,4	44,6
First phalanx			
Total length	12	13,5	88,9
Second phalanx			
Total length	8	11	72,7
Third phalanx			
Total length	6	10	60

The metric comparison of the skeletons of *Nonanomalurus soniae* and *Anomalurus peli* indicate that the two taxa have radically different skeletal proportions, despite having almost identical skull dimensions.

Brachial index, Crural index and Intermembral index of *Anomalurus peli* and *Nonanomalurus soniae*

The indices of the long bones of *Nonanomalurus* and *Anomalurus* confirm that they have radically different skeletal proportions (Table 6). In *Anomalurus* the distal long bones (radius, tibia) are as long as or slightly longer than the proximal elements (humerus, femur) whereas in *Nonanomalurus* the proximal elements are substantially longer than the distal ones. The intermembral indices of the two taxa are also markedly different, the hind limbs of *Anomalurus* being considerably longer than the forelimbs when compared to *Nonanomalurus*.

Table 6. Long bone indices of *Nonanomalurus soniae* and *Anomalurus peli*

Index	*N. soniae*	*A. peli*
Brachial index (radius/humerus)	76,4	100
Crural index (tibia/femur)	89	105,3
Intermembral index (humerus + radius / femur + tibia)	66,1	41

The distal limb elements of *Anomalurus* are as long as or longer than the proximal elements. In contrast the distal limb elements of *Nonanomalurus* are much shorter than the proximal elements. Visual comparison of a sample of rodents indicates that the proportions and overall form of the skeleton of *Nonanomalurus soniae* are closer to those of arboreal squirrels than they are to those of any of the anomalurids (Fig. 26). From this we infer that *Nonanomalurus soniae* probably occupied a squirrel-like niche in the Early Miocene forest that grew on the flanks of Napak Volcano.
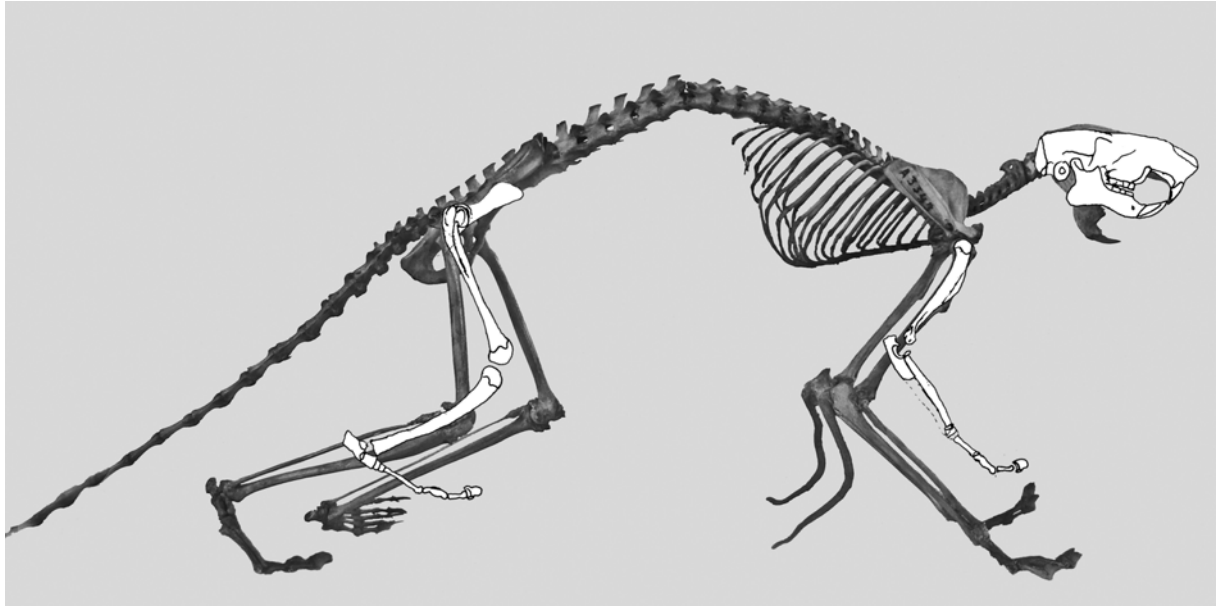
Figure 26. Skull and limb bones of *Nonanomalurus soniae* (in white) superposed on a mounted skeleton of *Anomalurus peli* (MNHN A 3343). The skulls of these two species are almost the same length, but the long bones of *Nonanomalurus* are considerably shorter than those of *Anomalurus*.

Family Anomaluridae Gill, 1872

Genus *Paranomalurus* Lavocat, 1973

Type species *Paranomalurus bishopi* Lavocat, 1973

Remarks
Lavocat (1973) included three species in *Paranomalurus* (*P. bishopi*, *P. soniae* and *P. walkeri*). The first and third in the list are morphologically similar and belong to the same genus, but have sufficiently different dimensions to represent two distinct species. "*P.*" *soniae*, in contrast is morphologically divergent from the other two species, but has approximately the same dimensions as *P. bishopi*. The extraction of "*P.*" *soniae* from the genus *Paranomalurus* impacts on the generic and species diagnoses, raising some of the species characters to the level of the genus.

Diagnosis : Large Anomaluridae with brachyodont teeth, palate relatively broad, upper molar rows subparallel and occlusal surface sloping only slightly outwards (from Lavocat, 1973, p. 173); skull roof only slightly overhanging the orbital cavity, bullae proportionally less developed than in *Anomalurus* and *Anomalurops*; upper molars as long as they are broad, lingual wall continuous, no sinus or internal fold; disposition of the valleys as in the extant genus *Anomalurus*; lower molars with distal lophid appreciably shorter mesio-distally than the mesial lophid; upper and lower incisors highly compressed mesio-distally.

Differential diagnosis : Differs from *Nonanomalurus* in possessing much more compressed incisors, and a continuous enamel wall in the upper cheek teeth closing off the transverse valleys lingually. Lower molars with distal lophid much shorter than the mesial lophid.

Species *Paranomalurus bishopi* Lavocat, 1973

Holotype : UM 7060 and 7061, skull in two parts, from Napak IX, Uganda.

Diagnosis : Large species of the genus (close in dimensions to *Anomalurus peli*); length of upper tooth row (P4/-M3/) 13 mm, length of lower tooth row (p/4-m/3) 15,4 mm; in lower cheek teeth, anterior

lobe much longer than the posterior one; four complete transverse valleys; a large external sinus (for original diagnosis see Lavocat, 1973, p. 173).

Description
Lavocat (1973) provided a thorough description of the skull, mandible and dentition of *Paranomalurus bishopi*. He did not have any postcranial fossils associated directly with the cranio-dental sample.

Species *Paranomalurus walkeri* Lavocat, 1973

Holotype : KNM SO 804, right maxilla containing P4/-M2/ from Songhor, Kenya.

Diagnosis : Small species of the genus; lower tooth row (p/4-m/3 ca 12,5 mm); upper teeth morphologically similar to those of *P. bishopi*, lower cheek teeth distinctly longer than broad, with a shorter anterior valley; well-marked buccal sinus of the anteroconid bordered by a projecting anteroconid situated on the buccal margin (for original diagnosis see Lavocat, 1973, p. 191).

Description
Lavocat (1973) provided a detailed description of the available cranio-dental remains of *Paranomalurus walkeri*. No postcranial bones have been found associated with the skull of this species. The available fossils indicate that the species is essentially a small version of *P. bishopi*, with very similar dental morphology.
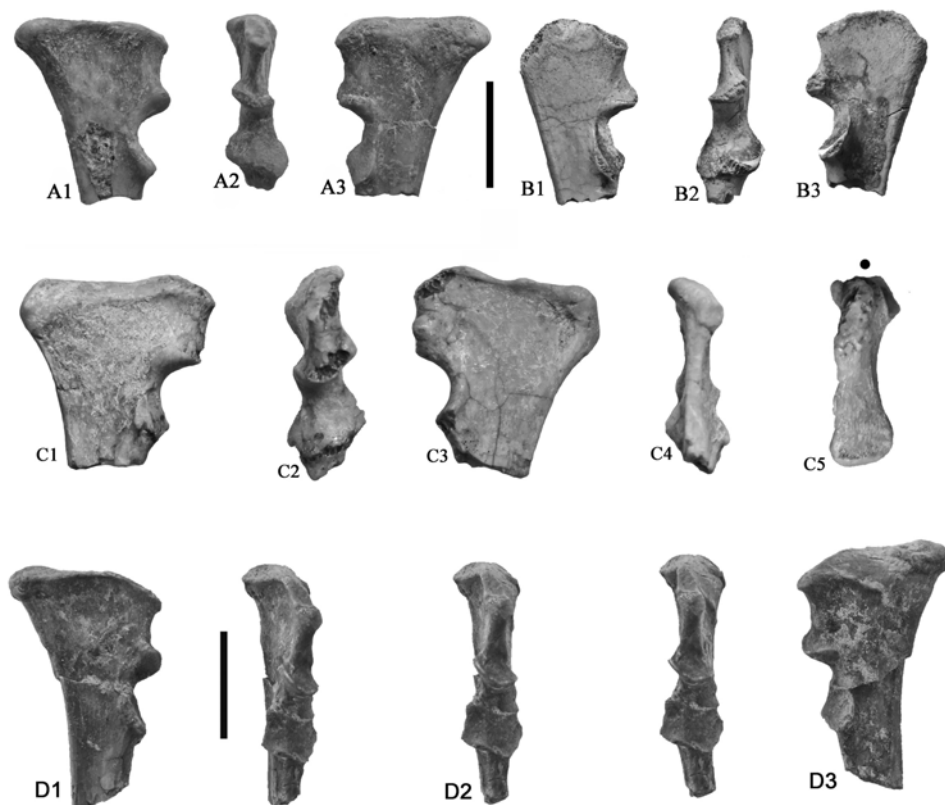

Figure 27. Anomalurinae proximal ulnae from Napak, Uganda, attributed to *Paranomalurus walkeri* (A, B, D) and *Paranomalurus bishopi* (C). A) Nap V 51'08, left ulna, A1 - medial, A2 - anterior (flexor), A3 - lateral views; B) Nap sans N° old collection right ulna of a juvenile with incompletely ossified epiphysis, B1 - medial, B2 - anterior, B3 - lateral views; C) Nap IV 185'11, right ulna, C1 - medial, C2 - anterior, C3 - lateral, C4 - posterior (extensor), C5 - proximal views, D) Nap XV 64'12, left ulna, D1) medial, D2) stereo triplet anterior view, D3) lateral view (dot shows the anterior edge) (scale : 10 mm).

Discussion

Much new cranio-dental material of *Paranomalurus* has been found, which confirms the presence of two species of the genus at several localities (Koru, Songhor, Napak). Lavocat (1973) had no specimens in which the postcranial skeleton was associated with the skull. The discovery of the associated skeleton and skull of *Nonanomalurus soniae* reveals not only that this species is dentally divergent from *P. bishopi* and *P. walkeri*, as was already demonstrated by Lavocat (1973), but that it probably differs postcranially from these species as well. This inference flows from the fact that we have found four proximal ulnae of anomalurine aspect at Napak (Fig. 27, Fig. 28), and Lavocat (1973, pp. 192-193) described a specimen of the same bone from Songhor, Kenya, which he attributed to Anomalurinae sp. The five available ulnae comprise two size groups, and we consider that the three small specimens probably belong to *P. walkeri*, and the large one to *P. bishopi*. If the ulnae of anomalurine aspect do indeed belong to *Paranomalurus*, as we infer, then they show that the postcranial skeletons of *Nonanomalurus* and *Paranomalurus* are highly divergent in morphology, the former showing no adapatations to gliding locomotion, the latter showing fully developed gliding adaptations as in extant *Anomalurus*.
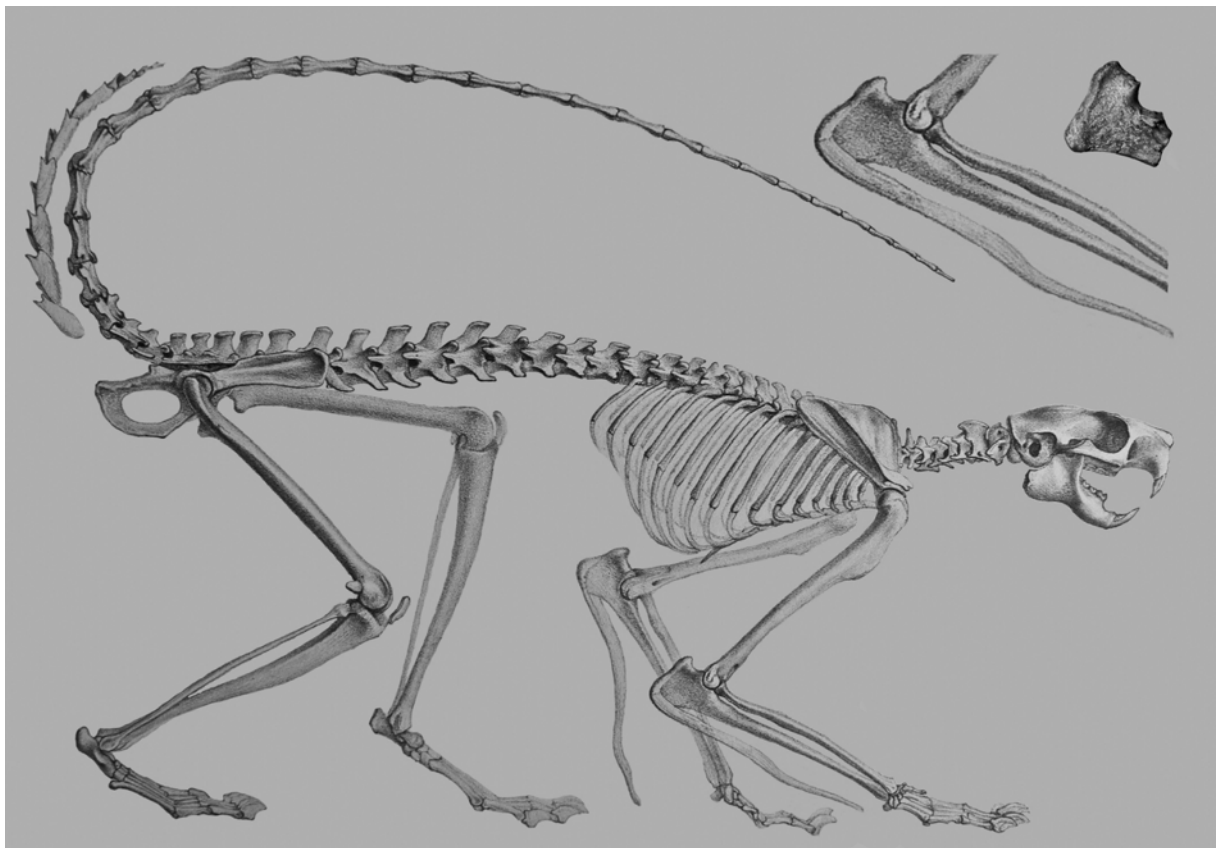

Figure 28. Skeleton of extant *Anomalurus peli* (modified from Blainville, 1839-1864) showing the expanded olecranon process of the ulna with the cartilaginous patagial strut attached (right elbow joint enlarged in top right corner and Nap IV 185'11, right ulna of *Paranomalurus bishopi* for comparison).

DISCUSSION

Lavocat (1973, pl. 8, fig. 3 ; pl. 38, figs 1-3) described an isolated proximal end of a left ulna. On account of its antero-posteriorly expanded olecranon process among other features which he considered to resemble extant anomalurid ulnae, he attributed the specimen (KNM SO 806) to an indeterminate anomalurine. The ulna was reported to be unusual in possessing a concave lateral surface, in contrast to extant anomalurids in which the concave surface is medial. However, Lavocat (1973, pl. 8., fig. 3) mis-identified the orientation of the bone, and called the medial side "lateral";

hence the supposed difference from the extant form disappears (the lateral view of the same bone is correctly labelled by Lavocat, 1973, pl. 38, fig. 2).

Comparison of the Songhor ulna and the four specimens from Napak, with that of the skeleton of *Nonanomalurus soniae*, reveals that they have highly divergent morphology and dimensions, indicating that whatever the Songhor ulna is, it is not attributable to *Nonanomalurus*, but is closer to *Anomalurus*. In *Nonanomalurus soniae*, the proximal ulna is considerably smaller and it is not antero-posteriorly expanded, nor is it proximo-distally elongated as in the Songhor specimen.

The Songhor fossil ulna is too large to represent *Zenkerella wintoni* but is the right size to represent *Paranomalurus walkeri*. Four proximal ulnae morphologically similar to the Songhor fossil were found at Napak (Nap V 51'08, an uncatalogued specimen from the old collections without precise locality data, Nap IV 185'11 and Nap 64'12). One of the specimens (Nap IV 185'11) is significantly larger than the others, and it is concluded that it represents the species *Paranomalurus bishopi*, while the smaller specimens probably belong to *P. walkeri*.

ASPECTS OF REPRODUCTION IN *NONANOMALURUS SONIAE*

Many rodents are r-strategists (several offspring at each birth with relatively short inter-birth intervals) while few are k-strategists (one or two infants at a time with longer inter-birth intervals). There is no sharp break between the spectrum of reproductive strategies, with many taxa falling between the extremes of r-strategists and k-strategists.

Among extant rodents, the spring hare *Pedetes* has one offspring (fewer than 1% twins) per birth but can have three pregnancies per year (Mills & Hes, 1997) and it is therefore a k-strategist. *Zelotomys*, in contrast, has between 5 and 11 pups per litter, and can be considered an r-strategist. *Otomys* is a different kind of r-strategist, giving birth to one to four pups per litter, but with up to seven litters per breeding season. *Anomalurus* gives birth to one to three pups per litter with two breeding seasons (April and September) (Haltenorth & Diller (1984). It therefore plots closer to the k-strategy end of the reproductive spectrum, than to the r-strategy end.

The fact that the skeleton of *Nonanomalurus soniae* described above was associated with the skeletal remains of a single foetus indicates that the species was probably a k-strategist.

PHYLOGENETIC RELATIONSHIPS OF *NONANOMALURUS*

The long bones of *Nonanomalurus* have closer morphological affinities to those of Pedetidae than they do to those of Anomaluridae, but this is most likely due to the fact that Nonanomaluridae and Pedetidae have retained a suite of plesiomorphic anomaluroid features. The distal epiphyses of the metatarsals of *Nonanomalurus* are solid, swollen and have a strongly developed central ridge ventrally and a globular dorsal surface.

The cheek teeth of *Nonanomalurus* have a central transverse valley (N° III) that opens buccally and lingually, giving the teeth a bilophodont aspect. The anterior and posterior lophs have shallow blind valleys that do not reach the buccal or lingual margins of the crowns. This also makes the teeth appear bilophodont, especially when they are worn deeply enough to wear away the blind valleys. In addition, the anterior and posterior loph(id)s are subequal in mesio-distal length and bucco-lingual breadth, another resemblance to the cheek teeth of Pedetidae, and a contrast with *Paranomalurus* in which the distal loph(id) is appreciably shorter than the anterior one (Lavocat, 1973).

The incisors of *Nonanomalurus* are not as highly compressed mesio-distally as those of *Paranomalurus*, *Idiurus* and *Zenkerella*, and in this respect they are closer to the proportions found in Pedetidae. The highly compressed incisors probably represent the derived condition, in which case the less compressed incisors of *Nonanomalurus* and Pedetidae are similar because they are plesiomorphic.

The otic bullae of *Nonanomalurus* are not as inflated as those of Pedetidae and they do not encroach onto the dorsal surface of the neurocranium (Pickford & Mein, 2011). In this respect they more closely resemble those of *Paranomalurus bishopi* and to a lesser extent those of *Anomalurus*, the differences between the two latter taxa already noted by Lavocat (1973).

There are thus dental and postcranial resemblances between *Nonanomalurus* and Pedetidae that do not occur in *Paranomalurus* and extant anomalurids, but this should perhaps not be pushed too far in terms of phylogenetic inferences, because the extant anomalurid genera *Idiurus* and *Zenkerella* also possess bilophodont cheek teeth, and *Zenkerella* is a non-volant anomalurid. Furthermore, there is a vast difference in cheek tooth hypsodonty in *Pedetes* and nonanomalurids, although the extinct genus *Megapedetes* is relatively brachyodont.

Resolution of the phylogenetic relationships between Pedetidae, Nonanomaluridae and Anomaluridae requires a complete study of the cranium, dentition and postcranial skeleton, including that of the non-volant anomalures such as *Zenkerella*. Such a study is beyond the scope of this article.

Also to be resolved are the relationships between anomaluroids from North Africa (*Kabirmys*, *Nementchamys*) and Myanmar (*Pondaungimys*) and Zegdoumyidae from North Africa and Namibia (*Glibia*, *Zegdoumys*) (Sallam *et al.*, 2010; Dawson *et al.*, 2003; Pickford, *et al.*, 2008). Our findings concerning *Nonanomalurus*, suggesting a Middle Eocene dichotomy among anomaluroids, accords with the results of Sallam *et al.*, (2010). However, none of the North African or Myanmar taxa are represented by post-cranial elements, making it difficult to make progress.

UNTANGLING FUNCTIONAL OSTEOLOGICAL FEATURES FROM TAXONOMIC ONES

The skeleton, Nap XV 170'07, unveils the difficulties that can be experienced by palaeontologists when they confine their comparisons to dentognathic remains. "*Paranomalurus*" *soniae* was considered by Lavocat (1973) to belong to Anomaluridae, a family of arboreal rodents, some of which are gliders, others non-volant. Its skeleton reveals that its limb bones are so divergent from those of *Anomalurus* that it is highly unlikely to belong to the same family. Apart from that, isolated postcranial elements from Napak reveal the existence of true anomalures at the same sites as *Nonanomalurus soniae*, a finding which indicates that the separation between Anomaluridae and Nonanomaluridae (nov. fam.) must have occurred a considerable time prior to the deposition of the Napak deposits (18.5-20 Ma). The four anomalurid ulnae from Napak and the specimen from Songhor, Kenya (KNM SO 806) the latter bone described and figured by Lavocat (1973), are compatible in dimensions to *Paranomalurus bishopi* for the large specimens and *Paranomalururs walkeri* for the smaller ones. Both these species are dentally divergent from *Nonanomalurus soniae* (see diagnoses in Lavocat, 1973).

The humerus and femur of *Nonanomalurus soniae* show features for enhanced joint mobility and they have thus converged in some aspects towards the corresponding bones in small arboreal primates, which explains why some palaeoprimatologists have been misled when interpreting incomplete isolated postcranial fossils. Several fossils from East African Early Miocene deposits hitherto thought to represent strepsirrhine primates (lorisids and galagids) turn out to belong to *Nonanomalurus*. Body weight estimates made using these misidentified fossils reveal that the results vary considerably depending upon which bone is used to calculate the weight and which animal model is in the mind of the calculator at the time of the study. It highlights some of the hazards of deducing locomotor repertoires on the basis of isolated articulations of animals - in this case the inference of slow climbing in extinct lorisids was based on remains of a rodent which was probably an active climber and leaper. Finally it exposes the weaknesses of arguments concerning evolution and phylogeny that flow from interpreting misidentified fossils.

Some features of the elbow and hip joint of *Nonanomalurus soniae* have been interpreted in terms of functional adaptations in lorisid primates (Gebo *et al.*, 1997; MacLatchy & Kityo, 2002). This appears to have been due the presence of osteological traits related to enhanced mobility of these articulations.

Because the arboreal environment is three dimensional and the arboreal substrate is discontinuous and highly complex in shape and orientation, mammals that live in it require enhanced mobility of the limb articulations, be they carnivores, rodents, primates, sloths or marsupials. In the case of the Napak supposed lorisid, osteological features that are signatures of arboreality in mammals in general, were taken to represent features of primates, without consideration of the possibility that they might also occur in other arboreal mammals. In the study of isolated postcranial bones that are thought to belong to primates, it is essential to examine all the mammals that might potentially have inhabited the same kind of environment. This applies particularly to arboreal taxa, but in general this advice is worth following for any taxon that possess highly mobile elbows and hip joints, such as burrowing mammals, the bones of which which have also, on occasion, been confused with those of primates (Leakey & Leakey, 1978) or aquatic mammals, which also tend to possess highly mobile shoulder and hip joints.

Figure 29. MUZM 30, initially interpreted as a lorisid distal right humerus by Gebo *et al*., 1997, is morphometrically similar to the distal humerus of *Nonanomalurus soniae*, Nap XV 170'07. Both specimens are broken at the same level, a point of weakness in the humerus of this species. The two specimens clearly belong to the same taxon.

Isolated and incomplete fossil postcranial bones have frequently proven problematic to palaeontologists. In particular, there is a tendency on the part of some palaeoanthropologists to attribute fragmentary non-primate fossils to primates, whereas the opposite rarely occurs. The case of

Hesperopithecus from North America is probably the most celebrated instance, in which a fossil peccary tooth was interpreted as being that of an anthropid ape (Osborn, 1922) but there are numerous publications in which African and Asian non-primate fossils have been identified as primates, including fish (a tooth of *Gymnarchus* identified as an incisor of a hominoid, Andrews, 1978), crocodiles (humerus taken for a hominoid clavicle : Le Gros Clark & Leakey, 1951) suids (isolated teeth taken to be those of hominoids : Andrews, 1978 ; Kelley, 2005 ; Lewis, 1934) anthracotheres (maxilla with two teeth identified as a cercopithecid : MacLatchy *et al.*, 2003) orycteropodids (femoral fragments identified as hominid : Leakey & Leakey, 1978) carnivores (femoral fragment identified as hominid: Leakey & Leakey, 1978) and unidentifiable mammal remains (small suiform scapula glenoid identified as *Morotopithecus* : Gebo *et al.*, 1997 ; MacLatchy *et al.*, 2000) among others. It is less common for primate fossils to be identified as non-primates, which indicates the presence of a bias in the interpretation of the fossil record.

A distal humerus and a proximal femur from Early Miocene (20-18 Ma) deposits at Napak, Uganda, were attributed to Lorisidae by Gebo *et al.*, (1997) and MacLatchy & Kityo (2002) (Fig. 29) and used to infer locomotor repertoires, to estimate body weight, and to deduce aspects of lorisid and galagid behaviour, evolution and phylogeny. The two fossils (MUZM 30, distal humerus and BUMP 20, proximal femur) were interpreted by these authors to indicate the presence of two taxa of Lorisidae at Napak, which were reported to differ principally in size, a small species estimated to weigh about 900 gm (Gebo *et al.*, 1997) and a second, larger species estimated to be « significantly larger than known Miocene and extant lorisoids » (MacLatchy & Kityo, 2002).

The anatomical features of the distal humerus of the "small" species were considered by Gebo *et al.*, (1997) to « suggest that forelimb function resembled arboreal quadrupedal and cautious climbing primates, with several functional similarities to extant lorises » whilst the femur (UM BUMP 20), which was attributed to the "large" species, was interpreted to provide evidence for slow climbing (MacLatchy & Kityo, 2002). Comparisons of these fossils with those of Early Miocene galagids (Walker, 1970 , 1974, 1978) and extant lorisids led to the suggestion that the Napak distal humerus « helps to document the beginning of lorisid locomotor adaptation and evolution in the forelimb » (Gebo *et al.*, 1997). In contrast, MacLatchy & Kityo (2002) wrote that the « timing and nature of the divergence of the lorisoid clade into bushbabies and slow lorises is poorly documented by the fossil record» but that the question could now be addressed on the basis of the Napak fossil femur which « suggests that the adaptive divergence of the two lorisid lineages was well under way by the Early Miocene ». Thus, to these authors, two fossils from the same rodent species and from the same site indicated two contrasting scenarios of the timing of the lorisid-galagid divergence, one well before the Early Miocene, one during the Early Miocene.

In contradiction to Gebo (1989) who wrote that the fossil lorisoid distal humeri from Kenya more closely resembled cheirogaleids (mouse lemurs and dwarf lemurs) than galagids in terms of the combination of a shallow olecranon fossa, the presence of a well-developed sulcus between the trochlea and the capitulum, and the small size of the articular surface laterally bordering the capitulum, Gebo *et al.*, (1997) concluded that they « more closely resembles galagids".

Clearly, therefore, there are difficulties in interpreting isolated and fragmentary postcranial specimens, with little sign of ending the uncertainties inherent in dealing with such incomplete material. There is evidently a bias among certain palaeoanthropologists for identifying fragmentary non-primate fossils as primates and then to employ them in wide-ranging interpretations of primate behaviour, locomotion, evolution and phylogeny.

MacLatchy & Rossie (2005b) appear to consider that it is necessary to understand the phylogeny of a taxon before it can be distinguished from other taxa at the generic level. This approach is generally invalid for a number of reasons, not least of which is that Identification, Taxonomy, Classification, Systematics and Phylogeny (ITCSP) are distinct human endeavours, related in a heirarchical way, but each of which can be practiced successfully without recourse to higher level inferences. For example, an experienced bird watcher can correctly identify the species to which a bird belongs, even on the

basis of a glimpse, without being aware of its systematic position or phylogeny, or indeed even if he holds an incorrect view of its systematics and phylogeny, or even if he does not understand or accept the concept of evolution. Likewise a systematician can propose robust hypotheses about the generic or family relationships of a species without being aware of its phylogenetic relationships.

Incorrectness of a higher level inference does not automatically invalidate a lower level one, although an error at a lower level always invalidates a higher level inference based on that lower level error. Evidence should be judged for correctness on the basis of data and arguments appropriate for solving issues at and beneath that level of the ITCSP heirarchy. For this reason, it is essential to identify organisms or, as is usually the case in palaeontology, parts of organisms, correctly before they can be used for determining higher level relations, just as it is essential to identify taxa correctly before valid systematic or eventually phylogenetic inferences can be proposed. For this reason, the phylogenetic relationships proposed for the Galagidae and Loridae (or Lorisidae) by Gebo *et al*., (1997) and MacLatchy & Kityo (2002), cannot be entertained because the fossils upon which they based their phylogenetic inferences were postcranial bones of a species of rodent incorrectly attributed by these authors to two distinct families of primates. Similarly, MacLatchy *et al*. (2003) proposed that fossils from Moroto II could throw light on the phylogenetic relationships between early monkeys and hominoids, but the "monkey" fossil mentioned in the text (a maxilla with D4/-M1/) is from a suiform, and is therefore inappropriate for such an endeavour, just as the scapula glenoid from Moroto I, attributed to *Morotopithecus bishopi* is not a valid basis for determining modes of locomotion and phylogenetic relationships in this primate because the scapula belongs to a suiform, *Morotochoerus ugandensis* (Pickford *et al*., 1999).

The description of a fossil « chimpanzee » femur (DeSilva *et al*., 2006) provides a recent example of this tendency. As a Late Pleistocene to Holocene human femur, which is what the Kikorongo (Uganda) specimen is, it was not particularly noteworthy, but reported as a late Miocene chimpanzee femur its newsworthiness was increased, not for what it could reveal about hominoid evolution since it is a poorly preserved fragment, but because chimpanzee fossils are extremely rare.

Even with genuine primate fossils, fragmentary remains that, had they belonged to non-primates would have been considered unpublishable have, on occasion, been subjected to repeated and often conflicting interpretations. East African material attributed to extinct strepsirrhines is no exception, with some specimens experiencing major changes in identification and interpretation. A proximal humerus (KNM SO 1028) for example, was identified by Walker (1970) as *Progalago dorae*, whereas Gebo (1989) claimed that the specimen was a procyonid. McCrossin (1992) in contrast, accepted its strepsirrhine status, but considered that its morphology linked it to Lorisidae rather than to Galagidae. Thus, if McCrossin (1992) is correct, then *Progalago* would be a lorisid rather than a galagid, contrary to the view of Walker (1970).

The discovery of articulated skeletons associated with cranio-dental remains often helps to clarify some of the claims made on the basis of incomplete and isolated post-cranial remains. The unearthing of an articulated skeleton of the anomaluroid rodent, *Nonanomalurus soniae* (Lavocat, 1973) at Napak, Uganda, provides constraints on the interpretation of the fossil record, and falsifies or renders doubtful some recent interpretations of lorisid and galagid phylogeny based on mis-identified fossils of this species.

The articulated skeleton of *Nonanomalurus* from Napak reveals that its postcranial skeleton is morphologically closer in several respects to that of Pedetidae than to that of Anomaluridae. However, the resemblances are probably due to shared primitive features, meaning that the relationships between Anomaluridae, Nonanomaluridae and Pedetidae still remain to be elucidated.

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