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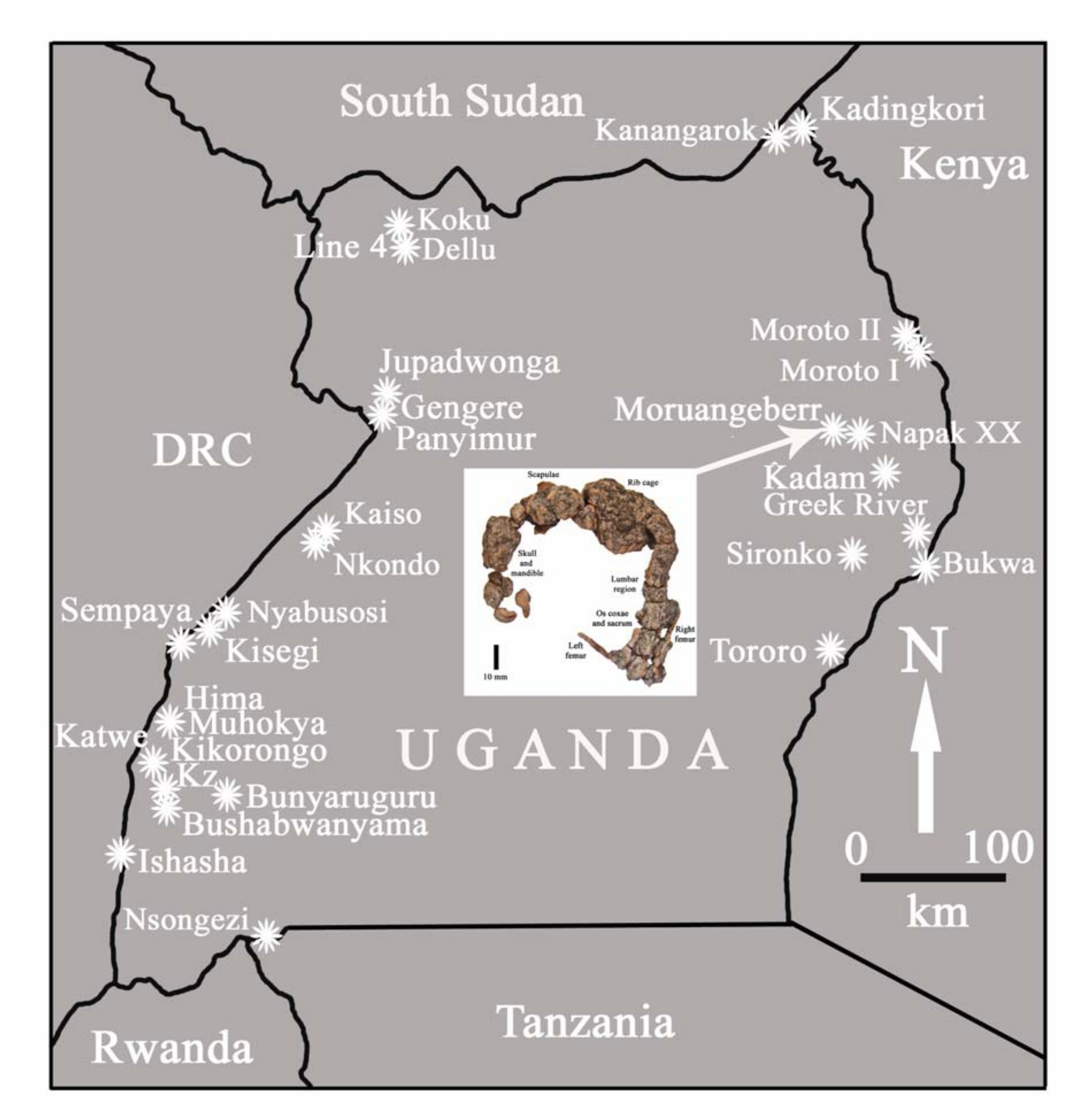

Uganda Museum, Kampala

Geo-Pal Uganda

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Uganda Museum, P.O. Box 5718, Kampala

Osteology of *Afrocricetodon songhori* Lavocat, 1973, from Napak, Early Miocene, Uganda: Keeping a low profile

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ABSTRACT

Afrocricetodon songhori, an extinct rodent, is common in the Early Miocene volcano-sedimentary deposits at Napak, Uganda. In 2011, a partial skeleton with skull and mandibles of the species was found at Napak V, which reveals that the rib cage is highly unusual in having antero-posteriorly expanded rib bodies which overlap each other, an expanded costal neck and head with an extremely complicated articular surface. The lateral surfaces of the thoracic vertebra have a correspondingly complex articular surface for the head of the rib, the neck and costal tubercle. The posterior ribs even make contact between the supra-tubercular apophysis and the transverse process of the vertebra. The external surface of the ribs and scapula are adorned with pustular bone. The scapular spine is markedly tilted anteriorly, and the scapular borders are thickened and reinforced. The spinous processes of the vertebrae are low and have a strongly developed dorsal ridge. The neurocranium is low and broad.

The aim of this paper is to put on record and describe the unusual morphology of the rib cage, thoracic vertebrae, and scapula of *Afrocricetodon songhori* and to hypothesise about the function of such a modified rib cage.

Key Words : Rodentia, Early Miocene, Africa, *Afrocricetodon*, skeleton, pustular ribs, predator avoidance

INTRODUCTION

Afrocricetodon songhori is a rodent common in Early Miocene deposits of East Africa (Songhor, Koru, Napak). Lavocat (1973) described the cranium, mandible and dentition, but he did not mention anything about the skeleton. A rib cage with 17 ribs preserved (8 on one side, 9 on the other) and several vertebrae was discovered at Napak V by W.W. Bishop, but at the time it was not associated with a skull, so its identification remained doubtful. The rib cage is peculiar in possessing antero-posteriorly expanded ribs with a pustular external bone surface, each rib overlapping the one behind it. In 2011, a second specimen was found at Napak V which is connected to the skull and mandible, confirming the identification as *Afrocricetodon songhori*. Examination of the old collections in the Uganda Museums reveals the presence of a skull and scapula in nodules similar to the 2011 specimen, and these could be parts of the same individual as the enigmatic rib cage found by W.W Bishop in 1962.

We describe the fossils, focussing on the peculiar morphology of the ribs and their corresponding vertebrae, and propose a functional analysis of the species in terms of predator avoidance or dissuasion.

MATERIALS AND METHODS

Specimen 1. Nap V, 129’11, associated skull and partial postcranial skeleton.
Specimen 2. Nap V, rib cage
Specimen 3. Nap V, left scapula.
Specimen 4. Nap V Aug’62, articulated mandibles and part of skull in a nodule of volcanic ash.
Specimen 5. Nap V, mandible in nodule.
Specimen 6. NHMUK M 32420 (Koru) right mandible in a limestone nodule associated with part of the vertebral column and two scapulae.
Specimen 7. NHMUK M 14310 (Koru) neurocranium.

Specimens 2, 3 and 4 could represent a single individual, as all are from Napak V, and occurred in tuffaceous nodules similar to the 2011 specimen.

Photographs of the fossils were taken prior to cleaning, and at various stages during preparation in order to record the positions of the bones relative to each other. Part of the sediment was removed by a combination of mechanical (micrograveur) and acid techniques (7 % formic acid) leaving enough matrix in place to preserve the skeleton in connection. Specimen N° 4 had already been cleaned prior to 1985, when the Uganda Palaeontology Expedition was launched, so there is no record of what it looked like before cleaning. It appears that a combination of mechanical and acid techniques was also used by whoever prepared that fossil.

In order to appreciate the articular relationship between ribs and vertebrae, plaster casts were made of the ribs and the lateral surfaces of the vertebrae, trimmed and then manipulated by hand into various articular positions. The resultant positions were then recorded by drawings.

The fossils were compared to specimens kept in the Uganda Museum (UM), the Natural History Museum, London (NHMUK) and the Muséum National d’Histoire Naturelle, Paris (MNHN).

We refer to Greene (1935) for the nomenclature of the rodent skeleton, and like this author we do not enter in long and detailed descriptions of each bone, but rely on the visual assessment of the specimens provided in the figures, many of which are in stereo. Some anatomical terms of the postcranial bones are from Sisson & Grossman (1953). Measurements are provided in mm.

GEOLOGICAL CONTEXT AND AGE

The articulated rodent skeletons described herein were found at Napak V, Uganda (Fig. 1). The deposits yield three species of tragulid (*Dorcatherium piggoti*, *Dorcatherium iririensis* and *Siamotragulus songhorensis*) which indicate that the deposits belong to the Napak Member, aged ca 20.5 – 20 Ma. The deposits are of volcano-sedimentary origin, more or less affected by pedogenesis. The volcanic ashes and palaeosols which accumulated on the flanks of Napak Volcano, supported a rich and diverse infauna and there is abundant evidence of plant roots (Musalizi *et al*., 2009). The articulated skeletons were fossilised within the palaeosols.

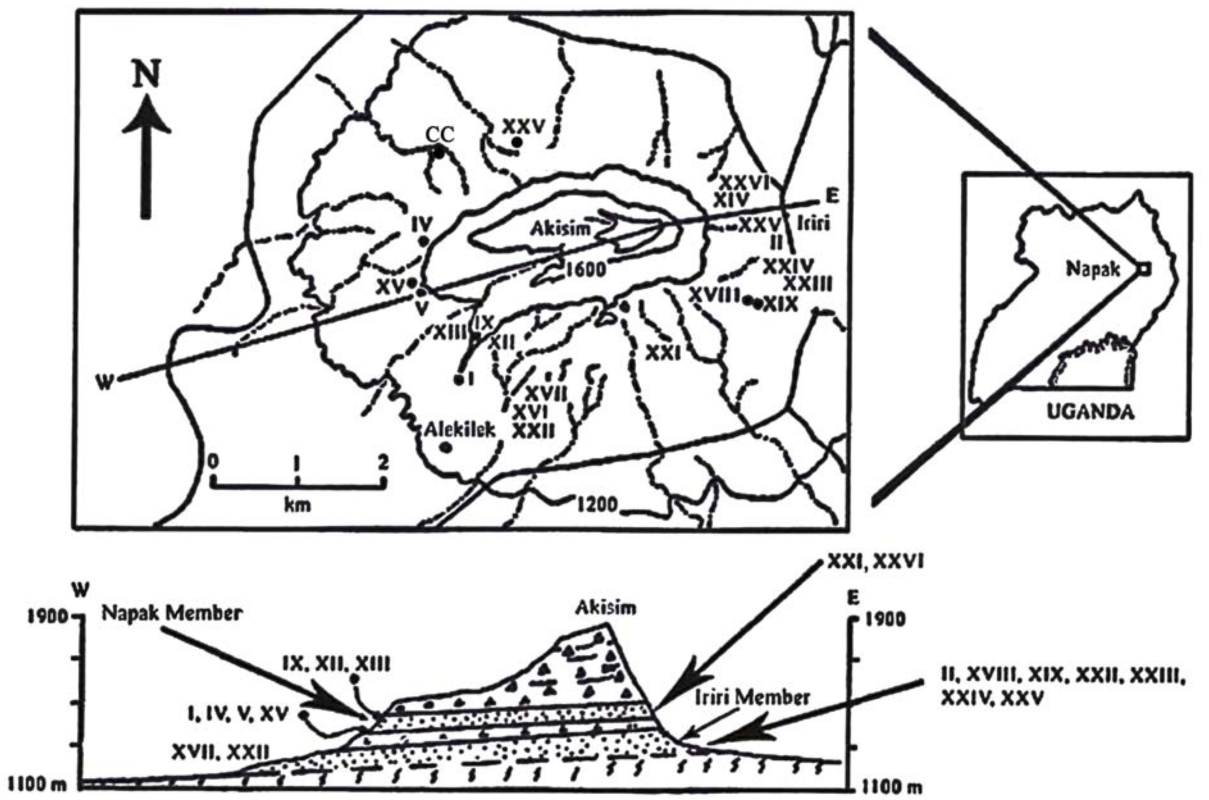

Figure 1. Location and regional stratigraphy of the Napak deposits. Napak V is in the Napak Member on the wetsern end of Akisim.

TAPHONOMY

When found, the specimen of *Afrocricetodon songhori* numbered Nap V 129’11, was curled up, lying on its left side, the head curled ventrally towards the rib cage. There has been some disturbance in the front part, and the autopodes are missing, probably having eroded away before the specimen was found. The lumbar region has rotated with respect to the thoracic region, so that the ventral side is downwards, the right femur aligned with the vertebral column, the left one poking out at a right angle towards the skull. This position suggests that the individual was curled up in a sleeping position when it died, and that putrefaction of the soft tissues and settling of the surrounding sediments has led to minor post-mortem displacement between the skeletal elements. The intact nature of the bulk of the skeleton indicates that the individual possibly died in a burrow or nest and was not greatly disturbed post-mortem by bioturbation or predation.

From a sedimentological point of view, it seems that the putrifying soft tissues of the individual caused differential induration of the immediately surrounding sediment (due to changes in pH, eH and moisture content of the surrounding sediment, for example) resulting in fossiliferous nodules which are more resistant to erosion than the surrounding tuffs. The sediment close to the bone is richer in calcite than the sediment further out. Thus, when the fossils weather out of the deposits they are enclosed in hard calcified tuffaceous nodules, unlike most of the fossils from Napak which weather out relatively devoid of matrix.

The fact that at least two partly articulated skeletons of *Afrocricetodon songhori* have been found at Napak V, suggests that the species lived in burrows in the soils on the flank of the volcano, and from time to time died inside their burrows and thereby avoided the attention of predators and scavengers. Alternatively the may have lived in nests constructed beneath fallen logs or branches.

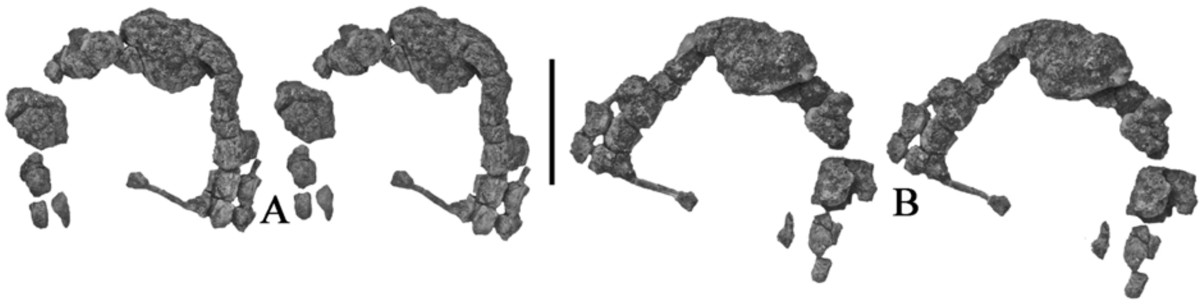

Figure 2. Nap V 129'11, articulated partial skeleton of *Afrocricetodon songhori*, from Napak V, prior to cleaning, A) stereo left lateral view of thorax and dorsal view of pelvic girdle, B) stereo right lateral view of thorax and ventral view of pelvic girdle. As found, the right side of the rib cage was up (scale : 10 cm).

SYSTEMATIC DESCRIPTION

Order Rodentia Bowdich, 1821

Family Cricetodontidae Schaub, 1925

Subfamily Afrocricetodontinae Lavocat, 1973

Genus *Afrocricetodon* Lavocat, 1973

Type species *Afrocricetodon songhori* Lavocat, 1973

Original diagnosis : Cricetodontids of large size, with the infra-orbital region of primitive aspect with large orifice. Anterior palatine orifices long, but not reaching the anterior margin of M1/ (as in *Protarsomys*). The overall characters of the teeth approach those of European Oligocene and Miocene forms. They are quite close morphologically to *Eucricetodon*, but of large dimensions. It differs from *E. collatus* by the more elongated proportions, by features of the upper and lower prelobe, and the weakness or absence of a clear mesoloph. There are also differences in the first lobe. The prelobe differentiates it from the teeth of *Protarsomys* which is much smaller (translated from Lavocat, 1973).

Emendation to diagnosis : Dorsal surface of scapula ornamented with small tubercles and low, sharp bony excrescences, borders of scapula and apex of scapular spine reinforced by a strong thickening. Scapular spine strongly tilted anteriorly. Ribs enlarged antero-posteriorly and elongated dorso-ventrally. Lateral surfaces of ribs ornamented with tubercles and low bony excrescences, each rib overlapping the anterior part of the succeeding rib, as in tiles on a roof. Articular surfaces of head, neck and tubercle of ribs enlarged with complex undulating surface topography, tubercle and supra-tubercular apophysis proximo-distally elongated with a deep slit between them; articular surface of the thoracic vertebrae complex with undulating topography, spinous processes of thoracic vertebrae low, posterior ribs with contact between the supra-tubercular apophysis and the transverse process of the vertebra.

Species *Afrocricetodon songhori* Lavocat, 1973

Diagnosis : Large species of the genus. Liaison of the prelobe to the first lobe of M1/ less progressive than in the species *Afrocricetodon korui*; posterior margin of the M2/ may be wide and at a right angle; internal cingulum often weakly developed (translated and modified from Lavocat, 1973).

Holotype : KNM SO 810, snout with upper molars.

Type locality and age : Songhor, Kenya, Early Miocene, 20-19 Ma.

<u>Description</u>

<u>Specimen 1</u>

The first specimen consists of large parts of an articulated skeleton associated with fragments of the skull and mandibles. The main nodule contains a left scapula, the vertebral column from the atlas to the sacrum, the ribs are preserved on both sides, and both os coxae are articulated to the sacrum. Both femora are articulated with their corresponding acetabula. The proximal half of the right tibia lies beneath the right femur. In sediment close to the skeleton some isolated bones (proximal humerus, two distal tibiae) were found which probably represent the same individual.

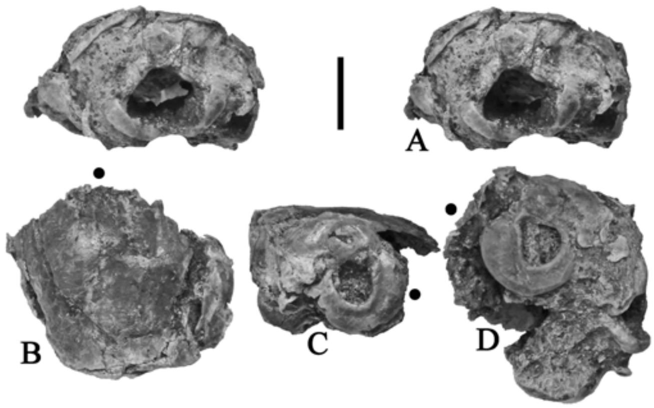

Figure 3. Nap V 129’11, neurocranium of *Afrocricetodon songhori* from Napak V, Uganda. A) stereo posterior view of foramen magnum and surrounding structures, B) dorsal view, C) right otic bulla, lateral view, D) left otic bulla, lateral view. Dots show the anterior side of the fossil (scale : 10 mm).

The skull is broken into four fragments. The neurocranium is slightly crushed and preserves both otic bullae and the foramen magnum but the specimen is in poor condition. In posterior view it is seen to be low and broad. The palate is broken into several pieces (now re-assembled) and shows some of the cheek teeth in a moderately worn state and the two mandibles are in the same nodule, all identifiable as *Afrocricetodon songhori*. The two upper incisors are present in a separate fragment; they are slender and measure about 1.3 mm mesio-distal and about 1.6 mm labio-lingual. There is also an isolated deeply worn left M1/ (Fig. 4).

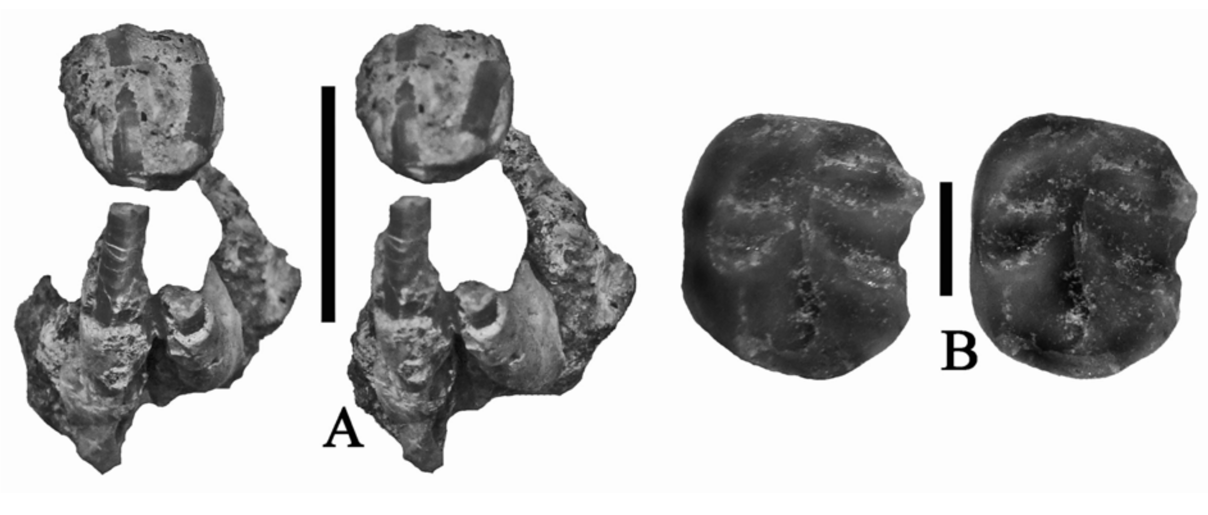

Figure 4. Nap V 129’11, *Afrocricetodon songhori* from Napak V, Uganda. A) stereo anterior view of upper and lower incisors (scale : 10 mm), B) left M1/ stereo occlusal view (scale : 1 mm).

The left mandible is damaged and has lost the cheek teeth, but the incisor which has lost its apex, measures 1.5 x 2.3 mm. The right mandible is preserved and contains the complete lower incisor.

The matrix around the anteriormost vertebra (atlas) slots into the foramen magnum with a snug fit, so it is likely that the vertebral column is complete from the axis to the sacrum. Indeed a small portion of the atlas is still stuck inside the foramen magnum on the left side. No caudal vertebrae were found in the surrounding soil.

The main part of the rib cage posterior to the scapula is almost 6 cm long, the lumbar part of the vertebral column about 4.5 cm, and the sacrum about 3 cm long. The right femur is 4.2 cm long (measured from the apex of the greater trochanter to the distal condyles). A proximal humerus is preserved.

In the post-scapular part of the rib cage there are nine ribs (or parts of ribs) on the each side. Under the the scapulae there are two pairs of shorter ribs which also show antero-posteriorly expanded bodies with pustular external surfaces and thickened leading edges. The heads, necks and tubercles of these anterior vertebrae are missing due to erosional damage prior to collecting. Unless some ribs are missing, then there were 11 pairs of ribs in *Afrocricetodon*, in contrast to the rat which has 13 pairs of ribs (Greene, 1935).

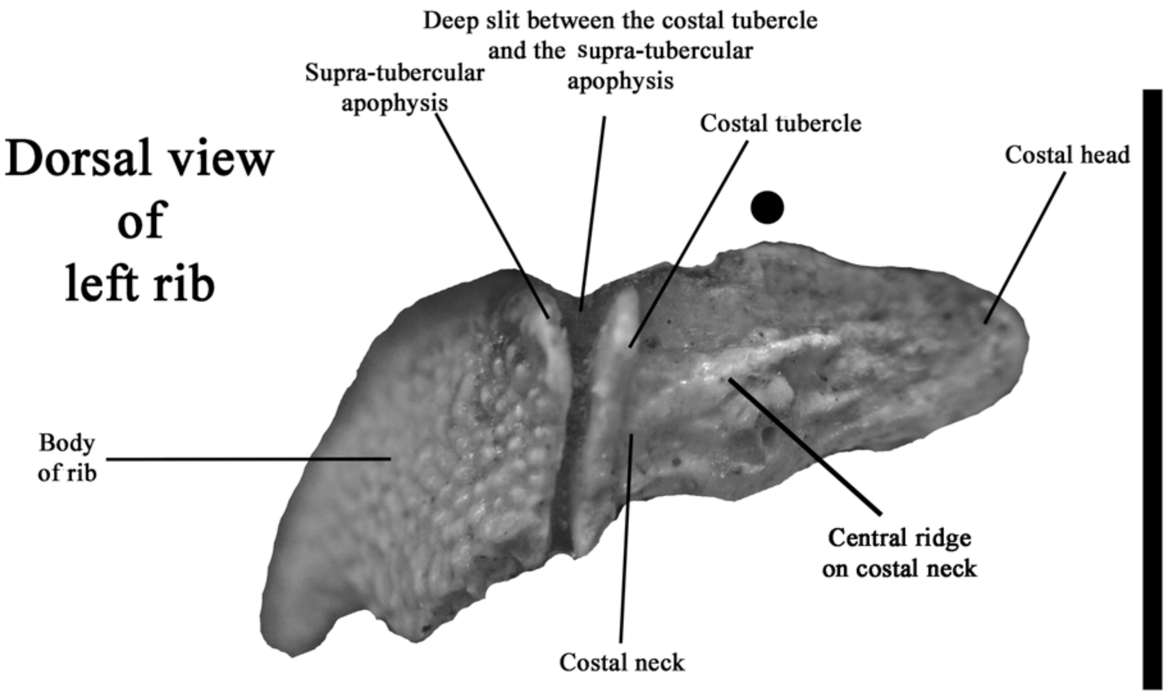

Figure 5. Nomenclature of a mid-series rib of *Afrocricetodon songhori* (part of specimen 2). The black dot shows the cranial side of the left rib. Note the tubercular outer surface of the rib (scale : 10 mm).

In specimen 1, the ribs are best preserved on the right side which was upwards in the sediment. In lateral view, the ribs show broad proximal parts, sub-parallel bodies narrowing in the ventral quarter, and terminating ventrally in a point in the first four ribs preserved (the others are damaged at their ventral extremities). The pointed ventral termination of the body of the rib corresponds to the costo-chondral junction. The even spacing between the ventral ends of the ribs in this specimen indicate that the sternal complex probably held the ribs in position until they were completely buried and could no longer shift relative to one another.

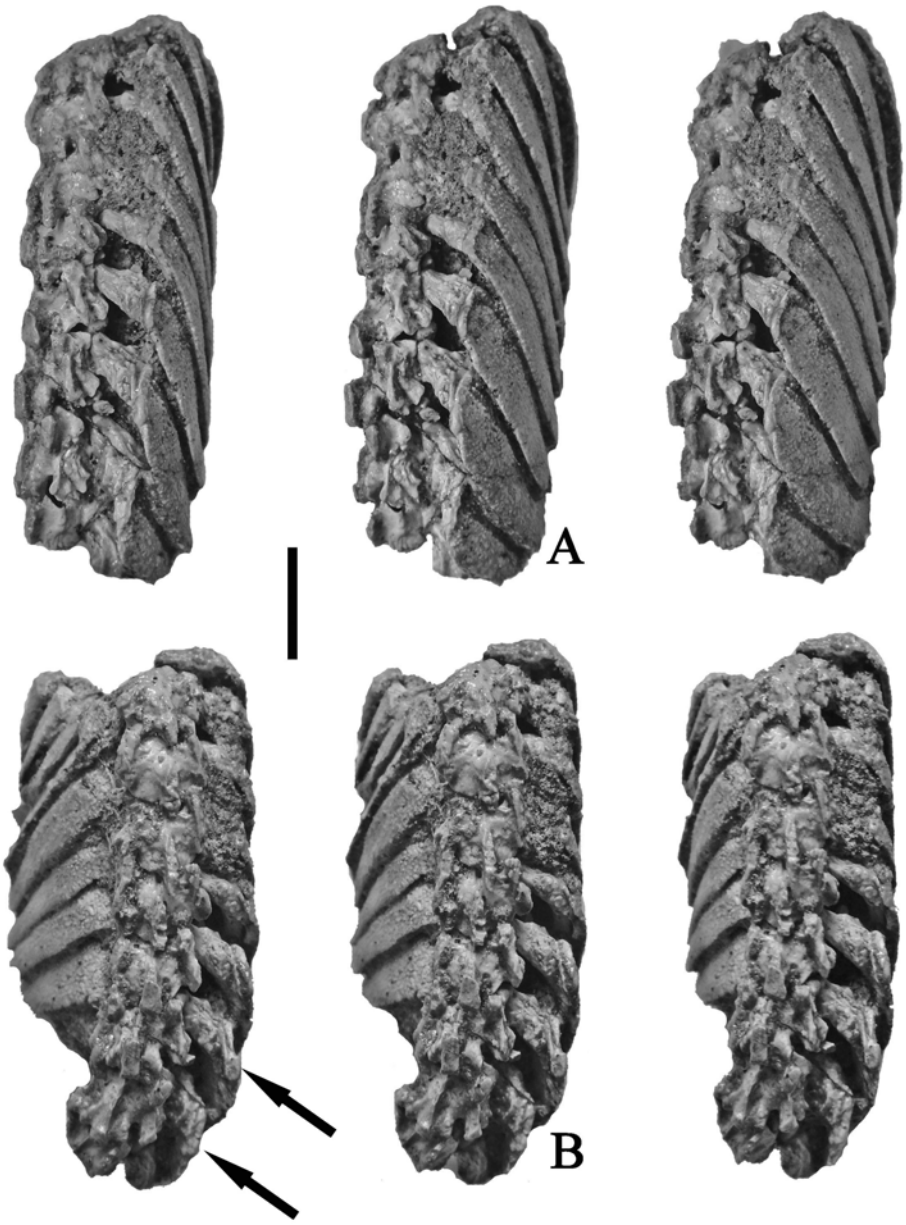

Figure 6. Stereo triplets of the rib cage of *Afrocricetodon songhori* Nap V 129'11. A) slightly oblique right lateral view of the vertebral column, to show the rib head morphology to maximum advantage, B) dorsal view of vertebral column. Arrows in (B) show contact facets on the supra-tubercular apophysis of the body of the last two ribs which articulate with the transverse processes of the corresponding vertebrae (scale : 10 mm).

The first rib exposed on the right side of the post-scapular complex differs from the others behind it by possessing a narrower supra-tubercular apophysis with a deep depression in it, beneath which is the blade-like body. In all the other ribs, the supra-tubercular apophysis is tall and elongated anterio-posteriorly into a ridge. The leading edge of each rib body is thickened, the trailing edge thin overlapping the thick part of the rib behind it.

Another extraordinary aspect of these ribs is that in the posterior ones there is contact between the supra-tubercular apophysis of the body with the transverse process of the vertebra. This indicates the existence of hyper-extension of the rib-vertebra articulation, with "locking" of the rib cage in an "open" position (Fig. 23), a highly unusual morphology in mammals.

In lateral views the ribs are inclined quite strongly towards the rear (Fig. 7).

Figure 7. Nap V 129’11, *Afrocricetodon songhori* stereo triplet of the right side of the rib cage. The anterior side is to the right of the image. Note the pointed ventral termination of the ribs, forming the costo-chondral junction (damaged in the five posterior ribs).

Lumbar region and pelvic girdle

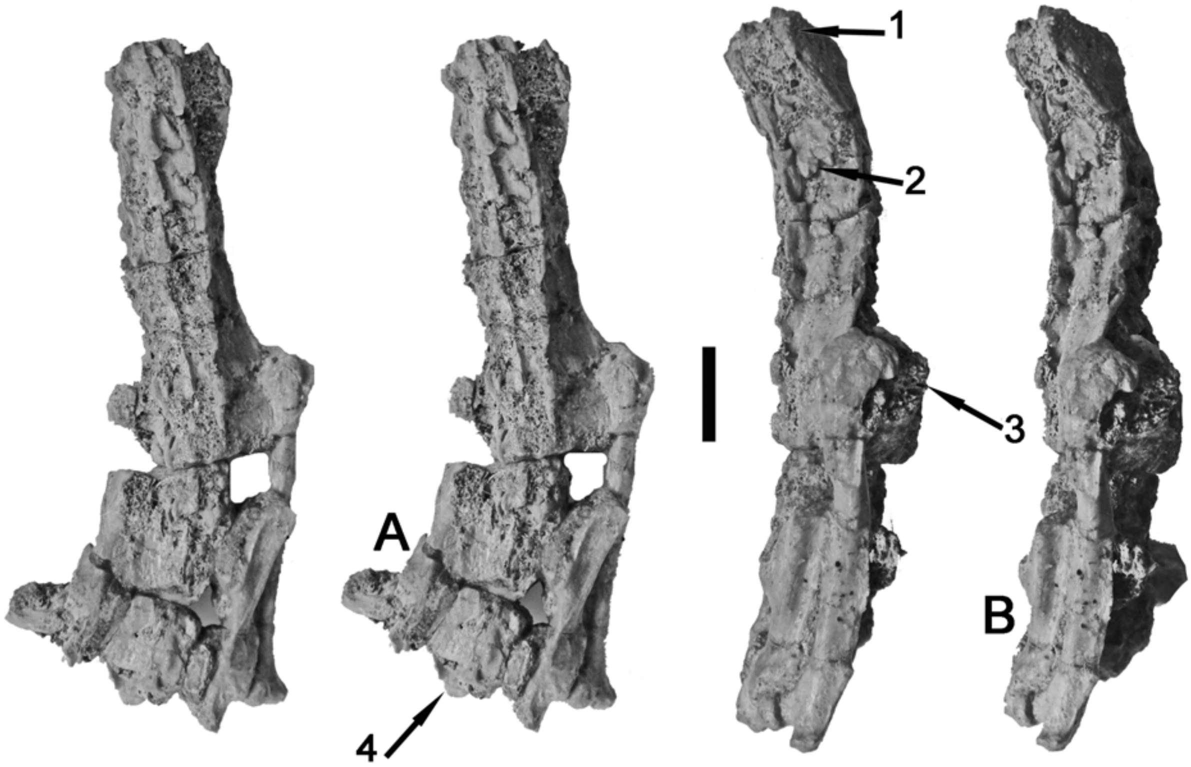

Figure 8. Lumbar region and pelvic girdle of *Afrocricetodon songhori* from Napak V, Uganda. A) stereo dorsal view, B) stereo right lateral view. 1) last rib on the right side, 2) complex vertebral apophysis, 3) proximal end of tibia beneath the femur, 4) caudal vertebra lodged inside the sacrum (scale : 10 mm).

Scapula

The left scapula is damaged but enough is preserved to show the thickened margin of the blade, the strongly anterior leaning scapular spine, and the pustular external bone surface.

Table 1. Measurements of the postcranial bones of Nap V 129'11, *Afrocricetodon songhori* from Napak, Uganda (dap - anteroposterior diameter; ddv – dorso-ventral diameter; dml – medio-lateral diameter).

Bone / Measurement taken	**Measurement (mm)**
Rib	
Dorso-ventral length of body of longest rib	32.3
Right humerus	
Head dap	6.2
Head dml	5.8
Left Femur	
Total length	41
Distal epiphysis dml	6.9
Distal epiphysis dap	6.2
Gap between condyles, posterior side	1.5
Breadth of patellar groove	2.3
Right femur	
Total length	42
Head dap	3.9
Head dml	2.7
Distal epiphysis dml	7
Distal right tibia	
Distal epiphysis dml	6.1
Distal epiphysis dap	5.4

Humerus

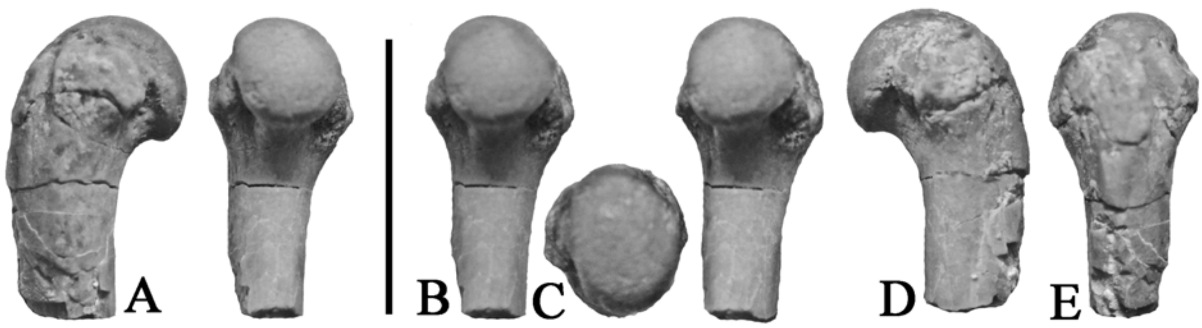

Figure 9. Nap V 129'11, proximal right humerus of *Afrocricetodon songhori* from Napak V, Uganda. A) medial, B) stereo triplet of the posterior side, C) proximal view, D) lateral, and E) anterior views (scale : 10 mm).

The proximal humerus of *Afrocricetodon songhori* has relatively small medial and lateral tuberosities, and a short, shallow intertuberal groove. The proximal epiphysis is incompletely fused to the diaphysis.

Femur

Figure 10. Nap V 129’11, right femur of *Afrocricetodon songhori* from Napak V, Uganda, in situ in the acetabulum of the os coxa, A) slightly oblique lateral view, B) cranial view (scale : 10 mm). The os coxa and sacrum have been darkened in order to highlight the femur.

The femur of *Afrocricetodon songhori* is long and slender. The head is hemispherical, posed on a short neck. The apex of the greater trochanter barely surpasses the top of the head. The third trochanter is elongated and extends to about the middle of the shaft. The patellar groove is narrow and shallow.

Tibia

The proximal end of the right tibia and about half the diaphysis is folded beneath the lumbar vertebrae, almost in articulation with the distal end of the right femur.

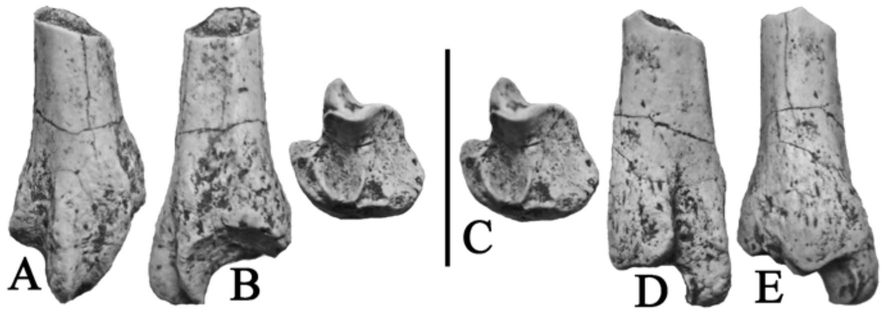

Figure 11. Nap V 129'11, distal right tibia of *Afrocricetodon songhori* from Napak V, Uganda, A) posterior, B) lateral (fibular) view, C) stereo distal view, D) medial view, E anterior view (scale : 10 mm).

The distal tibia is remarkable for the great depth and extent of the groove on the medial maleolus for the tendon of the flexor digitalis longus (Fig. 11 D) and for the strength of the anterior beak. The distal fibula is not fused to the tibia.

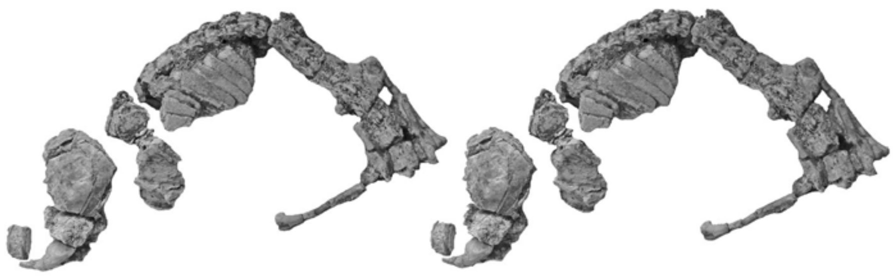

Figure 12. Stereo view of the ensemble of the skeleton of *Afrocricetodon songhori* from Napak V, after cleaning, left side.

<u>Specimen 2</u>
Scapula from Napak V
The dorsal surface of the scapula is ornamented with pustules and short low ridges of bone oriented proximo-distally, but the anterior, distal and posterior margins of the bone are smooth, as is the crest of the scapular spine. The scapular spine is inclined steeply towards the anterior side, overhanging the anterior part of the blade. The anterior margin of the scapula forms a ridge that borders the depression between the spine and the anterior margin. The ventral aspect of the scapula shows the development of a pustular bone surface, but not as exaggerated as on its dorsal surface or on the outer surfaces of the ribs.

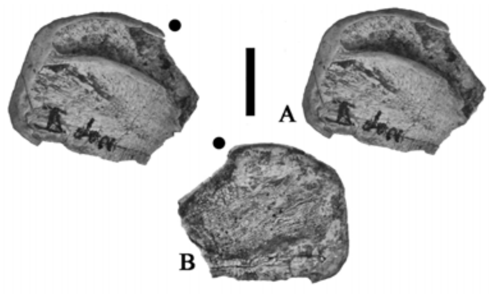

Figure 13. Nap V, left scapula of *Afrocricetodon songhori* from Napak V, Uganda. A) stereo lateral view, B) medial view (scale : 10 mm). Dots show the anterior border. Note the strong overhang of the scapular spine towards the anterior border of the blade.

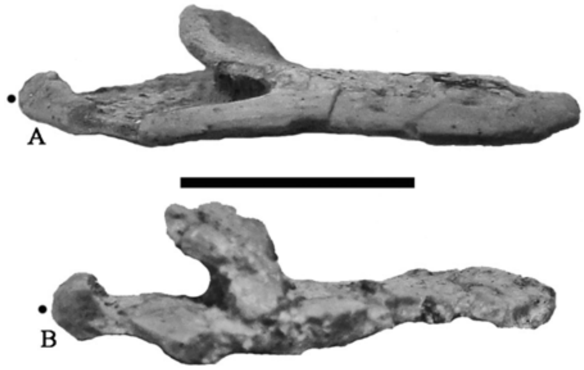

Figure 14. View of the vertebral margin of left scapulae of *Afrocricetodon* showing the thickened margins and the anteriorly leaning spine. A) Nap V; B) Nap V 129'11 (damaged vertebral margin and spine). Black dots show the anterior margin (scale : 10 mm).

Specimen 3

The rib cage from Napak V is crushed and some ribs are displaced, which complicates its interpretation. It preserves 9 ribs on the right side, and eight on the left.

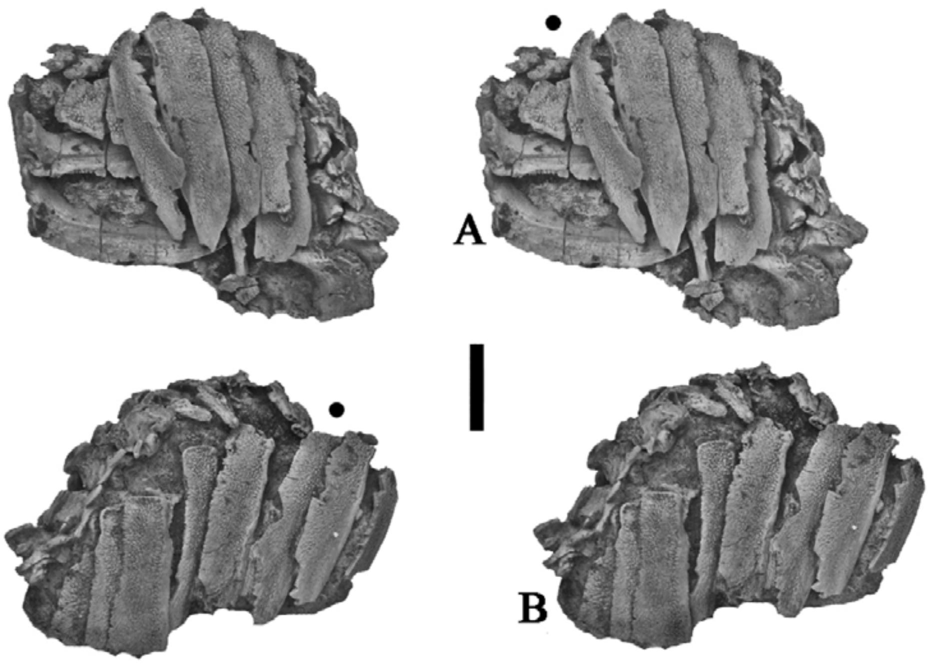

Figure 15. Rib cage of *Afrocricetodon songhori* from Napak V, Uganda, stereo views of A) left side, B) right side (scale : 10 mm). Dots show the anterior end of the vertebral column.

The bodies of the ribs of *Afrocricetodon* are cranio-caudally expanded, they overlap each other (the distal part of the rib overlies the proximal part of the rib behind it) they are dorso-ventrally elongated, their outer surfaces are ornamented with pustular bone, the cranial margins of the body of the ribs are smooth, and the head, neck and tubercle which articulate with the vertebrae are elongated, enlarged and angled slightly proximally. The cranial and caudal edges of each rib body are sub-parallel dorsally, narrowing to a point in the ventral quarter. Internally the surface of the ribs is smooth and is comprised of a thick anterior part and a thin posterior part which corresponds to the section that overlaps the outer surface of the next rib behind. There is a deep, narrow slit between the dorsal edge of each rib (ie the supra-tubercular apophysis) and the costal tubercle of its articular apophysis (Fig. 5).

The head and neck of the rib are expanded antero-posteriorly and have an irregularly rugose dorsal surface with a main central ridge running medio-laterally towards the costal tubercle but fading out before reaching it. The costal tubercle is mesio-distally elongated forming a long rounded ridge, separated from the mesio-distally elongated supra-tubercular apophysis by a narrrow, but deep, slit. The body of the rib descends ventrally from the supra-tubercular apophysis, the axis of the head of the rib and that of the body forming a right angle. The head points medially and slightly cranially (Fig. 5).

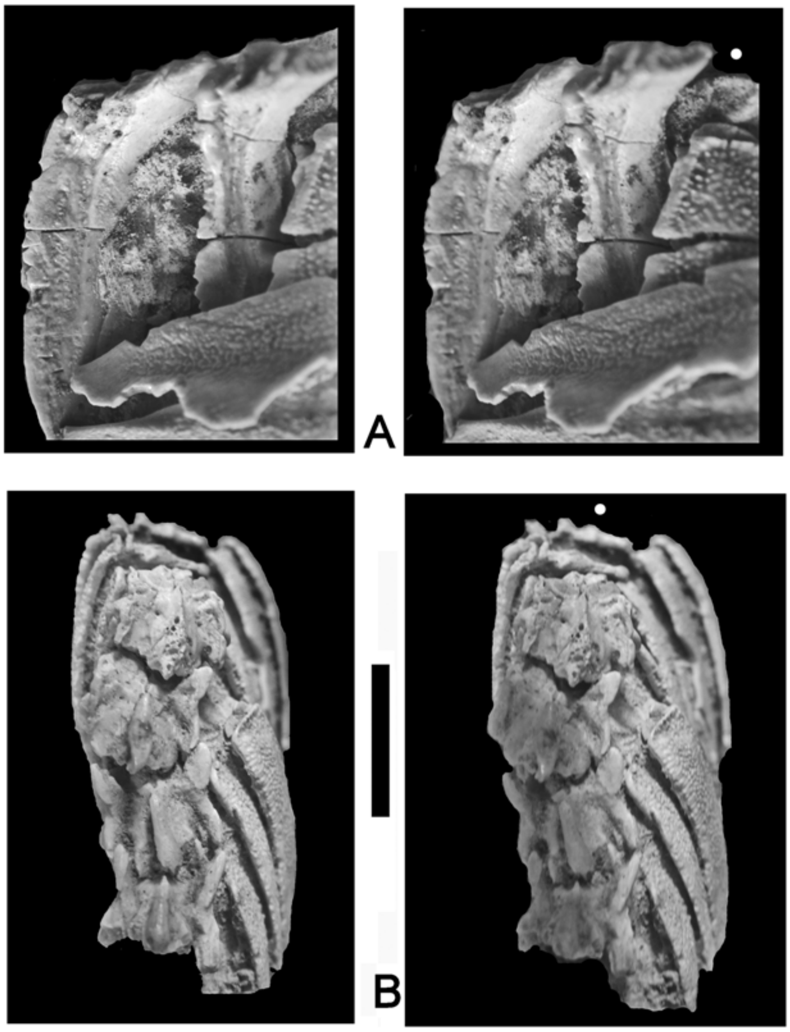

Figure 16. Rib cage of *Afrocricetodon songhori* from Napak V, Uganda. A) internal view of left ribs showing prominent posterior gutter, the costal groove, B) dorsal view of rib cage showing four thoracic vertebrae and the right ribs; the posterior part of each rib overlapping the anterior part of the rib behind it (scale : 10 mm). White dots show the anterior side of the rib cage.

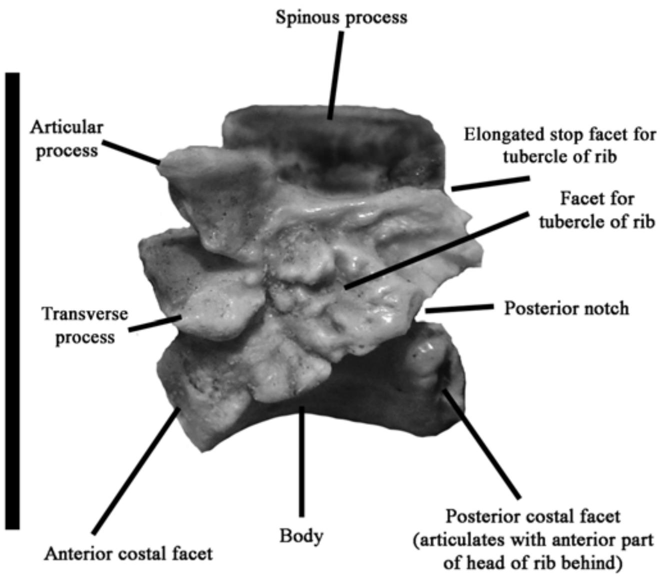

Figure 17. Nomenclature of a mid-series thoracic vertebra of *Afrocricetodon songhori* from Napak V, Uganda. The facet for the tubercle and neck of the rib is enlarged and comprises an undulating surface with its long axis running from antero-ventral to postero-dorsal. The spinous process and body have been darkened in order to highlight the articular facet for the tubercle and head of the rib (scale : 10 mm).

In the vertebral column, a complex articular surface extends over the entire lateral side of the each thoracic vertebra, angled from cranio-ventral to caudo-dorsal, the articulation for each rib arranged en echelon with respect to its neighbour. The articular surface is complex, with a sunken central zone characterised by an undulating surface topography which corresponds to the central ridge on the neck of the corresponding rib. The surface of this zone is traversed by low ridges of bone imparting a vermiform aspect to the articular surface above which the zygapophyses form strongly developed crests that overhang the articular surface. On the ribs, the cranial edge of the articular apophysis shows a raised central part bordered medially and laterally by lower areas. This means that the head of each rib articulates with two vertebrae as in mammals in general. The extent of the articular surfaces indicates that the degree of movement possible between the ribs and the vertebrae was greater than is usual in mammals, surpassing the amount of movement related to breathing. The bodies of the ribs overlap like tiles in a roof, but unlike tiles in a roof, each rib could move relative to its neighbours, and the zone of attachment of the rib cage was not fixed immovably to the vertebral column, but was flexible, such that the ensemble of ribs on each side could act in unison. The rib cage could thus expand and contract medio-laterally as well as cranio-caudally as the amount of overlap from rib to rib was increased or decreased, or as the vertebral column was flexed or extended.

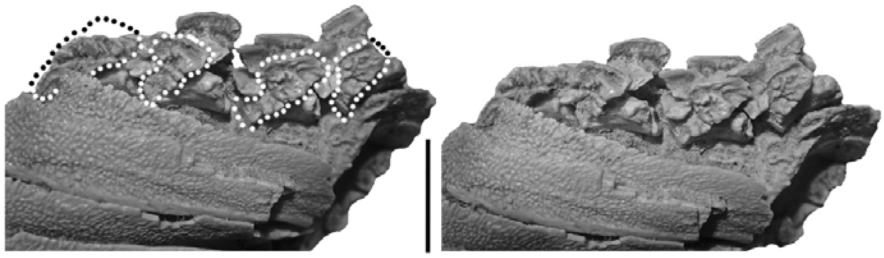

Figure 18. Stereo left lateral view of four thoracic vertebrae of *Afrocricetodon songhori* from Napak V, Uganda. Note the en echelon arrangement of the articular surfaces for the head, neck and tubercle of the ribs (outlined by dots) which angle from proximo-ventral to disto-dorsal (scale : 10 mm). The anterior side is to the left of the image.

Specimen 4

Labelled Nap V AUG'62 in the hand writing of S. Bishop, this specimen consists of the left and right mandibles slightly misaligned along the symphysis, and part of the palate in poor condition, all in a nodule of volcanic ash. R. Lavocat exposed the anterior tooth of the right mandible and the two incisors are visible in ventral view. The cheek tooth is typical of *Afrocricetodon* but Lavocat (1973) did not identify the species. It has three conical buccal cusps and two lingual ones. It is 3 mm in mesio-distal length; the breadth cannot be ascertained without further cleaning. The incisors are slender and measure 1.7 mm mesio-distal by 1.9 labio-lingual. Each of the mandibles shows a strong, sharp, almost straight masseteric ridge which terminates anteriorly beneath the mesial cheek tooth.

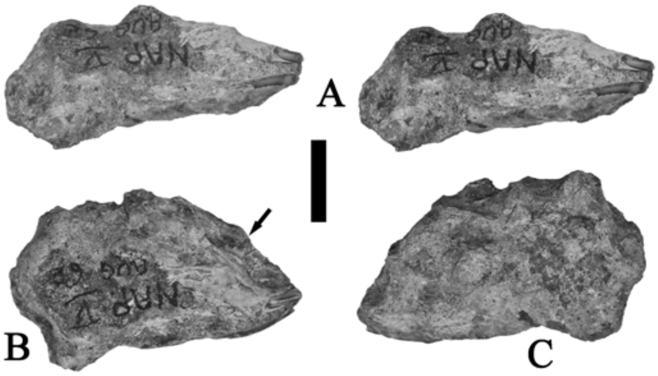

Figure 19. Nap V Aug'62, *Afrocricetodon songhori* mandible from Napak V still encased in its nodule, studied by Lavocat (1973) who exposed the right m/1. The same locality yielded a rib cage in a similar nodule, possible representing the same individual. A) stereo ventral view, B) right lateral view (arrow points to the m/1), C) left lateral view (scale : 10 mm).

Specimen 5

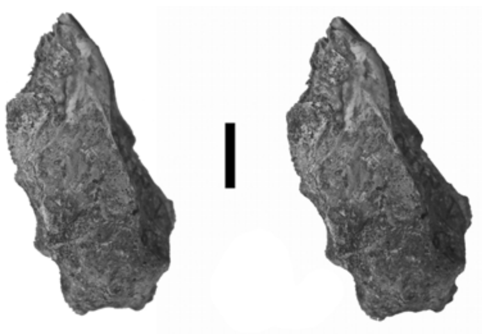

Figure 20. Nap V, Stereo image of a right mandible of *Afrocricetodon songhori* from Napak V, in its nodule prior to cleaning. Note the clear masseteric ridge (scale : 10 mm). Incisor is at the top of the image.

Species *Afrocricetodon korui* Lavocat, 1973

Diagnosis : Small species of the genus. Prelobe passing very progressively the first lobe. Lingual cingulum of upper molars well developed, diverticule of the lingual median valley between the protocone and longitudinal crest well marked (translated and modified from Lavocat, 1973).

Holotype : KNM KO 28, partial skull.

Type locality and age : Koru, Kenya, Early Miocene, 20-19 Ma.

Description

Specimen 6 is a nodule of pink tuffaceous limestone from Koru, Kenya, containing a right mandible, both scapulae, and several nuchal and thoracic vertebrae. The first molar has been exposed using a needle (Lavocat, 1973) and there are tool marks on the left side of the nodule either side of the scapular spine (Fig. 21). The scapular spine leans strongly anteriorly, and parts of the reinforced margins of the scapula and the thickened apex of the scapular spine are clearly visible. The lower first molar measures 2.3 x 1.8 mm, which is smaller than the equivalent tooth in *Afrocricetodon songhori* (Lavocat, 1973).

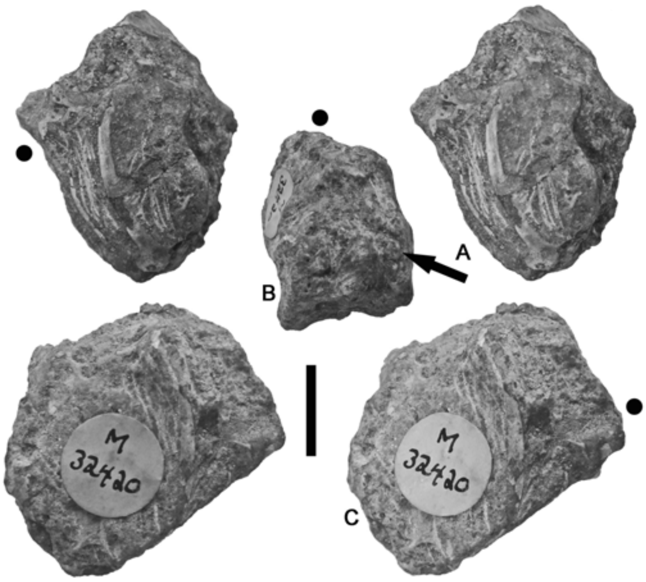

Figure 21. *Afrocricetodon korui* from Koru, Kenya, NHMUK M 32420, nodule containing right mandible, both scapulae and part of vertebral column A) left lateral stereo view, B) superior view showing teeth in mandible (arrow), C) right lateral stereo view. Black dots show anterior part of nodule (scale : 10 mm).

Specimen 7 (NHMUK M 14310) is a neurocranium of *Afrocricetodon korui* (Fig. 22). It is broader than tall, as in *Afrocricetodon songhori*, but it is appreciably smaller.

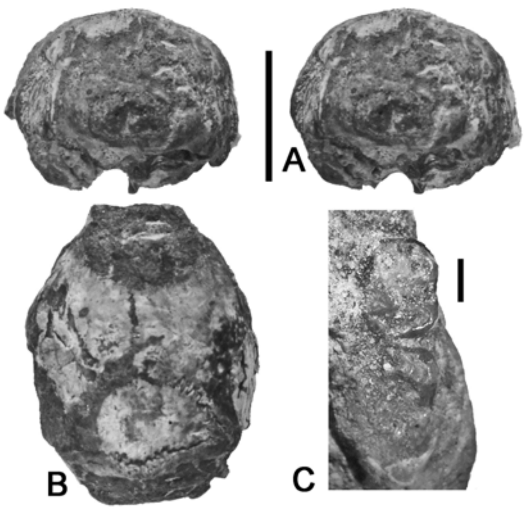

Figure 22. *Afrocricetodon korui* from Koru, Kenya, A-B) NHMUK M 14310, neurocranium, A) stereo posterior view, B) dorsal view (scale : 10 mm); C) NHMUK M 32420, right mandible, occlusal view of m/1 and part of m/2 (scale : 1 mm).

Table 2. Measurements (in mm) of *Afrocricetodon korui* from Koru, Kenya, and *Afrocricetodon songhori* from Napak, Uganda.

Measurement	***A. korui***	***A. songhori***
Breadth of neurocranium	17.2	28.0
Height of neurocranium	13.0	18.0
Height of scapula (glenoid to vertebral margin)	23.3	ca 30

The size difference between the specimens from Koru on the one hand, and Napak and Songhor, on the other, indicate that the two samples belong to distinct taxa. Lavocat (1973) separated them at the subspecies rank, but they are more probably full species, the view adopted here.

DISCUSSION

The rodents *Afrocricetodon songhori* and *Afrocricetodon korui* are common at several Early Miocene localities in Kenya and Uganda (Songhor, Koru, Napak). Well represented by cranio-dental remains, their postcranial skeletons have not been described, although it has long been suggested that ribs with pustular bone on the lateral surface probably represent this genus. In 2011, an articulated skeleton of *Afrocricetodon songhori* was excavated at Napak V which preserves the cranium, the axial skeleton from atlas to sacrum, the thoracic and pelvic girdles, and parts of the limbs (proximal humerus, both femora, two distal tibia). The rib cage comprises eleven pairs of ribs, nine in the post-scapular part, and two in the scapular part. Each rib is mesio-distally enlarged and overlaps the rib behind. The lateral surface of each rib is patterned with pustular bone. The head and neck of the ribs are highly modified as is the lateral surface of the corresponding vertebrae with which the ribs articulate. The scapula shows a patterned lateral bone surface and the vertebral, anterior and posterior margins are thickened.

The old collections from Napak V made by W.W. Bishop in 1962, contain a rib cage of the species (specimen 2) but because it was not directly associated with a skull or teeth, its identification remained uncertain. Examination of the fossils from this site housed in the Uganda Museum reveal that a skull, mandibles and scapula were collected at the same time, and could well belong to the same individual (specimens 3 and 4).

Taphonomic aspects of the fossils suggests that *Afrocricetodon songhori* may have lived in burrows in the soils and loose ash that accumulated on the flanks of Napak Volcano, or perhaps in nests constructed beneath fallen logs or branches. The fact that the species shows no obvious modifications of the postcanial skeleton for dedicated fossorial life, indicates that during its periods of activity it would emerge to the surface, returning to the burrow to rest, sleep, raising young or when in danger from predators. Today there are many small mammals such as Macroscelididae, which excavate shallow burrows in soft, dry soil, but which show few if any obvious skeletal modifications for a subterranean life. There are many animals that live beneath fallen logs, either permanently or occasionally, and many seek shelter beneath logs when disturbed or to build nests.

The hemispherical femoral head, the relatively short greater trochanter not surpassing the head and the anteriorly leaning scapular spine indicate that *Afrocricetodon songhori* was probably well adapted to climbing activity.

The function of the extraordinary rib cage and scapulae of *Afrocricetodon songhori* is enigmatic and demands explanation. Taking into account not only the strange rib cage, but also the peculiar scapula with its anteriorly leaning scapular spine, the low but broad neurocranium, and the low but reinforced spinous processes of the thoracric vertebrae, suggests that *Afrocricetodon songhori* was maintaining as low a profile as possible. This in turn suggests that it may have habitually entered low crevices or spaces such as cracks and fissures in trees, the spaces between tree trunks and bark that occur in fallen trees, or the gaps beneath logs lying on the forest floor. Many lizards (agamas in particular) employ such spaces in order to escape predators and to rest and reproduce (Spawls *et al.*, 2002).

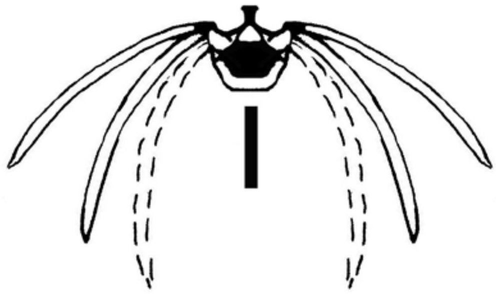

Figure 23. Anterior view of a section through the middle part of the rib cage of *Afrocricetodon,* with the ribs articulated in three positions. Dotted ribs represent a flexed "closed" position, the solid lines represent the ribs in partly extended and fully extended positions. The height of the rib cage in the fully extended "flattened" mode (including the spinous process of the vertebra) is only 2 cm, while in the normal mode it is slightly over 3 cm. Note the low spinous process of the thoracic vertebra (scale : 10 mm).

When the ribs of *Afrocricetodon* are in maximum extended position (Fig. 23) as shown when casts of ribs are articulated with the vertebrae, the body profile is extremely low, only about two centimetres tall, but in this position the body would be almost six centimetres broad. Thus, when the rib cage is in "flattened" mode, the individual could crawl into spaces as low as two centimetres and as broad as six centimetres.

This morphology alone does not explain why the rib bodies are expanded and covered in pustular bone. The presence of these morphological modifications suggest that the rib cage is strengthened for resisting breakage. It is possible that *Afrocricetodon* could wedge itself into low cracks and then inflate the rib cage in order to lock itself into the crevice so that it could not be pulled out easily. Some reptiles such as the flat pancake tortoise (*Malacochersus*) and agama lizards (*Agama*) behave like this in order to avoid predation (Spawls *et al*., 2002).

There are other possible explanations for the evolution of the strange rib cage of *Afrocricetodon,* but in our view they are less likely than the one described above, because they do not account for the peculiar scapular morphology, nor the relatively low and broad neurocranium which is about 1.8 cm tall by about 2.8 cm broad (exact measurements are not possible due to minor crushing and displacement of bone that has occurred to the brain case).

A reinforced rib cage could represent an adaptation which strengthens the anterior half of the body against crushing or constriction. Not only are the ribs of *Afrocricetodon* enlarged antero-posteriorly, but they also overlap each other and are patterned with pustular bone. Each rib has an elongated articulation with the vertebra, the articular surface being rugose and angled from antero-ventral to postero-dorsal. The articular surface is rugose which makes it difficult to dislocate. In the hyper-extended position, the rib cage is substantially more voluminous than is usually the case in mammals. The combined effect of these skeletal modifications is to make the rib cage more resistant to crushing than the rib cages of most rodents. It should be kept in mind that the rib cage is a dynamic structure, each rib being able to move relative to the others during breathing, arching the back, twisting the body left and right and so on. Add to this the strengthened scapulae with their pustular bone surface and reinforced margins, and one could be in the presence of a rodent with increased resistance to predation by crushing or constriction than rodents without these skeletal modifications. In the "open" position (Fig. 23) the rib cage would frustrate predators which ingest prey that correspond more or less to the dimensions of the skull. In other words, for some predators, such as small snakes, the prey would be too large to swallow. It is not beyond the realms of possibility that the rib cage would open to maximum volume as the prey is being swallowed, thereby stretching the throat of the predator and putting it in danger of rupturing or suffocating.

It is possible that *Afrocricetodon songhori* used its peculiar rib cage and anteriorly offset scapulae in an active way to avoid predation rather than just as a solid, resistant structure too large to ingest. By this we mean that if enveloped by a constrictor, the individual could move its scapulae and ribs actively to deter the predator, much as many beetles escape predation by moving their sharp legs in and out when captured, an effective method of avoiding predation or dissuading predators. Predators that experience this escape mechanism are less likely to try capturing the same prey species in the future.

Whilst the skeletal modifications of *Afrocricetodon* could be related to avoidance of predation by predators that crush or constrict their prey, there are other possible functional explanations. It is unlikely that the enlargement of the ribs and scapula of this species is related to aquatic life, not only because there are no indications of aquatic deposits at Napak, Songhor and Koru, where this rodent is common but also because its skeleton shows no modifications for aquatic or amphibious life. *Afrocricetodon* is most frequently associated with palaeosols. Being a small mammal capable of climbing activity and probably of burrowing in soft soil or hiding beneath fallen logs, it is conceivable that from time to time the burrows would collapse, and possession of a rib cage resistant to crushing could represent an adaptational advantage.

Some ant-eating mammals such as the South American mymecophage, *Cyclopes*, which, like *Afrocricetodon*, is about the size of a squirrel, have expanded and strengthened rib cages with overlapping ribs (Grassé, 1955). The animal is predominantly arboreal.

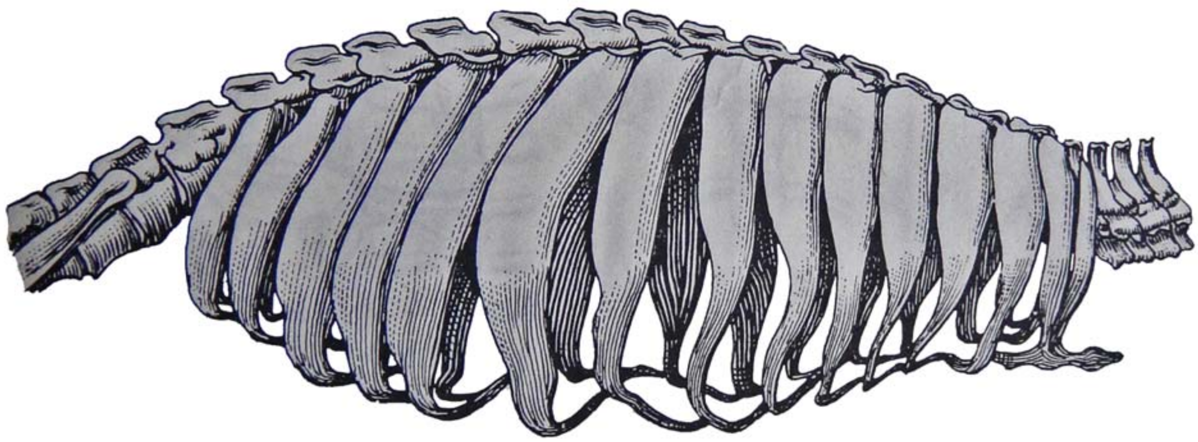

Figure 24. Rib cage of the Silky Anteater of South America (*Cyclopes*) with antero-posteriorly expanded ribs which overlap one another (modified from Grassé, 1955). The similarities in the rib morphologies of *Afrocricetodon* and *Cyclopes* represent convergence. The lumbar region in *Cyclopes* is very short (two vertebrae intervene between the os coxa and the last rib), whereas that of *Afrocricetodon* is long (five vertebrae between the os coxa and the last rib).

Pustular bone surfaces occur in some other small mammals, including the extant cricetid rodent *Lophiomys*, which sports such bone on its cranial roof (Aguilar & Thaler, 1987; Aguilar & Michaux, 1990). The function of such bone is unknown, although it is usually associated with thickening of the bones which make them more resistant to breakage and crushing. *Lophiomys* secretes a toxic substance in a flank gland which is reputed to kill dogs which bite it (Haltenorth & Diller, 1984). There is no evidence that *Afrocricetodon* did likewise, but predator dissuasion often relies on two or more strategies. In the case of *Lophiomys*, a combination of strengthened skull roof, behaviour (double hiss sound, growls, raised dorsal mane, longitudinal flank band – black, white and brown warning coloration - exposed towards the predator, and bites) and a flank gland secreting a toxic substance, comprise an effective predator dissuasion package for a species of slow-moving rodent.

In conclusion, *Afrocricetodon songhori* is an Early Miocene African rodent with a highly modified post-cranial skeleton. Several behavioural scenarios are proposed to explain the function of such a peculiar skeleton, of which the most likely is an adaptation for crawling into low crevices or gaps beneath fallen logs in order to avoid predation.

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