

Systematic palaeontology (vertebrate palaeontology)

The African species *Megantereon whitei* from the Early Pleistocene of Monte Argentario (South Tuscany, Central Italy)

Raffaele Sardella^{a,*}, Mauro Petrucci^a, Lorenzo Rook^b

^a Dipartimento di Scienze della Terra, Sapienza Università di Roma, P.le A. Moro 5, 00185 Roma, Italy

^b Dipartimento di Scienze della Terra, Università di Firenze, Via La Pira 4, 50121 Firenze, Italy

^c Istituto Italiano di Paleontologia Umana, Piazza Mincio 2, 00198 Roma, Italy

Received 1st September 2008; accepted after revision 24 September 2008

Available online 12 November 2008

Written on invitation of the editorial board

Abstract

A partial skull and articulated postcranial elements of *Megantereon whitei* have been recorded during the 1950s from a karst deposit in the Monte Argentario area (Grosseto). These fossils recently became available for study. The bones are quite well preserved, included in a hard reddish matrix with calcareous clasts. The fossil is part of a faunal assemblage referred to the Late Villafranchian (Early Pleistocene). *M. whitei* from Monte Argentario is characterised by elongated upper canines, stronger than those of the Upper Valdarno (Tuscany) specimens and similar to the Pirro Nord (Apulia) fossil. The manus is robust, the first phalanges are quite long in comparison to the metacarpals. The Early Pleistocene European *M. whitei* represents an African element that took part in the faunal dispersal from Africa to Europe that occurred at the Plio-Pleistocene transition. **To cite this article: R. Sardella et al., C. R. Palevol 7 (2008).**

© 2008 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

Résumé

L'espèce africaine *Megantereon whitei* du Pléistocène inférieur du Mont Argentario (Sud de la Toscane, Italie centrale). Un crâne incomplet associé à des restes postcrâniens de *Megantereon whitei* a été collecté pendant les années 1950 dans des dépôts karstiques de la région du Monte Argentario (Grosseto), mais leur étude n'a commencé qu'il y a peu. Les os sont bien préservés, mais inclus dans une gangue très dure avec des éclats de calcaire. Le fossile appartient à un ensemble faunique daté du Villafranchien tardif (Pléistocène inférieur). Le spécimen de *M. whitei* du Monte Argentario est caractérisé par des canines supérieures allongées, plus fortes que celles des exemplaires du Val d'Arno supérieur (Toscane) et semblables au fossile de Pirro Nord (Apulie). La main est robuste, avec des premières phalanges assez longues, relativement aux métacarpiens. Le *M. whitei* du Pléistocène inférieur européen représente un élément africain qui appartient à la dispersion faunique de la limite Plio-Pléistocène d'Afrique vers Europe. **Pour citer cet article : R. Sardella et al., C. R. Palevol 7 (2008).**

© 2008 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

Keywords: *Megantereon*; Plio-Pleistocene; Villafranchian; Africa; Europe; Italy; Dispersal event

Mots clés : *Megantereon* ; Plio-Pléistocène ; Villafranchien ; Afrique ; Europe ; Italie ; Dispersion

* Corresponding author.

E-mail address: raffaele.sardella@uniroma1.it (R. Sardella).

1. Introduction

In 1958, Baschieri and Segre [2] described a “terra rossa” deposit with vertebrate fossil remains at Monte Argentario (South Tuscany, Central Italy). The geological structure of Monte Argentario is characterised by Permo-Trias calcareous and dolomitic rocks, which were affected by karst activity during the Plio-Pleistocene [4]. Today, Monte Argentario is linked to the mainland by three sandy connections (tomboli).

Baschieri and Segre, on the basis of indications by previous authors [5,8,24] identified the reddish continental deposits (cemented “terra rossa”) in the area of old quarries and collected several bones of fossil vertebrates, in some cases articulated and well preserved. They referred the faunal assemblage, characterised by the occurrence of the Tuscan rhino and machairodont felid (in their original words: “fauna a *Rinoceronte etrusco e macairodo*”) to the Villafranchian, and provided the following faunal list: *Castor* sp., *Lepus etruscus*, *Machairodus crenatidens*, *Panthera pardus*, *Lynx issiodorensis*, *Ursus etruscus*, *Hyaena* sp., *Canis falconeri*, *Dicerorhinus etruscus*, *Leptobos* cf. *L. etruscus* and Tragulidae indet. [2].

Almost all of the fossil bones were stored in Rome at the Istituto Italiano di Paleontologia Umana. In 1992–94, one of us (RS) had the opportunity to study the saber-toothed cat for his PhD dissertation. Sardella [21] referred the craniodental remains and the partial articulated skeleton to *Megantereon* ex gr *cultridens* (advanced form); he also recognized the occurrence of an associated second saber tooth felid, *Homotherium*, represented only by a fragmentary humerus [21,22].

A preliminary reconsideration of the fossil collection yields the following updated faunal list: *Ursus* cf. *U. etruscus*, *Canis* sp., *Pachycrocuta brevirostris*, *Lynx issiodorensis*, *Panthera* ex gr. *toscana-gombaszoegensis*, *Homotherium* sp., *Megantereon whitei*, *Stephanorhinus* cf. *hundsheimensis*, *Leptobos* sp., *Bovidae* indet. [22]. The Monte Argentario faunal assemblage can be referred to the Early Pleistocene (Late Villafranchian, Farneta Faunal Unit) [9,23].

The entire Monte Argentario faunal collection is under revision. The larger breccia blocks (in particular, the *Megantereon* partial articulated skeleton) are going to be properly restored and prepared. In addition, new field activities to rediscover the fossil deposits are planned for 2009 in agreement with the local officers from the Soprintendenza Archeologica per la Toscana.

2. *Megantereon*

The genus *Megantereon* includes Plio-Pleistocene jaguar-sized, short limbed, dirk-toothed cats with a stoutly built postcranial skeleton, in which the robust distal limb bones indicate an ambushing hunting method. Taxonomy and evolution of this felid have been discussed in several papers issued during recent decades and different interpretations have been provided [7,10,12,13,16,17,22,26,29]. Of particular concern is the debate on the taxonomy of the Old World Plio-Pleistocene *Megantereon*.

All the authors agree to refer Pliocene European specimens to *M. cultridens*. Different interpretations are proposed for Early Pleistocene European forms.

Turner [26] considered the differences recorded into the Eurasian and African sample of *Megantereon* as due to sexual dimorphism, comparing the data to those of the living leopard. Other authors [8,15] claimed a convergent evolution of the European samples of *M. cultridens* with the African *M. whitei*, due to the paleoclimatic and paleoenvironmental conditions prevalent at the end of Pliocene. They named this form *M. cultridens adroveri* [10,17].

Sardella [22] suggested the use of open taxonomy including the Early Pleistocene European specimens in *Megantereon* ex gr. *cultridens* (advanced form).



Fig. 1. Location of the Italian localities with *Megantereon*.

Fig. 1. Localisation des sites italiens à *Megantereon*.

Martínez-Navarro and Palmqvist [12,13] suggested that the Early Pleistocene European *Megantereon* represent a dispersal of the African form *M. whitei* that replaced *M. cultridens* at the Plio-Pleistocene transition. This hypothesis seems to have recently reached a larger consensus [16].

The two species differ mainly in the following craniodental features:

- *M. cultridens* cheek teeth tend to be larger than those of *M. whitei*, and their proportions are different;
- *M. cultridens* has on average the smallest upper canines, although the sample size and range for *M. cultridens* are greater than for *M. whitei*.

The Italian sample includes informative specimens. In particular, for several years the latest Pliocene Upper Valdarno fossils [6,7] constituted a rich basis for comparison in *Megantereon* studies. *Megantereon* remains have also been discovered in the Middle-Late Villafranchian faunal assemblages from the Late Pliocene



Fig. 2. The specimen ARG 31 from Monte Argentario stored at the Istituto Italiano di Paleontologia Umana (Roma). Scale bar: 5 cm (photo R. Sardella).

Fig. 2. Le spécimen ARG 31 du Monte Argentario, conservé à l'Istituto Italiano di Paleontologia Umana (Rome). Échelle: 5 cm (photo R. Sardella).

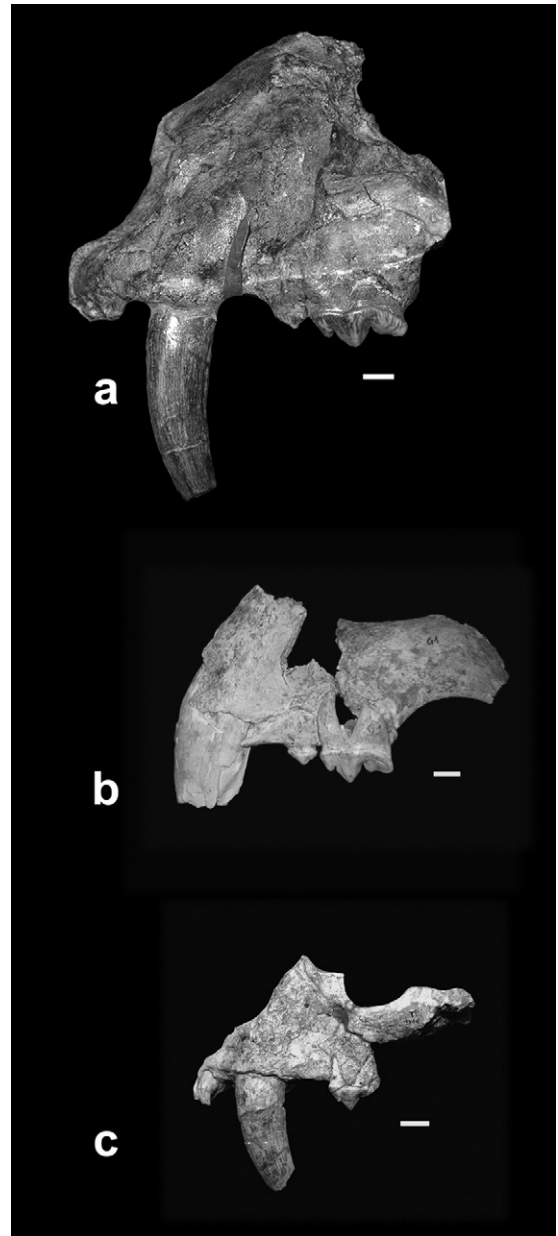


Fig. 3. *Megantereon* skulls from Italian localities (photos A. Cipullo and R. Sardella). a: *M. cultridens* (IGF 830) from Sammezzano, Upper Valdarno, Tuscany (stored at the Museo di Paleontologia di Firenze). b: *M. whitei* (G1) from Pirro Nord, Apulia (stored at the Dipartimento di Scienze della Terra, Sapienza Università di Roma). c: *M. whitei* (ARG31) from Monte Argentario, Tuscany (stored at the Istituto Italiano di Paleontologia Umana, Roma). Scale bar: 1 cm.

Fig. 3. Crânes de *Megantereon* des localités italiennes (photos A. Cipullo et R. Sardella). a: *M. cultridens* (IGF 830) de Sammezzano, Haut Valdarno, Toscane (conservé au Museo di Paleontologia de Florence). b: *M. whitei* (G1) de Pirro Nord, Apulie (conservé au Dipartimento di Scienze della Terra, Sapienza Università de Rome). c: *M. whitei* (ARG31) du Monte Argentario, Toscane (conservé à l'Istituto Italiano di Paleontologia Umana, Rome). Échelle: 1 cm.

Table 1

Measurements (in mm) of metacarpals of *Megantereon* from Sénèze, Pirro Nord, Monte Argentario and Villa S. Faustino (see text for the chronology of the localities).

Tableau 1 Mesures (en mm) des métacarpes de *Megantereon* de Sénèze, Pirro Nord, Monte Argentario et Villa S. Faustino (voir texte pour la chronologie des localités).

Locality	Age	Element	Coll	GL	BP	DP	BM	DM	BD	DD
Sénèze	Late Pliocene	MC II	SE 311	77.8	20.18	24.01	11.44	12.06	18.03	17.43
Pirro Nord	Early Pleistocene	MC II	G 12	75	18	21	11.5	11	18	14
Sénèze	Late Pliocene	MC III	SE 311	84.6	20.7	21.4	12.7	10.8	19.4	17.9
Villa S. Faustino	Late Pliocene	MC III	BT 16	91	22	22.7	12.8	12.4	21.5	17.5
Argentario	Early Pleistocene	MC III	ARG 30	86						
Pirro Nord	Early Pleistocene	MC III	G 13	81.5	20	20	12.8	10	18.5	16
Sénèze	Late Pliocene	MC IV	SE 311	83.41	14.8	18.6	10.6	10.3	17.3	13.85
Pirro Nord	Early Pleistocene	MC IV	G 14	77	15	17.5	10.5	10.2	16.5	15.5
Argentario	Early Pleistocene	MC IV	ARG 30	78.7						
Sénèze	Late Pliocene	MC V	SE 311	69	16.8	17.4	10.2	10.5	16	16.5
Villa S. Faustino	Early Pleistocene	MC V	BT 17	72	15.2	18	10	10.6	17	16
Pirro Nord	Early Pleistocene	MC V	G 15	65	16.8	16.5	11	10	16	13.8
Argentario	Early Pleistocene	MC V	ARG 30	68						

GL: greatest length; BP: proximal breadth; DP: proximal depth; BM: medium breadth; DM: medium depth; BD: distal breadth; DD: distal depth.

sites of Collepardo, Olivola and Villa S. Faustino (previously referred to the Early Pleistocene), and the Early Pleistocene sites of Monte Argentario and Pirro Nord [1,7,9,22] (Fig. 1).

3. The *Megantereon* specimen from Monte Argentario

The *Megantereon* material from Monte Argentario, here referred to the species *M. whitei*, is represented by a right mandible with p4 and m1 (ARG34), part of a skull (ARG31, left dental and maxilla with teeth) and some elements of an articulated skeleton (ARG30) including the right upper canine, left mandible with teeth, an axis, and the left forelimb (humerus, ulna and radius, II to V metacarpal, first phalanges) (Fig. 2).

The upper incisors are strong: a diastema separates them from the upper canine. The upper canines are proportionally stronger than in the Tuscan specimens from Upper Valdarno. Such a feature seems to be typical of *M. whitei* and is even more evidenced in the specimen G1 from Pirro Nord [16,22] (Fig. 3).

P3 in ARG31 is reduced, P4 is posteriorly damaged (the carnassial blade is missing), but shows the typical morphology of the genus. The left hemimandible is almost complete. The mental profile is almost vertical, p3 is missing but, judging from the alveolus, was single rooted and reduced. Both p4 and m1 are quite well preserved.

Possibly some cervical vertebrae and the left forelimb of the animal are included in the rock block. At present all the measurements cannot be taken, because

the bones are still included in the matrix. The restoration of the specimen will start within 2008 and hopefully new elements of the skeleton may be found. Comparison with the manus of *M. cultridens* from Sénèze [3] and *M. whitei* from Pirro Nord reveals great similarities. Metacarpals have strong diaphyses and quite long first phalanges, similar to those of extant felids. The humerus, ulna and metacarpals are much stouter and stronger in *Megantereon* than in *Panthera*, which is confirmed by the Monte Argentario specimens (Table 1). Such features of the forelimb of *Megantereon* are closely related to ambush behaviour [25]. The powerfully developed forelimbs suggest that this felid killed the prey (cervids and equids) biting them in the throat, after immobilizing them with the forelimbs [15,27]. A more detailed analysis on the postcranial skeleton of *Megantereon* is under progress and will point out further differences between *M. cultridens* and *M. whitei*.

4. Conclusions

The taxonomy of *Megantereon* is based mainly on craniodental features because of the scantiness of the fossil record. Valuable new data will be provided by the detailed study of the outstanding Chinese fossil sample [18] and by the analysis of the postcranial skeleton.

The Italian fossil record, and in particular the specimen from Monte Argentario, is interesting for both taxonomic and morpho-functional points of view. The available data suggest that the Early Pleistocene European dirk-toothed cats can be assigned to *M. whitei* that replaced *M. cultridens* at Plio-Pleistocene transition.

The dispersal of *M. whitei* into Europe occurred concurrently with other African species [11,19,28]. The Levantine Corridor is the principal path of dispersal between Africa and Eurasia and it is evident that the influence of forms of African origin in the Early Pleistocene of the Levant, as at the 'Ubeidiya site (Israel) [14,25], where the occurrence of (among others) *Homo*, *Theropithecus* sp., *Hippopotamus gorgops*, *Kolpochoerus olduvaiensis*, *Pelorovis oldowayensis*, *Megantereon* cf. *whitei*, *Crocota crocuta*, is documented. However, only few of these African species expanded their range into northernmost regions of Eurasia. This group is composed together with *M. whitei* by *T. oswaldi*, *Hippopotamus antiquus* and, obviously, *Homo* [9,18,20]. This assemblage (or representatives of this assemblage) has(ve) been partially found in western Europe, in Spain (Venta Micena, Fuente Nueva-3, Barranco León-5, Cueva Victoria and Incarcal), France (Sainzelles), Italy (Pirro Nord), Germany (Untermassfeld), Greece (Apollonia and Ravin de Voulgarakis) [9]. Monte Argentario provides further evidence of this assemblage in western Europe.

Acknowledgments

We thank the RHOI initiative and Prof. L. De Bonis for inviting us to contribute to the Carnivora working group meeting. This paper is framed within a larger project of revision and study of the Monte Argentario fauna developed by one of us (RS) under the Istituto di Paleontologia Umana (IIPU, Rome) support.

References

- [1] P. Ambrosetti, G. Basilici, L. Capasso Barbato, M.G. Carboni, G. Di Stefano, D. Esu, E. Gliozzi, C. Petronio, R. Sardella, E. Squazzini, Il Pleistocene Inferiore nel Ramo Sud occidentale del Bacino Tiberino (Umbria): aspetti litostratigrafici e biostratigrafici, *Il Quaternario* 8 (1995) 19–36.
- [2] F. Baschieri, A.G. Segre, Notizie su un ritrovamento di fauna a Rinoceronte etrusco e Macairodo all'Argentario (prov. di Grosseto), *Quaternaria* 4 (1958) 195–197.
- [3] P. Christiansen, J.S. Adolfssen, Osteology and ecology of *Megantereon cultridens* SE311 (Mammalia; Felidae; Machairodontinae), a sabrecat from the Late Pliocene – Early Pleistocene of Senéze, France, *Zool. J. Linn. Soc.* 151 (2007) 833–884.
- [4] F.A. Decandia, A. Lazzarotto, Le unità tettoniche del Monte Argentario (Toscana meridionale), *Mem. Soc. Geol. Ital.* 20 (1980) 385–393.
- [5] A. D'Achiardi, L. Busatti, Ossa animali e resti dell'industria umana rinvenuti in una breccia ossifera sul M. Argentario, *Nuovo Cimento Ser. I* (1879) 67.
- [6] E. Fabrini, I *Machairodus* (*Megantereon*) del Valdarno Superiore, *Boll. Reg. Com. Geol. Ser. 3* (1) (1890) 1–43.
- [7] G. Ficcarelli, The Villafranchian machairodonts of Tuscany, *Paleontogr. Ital.* 71 (1979) 17–26.
- [8] C.I. Forsyth Major, L. Busatti, Di una breccia ossifera sul M. Argentario, *Atti Soc. Tosc. Sci. Nat., Proc. Verb.* 3 (1882) 113.
- [9] E. Gliozzi, L. Abbazzi, P. Argenti, A. Azzaroli, L. Caloi, L. Capasso Barbato, G. di Stefano, D. Esu, G. Ficcarelli, O. Girotti, T. Kotsakis, F. Masini, P. Mazza, C. Mezzabotta, M.R. Palombo, C. Petronio, L. Rook, B. Sala, S. Sardella, E. Zanalda, D. Torre, Biochronology of selected Mammals, Molluscs and Ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of the art, *Riv. Ital. Paleontol. Stratigr.* 103 (1997) 369–388.
- [10] H. Hemmer, Die Feliden aus dem Epivillafranchium von Untermassfeld, in: R. D. Kahlke, (Ed.), *Das Pleistozän von Untermassfeld bei Meiningen (Thüringen)*, Römisch-Germanisches Zentralmuseum 40 (2001) 699–782.
- [11] B. Martínez-Navarro, Hippos, pigs, bovids, sabertoothed tigers, monkeys and hominids: Dispersals during Late Pliocene and Early Pleistocene times through the Levantine Corridor, in: N. Goren-Inbar, J.D. Speth (Eds.), *Human Paleoecology in the Levantine Corridor*, Oxbow Books, Oxford, 2004, pp. 37–51.
- [12] B. Martínez-Navarro, P. Palmqvist, Presence of the African Machairodont *Megantereon whitei* (Broom, 1937) (Felidae, Carnivora, Mammalia) in the Lower Pleistocene Site of Venta Micena (Orce, Granada, Spain), with some considerations on the origin, evolution and dispersal of the genus, *J. Archaeol. Sci.* 22 (1995) 569–582.
- [13] B. Martínez-Navarro, P. Palmqvist, Presence of the African Saber-toothed Felid *Megantereon whitei* (Broom, 1937) (Mammalia, Carnivora, Machairodontinae) in Apollonia-I (Mygdonia Basin, Macedonia, Greece), *J. Archaeol. Sci.* 23 (1996) 869–872.
- [14] B. Martínez-Navarro, M. Belmaker, O. Bar-Yosef, The large carnivores from 'Ubeidiya (Early Pleistocene, Israel): biochronological and biogeographical implications, *J. Hum. Evol.* (in press).
- [15] P. Palmqvist, D.R. Gröcke, A. Arribas, R.A. Fariña, Paleocological reconstruction of a Lower Pleistocene large mammal community using biogeochemical ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{18}\text{O}$, Sr:Zn) and ecomorphological approaches, *Paleobiology* 29 (2003) 205–229.
- [16] P. Palmqvist, V. Torregrosa, J.A. Pérez-Claros, B. Martínez-Navarro, A. Turner, A re-evaluation of the diversity of *Megantereon* (Mammalia, Carnivora, Machairodontinae) and the problem of species identification in extinct carnivores, *J. Vertebr. Paleontol.* 27 (2007) 160–175.
- [17] J. Pons-Moyà, Los carnívoros (Mammalia) de Venta Micena (Granada, España), *Paleontol. Evol. Mem. Esp.* 1 (1987) 109–128.
- [18] Z. Qiu, T. Deng, B. Wang, Early Pleistocene mammalian fauna from Longdan, Dongxiang, Gansu, China, *Paleontol. Sin.*, N. Ser. C 191 (2004) 1–198, in Chinese with English summary.
- [19] H.J. O'Regan, L.C. Bishop, S. Elton, A. Lamb, A. Turner, Afro-Eurasian mammalian dispersal routes of the Late Pliocene and Early Pleistocene and their bearing on earliest hominin movements, *Cour. Forsch. Inst. Senckenberg* 256 (2006) 305–314.
- [20] L. Rook, B. Martínez-Navarro, F.C. Howell, Occurrence of *Theropithecus* sp. in the Late Villafranchian of southern Italy and implication for Early Pleistocene "out of Africa" dispersals, *J. Hum. Evol.* 47 (2004) 267–277.
- [21] R. Sardella, Sistematica e distribuzione stratigrafica dei Macairodontini dal Miocene Superiore al Pleistocene, PhD dissertation, Bologna, Firenze, Modena and Roma "La Sapienza" Universities, Rome (1994) 137 p.

- [22] R. Sardella, The Plio-Pleistocene dirk-toothed cat *Megantereon* ex gr. *cultridens* (Mammalia, Felidae, Macharodontinae) with comments on taxonomy, origin and evolution, N. Jahrb. Geol. Paläontol. Abh. 207 (1998) 1–36.
- [23] R. Sardella, The Late Villafranchian *Panthera* ex gr. *toscana-gombaszoegensis* from Monte Argentario (Grosseto, South Tuscany, Central Italy), Cour. Forsch. Inst. Senckenberg 256 (2006) 23–27.
- [24] A.G. Segre, Giacimenti pleistocenici con fauna e industria litica a Monte Argentario (Grosseto), Riv. Sci. Preist. 14 (1959) 1–18.
- [25] E. Tchernov (Ed.), The Lower Pleistocene Mammals of 'Ubeidiya (Jordan Valley), Mem. Trav. Cent. Rech. Fr. Jérus. 5 (1986) 1–405.
- [26] A. Turner, *Megantereon cultridens* (Cuvier) (Mammalia, Felidae, Machairodontinae) from Plio-Pleistocene deposits in Africa and Eurasia, with comments on dispersal and the possibility of a New World origin, J. Paleontol. 61 (1987) 1256–1268.
- [27] A. Turner, M. Antón, The Big Cats and Their Fossil Relatives, Columbia University Press, New York, 1997, 256 p.
- [28] A. Turner, H.J. O'Regan, Afro-Eurasian mammalian fauna and early hominin dispersals, in: M.D. Petraglia, B. Allchin (Eds.), The Evolution and History of Human Populations in South Asia, Springer, New York, 2005, pp. 23–39.
- [29] L. Werdelin, M.E. Lewis, Carnivora from the South Turkwell hominid site, northern Kenya, J. Paleontol. 74 (2000) 1173–1180.