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New fossils of Giraffoidea (Mammalia: Artiodactyla) from the Lothidok Formation (Kalodirr Member, Early Miocene, West Turkana, Kenya) contribute to our understanding of early giraffoid diversity

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Abstract

Excavations at Kalodirr and Moruorot from the Lothidok Formation (ca. 17 mya) in the West Turkana Region of Kenya have yielded several cranial appendages, dentitions and postcranial fossils that can be attributed to either Climacoceratidae or the Giraffidae. An additional unusual and unique fossil, we describe in this paper for the first time, is, in our opinion, a novel stem-giraffoid cranial appendage. The *Climacoceras* from Kalodirr is the oldest representative of the genus, extending Climacoceratidae into the Early Miocene. We establish that by the end of the Early Miocene in Africa the Giraffoidea included at least two families, Climacoceratidae and Giraffidae, distinguished by different types of cranial appendages. Furthermore, the Giraffidae include at least two distinct lineages, represented by distinctive ossicones found at Kalodirr and Moruorot. Thus, we recognize that unlike at older sites where only *Canthumeryx* is recognized, by the later part of the early Miocene, Giraffoidea communities in East Africa include as many as three genera, and perhaps even four. This pattern of diversity in giraffoid communities persisted into the Middle Miocene and beyond.

Key words: Giraffoidea, Giraffidae, Climacoceratidae, Early Miocene, Kalodirr, Moruorot, East Africa, ruminant evolution.

1. Introduction

In Africa, *Canthumeryx sirtensis* from the Hiwegi Formation of Rusinga Island and from Loperot in West Turkana is the oldest known member of the Giraffoidea and the Giraffidae (contra Clauss & Rössner 2014 who accidently placed it in Pecora indet.), placing the Giraffoidea in Africa prior to 18 million years ago (Grossman et al. in press). *C. sirtensis* is found throughout much of East and North Africa during the Early and into the Middle Miocene (Harris et al. 2010). However, evidence in Africa of other Early Miocene giraffoid and giraffid taxa is extremely scarce. Nevertheless, recent discoveries at Kalodirr and Moruorot of the Lothidok Formation of West Turkana (Kenya) demonstrate that by the end of the Early Miocene *C*. sirtensis was not the sole giraffoid or giraffid taxon present in Africa (Harris et al. 2010;). The purpose of this paper is to describe a new possible cranial appendage from the Lothidok Formation (specifically Moruorot) and discuss additional new fossils (from Moruorot and Kalodirr), and discuss the implications of the diversity of giraffoids from the Lothidok formation on our understanding of giraffoid and giraffid evolution.

1.1 Location and age of the sites (Fig. 1)

Kalodirr is located at the headwater of the Kalodirr River (3°20’N, 35°45’E) between the Lokipenata Ridge and the Basalt Hills to the east. Not far from Kalodirr, the Moruorot localities are found on the flanks of Moruorot Hill (3°17’ N, 35°50’ E) (Leakey & Leakey 1986a, b; Boschetto et al. 1992). All the fossils from Kalodirr and Moruorot are found in sediments of the Early Miocene Lothidok Formation constrained using K/Ar dating to 17.5±0.2-16.8±0.2 Ma (Boschetto et al. 1992).

1.2 Habitat reconstructions

Sedimentological analyses indicate deposition via small meandering stream channels (Boschetto 1988; Grossman & Holroyd 2009) at Kalodirr and Moruorot. Environmental reconstructions for the Kalodirr and Moruorot localities using the mammalian faunal assemblage suggest seasonally wet, closed-habitat woodland rather than forest (Leakey et al. 2011). Further support for this interpretation is provided by several plant fossils from Kalodirr including broad lea-

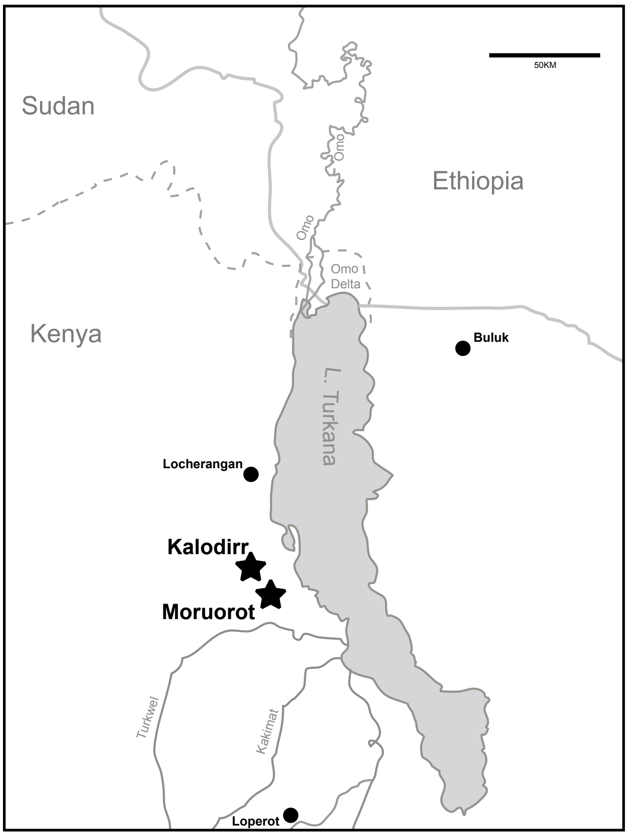

Figure 1: Location of Kalodirr and Morurot fossil sites, Lothidok Fm., West Turkana, Kenya.

ved forms, some possessing an acuminate tip („drip tip“) indicating seasonally wet conditions (Boschetto 1988). Several fish, a pelomedusid turtle, and crocodilian fossils from the sites indicate the presence of lacustrine or fluvial water.

2. Material and Methods

In this paper we provide a compilation of published giraffoid materials from the Lothidok Formation. All of the material was examined by at least one of us in person and identifications were confirmed. In addition, we describe a new cranial appendage from Moruorot. We provide descriptions using standard anatomical terminology. We also compare the giraffoid community from the Lothidok Formation with published records of Early and Middle Miocene Giraffoidea from Africa.

2.1 Abbreviations

2.1.1 Museum collections

Specimens in museum collections have the following prefixes: **KNM**, Kenyan National Museums, Nairobi, Kenya. For KNM localities are indicated by WK for Kalodirr, MO and Mt for Moruorot, RU for Rusinga Island, MB for Maboko Island, and FT, for Fort Ternan. Other institutional indicators are **UCMP**, University of California Museum of Paleontology, Berkeley, California; **BMM**, Fossil Mammal Section, Department of Palaeontology, British Museum (Natural History) London, UK; **UB**, Department of Geology, University of Bristol, Bristol, UK.

2.1.2 Dental terminology

Lower dentition is noted by lower case letters (e.g. m1 for first lower molar) while upper dentition is noted by upper case letters (e.g. M3 for third upper molar)

3. Results

3.1 Systematic plaeontology

Order Artiodactyla Owen, 1848

Superfamily Giraffoidea Gray, 1821

Diagnosis: (Harris et al. 2010) Ruminant artiodactyls with a bilobed lower canine but lacking first premolars. The stomach is four chambered in extant forms, but there is no gall bladder.

Family Climacoceratidae Hamilton, 1978

Diagnosis: (modified from Hamilton 1978). Giraffoids having large cranial appendages carrying many tines.

Genus *Climacoceras* MacInnes, 1936

Diagnosis: (Hamilton 1978) Climacoceratids in which the premolar row is reduced in length relative to the molar row, cheek teeth hypsodont.

Type Species: *Climacoceras africanus* MacInnes, 1936

Climacoceras sp. nov.

Referred Material: KNM-WK 18272, Cranial appendage

Type Locality: Kalodirr, Kalodirr Member of the Lothidok Formation, early Miocene, Kenya

Description: A fragment of a left cranial appendage that was assigned by Harris et al. (2010) to *Cl. africanus,* a species known from younger Middle Miocene localities such as Maboko Island (MacInnes 1936). However, KNM-WK 18272 differs from *Cl. africanus* by the flattened cross-section of its main beam and possession of a groove on both sides of the beam. This differs from *Cl. africanus* or *Cl. gentryi* as both latter species have a rounded beam with no groove.

Family Giraffidae Gray, 1821

Genus et species nov.

Referred Material: KNM-WK 18087, left ossicone

Description: KNM-WK 18087 is a left ossicone whose formal description is part of a paper currently in review. In brief, the base is quadrangular in shape while the shaft is oval and compressed as it progresses towards the apex. Anteriorly, the ossicone forms a dull keel along the large curvature of the bone. At the base there is a small lateral flange and a small depression is just medial to the flange. Dorsally, two faint ridges are present. The ventral surface is dome-shaped. A median notch separates the two growths observed on the apex. Also, a lattice of small bumps covers the apex. Near its base, the shaft is smooth and dispalys very fine striations. This combination of features is unique among Giraffoidea.

Subfamily Canthumerycinae Hamilton, 1978

Canthumeryx sirtensis Hamilton, 1973

Referred Material: KNM-WK 17089, ossicone; KNM-WK 17099, ossicone; KNM-MO 17116 ossicone; KNM-WK 17086 right mandible with alveolus and broken crown of dp3, dp4-p4; KNM-WK 18199 isolated M1, M2, M3; KNM-MO 65 Right mandible fragment with m3; KNM-MO 73 Right M3; KNM-MO 17115 left M2; UCMP 42058 Partial skeleton; UCMP 41878 p4, UCMP 41873 P3; UCMP 41981 P4-M1.

cf. *Canthumeryx sirtensis* Hamilton, 1973

Referred Material: KNM-WK 16967 Left mandible with p4-m1, m2-m3; KNM-WK 17126 left mandible with m2-3.

Family incertae sedis

Genus et species nov.
(Fig. 2)

Referred Material: UCMP 40461, cranial appendage

Type Locality: Moruorot, Kalodirr Member, Lothidok Formation, early Miocene, Kenya.

Diagnosis: UCMP 40461 can be differentiated from other Giraffoidea by having a concave base, relatively even beam and two short tines coming off the beam. We recognize UCMP 40461 as a cranial appendage because it has only a single attachment surface on what we recognize as its proximal end and lacks any attachment facets on any of its other surfaces, thus excluding the possibility of this being a calcaneus, a pachyostotic cervical rib, or any other bone we are aware of. Additionally, it possesses several bumps that resemble the cranial appendages of other ruminant taxa such as sivathere giraffids, lagomerycids (e.g. Azanza and Ginsburg 1997) and *Orangemeryx hendeyi* (Morales et al. 1999). The bumps of UCMP 40461 are reminiscent of knobs in the ossicones of *Sivatherium* as well as the tines of *Climacoceras* spp. and to a lesser extent those of *O. hendeyi*. However, UCMP 40461 differs from Giraffidae because giraffid ossicones typically are wider at their base and taper distally, whereas UCMP 40461 appears to have a beam that is relatively uniform throughout as seen in *Cl. africanus* and in *O. hendeyi*.

Description: UCMP 40461 is a relatively complete cranial appendage (Fig. 2C). The shaft is of uniform thickness. The base is not appreciably wider than the distal part. The base has a surface that in our observation was unattached to the skull at the time of death. The surface of the base is concave and is composed of very fine small rounded bony ossifications. These are finer, flatter and more densely packed together than those of the ossicones of either *Okapia* or *Giraffa*. By the edge of the base, radiating channels of space indicate that the core is developmentally ordered. The growth was apparently from the center outward. This is common in other cranial appendages including bovid horns and giraffe ossicones. On the external side of the base a layer is discernible. This layer albeit a thin one is suggestive of a cortex. Cortices can be found in antlers, ossicones and horns, again indicating an active growth on the surface. Two very short tines are present. The tines are similar in thickness to the beam. The tines face in two opposite directions. The proximal tine is connected to the base by a robust ridge which spirals down to the base. The outer edge of the long axis is slightly bowed out, so that there is a concave surface and a convex surface. The apex is as dull as the tines. The external surface is smooth unlike giraffe ossicones but similar to *Climacoceras* spp. and palaeomerycid cranial appendage surfaces.

3.2 Summary of fossil Giraffoidea and stem-Giraffoidea in Afro-Arabia during the Early and Middle Miocene

Table 1 summarizes the Giraffoid community of Kalodirr and Moruorot including the newly described cranial appendage from Moruorot and compares them with those of major Early- and Middle Miocene sites in East Africa, North Africa, South Africa, and the Arabian plate where giraffoids and stem-giraffoids are known.

4. Discussion

4.1 Taxonomic Affiliation of UCMP 40461

UCMP 40461 is unique in its morphology and we

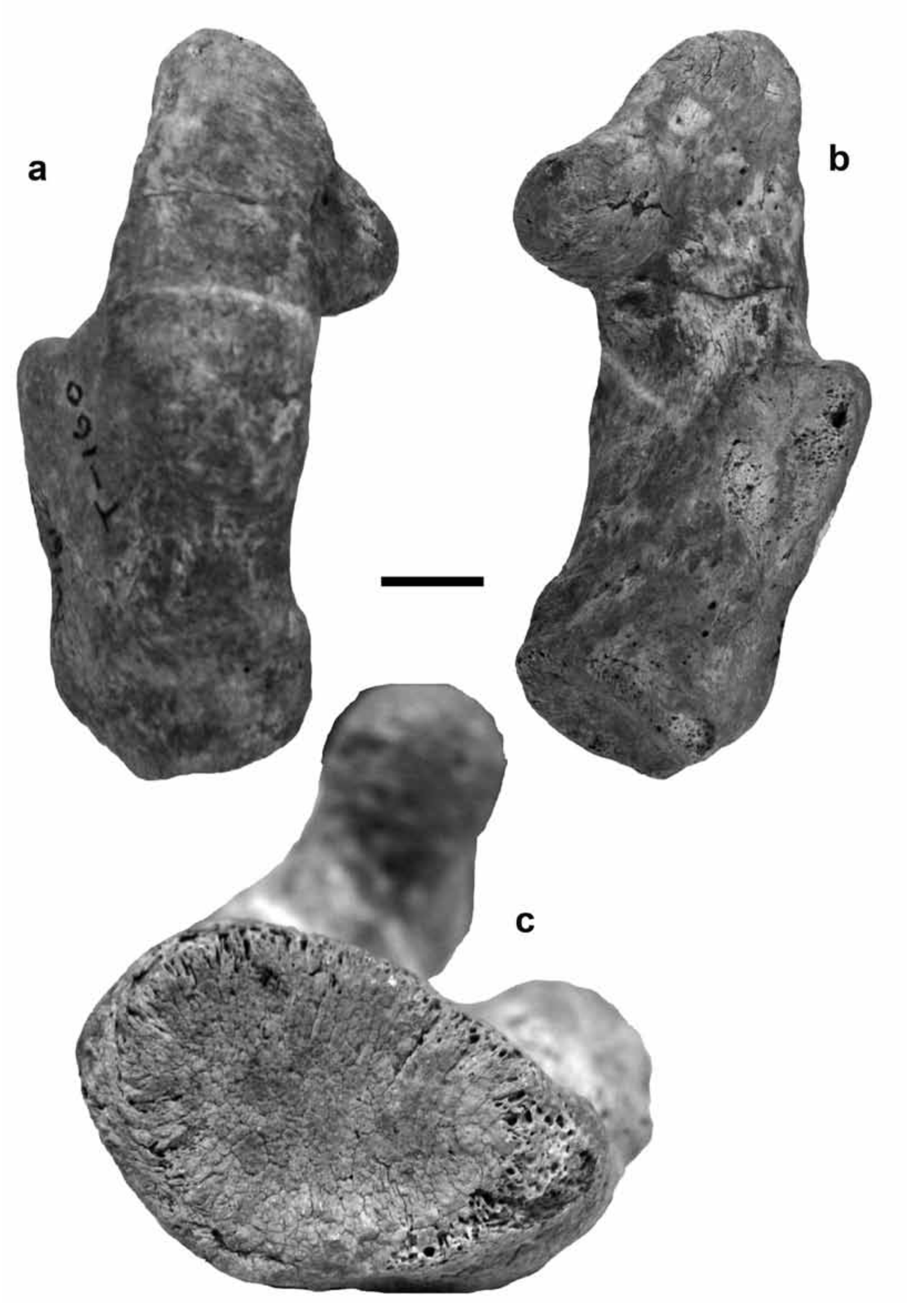

Figure 2: UCMP 40461, cranial appendage from Moruorot, Lothidok Fm. West Turkana, Kenya. Scale bar equals 1cm. **(a)** Lateral view. **(b)** Medial view. **(c)** Base.

cannot at present comfortably align UCMP 40461 with any other known ruminants. The base of UCMP 40461 appears unfused. Whether this means that it had detached from a pedicle (as a cervid antler would) or is merely a younger individual of a giraffoid in which fusion of the cranial appendage to the frontal (as in Giraffidae) simply did not occur yet, cannot be determined. Figure 3 presents the three most possible hypotheses about the phylogenetic relationships of UCMP 40461.

The unattached nature of UCMP 40461 suggests that UCMP 40461 may be a stem-Cervidae (Fig. 3.1). Cervidae antlers detach and the base of a fallen antler is convex in most crown cervids, wheras in UCMP 40461 the base is concave. However, in the primitive deer *Stephanocemas*, the base of the antler

Table 1: Distribution of fossil Giraffoidea and stem-Giraffoidea in Early and Middle Miocene Afro-Arabia.

REGION	EAST AFRICA							NORTH AFRICA		ARABIAN PLATE		SOUTH AFRICA
AGE	E. Miocene					M. Miocene		E. Miocene		E. Miocene	M. Miocene	E. Miocene
SITE	Loperot	Rusinga Island	Buluk	Lothidok Formation Kalodirr	Moruorot	Maboko Island	Fort Ternan	Gebel Zelten	Wadi Moghara	Yeroham	Al-Sarrar	Arrisdrift
Crown-Giraffoidea												
Climacoceratidae												
Climacoceras sp.				X								
Climacoceras africanus						x						
Climacoceras gentryi							x					
Giraffidae												
Genus et species nov.				x								
Canthumeryx sirtensis	x	x	x	x	x	x		x	x	x	x	
Giraffokeryx primaevus							x					
Stem-Giraffoidea												
Prolibytherium magnieri								x	x			
Orangemeryx hendeyi												x
UCMP 40461					x							
TOTAL of species number	1	1	1	4		2	2	2	2	1	1	1

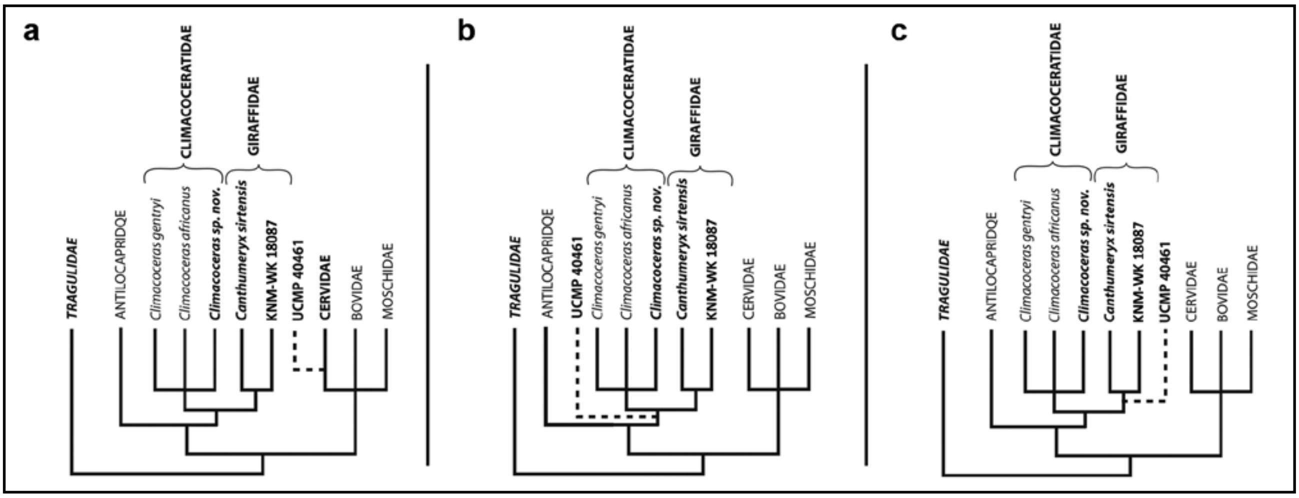

Figure 3: Three different hypotheses on the phylogenetic position of UCMP 40461 in relation to fossil Giraffoidea from Kalodirr and Moruorot. Ruminant phylogeny used follows Bininda-Emonds et al. (2007), Marcot (2007), Spaulding et al. (2010). Bold names represent taxa present at the Kalodirr Member, Lothidok Formation localities according to each hypothesis. **(a)** Member of the Cervoidea; **(b)** Stem-Giraffoidea; **(c)** Sister-taxon of the Giraffidae.

appears concave as well (e.g. Azanza and Ginsburg 1997; Wang et al. 2009). But, when antlers fall off, even in primitive deer, the base looks different from UCMP 40461. Antlers are naturally shed by hormonal changes in the haversian systems of the pedicle. As a result, the bone does not have a cortex surrounding the base. UCMP 40461 has a concavity similar in appearance to a typical attachment surface, with a cortical cover over spongy bone. Typically the base of a modern antler has a characteristic burr, a growth of bone surrounding the base like a corona, but such a burr is not present in very early Cervoidea (e.g. Azanza and Ginsburg 1997) or in UCMP 40461. Given that no Cervidae are recognized in Africa until the Pleistocene (Gentry 2010), we prefer to exclude UCMP 40461 from the Cervidae at this time.

Among the Giraffoidea cranial appendages appear to develop in at least two different ways. *Climacoceras* cranial appendages are apophyseal in nature developing as direct extensions of the frontal bone (e.g. Azanza et al. 2003). By contrast, ossicones are "epiphyseal" in the nature of their development, in that they ossify from a separate cartilaginous matrix within the dermis independent of the cranial bones. Ossicones may fuse to the frontal or other bones of the cranial vault later in life. It is important to note that "epiphyseal" does not imply similarity in growth with the epiphysis of a long bone merely that ossicones form separately from the frontal bone (e.g. Geraads 1991).

It is possible that UCMP 40461 represents either a stem-Giraffoidea (Fig.3.2.) or an unusual Giraffidae (Fig.3.3). Because UCMP 40461 is unattached it clearly is reminiscent of "epiphyseal" ossicones of the Giraffidae in that regard. Also, the concave nature of the base of UCMP 40461 is somewhat similar to giraffids where the base is also concave prior to fusing with the skull. However, UCMP 40461 has a beam that maintains relatively even dimensions along its entire length, unlike the ossicones of Giraffidae which are typically conical with a wider base tapering to a point. Knobs are found in Sivatherrine Giraffidae, however in *Sivatherium* the knobs are developed in only one direction: posterolateral, whereas in UCMP 40461 the knobs point in different directions. Also, the very uniform morphology of the base of UCMP 40461 is not reminiscent of giraffids. It is unlikely that UCMP 40461 represents a third lineage of Giraffidae at Kalodirr and Morurot. Thus, it is prudent at this point to exclude UCMP 40461 from Giraffidae and include it only in the Giraffoidea.

Comparisons with non-Giraffidae members of the Giraffoidea do not immediately align UCMP 40461 with any known taxon. UCMP 40461 is unlike *Climacoceras* (Giraffoidea: Climacoceratidae) or *Orangemeryx* (regarded as a stem-Giraffoidea by some (e.g. Morales et al. 1999) but identified as Pecora indet. by others (e.g. Cote 2010). In the latter two taxa the cranial appendage is a direct extension of the frontal bone (MacInnes 1936; Azanza et al. 2003), but in UCMP 40461 the cranial appendage is separate from the skull, and is clearly not an extension of the frontal bone. Compared to *Climacoceras*, UCMP 40461 has shorter, more robust tines and a shorter beam. In *O. hendeyi* the tines are found at the distal terminus of the beam, very different from the arrangement seen in UCMP 40461. When comparing UCMP 40461 with the cranial appendages of the enigmatic pecoran *Prolibytherium magnieri* from Gebel Zelten in Libya (see Cote 2010), it is obvious that many differences exist. *P. magnieri* has large, wing-shaped, and very flat cranial appendages. These are fused to the frontal and parietal bones of the skull. The cranial appendages extend anteriorly and posteriorly appearing as a shield overlying the roof of the skull (Hamilton 1973; Harris et al. 2010). Careful examination of the type specimen cranial appendages of *P. magnieri* reveals that theses appendages are formed by two flat plates surrounding a hollow interior. UCMP 40461 is much smaller, not flat or wing-like, and is not hollow. Therefore, we can comfortably distinguish UCMP 40461 from *P. magnieri*.

While we refrain from naming a new taxon until we can associate the cranial appendage with other gnatho-dental and postcranial materials that help resolve its phylogenetic relationships, our current working hypothesis recognizes UCMP 40461 as a cranial appendage, that is most similar to the Giraffoidea but unlike any known lineage of the Giraffoidea. We currently recognize UCMP 40461 as a stem Giraffoidea (Fig.3.2), albeit one that is different from the stem Giraffoidea *Orangemeryx hendeyi* from Namibia or *Prolibytherium magnieri* from North Africa.

4.2 Implications of the Giraffoidea community (including stem-Giraffoidea) of the Lothidok Formation

Fossils from Kalodirr represent the earliest known occurrence of the genus *Climacoceras* extending the temporal range of the genus into the Early Miocene. Kalodirr also represents the most northerly range of the genus *Climacoceras*. Based on available evidence, it appears that the habitat preferred by *Climacoceras* spp. was not a closed-canopy forest because habitat reconstructions of Kalodirr (Leakey et al. 2011), Maboko (e.g. Retallack et al. 2002), and Fort Ternan (e.g. Cerling et al. 1997) all suggest woodland environments.

Canthumeryx sirtensis is found in North and East Africa and has a wide temporal range and a wide geographic range. *C. sirtensis* is found in sediments older than 18 years at Loperot (Grossman 2013) and Rusinga Island (Peppe et al. 2011). C. *sirtensis* is also found in sediments as young as 16 million years old Maboko (Andrews et al. 1981) and Al-Sarrar (Thomas et al. 1982). In older sites such as Rusinga Island or Loperot *C. sirtensis* is the only member of the Giraffoidea currently recognized, although other pecorans are found at those sites. In East Africa, fossils from Kalodirr and Morurot (ca. 17 million years ago, Boschetto 1992) represent the oldest occurrences of a giraffoid community. In North Africa *C. sirtensis* is not found with other crown Giraffoidea but it is found with *P. magnieri* (Hamilton 1973; Miller 1999), a taxon which may belong in the Giraffoidea, but then again may not (Cote 2010; Harris et al. 2010).

The Giraffoidea community of the Kalodirr Member of the Lothidok Formation includes *Climacoceras* sp., the taxon represented by UCMP 40461, and two giraffids: *C. sirtensis* and Giraffidae gen. et sp. nov. (see previous description in text), a genus and species of giraffid with larger and more robust ossicones than *C. sirtensis*. The new genus shares some similarities with later *Giraffokeryx* and even more so with *Sivatherium.* Whether these similarities represent phylogenetic affinities or merely phenetic homoplasy requires recovery of more material. What is certain is that Giraffidae of the Lothidok Formation include at least two distinct lineages. In the Middle Miocene the Giraffoidea communities found in Maboko Island includes *Cl.* africanus and *C. sirtensis*, following the pattern established at Kalodirr and Moruorot. Thus, the sites of the Lothidok Formation represent the first instance of a diverse giraffoid community, some of whose members provide a link between the Early and Middle Miocene.

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5. References

Andrews P, Meyer GE, Pilbeam DR, Van Couvering JA, Van Couvering JAH. 1981. The Miocene fossil beds of Maboko Island, Kenya: geology, age, taphonomy and palaeontology. Journal of Human Evolution 10, 35-48.

Azanza B, Ginsburg L. 1997. A revision of the large lagomerycid artiodactyls of Europe. Palaeontology 40, 461-486.

Azanza B, Morales J, Pickford M. 2003. On the nature of the multibranched cranial appendages of the climacoceratid *Orangemeryx hendeyi*. Memoires of the Geological Survey of Namibia 19, 345-357.

Bininda-Emonds ORP, Cardillo M, Jones KE, MacPhee RDE, Beck RMD, Grenyer R, Price SA, Vos RA, Gittleman JL, Purvis A. 2007. The delayed rise of present-day mammals. Nature 446, 507-512.

Boschetto HB. 1988. Geology of the Lothidok Range. M.S. thesis, University of Utah, Utah, 203 p.

Boschetto HB, Brown FH, McDougall I. 1992. Stratigraphy of the Lothidok Range, Northern Kenya, and K/Ar ages of its Miocene primates. Journal of Human Evolution 22, 47–71.

Cerling TE, Harris JM, Ambrose SH, Leakey MG, Solounias N. 1997. Dietary and environmental reconstruction with stable isotope analyses of herbivore tooth enamel from the Miocene locality of Fort Ternan, Kenya. Journal of Human Evolution 33, 635–650.

Clauss M, Rössner GE. 2014. Old world ruminant morphophysiology, life history, and fossil record: exploring key innovations of a diversification sequence. Annales Zoologici Fennici 51, 80-94.

Cote SM. 2010. Pecora *Incertae Sedis*. In L Werdelin, WJ Sanders (Eds), Cenozoic Mammals of Africa. Berkeley, CA, University of California Press, 731-740.

Gentry AW. 2010. Cervidae. In: L Werdelin, WJ Sanders (Eds), Cenozoic Mammals of Africa. Berkeley, CA, University of California Press, 813-814.

Geraads D. 1991. Derived features of giraffoid ossicones. Journal of Mammalogy. 72, 213-214.

Gray JE. 1821. On the natural arrangement of vertebrose animals. London Medical Repository 15, 296-310.

Grossman A. 2013. Primate paleocommunities in the early Miocene of Africa: Why are apes and monkeys so rarely found together? American Journal of Physical Anthropology 150, 138.

Grossman A, Holroyd P. 2009. *Miosengi butleri*, gen. et sp. nov., (Macroscelidea) from the Kalodirr Member, Lothidok Formation, Early Miocene of Kenya. Journal of Vertebrate Paleontology 29, 957-960.

Grossman A, Liutkus-Pierce C, Kyongo B, M'Kirera F. In press. Catarrhine paleocommunities in the early and Middle Miocene of Africa: Why are apes and monkeys not always found together? International Journal of Primatology.

Hamilton WR. 1973. The Lower Miocene Ruminants of Gebel Zelten, Libya. Bulletin of the British Museum (Natural History) Geology 24, 73-150.

Hamilton WR. 1978. Fossil Giraffes from the Miocene of Africa and a Revision of the Phylogeny of the Giraffoidea. Philosophical Transactions of the Royal Society of London B 283, 165-229.

Harris JM, Solounias N, Geraads D. 2010. Giraffoidea. In: L Werdelin, WJ Sanders (Eds), Cenozoic Mammals of Africa. Berkeley, CA, University of California Press, 797-811.

Leakey RE, Leakey MG. 1986a. A new Miocene hominoid from Kenya. Nature 324, 143-146.

Leakey RE, Leakey MG. 1986b. A second new Miocene hominoid from Kenya. Nature 324, 146-148.

Leakey M, Grossman A, Gutiérrez M, Fleagle JG. 2011. Faunal change in the Turkana Basin during the Late Oligocene and Miocene. Evolutionary Anthropology: Issues, News, and Reviews 20, 238-253.

MacInnes D. 1936. A new genus of fossil deer from the Miocene of Africa. Journal of the Linnean Society of London, Zoology 39, 521-530.

Marcot JD. 2007. Molecular phylogeny of terrestrial artiodactyls. In: DR Prothero, SE Foss (Eds), The Evolution of Artiodactyls. Baltimore, MD, Johns Hopkins University Press, 4–18.

Miller ER. 1999. Faunal correlation of Wadi Moghara, Egypt: implications for the age of *Prohylobates tandyi*. Journal of Human Evolution 36, 519-533.

Morales J, Soria D, Pickford M. 1999. New stem giraffoid ruminants from the early and middle Miocene of Namibia. Geodiversitas 21, 229-253.

Owen R. 1848. Description of teeth and portions of jaws of two extinct anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the NW coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. Quarterly Journal of the Geological Society of London 4, 104-141.

Peppe DJ, Deino AL, McNulty KP, Lehmann T, Harcourt-Smith WEH, Dunsworth HM, Fox DL. 2011. New age constraints on the early Miocene faunas from Rusinga and Mfangano Islands (Lake Victoria, Kenya). American Journal of Physical Anthropology 144, 237.

Retallack GJ, Wynn JG, Benefit BR, McCrossin ML. 2002. Paleosols and paleoenvironments of the middle Miocene, Maboko Formation, Kenya. Journal of Human Evolution 42, 659-703.

Spaulding M, O'Leary MA, Gatesy J. 2009. Relationships of Cetacea (Artiodactyla) among mammals: increased taxon sampling alters interpretations of key fossils and character evolution. PLoS ONE 4, 1–14. (doi:10.1371/journal.pone.0005361)

Thomas H, Sen S, Khan M, Battail B, Ligabue G. 1982. The lower Miocene fauna of Al-Sarrar (Eastern Province, Saudi Arabia). ‚Atlal', Journal of Saudi Arabian Archaeology 5, 109-136.

Wang X, Xie G, Dong W. 2009. A new species of crownantlered deer *Stephanocemas* (Artiodactyla, Cervidae) from the middle Miocene of Qaidam Basin, northern Tibetan Plateau, China, and a preliminary evaluation of its phylogeny. Zoological Journal of the Linnean Society 156, 680-695.

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