

A new genus and species of Felidae (Mammalia) from Rusinga Island, Kenya, with notes on early Felidae of Africa

Un nuevo género y especie de Felidae (Mammalia) de la isla de Rusinga, Kenia, con notas sobre los primeros Felidae de África

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ABSTRACT

The lower Miocene (Burdigalian) deposits of the Hiwegi Fm., Rusinga Island, Kenya, have yielded a single specimen of a small felid. This specimen, here identified as the holotype of a new genus and species, is of the size of the smallest living Felidae. It shows some features of primitive, “*Pseudaelurus*-grade” cats, but also features of both morphology and metrics that are intermediate between this grade and modern Felidae, suggesting a transitional taxon. This is in contrast with *Diamantofelis* and *Namafelis* from Namibia, which, though aberrant, are more clearly of “*Pseudaelurus*-grade”. The Rusinga specimen is the most derived felid specimen of the lower Miocene.

Keywords: Africa, Kenya, Rusinga, lower Miocene, Felidae.

RESUMEN

Los depósitos del Mioceno inferior de la formación Hiwegi, en la Isla de Rusinga (Kenia), han proporcionado un espécimen aislado de un pequeño félido. Esta pieza, identificada aquí como holotipo de un nuevo género y especie, es del tamaño del félido actual más pequeño. Presenta algunos caracteres de los félidos primitivos de “grado *Pseudaelurus*”, pero también rasgos tanto métricos como morfológicos que son intermedios entre este grado y los Felidae modernos, sugiriendo que se trata de un taxón transicional. Por el contrario, *Diamantofelis* y *Namafelis* de Namibia, aunque de morfología aberrante, son más claramente del “grado *Pseudaelurus*”. El espécimen de Rusinga es el félido más derivado del Mioceno inferior.

Palabras clave: África, Kenia, Rusinga, Mioceno inferior, Felidae.

Introduction

The earliest history of the Felidae in Africa is brief yet difficult to interpret. From ca 12.5 Ma (middle Serravallian) onwards there is a reasonably continuous record, including taxa such as *Machairodus* that are also well known from other continents (Sardella & Werdelin, 2007; Werdelin & Peigné, 2010). However, before this time there are only two published records of Felidae, both from Arrisdrift in Namibia, dated to ca 17-17.5 Ma (i.e. middle-upper Burdigalian) on biostratigraphy

(Pickford & Senut, 2003). Other records of early Felidae in Africa, such as *Pseudaelurus africanus* (Andrews, 1914) are currently referred to *Afrosmilus*, which is now considered to belong to the distinct family Barbourfelidae (Morales *et al.*, 2001).

Two species, *Diamantofelis ferox* and *Diamantofelis minor*, were originally described from Arrisdrift (Morales *et al.*, 1998), with the latter subsequently transferred to a separate genus, *Namafelis* (Morales *et al.*, 2003). These two species share a number of traits, as indicated by their original

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placement in a single genus (Morales *et al.*, 1998). From the perspective of functional morphology and ecology, their most important features are those that differentiate them from *Afrosmilus* [and, by implication, from the Barbourfelidae as a whole (Morales *et al.*, 2001)]. These features include a rounded symphysis, non-compressed canine, and short post-canine diastema. However, *Diamantofelis* and *Namafelis* also share some features that distinguish them from contemporary Eurasian Felidae of the genera *Pseudaelurus* and *Styriofelis* (Werdelin *et al.*, 2010), including a short and high mandible, and shorter diastema. In addition, at least *N. minor* has a well developed talonid on m1, with a single, centrally positioned cusp, somewhat reminiscent of the m1 of the hyenid *Chasmaporthetes* (Kurtén & Werdelin, 1988). The only other presumed felid with an m1 talonid of similar appearance is *Pratifelis kansensis* (Hibbard, 1934) of the Hemphillian of Kansas, USA (late Miocene or earliest Pliocene), though the latter is a much larger species, and differs considerably in other respects from the Namibian forms. The relationships of the Arrisdrift species to other felids and, indeed, the question of whether they are felids at all [and not very aberrant barbourfelids - cf. (Werdelin *et al.*, 2010)], are still moot.

In this communication I report on a third felid specimen from the Burdigalian of Africa. This specimen, from Rusinga Island in Lake Victoria, eastern Africa, is clearly a felid and very distinct from *Diamantofelis* and *Namafelis*. Despite having been recovered in 1949 (according to the field number), this specimen has only been mentioned in the paleontological literature once (Werdelin & Peigné, 2010) - erroneously as coming from Songhor - and then only as Felidae indet. It was not discussed in either of the two previous works on lower Miocene carnivores from eastern Africa (Savage, 1965, Schmidt-Kittler, 1987). The specimen shows a number of interesting traits and opens up new possibilities regarding the early evolution of Felidae in general and Felinae (the extant cats) in particular.

Material and methods

The felid specimen from Rusinga consists of a small portion of a right mandibular ramus incorporating complete p4-m1, housed in the Paleontology Department, National Museums of Kenya, Nairobi. Comparative material of *Pseudaelurus* sp. has been studied by me at various times in various

museums, and more recently from the published literature. The majority of measurements of *Pseudaelurus* spp. were kindly provided by Dr. Stéphane Peigné, Paris and Dr. Manuel J. Salesa, Madrid. Measurements of extant felids as well as of the Rusinga specimen were taken by me with digital calipers to the nearest 1/100 mm and rounded to the nearest 1/10 mm. The measurements used are Lp4, Lm1: greatest mesiodistal length of tooth; Wp4, Wm1: greatest buccolingual width of tooth; Ltm1: greatest length of trigonid of tooth. Standard anatomical terminology has been used throughout. Institutional abbreviations are: KNM: Kenya National Museums. I am using marine stage names to simplify stratigraphic terminology and comparisons.

Systematic paleontology

Order Carnivora Bowdich, 1821

Suborder Feliformia Kretzoi, 1945

Family Felidae Fischer von Waldheim 1817

Genus *Asilifelis* gen. nov.

Type species: *Asilifelis coteae* gen. et sp. nov.

Diagnosis and description: As for species, below.

Differential diagnosis: Differs from *Proailurus* in absence of m2, taller paraconid more equal to protoconid on m1, metaconid lost. Differs from *Styriofelis* in p4 with less prominent mesial accessory cusp, m1 with better developed paraconid (more equal to protoconid in size), metaconid completely lost (sometimes present in *Styriofelis*), and talonid much more reduced. Differs from *Diamantofelis* in much less prominent p4 mesial accessory cusp, much more reduced m1 talonid. Differs from *Namafelis* in (apparently) taller main cusp of p4, much more reduced m1 talonid. Differs from all of these in much smaller size.

Etymology: From Swahili *asili*, origin, ancestor.

Occurrence: R106, Rusinga Island, Kenya; Hiwegi Fm., Fossil Bed Mb. The dating of the Hiwegi Fm. is currently in revision, but is now considered to be between 18-20 Ma, i.e. lower - middle Burdigalian (Peppe *et al.*, 2011).

Species *Asilifelis coteae* sp. nov. (Fig. 1A-C)

Diagnosis: Felidae of very small size, matching the smallest extant members of the family; p4 short, with accessory cusp development intermediate between '*Pseudaelurus*-grade' and '*Felis*-grade' Felidae; m1 with paraconid size relative to protoconid as in extant Felidae; metaconid absent; talonid reduced to almost the degree seen in extant Felidae.

Holotype: KNM RU 18349, fragment of right mandibular ramus with complete p4-m1 (Fig. 1A-C).

Etymology: For Susanne Cote, who opened my eyes to the wonders of the lower Miocene faunas of eastern Africa.

Description: The specimen includes a small portion of the ramus from just mesial to p4 to the mesial end of the ramus' ascent towards the coronoid process, with a small portion of the masseteric fossa preserved. The latter extends to just distal to the m1 talonid. Neither mental foramina nor any portion of the symphysis are preserved.

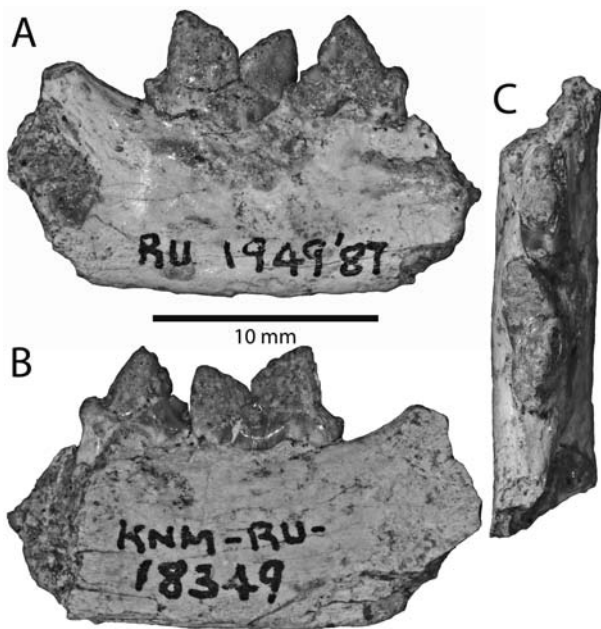


Fig. 1.—The holotype specimen of *Asilifelis coteae*, gen. et sp. nov., in A) buccal, B) lingual, and C) occlusal view. Photographs ©Kenya National Museums.

Both p4 and m1 are essentially complete, lacking only minute fragments chipped off the major cusps. They are somewhat imbricated, so that the distolingual end of the p4 overlaps the mesiobuccal end of the m1. There is a slight crack along the base of the m1 protoconid on the buccal side.

The p4 is slender, with a prominent mesial accessory cusp and cingulum. The main cusp is tall. Its relative height is greater than that of most extant Felidae and considerably greater than that of other lower Miocene Felidae. It approaches *Felis nigripes* in this respect, though the p4 of the latter is relatively taller still. Distally, the accessory cusp is prominent but relatively low. The tooth is then terminated by a short cingulum that extends around the distal end of the tooth.

The m1 is much longer than the p4. Both paraconid and protoconid are strongly developed, with the latter slightly taller than the former. The preparacristid is nearly vertical, as is the postprotocristid. The metaconid is entirely absent and the talonid is short and very low. The distal end of the tooth has a short cingulum and minute cingulum cusp. This cingulum extends along the lingual side of the tooth to the distal end of the paraconid.

Measurements (in mm): Lp4: 5.5; Wp4: 2.4; Lm1: 7.4; Wm1: 2.8; Ltm1: 6.7.

Morphologic and metric comparisons

The first thing to note about RU 18349 is that it is strikingly modern in appearance compared to contemporary Felidae. Given the very small size of the specimen, we can limit our comparisons to

only a few taxa: living species of the genus *Felis*, especially those with African distributions: *F. silvestris lybica*, *F. chaus*, *F. margarita*, and *F. nigripes*; the smallest species of “*Pseudaelurus*-grade”, *Styriofelis turnauensis*, and the recently described *S. vallesiensis* (Salesa *et al.*, in press); and finally the only other African Felidae of ‘*Pseudaelurus*-grade’ - *Diamantofelis ferox* and *Namafelis minor* (Morales *et al.*, 2003, Morales *et al.*, 1998). To place the latter metrically, comparisons with larger pseudaelurines such as *P. quadridentatus* and *S. lorteti* were also made.

To simplify the following comparisons, Figs. 2A and 3A illustrate metric relationships of extant Felidae and show that the small available samples of *F. margarita* and *F. s. lybica* do not differ from the larger sample of *F. chaus* except in size. Therefore, the two former species are removed from the comparisons with fossil taxa. *Felis nigripes* on the other hand, does differ from *F. chaus* and is retained in these comparisons.

Compared to the fossil taxa listed above, RU 18349 has a markedly reduced m1 talonid, reflected in the relatively short m1 seen in Figure 2B, where RU 18349 falls with *F. nigripes* and close to the extension of the regression line for *F. chaus*. It should also be noted that all but one of the specimens of *S. vallesiensis* fall within the 95% confidence ellipse for *F. chaus*. This suggests that the former species may be transitional in some respects between the ‘*Pseudaelurus*-grade’ and the ‘*Felis*-grade’. To provide comparisons for *D. ferox* and *N. minor*, Fig. 2C includes a sample of *Pseudaelurus quadridentatus*, as well as some *Styriofelis lorteti* specimens. This diagram shows that *S. turnauensis* that has a somewhat aberrant regression of m1 length and width, and that *D. ferox* is very close to *P. quadridentatus* in the metrics of this tooth, while *N. minor* lies close to the regressions of both *S. turnauensis* and *S. vallesiensis*.

That the m1 of extant cats is shorter due to the reduction of the talonid also in part explains the relatively shorter m1 in relation to p4 seen in these animals (Fig. 3B). This figure shows three distinct regressions: one for extant *Felis*, one for *S. turnauensis*, and an intermediate one for *S. vallesiensis*. This once again demonstrates the transitional character of the latter taxon. Both *F. nigripes* and RU 18349 fall on or near the extended line from *S. vallesiensis*, with RU 18349 slightly above it. This suggests that despite the reduced talonid and other characters of the Rusinga specimen, it is still par-

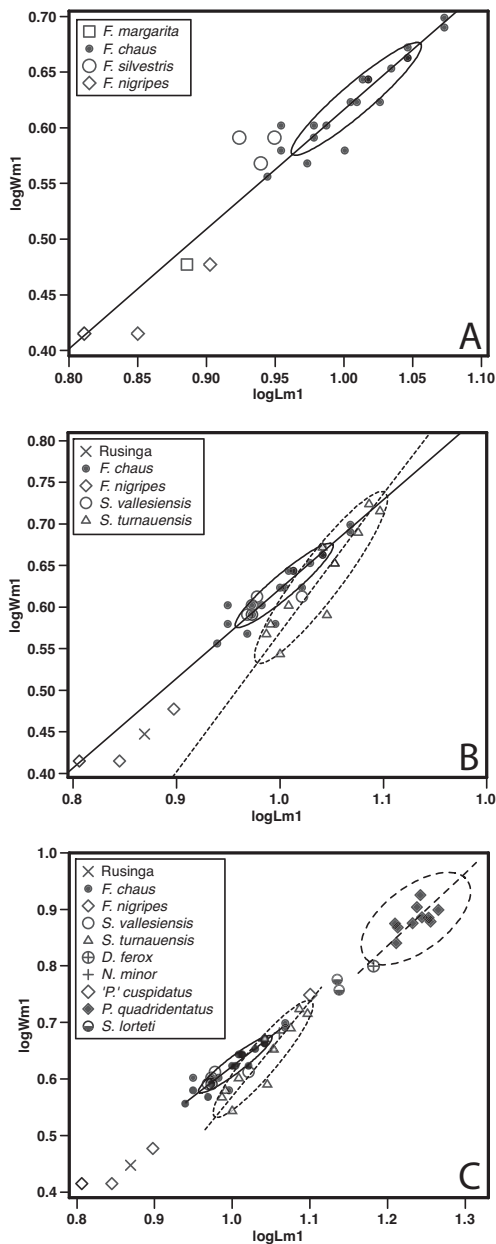


Fig. 2.—Bivariate diagrams of length and width of m1 of selected Felidae as labeled. A) Extant Felidae, with regression line and 95% confidence ellipse for *F. chaus*. All species fall near the regression line for *F. chaus*. For this reason, *F. silvestris* and *F. margarita* have been eliminated from the overall comparison. *F. nigripes* is retained because of its similarity in size to the Rusinga specimen. B) Overall comparison of extant and extinct Felidae, with regression lines and 95% confidence ellipses for *F. chaus* (solid lines) and *S. turnauensis* (dashed lines). The regressions differ considerably in slope, and the Rusinga specimen falls nearer the *F. chaus* regression. C) Comparison of extant and extinct taxa incorporating some larger species. Regression lines and 95% confidence ellipses are shown for *F. chaus* (solid lines), *S. turnauensis* (short dashes), and *P. quadridentatus* (long dashes). Note the position of *D. ferox* very near the 95% confidence ellipse of *P. quadridentatus*.

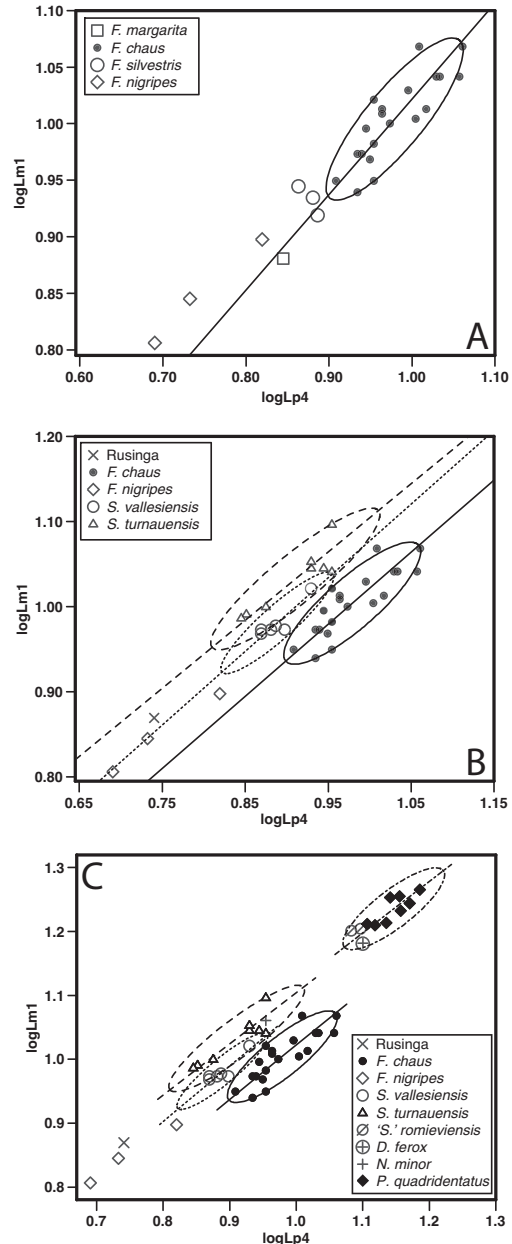


Fig. 3.—Bivariate diagrams of length of p4 and m1 of selected Felidae as labeled. A) Extant Felidae, with regression line and 95% confidence ellipse for *F. chaus*. *Felis silvestris* and *F. margarita* fall near the regression line for *F. chaus* and have been eliminated from the overall comparison. *F. nigripes* differs, and has been retained. B) Overall comparison of extant and extinct Felidae, with regression lines and 95% confidence ellipses for *F. chaus* (solid lines), *S. turnauensis* (dashed lines), and *S. vallesiensis* (dotted lines). The regressions are similar in slope but differ in location. The Rusinga specimen falls near the *S. vallesiensis* regression, as does *F. nigripes*. C) Comparison of extant and extinct Felidae including some larger species. Regression lines and 95% confidence ellipses are shown for *F. chaus* (solid lines), *S. turnauensis* (dashed lines), *S. vallesiensis* (dotted lines), and *P. quadridentatus* (dash-dot lines). Note the position of *D. ferox* within the *P. quadridentatus* 95% confidence ellipse, and that the regression for the latter taxon is very similar to that of *S. turnauensis* (but not *S. vallesiensis*).

tially of 'Pseudaelurus-grade' and not yet a modern-type feline.

To better place *Diamantofelis* and *Namafelis* metrically in relation to Eurasian pseudaelurines, a third diagram of p4 versus m1 length incorporating larger species was made (Fig. 3C). The smaller *Namafelis minor* lies comfortably within the 95% confidence ellipse of *S. turnauensis*, while the relative lengths of p4 and m1 in the larger *D. ferox* are within the 95% confidence ellipse of *P. quadridentatus*.

Apart from the features discussed above, that leave traces in the metrics of the specimens, the only noteworthy feature of RU 18349 lies in the relatively low mesial and distal accessory cusps on p4. In felids of 'Pseudaelurus-grade' these accessory cusps are generally larger and more distinctly set off from the main cusp. At the same time, they are less appressed to the main cusp than in the majority of small extant Felidae, thus again representing something of a transitional form between the 'Pseudaelurus-grade' and 'Felis-grade' cats. Both *D. ferox* and *N. minor* are of 'Pseudaelurus-grade' in this respect.

Discussion

The existence of a member of the Felidae as derived as *Asilifelis coteae* gen. et sp. nov. in the Burdigalian of Africa is surprising. In Eurasia and North America, the Burdigalian is the time of diversification of felids of 'Pseudaelurus-grade', including the genera *Pseudaelurus*, *Styriofelis*, and *Hyperailurictis* (Werdelin *et al.*, 2010). It is not until much later, around the beginning of the Tortonian (11.6 Ma) that felids of 'Felis-grade' appear, with the first appearance of *Pristifelis attica* (Salesa *et al.*, in press). At the same time, since the only felids of 'Pseudaelurus-grade' are the aberrant *D. ferox* and *N. minor* (the felid status of which has still to be determined), it is not unreasonable that there is room for one or several small felids in the ecosystems.

The importance of *A. coteae* gen. et sp. nov. thus is two-fold: its presence as the only member of its family in eastern Africa until the latest middle Miocene, and its derived nature. With regard to the first, it may be that the plethora of small Viverridae and Herpestidae in the lower Miocene of Africa (Morlo *et al.*, 2007, Savage, 1965, Schmidt-Kittler, 1987, Werdelin & Peigné, 2010) excluded Felidae from these ecosystems. Alternatively, African Felidae

may primitively have favored habitats that are poorly or not at all sampled at these early African localities. A similar cause may explain the presence of the ursid *Hemicyon* sp. at Rusinga, approximately 10 million years before the next occurrence of Ursidae on the continent.

The derived nature of the specimen is equally hard, if not harder, to explain. One could speculate that competition from the many Viverridae and Herpestidae forced a precocious evolution of the lineage into a part of hypercarnivore niche space that Felidae did not reach elsewhere until much later. With only one specimen available, there are not enough data to evaluate this possibility. Nor can we know whether this African lineage migrated out of Africa to become the founder of the modern Felidae radiation - a possibility that does not militate against the reconstruction of the earliest Felidae ancestor as coming from Asia (Johnson *et al.*, 2006), since this only refers to extant Felidae, not to any possible stem lineage taxa. An origin from African antecedents would at least explain why fully evolved Felidae of extant grade, such as *P. attica* and *Machairodus*, appear so abruptly in Eurasia near the beginning of the Tortonian. But again, without more material, this rapidly enters the realm of pure speculation.

Diamantofelis ferox and *N. minor* are clearly 'Pseudaelurus-grade' forms. Whether they belong to this grade-group or are not felids at all cannot be determined from metric analysis at this time and is still a moot point. They match Eurasian pseudaelurines in dental metrics, and, interestingly, show a size difference typical of sympatric Eurasian pseudaelurines. However, as pointed out by Morales *et al.*, (1998, 2003), they share certain dental features with *Afrosmilus* and the possibility that they are conical-toothed barbourofelids must be entertained. At all events, they are less derived than *A. coteae* gen. et sp. nov. and the relationship between them must be distant, involving separate migrations into Africa from Eurasia in the late Oligocene or early Miocene.

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References

- Andrews, C.W. (1914). On the Lower Miocene vertebrates from British East Africa, collected by Dr. Felix Oswald. *Quarterly Journal of the Geological Society of London*, 70: 163-186. doi:/10.1144/GSL.JGS.1914.070.01-04.11
- Bowdich, T.E. (1821). *An analysis of the natural classifications of Mammalia for the use of students and travellers*. J. Smith, Paris, 115 pp.
- Fischer von Waldheim, G. (1817). *Adversaria Zoologica, fasciculus primus. Mémoires de la Société des Naturalistes de Moscou*, 5: 357-446.
- Hibbard, C.W. (1934). Two new genera of Felidae from the Middle Pliocene of Kansas. *Transactions of the Kansas Academy of Sciences*, 37: 239-255. doi:/10.2307/3625308
- Johnson, W.E.; Eizirik, E.; Pecon-Slattey, J.; Murphy, W.J.; Antunes, A.; Teeling, E. & O'Brien, S.J. (2006). The Late Miocene radiation of modern Felidae: a genetic assessment. *Science*, 311: 73-77. doi:/10.1126/science.1122277
- Kretzoi, M. (1945). Bemerkungen über das Raubtiersystem. *Annales Historico-Naturales Musei Nationalis Hungarici*, 38: 59-83.
- Kurtén, B. & Werdelin, L. (1988). A review of the genus *Chasmaporthetes* Hay, 1921 (Carnivora, Hyainidae). *Journal of Vertebrate Paleontology*, 8: 46-66. doi:/10.1080/02724634.1988.10011683
- Morales, J.; Pickford, M.; Fraile, S.; Salesa, M.J. & Soria, D. (2003). Creodonta and Carnivora from Arrisdrift, early Middle Miocene of southern Namibia. *Memoirs of the Geological Survey of Namibia*, 19: 177-194.
- Morales, J.; Pickford, M.; Soria, D. & Fraile, S. (1998). New carnivores from the basal Middle Miocene of Arrisdrift, Namibia. *Eclogae geologicae Helvetiae*, 91: 27-40.
- Morales, J.; Salesa, M.J.; Pickford, M. & Soria, D. (2001). A new tribe, new genus and two new species of Barbourofelinae (Felidae, Carnivora, Mammalia) from the Early Miocene of East Africa and Spain. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, 92: 97-102. doi:/10.1017/S0263593300000067
- Morlo, M.; Miller, E.R. & El-Barkooky, A.N. (2007). Creodonta and Carnivora from Wadi Moghra, Egypt. *Journal of Vertebrate Paleontology*, 27: 145-159. doi:/10.1671/0272-4634(2007)27[145: CACFWM]2.0.CO;2
- Peppe, D.J.; Deino, A.L.; McNulty, K.P.; Lehmann, T.; Harcourt-Smith, W.E.H.; Dunsworth, H.M. & Fox, D.L. 2011. New age constraints on the early Miocene faunas from Rusinga and Mfangano Islands (Lake Victoria, Kenya). *American Journal of Physical Anthropology*, 52 (supplement): 237.
- Pickford, M. & Senut, B. (2003). Miocene paleobiology of the Orange River Valley, Namibia. *Memoirs of the Geological Survey of Namibia*, 19: 1-22.
- Salesa, M.J.; Antón, M.; Morales, J. & Peigné, S. (in press). Systematics and phylogeny of the small felines (Carnivora, Felidae) from the Late Miocene of Europe: a new species of Felinae from the Vallesian of Batallones (MN 10, Madrid, Spain). *Journal of Systematic Palaeontology*.
- Sardella, R. & Werdelin, L. (2007). *Amphimachairodus* (Felidae, Mammalia) from Sahabi (latest Miocene - earliest Pliocene, Libya), with a review of African Miocene Machairodontinae. *Rivista Italiana di Paleontologia e Stratigrafia*, 113: 67-77.
- Savage, R.J.G. (1965). Fossil mammals of Africa: 19. The Miocene Carnivora of East Africa. *Bulletin of the British Museum (Natural History), Geology*, 10: 241-316.
- Schmidt-Kittler, N. (1987). The Carnivora (Fissipedia) from the Lower Miocene of East Africa. *Palaeontographica, Abt. A*, 197: 85-126.
- Werdelin, L. & Peigné, S. (2010). Carnivora. In: *Cenozoic Mammals of Africa* (Werdelin, L. & Sanders, W.J., eds.). University of California Press, Berkeley, 609-663.
- Werdelin, L.; Yamaguchi, N.; Johnson, W.E. & O'Brien, S.J. (2010). Felid phylogeny and evolution. In: *The Biology and Conservation of Wild Felids* (Macdonald, D.M. & Loveridge, A., eds.). Oxford University Press, Oxford, 59-82.

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