A new species of *Mioeuoticus* (Lorisiformes, Primates) from the early Middle Miocene of Kenya

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Abstract We here describe a prosimian specimen discovered from the early Middle Miocene (~15 Ma) of Nachola, northern Kenya. It is a right maxilla that preserves P⁴–M³, and is assigned to a new species of the Miocene lorisid genus *Mioeuoticus*. Previously, *Mioeuoticus* was known from the Early Miocene of East Africa. The Nachola specimen is therefore the first discovery of this genus from the Middle Miocene. The presence of a new lorisid species in the Nachola fauna indicates a forested paleoenvironment for this locality, consistent with previously known evidence including the abundance of large-bodied hominoid fossils (*Nacholapithecus kerioi*), the dominance of browsers among the herbivore fauna, and the presence of plenty of petrified wood.

Key words: Middle Miocene, *Mioeuoticus*, Lorisidae, Prosimians, East Africa

Introduction

Although there are relatively abundant fossils of adapoid and omomyoid prosimians known from the Eocene of North America and Europe, prosimian fossils more closely related to living taxa are relatively rare in the fossil record. The fossil record of tarsiers is very poor (Gunnell and Rose, 2002; Rossie et al., 2006; Ni et al., 2013). Living lemurs are restricted to Madagascar, and no fossil lemurs are known prior to the Late Pleistocene (Godfrey and Jungers, 2002). Fossil lorisiforms are known from Africa and South Asia. In Africa, there are three genera (one lorisid: *Mioeuoticus*, and two galagids: *Progalago*, *Komba*) from the Early to early Middle Miocene (20–15 Ma), and one genus (*Galago*) from the Plio-Pleistocene (Phillips and Walker, 2000; Harrison, 2010). In Egypt, Pickford et al. (2006) reported the presence of *Galago* in the Late Miocene (~10 Ma). Two upper molars of galagid indet. were known from the Late Miocene (10–9 Ma) of Namibia (Conroy et al., 1993; Rasmussen and Nekaris, 1998). A galagid maxillary fragment with two upper molars was recently discovered from the Late Miocene of Kenya (~9.9 Ma) (Kunimatsu et al., 2017). Prior to the Miocene, stem galagids such as *Saharagalago* (~37 Ma) and

Wadilemur (~34 Ma), and a possible lorisid or stem lorisiform (*Karanisia*; ~37 Ma) are known from the Fayum area in Egypt, supporting the hypothesis of an ancient Afro-Arabian origin for crown strepsirrhines and an Eocene divergence of extant lorisiform families (Seiffert et al., 2003, 2005; Seiffert, 2012). In addition, Pickford (2015) described a new lorisid genus, *Namaloris rupestris*, based on an upper molar discovered from the Eocliiff Limestone site EC 9 (Bartonian: 41.3–38.0 Ma) in Namibia. Another enigmatic primate, *Notnamaia bogenfelsi*, is known from the Lutetian (47.8–41.3 Ma) of Namibia (Pickford et al., 2008; Pickford and Uhen, 2013), and was originally considered to be an anthropoid (Pickford et al., 2008). Later, Godinot (2015) considered that *N. bogenfelsi* had overall similarities with European anchomomyin adapoids, although he also recognized that the former showed some significant differences from the latter.

In this article, we describe a new species of *Mioeuoticus*, based on material discovered from the early Middle Miocene deposits in Nachola, northern Kenya. Previously, this genus was known only from the Early Miocene, including two species, one from Napak I in Uganda (*M. bishopi*, ~19–18 Ma) and the other from Rusinga Island (*M. shipmani*, ~18 Ma) in Kenya (Phillips and Walker, 2000). In addition, Harrison (2010) proposed that the specimens previously assigned to *Progalago songhorensis* from Songhor and Rusinga in Kenya (~19–18 Ma) should be included in the hypodigm of *M. bishopi*. A talus from Koru (~20–19 Ma) and a calcaneus from Songhor (~19 Ma) in Kenya have been

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tentatively assigned to *Mioeuoticus* (Gebo, 1986, 1989). A loris-like distal humerus (MUZM 30) compatible in size with *Mioeuoticus* was reported from Napak (Gebo et al., 1997), but Pickford (2012) refuted its primate affinity, suggesting that it belongs to *Paranomalous bishopi*, an arboreal rodent. The new species from Nachola is therefore the first discovery of this genus in the Middle Miocene.

Nachola is located west of the township of Baragoi in northern Kenya. Through a long-term field project conducted since the early 1980s, the Kenya–Japan Joint Expedition has recovered hundreds of primate fossils, most of which are attributed to a large-bodied Miocene hominoid *Nacholapithecus kerioi* (Ishida et al., 1984, 1999, 2004; Nakatsukasa et al., 1998, 2003; Kunitatsu et al., 2004; Nakatsukasa and Kunitatsu, 2009). The Nachola primate fauna also includes a nyanzapithecine small catarrhine (*Nyanzapithecus harrisoni*) (Kunitatsu, 1992, 1997), a victoriapithecine monkey, and *Komba* sp. (Tsujikawa and Nakaya, 2005). In Nachola, fossils have been discovered from the lower part of the Aka Aithuth Formation. The chronological age of the fossiliferous deposits dated by the K–Ar method is 16.4–15.3 Ma (Sawada et al., 2006). A more recent analysis of anorthoclase grain samples from the fossil-bearing horizon, from which primates and the majority of other vertebrate fossils were obtained, yielded a ^{40}Ar – ^{39}Ar age of 14.77 ± 0.10 Ma, in which the authors have confidence (Nakatsukasa and Kunitatsu, 2009). The fauna from this horizon (Tsujikawa and Nakaya, 2005) corresponds to the faunal set IIIb by Pickford (Pickford, 1981; Pickford and Morales, 1994), which is in accord with the results of K–Ar and ^{40}Ar – ^{39}Ar dating.

Systematics

Order Primates Linnaeus, 1758
 Suborder Strepsirrhini Geoffroy, 1812
 Infraorder Lorisiformes Gregory, 1925
 Superfamily Lorisioidea Gray, 1821
 Family Lorisidae Gray, 1821
 Subfamily Mioeuoticiinae Harrison, 2010
 Genus *Mioeuoticus* Leakey, 1962
Mioeuoticus kichotoi sp. nov.

Diagnosis. Upper P^4 is subtriangular in occlusal outline, having two main cusps. Upper M^1 and M^2 have a square occlusal outline with the hypocone being well developed. Hypocone is not developed in upper M^3 , whose occlusal outline is consequently more triangular than in the anterior molars. Buccal cingulum is well developed on all upper molars.

Differential diagnosis. The new species is different from *Komba* and *Progalago* in the occlusal outline of the upper molars, which is subsquare in M^1 and M^2 , and triangular in M^3 , lacking the concavity on the distal margin in the latter taxa. Hypocone on M^1 and M^2 located distal to the protocone, hence differing from the more distolingual position of the hypocone in *Komba* and *Progalago*. Differs from both *M. bishopi* and *M. shipmani* in having upper molars proportionally more elongate in mesiodistal direction and in relative molar size: In *M. kichotoi*, upper M^2 is slightly larger than M^1 and similar in size to M^3 , while the upper molars

become smaller from M^1 to M^3 in *M. bishopi*. In *M. shipmani*, M^2 is the largest molar with M^1 being similar in size to M^3 . Further differs from *M. bishopi* in having upper P^4 slightly smaller and more triangular in occlusal outline, larger upper M^2 – M^3 , hypocone on M^1 – M^2 being separated from the protocone by a groove, and better developed crista obliqua. Further differs from *M. shipmani* in smaller dental size, proportionally shorter upper P^4 , and narrower buccal cingulum on upper molars.

Holotype. KNM-BG 48081

Type locality. Site BG-K, Nachola village near Baragoi town, northern Kenya

Horizon. Lower part of the Aka Aiteputh Formation

Age. Early Middle Miocene (~15 Ma)

Etymology. After Mzee Kichoto, who has for years contributed much to maintaining the field camp in Nachola as the head of the local camp workers.

Hypodigm. Holotype only

Description

The holotype (KNM-BG 48081) is a right maxillary fragment with P^4 – M^3 (Figure 1, Figure 2, Table 1). It preserves a part of the palatal process and orbital floor. There is a small foramen piercing the orbital floor reaching to the palatal ceiling near the mesiolingual corner of the M^2 crown. P^4 is subtriangular in occlusal outline and is two-rooted (Figure 3). The buccal portion of the crown is longer mesiodistally than the lingual portion, with oblique and concave mesial and transverse distal margins. There are two main cusps (paracone and protocone). A chip of enamel is missing from the protocone. The paracone is larger in area than the protocone. The paracone is buccolingually narrower than the me-

Figure 1. The holotype (KNM-BG 48081) of *Mioeuoticus kichotoi*, a right maxilla with P^4 – M^3 : (a) occlusal view (stereo); (b) linguocclusal view; (c) buccal view. Scale bar = 5 mm.

Figure 2. 3D digital models of the holotype (KNM-BG 48081) of *Mioeoticus kichotoi*, based on the CT scanning data: (a) occlusal view; (b) superior view; (c) buccal view; (d) lingual view; (e) posterior view; (f) anterior view. Scale bar = 5 mm.

siodistal length of the cusp. The preparacrista is longer than the postparacrista, and a style is well developed at the base of the preparacrista.

M¹ is tetracuspoid, and is almost square in occlusal outline, but the buccal margin is slightly longer mesiodistally than the lingual margin with a slightly oblique mesial margin. The cusps are low. The protocone is the largest cusp, but is slightly lower than the buccal cusps. The paracone is slightly larger than the metacone, and both of them are buccolingually narrower relative to their mesiodistal length. The hypocone is well developed, occupying the distolingual corner of the crown, but is lower and more rounded than the other three cusps. The hypocone is separated from the protocone by a groove. The preprotocrista runs mesiobuccally and merges with the mesial marginal ridge. The postprotocrista

Figure 3. CT image of the holotype maxilla in a horizontal section slightly above the cervical region of the cheek teeth, showing the roots of P⁴–M³. White arrows indicate the two roots of P⁴.

runs distally and slightly buccally at first, and then turns to a more distobuccal direction. It meets with the lingual ridge from the metacone to make a low crista obliqua. Although the buccal surface of the crown is eroded, the preserved morphology indicates that the buccal cingulum is well developed, being almost continuous along the buccal aspect except that it might be briefly interrupted on the buccal face of the paracone. There is neither paraconule nor metaconule.

M² is basically similar to M¹, but the crown is relatively broader buccolingually (Table 2). Consequently, the trigon basin is also relatively broader. The hypocone is more lingually placed relative to the protocone, and the degree of lingual displacement of the hypocone is more marked than in M¹. A chip of enamel is missing from the metacone apex. The buccal surface is somewhat eroded, but it is apparent that the buccal cingulum is prominently developed all over the buccal aspect, though there may be a slight interruption on the buccal face of the paracone.

M³ is different from the anterior two molars in lacking the

Table 1. Dental measurements of *Mioeoticus* species

Taxon	Acc. No.	Locality	P ⁴		M ¹		M ²		M ³	
			MD	BL	MD	BL	MD	BL	MD	BL
<i>M. kichotoi</i>	KNM-BG 48081	Nachola	2.1	2.8	3.5	3.7	3.5	4.1	3.5	4.0
<i>M. shipmani</i>	KNM-RU 2052	Rusinga	2.8	3.2	3.9	4.5	3.8	5.1	3.7	4.6
<i>M. bishopi</i>	NAP.I.3 6/58*	Napak	2.3	3.1	3.4	3.9	3.1	3.9	2.9	3.4
	KNM-SO 1312	Songhor	—	—	—	—	3.1	4.0	—	—
	KNM-RU 3415	Rusinga	—	—	—	—	3.2	4.2	—	—
<i>M. bishopi</i> mean			2.3	3.1	3.4	3.9	3.1	4.0	2.9	3.4

* Data from Phillips and Walker (2000).

Table 2. Crown area (MD $\times$ BL) and proportion (MD/BL) of *Mioeoticus* species

Taxon	Acc. No.	Locality	MD $\times$ BL (mm ²)				MD/BL (%)			
			P ⁴	M ¹	M ²	M ³	P ⁴	M ¹	M ²	M ³
<i>M. kichotoi</i>	KNM-BG 48081	Nachola	5.9	13.0	14.4	14.0	75.0	94.6	85.4	87.5
<i>M. shipmani</i>	KNM-RU 2052	Rusinga	9.0	17.6	19.4	17.0	87.5	86.7	74.5	80.4
<i>M. bishopi</i>	NAP.I.3 6/58*	Napak	7.1	13.3	12.1	9.9	74.2	87.2	79.5	85.3
	KNM-SO 1312	Songhor	—	—	12.4	—	—	—	77.5	—
	KNM-RU 3415	Rusinga	—	—	13.4	—	—	—	76.2	—
<i>M. bishopi</i> mean			7.1	13.3	12.6	9.9	74.2	87.2	77.7	85.3

* Calculated using data from Phillips and Walker (2000).

Figure 4. Crown areas (MD $\times$ BL in mm²) of P⁴–M³ in *Mioeoticus* species. As for *M. bishopi*, only the type specimen (NAP.I.3 6/58) is used in this graph.

hypocone and having a more triangular occlusal outline. It is therefore a tricuspid tooth. The protocone is the largest cusp as in the anterior molars. The metacone is much smaller than the paracone. The distal cingulum and distal marginal ridge are developed between the distal bases of the metacone and protocone. The lingual end of the distal cingulum is slightly swollen. The postprotocrista runs distobuccally to meet the lingual ridge of the metacone, forming a crista obliqua. The buccal cingulum is well developed, forming a wide ledge that is continuous along the buccal aspect of the crown, although the cingulum fades out shortly on the buccal face of the paracone. A chip of enamel is missing from the paracone apex.

Comparisons

M. kichotoi is clearly distinguished from the two previously known species of the genus in having more elongate upper molars, and relative upper molar size from M¹ to M³, as described in the differential diagnosis. In dental size, *M. kichotoi* is smaller than *M. shipmani*, and is similar in M¹ and P⁴ and moderately larger in M² and M³ compared to the type species *M. bishopi* (Table 1, Table 2, Figure 4). The P⁴ morphology of *M. kichotoi* shows some resemblance to that

of *M. shipmani*, such as less square occlusal outline, but the crown is relatively shorter than in *M. shipmani* and in this respect, the Nachola species is similar to *M. bishopi*. The MD/BL proportion of the upper molars (Table 2, Figure 5) appears to show different tendencies between *M. kichotoi* and *M. shipmani*. The former acquired more elongate and narrower molar crowns, and the latter shorter and broader crowns, if we assume that they were derived from the intermediate condition in the oldest species *M. bishopi*. However, given the paucity of available lorid fossils, it may be premature to deduce much about their phylogenetic relationships.

Body mass estimates

Body mass estimates for *M. kichotoi* (KNM-BG 48081), *M. shipmani* (KNM-RU 2502) and *M. bishopi* (UMP-NAP.I.3 6/58) were calculated from crown areas (MD $\times$ BL) using the formulae for extant prosimians in Egi et al. (2004). The body mass estimates vary depending on which tooth is used (Table 3). The ranges of body mass estimates are 0.46–1.39 kg for *M. kichotoi*, 0.75–1.72 kg for *M. shipmani*, and 0.58–0.84 kg for *M. bishopi*. The multiregression formula gives body mass estimates as 0.70 kg for *M. kichotoi*,

Figure 5. Crown proportion (MD/BL in %) of P⁴–M³ in *Mioeuoticus* species. As for *M. bishopi*, only the type specimen (NAP.1.3 6/58) is used in this graph.

Table 3. Body mass estimates (kg)

	<i>M. kichotoi</i>	<i>M. shipmani</i>	<i>M. bishopi</i>
P ⁴	0.46	0.75	0.59
M ¹	0.64	0.93	0.66
M ²	0.75	1.13	0.58
M ³	1.39	1.72	0.84
Multiregression	0.70	1.05	0.61

1.05 kg for *M. shipmani*, and 0.61 kg for *M. bishopi*. *M. shipmani* is apparently much heavier than the other two species. *M. kichotoi* is roughly similar to or slightly heavier than *M. bishopi*.

Discussion

The new prosimian material discovered from the Aka Aituputh Formation in Nachola is attributed to a new species of *Mioeuoticus*. At present, the fossil record of lorisoid primates is fairly poor, and *Mioeuoticus* is the only genus attributed to the Lorisidae in the Miocene African fossil record, although there are a few specimens of indeterminate lorisids known from Chamtwara (~19 Ma), Fort Ternan (~14 Ma), and Lukeino (~6 Ma) in Kenya (Harrison, 2010; Pickford, 2012). The previously known species of *Mioeuoticus* were confined to a relatively short period of the Early Miocene (19–18 Ma) (Harrison, 2010). The new species *M. kichotoi* from Nachola (~15 Ma) is the first discovery of *Mioeuoticus* from the Middle Miocene, and is the latest known occurrence of this genus in the fossil record, extending the chronological distribution of the genus by ~3 million years younger.

A left maxilla with P⁴–M³ of a lorisid is known from another Middle Miocene locality, Fort Ternan, in Kenya, but its

dental morphology is so different from that of *Mioeuoticus* that the Fort Ternan lorisid is considered to belong to a distinct genus and species which is more derived than *Mioeuoticus* and is most similar to extant *Perodicticus* (Harrison, 2010). The discovery of *M. kichotoi* from Nachola increases the diversity of prosimians in the African Middle Miocene.

The extant lorisids are restricted to tropical/subtropical forests in Sub-Saharan Africa and South to Southeast Asia (Mittermeier et al., 2013). They are arboreal primates, and their locomotion is characterized by slow and cautious movements in trees. The extant African lorisids include angwantibos (*Arctocebus* spp.), pottos (*Perodicticus potto*), and false pottos (*Pseudopotto martini*), while slender lorises (*Loris* spp.) and slow lorises (*Nycticebus* spp.) are distributed in tropical rainforests to deciduous forests in Asia (Schwartz, 1996; Groves, 2001; Butynski et al., 2013; Mittermeier et al., 2013; Kingdon, 2015). The estimated body weight of ~0.7 kg for *M. kichotoi* is slightly smaller than *P. potto* (0.8–1.6 kg), but considerably larger than angwantibos (0.23–0.47 kg for *A. calabarensis*; 0.20–0.27 kg for *A. aureus*) (Kingdon, 2015).

M. bishopi was originally known from Napak, Uganda (Harrison, 2010). Recently, Harrison (2010) suggested that some specimens from Songhor and Rusinga, Kenya, should also be assigned to this taxon. *M. shipmani* is known from Rusinga (Philips and Walker, 2000). The fossil terrestrial gastropods collected from Napak indicate the presence of woodland to forest environments in this area around 20–18.5 Ma, although some taxa suggest that patches of more open environments may have existed occasionally (Pickford, 2004). The abundance of tragulid fossils at Napak (Pickford, 2002) may indicate the presence of forested environments, although caution is necessary as the microwear analysis of the early Miocene African tragulids from Rusinga and Song-

hor shows diverse diets from grazers to browsers, suggesting that those fossil tragulids may have been adapted to more diverse environments than extant tragulids (Ungar et al., 2012).

The vertebrate fossil assemblages from Rusinga include both forest dwellers and those that more likely inhabited open environments, suggesting that the environments of Rusinga may have been variable lowland forests including both wetter/closed and drier/open habitats (Andrews and Couvering, 1975; Andrews et al., 1997; Nesbit Evans et al., 1981; Ungar et al., 2012). Paleobotanical and paleosol studies also support the paleoenvironmental reconstruction for Rusinga as having forested to woodland environments in a strongly seasonal and warm climate (Collinson et al., 2009; Maxbauer et al., 2013).

Plenty of petrified wood was discovered from the same stratigraphic level as the primate fossils in Nachola, suggesting the presence of forests in the paleoenvironment (Suzuki, 1987). A large-bodied hominoid *N. kerioi* is the most abundant taxon in the Nachola fauna (Tsujikawa and Nakaya, 2005). The locomotion pattern of *N. kerioi* is reconstructed as arboreal quadrupedalism with enhanced functions of the forelimbs for climbing and clambering (Rose et al., 1996; Ishida et al., 2004; Nakatsukasa et al., 1998, 2007, 2012; Nakatsukasa and Kunimatsu, 2009), suggesting that they would have needed relatively dense tree covers. The majority of the herbivorous mammals from Nachola are browsers. Although there are a few hypsodont taxa such as a rhinocerotid and a bovid, they are rare in the Nachola mammalian fauna (Tsujikawa and Nakaya, 2005).

The presence of a new lorid species *M. kichotoi* described in this article further supports a forested paleoenvironment for Nachola, which is consistent with the abundance of a large-bodied, arboreal quadrupedal hominoid (*N. kerioi*) and the dominance of browsers among herbivore mammals in the mammalian fauna of this locality, as well as the presence of plenty of petrified wood (Suzuki, 1987; Tsujikawa and Nakaya, 2005).

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References

Andrews P. and Couvering J.A.H.V. (1975) Palaeoenvironments in the East African Miocene. In: Szalay F. (ed.), *Approaches to*

- Primate Paleobiology. Karger, Basel, pp. 62–103.
- Andrews P., Bugun D.R., and Zylstra M. (1997) Interrelationships between functional morphology and paleoenvironments in Miocene hominoids. In: Begun D.R., Ward C.V., and Rose M.D. (eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*. Plenum Press, New York, pp. 29–58.
- Butynski T.M., Kingdon J., and Kalina J. (eds.) (2013) *Primates*. Bloomsbury, London.
- Collinson M.E., Andrews P., and Bamford M.K. (2009) Taphonomy of the early Miocene flora, Hiwegi Formation, Rusinga Island, Kenya. *Journal of Human Evolution*, 57: 149–162.
- Conroy G., Pickford M., Senut B., and Mein P. (1993) Additional Miocene primates from the Otavi Mountains, Namibia. *Comptes Rendus de l'Académie des Sciences, Paris, serie II*, 317: 987–990.
- Egi N., Takai M., Shigehara N., and Tsubamoto T. (2004) Body mass estimates for Eocene eosimiid and amphipithecoid primates using prosimian and anthropoid scaling models. *International Journal of Primatology*, 25: 211–236.
- Gebo D.L. (1986) Miocene lorids—the foot evidence. *Folia Primatologica*, 47: 217–225.
- Gebo D.L. (1989) Postcranial adaptation and evolution in Loridae. *Primates*, 30: 347–367.
- Gebo D.L., MacLatchy L., Kityo R., Deino A., Kingston J., and Pilbeam D. (1997) A hominoid genus from the early Miocene of Uganda. *Science*, 276: 401–404.
- Godfrey L.R. and Jungers W.L. (2002) Quaternary fossil lemurs. In: Hartwig W.C. (ed.), *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp. 97–121.
- Godinot M. (2015) Fossil record of the primates from the Paleocene to the Oligocene. In: Henke W. and Tattersall I. (eds.), *Handbook of Paleoanthropology*. Springer-Verlag, Berlin, pp. 1137–1259.
- Groves C. (2001) *Primate Taxonomy*. Smithsonian Institution Press, Washington DC.
- Gunnell G.F. and Rose K.D. (2002) Tarsiiformes: evolutionary history and adaptation. In: Hartwig W.C. (ed.), *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp. 45–82.
- Harrison T. (2010) Later Tertiary Loridiformes. In: Werdelin L. and Sanders W.J. (eds.), *Cenozoic Mammals of Africa*. University of California Press, Oakland, pp. 333–349.
- Ishida H., Pickford M., Nakaya H., and Nakano Y. (1984) Fossil anthropoids from Nachola and Samburu Hills, Samburu District, Kenya. *African Study Monographs, Supplementary Issue*, 2: 73–85.
- Ishida H., Kunimatsu Y., Nakatsukasa M., and Nakano Y. (1999) New hominoid genus from the Middle Miocene of Nachola, Kenya. *Anthropological Science*, 107: 189–191.
- Ishida H., Kunimatsu Y., Takano T., Nakano Y., and Nakatsukasa M. (2004) *Nacholapithecus* skeleton from the Middle Miocene of Kenya. *Journal of Human Evolution*, 46: 69–103.
- Kingdon J. (2015) *The Kingdon Field Guide to African Mammals*, 2nd ed. Princeton University Press, Princeton.
- Kunimatsu Y. (1992) New finds of a small anthropoid primate from Nachola, northern Kenya. *African Study Monographs*, 13: 237–249.
- Kunimatsu Y. (1997) New species of *Nyanzapithecus* from Nachola, Northern Kenya. *Anthropological Science*, 105: 117–141.
- Kunimatsu Y., Ishida H., Nakatsukasa M., Nakano Y., Sawada Y., and Nakayama K. (2004) Maxillae and associated gnathodental specimens of *Nacholapithecus kerioi*, a large-bodied hominoid from Nachola, northern Kenya. *Journal of Human Evolution*, 46: 365–400.
- Kunimatsu Y., Nakatsukasa M., Sakai T., Saneyoshi M., Sawada Y., and Nakaya H. (2017) A newly discovered galagid fossil from Nakali, an early Late Miocene locality of East Africa. *Journal of Human Evolution*, 105: 123–126.
- Maxbauer D.P., Peppe D.J., Bamford M., McNulty K.P.,

- Harcourt-Smith W.E.H., and Davis L.E. (2013) A morphotype catalog and paleoenvironmental interpretations of early Miocene fossil leaves from the Hiwegi Formation, Rusinga Island, Lake Victoria, Kenya. *Palaeontologia Electronica*, 16: 28A.
- Mittermeier R.A., Rylands A.B., and Wilson D.E. (eds.) (2013) *Primates*. Lynx Edicions, Barcelona.
- Nakatsukasa M. and Kunimatsu Y. (2009) *Nacholapithecus* and its importance for understanding hominoid evolution. *Evolutionary Anthropology*, 18: 103–119.
- Nakatsukasa M., Yamanaka A., Kunimatsu Y., Shimizu D., and Ishida H. (1998) A newly discovered *Kenyapithecus* skeleton and its implications for the evolution of positional behavior in Miocene East African hominoids. *Journal of Human Evolution*, 34: 657–664.
- Nakatsukasa M., Tsujikawa H., Shimizu D., Takano T., Kunimatsu Y., Nakano Y., and Ishida H. (2003) Definitive evidence for tail loss in *Nacholapithecus*, an East African Miocene hominoid. *Journal of Human Evolution*, 45: 179–186.
- Nakatsukasa M., Kunimatsu Y., Nakano Y., Egi N., and Ishida H. (2007) Postcranial bones of infant *Nacholapithecus*: ontogeny and positional behavioral adaptation. *Anthropological Science*, 115: 201–213.
- Nakatsukasa M., Kunimatsu Y., Shimizu D., Nakano Y., Kikuchi Y., and Ishida H. (2012) Hind limb of the *Nacholapithecus kerioi* holotype and implications for its positional behavior. *Anthropological Science*, 120: 235–250.
- Nesbit Evans E.M., Van Couvering J.A.H., and Andrews P. (1981) Palaeoecology of Miocene sites in western Kenya. *Journal of Human Evolution*, 10: 99–116.
- Ni X., Gebo D.L., Dagosto M., Meng J., Tafforeau P., Flynn J.J., and Beard C.K. (2013) The oldest known primate skeleton and early haplorhine evolution. *Nature*, 498: 60–64.
- Phillips E.M. and Walker A. (2000) A new species of fossil lorisid from the Miocene of East Africa. *Primates*, 41: 367–372.
- Pickford M. (1981) Preliminary Miocene mammalian biostratigraphy for Western Kenya. *Journal of Human Evolution*, 10: 73–97.
- Pickford M. (2002) Ruminants from the Early Miocene of Napak, Uganda. *Annales de Paléontologie*, 88: 85–113.
- Pickford M. (2004) Palaeoenvironments of Early Miocene hominoid-bearing deposits at Napak, Uganda, based on terrestrial molluscs. *Annales de Paléontologie*, 90: 1–12.
- Pickford M. (2012) Lorisine primate from the Late Miocene of Kenya. *Journal of Biological Research-Bollettino della Società Italiana di Biologia Sperimentale*, 85: 47–52.
- Pickford M. (2015) Late Eocene lorisiform primate from Eocliff, Sperrgebiet, Namibia. *Communications of the Geological Survey of Namibia*, 16: 194–199.
- Pickford M. and Morales J. (1994) Biostratigraphy and palaeobiogeography of East Africa and the Iberian peninsula. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 112: 297–322.
- Pickford M. and Uhen M.D. (2013) *Namaia* Pickford et al., 2008, preoccupied by *Namaia* Green, 1963: proposal of a replacement name. *Communications of the Geological Survey of Namibia*, 15: 91.
- Pickford M., Wanas H., and Soliman H. (2006) Indications for a humid climate in the Western Desert of Egypt 11–10 Myr ago: evidence from Galagidae (Primates, Mammalia). *Comptes Rendus Palevol*, 5: 935–943.
- Pickford M., Senut B., Morales J., Mein P., and Sanchez I. M. (2008) Mammalia from the Lutetian of Namibia. *Memoir of the Geological Survey of Namibia*, 20: 465–514.
- Rasmussen D.T. and Nekaris K.A. (1998) Evolutionary history of lorisiform primates. *Folia Primatologica*, 69: 250–285.
- Rose M.D., Nakano Y., and Ishida H. (1996) *Kenyapithecus* postcranial specimens from Nachola, Kenya. *African Study Monographs Supplementary Issue*, 24: 3–56.
- Rossie J.B., Ni X., and Beard C.K. (2006) Cranial remains of an Eocene tarsier. *Proceedings of the National Academy of Sciences, USA*, 103: 4381–4385.
- Sawada Y., Saneyoshi M., Nakayama K., Sakai T., Itaya T., Hyodo M., Mukokya Y., Pickford M., Senut B., Tanaka S., Chujo T., and Ishida H. (2006) The ages and geological backgrounds of Miocene hominoids *Nacholapithecus*, *Samburupithecus*, and *Orrorin* from Kenya. In: Ishida H., Tuttle R.H., Pickford M., Ogiwara N., and Nakatsukasa M. (eds.), *Human Origins and Environmental Backgrounds*. Springer, New York, pp. 71–96.
- Schwartz J.H. (1996) *Pseudopotto martini*: a new genus and species of extant lorisiform primate. *Anthropological Paper of the American Museum of Natural History*, 78: 1–14.
- Seiffert E.R. (2012) Early primate evolution in Afro-Arabia. *Evolutionary Anthropology*, 21: 239–253.
- Seiffert E.R., Simons E.L., and Attia Y. (2003) Fossil evidence for an ancient divergence of lorises and galagos. *Nature*, 422: 421–424.
- Seiffert E.R., Simons E.L., Ryan T.M., and Attia Y. (2005) Additional remains of *Wadilemur elegans*, a primitive stem galagid from the late Eocene of Egypt. *Proceedings of the National Academy of Sciences, USA*, 102: 11396–11401.
- Suzuki M. (1987) A preliminary description of fossil woods collected from Site BG-X, west of Baragoi, Kenya. *African Study Monographs, Supplementary Issue*, 5: 163–167.
- Tsujikawa H. and Nakaya H. (2005) Geologic age and palaeoenvironments of mammalian faunas from Samburu Hills, Northern Kenya. *Chikyu Monthly*, 27: 603–611.
- Ungar P.S., Scott J.R., Curran S.C., Dunsworth H.M., Harcourt-Smith W.E.H., Lehmann T., Manthi F.K., and McNulty K.P. (2012) Early Neogene environments in East Africa: evidence from dental microwear of tragulids. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 342–343: 84–96.