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The cheetah *Acinonyx pardinensis* (Croizet et Jobert, 1828) s.l. at the hominin site of Dmanisi (Georgia) – A potential prime meat supplier in Early Pleistocene ecosystems

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ABSTRACT

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1. Introduction

In addition to a rich, contemporaneous vertebrate faunal record, the fossil site of Dmanisi in southern Georgia, 85 km SW of Tbilisi (Fig. 1), has yielded a large amount of hominin cranial, dental and postcranial elements (Gabunia et al., 2000; Vekua et al., 2002; Rightmire et al., 2006; Lordkipanidze et al., 2007; Martínón-Torres et al., 2008). By placing the Dmanisi faunal assemblage at around the Olduvai/Matuyama palaeomagnetic boundary (Lordkipanidze et al., 2007), the corresponding hominin remains appear to be the stratigraphically oldest indication of *Homo* outside of Africa. These remains demonstrate the advance of humans from Africa via the Levantine Corridor and into Transcaucasia at the onset of the Late Villafranchian, around 1.8 Ma.

Before the discovery of an almost complete set of skeletal elements of a large cat's foreleg at Dmanisi, two machairodonts, *Homotherium crenatidens* (Weithofer, 1889) and *Megantereon cultridens* (Cuvier, 1824), were the only felids known from the

mammal assemblage of the site (Vekua, 1995). After the subsequent discovery of a mandible of an Eurasian jaguar (recently named *Panthera onca georgica* Hemmer, Kahlke et Vekua, 2010), the limb bones in question were attributed to this species, as it was impossible to relate them morphologically to a machairodontine cat (Vekua, 2001). In addition to the three cat species so far recorded at Dmanisi, the guild of western Palaearctic large felids around 1.8 Ma comprised the Eurasian puma, *Puma pardoides* (Owen, 1846) (Hemmer, 2004), and the large cheetah, *Acinonyx pardinensis* (Croizet et Jobert, 1828). In view of the existence of many open landscape dwellers in the herbivore record, and a correspondingly reconstructed landscape pattern, the presence of, at least, the latter of these felid species was expected in the Dmanisi palaeo-ecosystem.

A re-examination of the above-mentioned postcranial felid material from Dmanisi did, in fact, result in the discovery of a cheetah. Based on the comparative description and evaluation of the most diagnostic skeletal elements of its foreleg, the taxonomic affiliation of this new element of the Dmanisi fauna is discussed here, along with a review of the relevant material from Eurasian Plio- and Early Pleistocene localities. By applying different prediction equations, a body mass estimation of this large predator has

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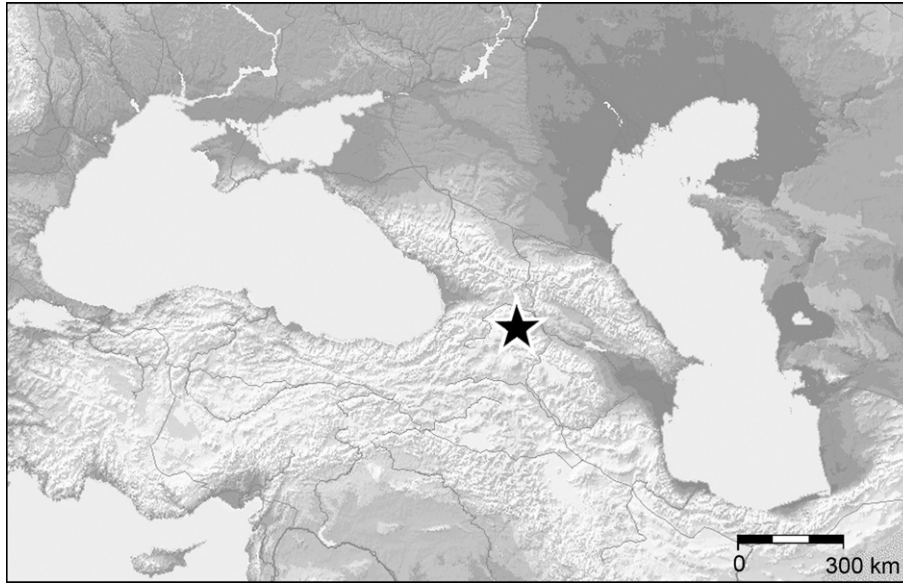


Fig. 1. Geographic position of the Early Pleistocene hominin site of Dmanisi (Georgia).

been calculated. Combined with its inferred hunting success, this new data provides a clearer understanding of the role of cheetahs within Early Pleistocene ecosystems.

2. Material and methods

Based on a number of studies on different faunal elements, in addition to new observations, we present here an updated vertebrate faunal list for the site of Dmanisi. The attribution of the majority of recorded species to corresponding biotopes, through consideration of the given geological and topographic situation, has enabled a reconstruction of the Dmanisi palaeo-landscape pattern during the period of site formation to be put forward.

The studied felid material was found during the 1997 field campaign (square 63/59) and is stored in the collection of the Georgian National Museum Tbilisi (inventory numbers: Scapula D1999, Humerus D2000, Radius and Ulna D2001, Metacarpals II–V D2002a–d, phalanx I–III D2003–2005). The most diagnostic elements are presented in this study. Some unpublished Late Plio- and Early Pleistocene humerus fragments from Villafranca d'Asti (Italy) (NHMB V.J.133) and St. Vallier (France) (NHMB St.V.265, 266) were studied in the Basel Natural History Museum. Measuring was done by H.H. using classic dimensions. The set of specific measurements published by Schütt (1970) was used for the distal humerus diagnosis.

To estimate the body mass of the newly discovered Dmanisi cat, a set of prediction equations was calculated based on the metacarpal shaft minimum diameters. The following data were used to this end: body masses were taken as species means, or as male and female means, respectively (if the available metacarpal data were clearly assignable to a sex), based on Nowell and Jackson (1996) and Piechocki (1986). These data were rounded as follows: to the nearest ½ kg for means lower than 5 kg; to the nearest 1 kg for cats weighing more than 5 but less than 20 kg; to the nearest 5 kg for the range between 20 and 50 kg; to the nearest 10 kg for specimens weighing more than 50 but less than 200 kg (cf. Hemmer, 2004). Metacarpal shaft dimensions were collected from Del Campana (1916, 1954), Hooijer (1947), Thenius (1954), Kurtén (1965, 1978), Björk (1970), Clot and Besson (1974), Kurtén and Crusafont-Pairó (1977), Van Valkenburgh et al. (1990), Morgan and Seymour

(1997), García García (2003, p. 100), and Morales et al. (2003). Dimensions of *Felis catus* were taken by one of the authors (H.H.).

Used alongside behavioural data observed from extant cheetahs, both the updated palaeoenvironmental data from Dmanisi and the morphometric analysis of the discussed felid remains, have shed light on the palaeoecological role played by large sized cheetahs in Early Pleistocene ecosystems of the western Palearctic.

3. Early Pleistocene fauna and palaeo-landscape reconstruction of the Dmanisi site

3.1. Vertebrate faunal assemblage

Apart from the hominin record, the Dmanisi fossil vertebrate assemblage has so far produced the remains of 50 taxa of amphibians and reptiles (8), birds (3) and mammals (39): *Bufo viridis* Laurenti, 1768, *Anura* gen. et sp. indet., *Testudo graeca* Linnaeus, 1758, *Lacerta* ex. gr. *viridis* Laurenti, 1768, *Sauria* gen. et sp. indet., cf. *Elaphe quatuorlineata* (Lacépède, 1789), *Colubines* gen. et sp. indet., *Serpentes* gen. et sp. indet., *Struthio dmanisensis* Burchak-Abramovich et Vekua, 1990, *Gallus dmanisiensis* Bendukidze et Burchak, 2001, *Strix gigas* Bendukidze et Burchak, 2006, *Ochotona* ex gr. *Ochotona lagreli minor* Bohlin, 1942, *Hypolagus* cf. *brachygnathus* Kormos, 1934, *Marmota* sp., *Cricetus* sp., *Miomys tornensis* Jánossy et van der Meulen, 1975, *Miomys ostramocensis* Jánossy et van der Meulen, 1975, *Gerbillus* sp., *Paramerion obediensis* (Haas, 1966), *Apodemus dominans* Kretzoi, 1959, *Hystrix* sp., *Beremendia fissidens* (Petényi, 1864), *Lynx issiodorensis* (Croizet et Jobert, 1828), *Panthera onca georgica* Hemmer, Kahlke et Vekua 2010, *Megantereon cultridens* (Cuvier, 1824): pending relation to the African *Megantereon whitei* (Broom, 1937), *Homotherium crenatidens* (Weithofer, 1889), *Pachycrocuta perrieri* (Croizet et Jobert, 1828), *Pachycrocuta* sp., *Canis etruscus* Forsyth Major, 1877, *Vulpes alopecoides* Forsyth Major, 1877, *Ursus etruscus* Cuvier, 1812, *Ursus* sp., *Meles* sp., *Martes* sp., *Insectivora* gen. et sp. indet., *Dama* (= *Pseudodama* = *Cervus* s.l.) cf. *nestii* Forsyth Major, 1879, *Cervus abesalomi* Kahlke, 2001 (= *Cervus perrieri* Croizet et Jobert, 1828 sensu Vekua, 1995), *Eucladoceros* aff. *tegulensis* (Dubois, 1904) [= *E. aff. senezensis* (Depéret, 1910)], *Palaeotragus* sp., *Bison* (*Eobison*) *georgicus* (Burchak-Abramovich et Vekua, 1994), *Pontoceros* sp.,

Antilopini gen. et sp. indet., *Gallagoral meneghinii sickenbergii* Kostopoulos, 1996, *Soergelia* cf. *minor*, Ovibovini gen. et sp. indet., *Capra dalii* Bukhsianidze et Vekua 2006, *Equus stenonis* Cocchi, 1867, *Equus* sp. aff. *altidens* von Reichenau, 1915, *Stephanorhinus etruscus* (Falconer, 1859), *Mammuthus meridionalis meridionalis* (Nesti, 1825) (compiled under consideration of the contributions by Vekua and Gabunia, 1989; Gabunia and Vekua, 1993; Vekua, 1995; Bukhsianidze, 2005, 2006; Bukhsianidze and Vekua, 2006; Lordkipanidze et al., 2007; Palmqvist et al., 2007; Vekua et al., 2008; Furió et al., 2010; Hemmer et al., 2010).

Whereas the Late Pliocene faunas of Transcaucasia show remarkable affinities to Africa, as recorded from the c. 3 Ma old site of Kvabebi in eastern Georgia (Vekua, 1972; updated faunal lists in Hemmer et al., 2004; Agustí et al., 2009), the northern dispersal of African species into Eurasia was more limited during the Middle (c. 2.6–1.8 Ma) and Late Villafranchian (c. 1.8–1.2 Ma) (Kahlke et al., 2011). The earliest Late Villafranchian fauna of Dmanisi is of, predominantly, Eurasian character. Several of the faunal elements recorded at Dmanisi are also common in the Middle Villafranchian contexts of Western Asia and Europe: *Gallagoral meneghinii sickenbergii*, *Eucladoceros* aff. *tegulensis*, *Palaeotragus* sp., *Mammuthus meridionalis* (typical form) and *Pachycrocuta perrieri*. More modern forms comprise *Bison* (*Eobison*) *georgicus*, *Pontoceros* sp., *Dama* cf. *nestii*, and the elaphine *Cervus abesalomi*.

3.2. Palaeo-landscape reconstruction after the vertebrate record

The fossil bone concentrations at the site of Dmanisi were accumulated in a broad river valley whose floor consisted of basalts and volcanoclastic alluvials, near to the confluence of two successively incising river branches (Džaparidze et al., 1989). However, the Dmanisi taphocenosis does not only include species which inhabited valley floodplains. Lake and river landscapes with their wet biotopes and open water bodies attract many species and are regularly frequented for drinking, and in some cases for food resources, by species roaming in both the immediate surroundings, as well as in the broader environs of the valley. Qualitative analyses can be performed on indicator species, which enable the different types of habitats present in the Dmanisi region during the site formation to be described. In order to quantify the share held by each of the different type of habitats, an unbiased quantitative representation of all faunal elements is required. As far as the taphonomic evidence is understood (Tappen et al., 2007), this prerequisite is lacking at Dmanisi. Nevertheless, the available palaeozoological record provides a detailed picture of the shape of the landscape whilst the Dmanisi fossil site was evolving.

The immediate vicinity of (at least seasonal) fluviolimnic water bodies is indicated by the geographic position of the site in a flat river valley, now forming a promontory above the confluence of the Mashavera and Pinezaouri Rivers. In the more stable areas of the palaeo-valley, the presence of a gallery forest is supported by the numerous cervid remains recovered from the site. In addition to the frequently recorded *Eucladoceros* aff. *tegulensis*, *Cervus abesalomi* must also be assigned to wooded biotopes. However, the regular occurrence of *Dama* cf. *nestii* in more open landscapes cannot be excluded (cf. Hemmer, 2001). *Bison* (*Eobison*) *georgicus* might have been predominantly a woodland inhabitant, as were all of the, so far identified, members of the subgenus *Eobison* (Kahlke, 1999, p. 109). Jaguars (*Panthera onca georgica*) roamed in different climatic and vegetation zones of Eurasia from the latest Middle Villafranchian onwards up to the early Middle Pleistocene. These cats preferred areas where gallery forests provided a suitable spectrum and quantity of prey (Hemmer et al., 2003). Dirktooth cats (*Megantereon*) chiefly hunted in forest habitats, as has been shown by both comparative morphology as well as biogeochemical

data (Hemmer, 2001; Palmqvist et al., 2007). The records of *Strix*, *Meles* and *Apodemus dominans* also support the idea of gallery forest biotopes in the vicinity of the Dmanisi site.

Stephanorhinus etruscus and *Mammuthus meridionalis meridionalis* lived in open wooded areas as well as in savannah like landscapes (Kahlke, 2006). Garutt and Bajguševa (1981) were able to demonstrate that the high and relatively short stature of the Southern Elephants allowed them to forage on leaves, branches and bark. It is likely that their dietary spectrum showed a marked seasonal variation. Whereas fresh steppe vegetation may have been preferred in spring and at the beginning of summer, arboreal forage probably became more important later in the year. The woodland steppes and tree savannahs would also have been a natural habitat for *Palaeotragus* (Godina, 1979) and so, away from the gallery forest, landscapes with minor tree vegetation and open areas have to be assumed.

The overall picture of the Dmanisi fauna is characterised by numerous species typically associated with open environments. In addition to *Struthio dmanisensis*, *Hypolagus* cf. *brachygnathus*, *Cricetus*, *Gerbillus*, *Paramerion* *obeidiensis* and the equids, as well as members of the Antilopini group, all indicate the presence of savannah to steppe conditions away from the river valley. The *Lacerta viridis* prefers sunny areas near to dense shrub vegetation, and *Bufo viridis* is able to live in open steppe biotopes. Furthermore, the presence of certain carnivore species in the fossil record, e.g. *Vulpes alopecoides* with its more or less developed affinity to open steppe biotopes (Kahlke, 1999), also support the idea of a predominantly open environment for the Dmanisi palaeo-landscape. If the recorded *Pachycrocuta perrieri* is, indeed, a brown hyaena, as discussed (Turner, 1990), its habitat preferences would, most likely, have been similar to that of the extant south African *Hyaena brunnea*, which roams predominantly in dry savannah, steppe and semi-desert landscapes. Meanwhile, the presence of *Testudo graeca* and *Hystrix* are indicative of temperate Mediterranean climatic parameters.

The presence of the gallinaceous bird, *Gallus dmanisensis*, suggests the existence of a plain at the foothills of a mountainous landscape, most probably with bush cover (Bendukidze and Burchak, 2001). The occurrence of *Soergelia* cf. *minor* seems to be an indicator of a more pronounced palaeo-relief or possibly even mountainous conditions. Picas, like the recorded *Ochotona* ex gr. *Ochotona lagreli minor*, are found in areas of broken rock and talus that are surrounded by suitable vegetation. They are most commonly seen at the interface between meadow habitat and open rocky terrain. Typical inhabitants of rocky mountain areas are the recorded ibex *Capra dalii*, which would have avoided open plains, as well as *Gallagoral meneghinii sickenbergii*, which has been characterised, using ecological analogies, to extant *Nemorhaedus* and *Capricornis* (Guérin, 1965).

Some of the recorded carnivore species, i.e., *Lynx issiodorensis*, *Homotherium crenatidens*, *Canis etruscus* and *Ursus etruscus*, did not require specialised habitats, but could adapt well to any of the landscape components described above.

The combination of topographic and vertebrate palaeontological information provides strong evidence of the existence of a fairly differentiated landscape pattern around the site of Dmanisi. The flat river valley, c. 1,300 m above sea-level, would have contained open water bodies and areas of wet ground throughout the year. Other parts of the valley floodplain were covered by gallery forests. Due to the lithologic features of their volcanic subsoil, the flanking slopes of the river valley would have been significantly dryer and poorer in tree cover. They would have been dominated by a lower diversity of dense shrub vegetation lying adjacent to more open areas. On the south to southeast facing exposed slopes dry meadows would have developed. Extended grasslands characterised the site vicinity in the adjacent higher ground outside of the valley. In addition to dry

savannahs, even semi-desert like areas could have existed in the Dmanisi area. Over distances of just a few kilometres, cuesta scarps of basaltic lavas (today's relative height 75–150 m) would have led to the formation of broken rocks, taluses and rocky terrain, in which ibexes and gorals would have found suitable habitats. These animals were probably related to corresponding populations in the Džavacheti mountain chain (up to 3000 m above sea-level) some 20 km west of the site.

The palaeo-landscape of the Dmanisi area showed remarkable gradients in its relief as well as in its humidity and vegetation character. Over a distance of some kilometres the landscape pattern appears to have changed dramatically, from that of a forested valley floor and slopes with shrub vegetation, to tree savannah and open grasslands, and up to semi-arid areas and rocky terrains. Whereas the ecological niche of deer and bison hunters, in the more forested areas, was occupied by the jaguar and the dirktooth, the more ubiquitous elephant and rhino populations were most probably exploited by the large sabretooth. However, the presence of a specialized hunter which targeted the antelope to horse sized game, in the predominantly dryer and more open areas of the site's vicinity, had, until now, been absent from the fossil record.

4. Morphometric analysis of the Dmanisi *Acinonyx* remains

4.1. Brachial index

The availability of associated and complete long bones of an anterior limb has enabled the first substantial attempt using the brachial (humeroradial) index (radius length/functional humerus length $\times 100$), as calculated for large felids, e.g. by Vereshchagin (1971) or by Gonyea (1976). An index value of 99.5 was obtained for the Dmanisi cat. This value differs from the means of both *Panthera onca* (86.8 ± 2.08) and *Panthera pardus* (90.5 ± 1.46) by over 6 standard deviations, and from *Panthera tigris* (89.8 ± 0.89) by > 10 s. These extant pantherine species must, therefore, be excluded as candidates in the identification of the Dmanisi find. The humeroradial ratio of the Dmanisi cat fits the distribution recorded for extant *Panthera leo* (98.3 ± 2.22) (means and standard deviations by Gonyea, 1976), as well as the variability of *Acinonyx jubatus*. Two data sets were published for this species, 103.3 ± 1.45 (Gonyea, 1976) and $96.7\text{--}104.2$ (Vereshchagin, 1971). In view of low standard deviations found in extant large felids, the brachial index also qualifies as a useful tool in the definite discrimination between the Dmanisi cat and the Pliocene–Pleistocene machairodont species *Homotherium crenatidens* (89.5), *Megantereon cultridens* (81.6), and *Dinofelis barlowi* (80.5 ± 0.50) (data by Marean, 1989; see also Werdelin and Lewis, 2001). Furthermore, the brachial index of the Dmanisi cat excludes identification with the Blancan/Irvingtonian North American cheetah-like, but puma-related (Barnett et al., 2005), cat, *Miracinonyx inexpectatus* (91.1 respectively around 90; Van Valkenburgh et al., 1990). In contrast, the associated long bones of a large European cheetah from Étouaires (France), dated to the end of the Lower Villafranchian (MN 16), have a humeroradial ratio which matches the value of the Dmanisi individual. The humerus length of the Étouaires specimen has been given as 267 mm and the radius length as 268 mm by Croizet and Jobert (1828). Van Valkenburgh et al. (1990) measured the radius length (cast) as 266 mm (a humerus length of 260 mm cited by these authors in their Table 3 obviously is the result of a print error, as Fig. 6 of their paper shows nearly the same humerus as radius lengths). Savage (1960) gave the radius length, using the same cast as Van Valkenburgh et al. (1990), as c. 269 mm. In view of these different values, Croizet and Jobert's measurements on the originals have been used in this study, resulting in a brachial index of 100.4.

The Early Pleistocene cat from Dmanisi discussed here largely predates the first appearance of the lion in Eurasia during the early Middle Pleistocene. Moreover, the Eurasian cave lion's radius is relatively shorter (brachial index 91.5 after Vereshchagin, 1971) than that of the recent African lion (see above). Consequently, the brachial index of the Dmanisi foreleg also excludes a *Panthera leo* diagnosis. Using the brachial index diagnostic tool, therefore, the genus *Acinonyx* is considered to be the only suitable candidate adequately fitting the Dmanisi measurements.

4.2. Foreleg skeletal elements

4.2.1. Humerus

The humerus is strikingly slender, especially the distal region, when compared to other large-sized felids (Fig. 2, Table 1). A jaguar's humerus of the same length would have a 25% larger distal transverse diameter than that recorded in the Dmanisi fossil ($\log \text{distTD} = 1.16 \log L - 0.95$, $n = 6$, $r = 0.978$; basic data for this allometric equation: 1 extant + 5 Pleistocene American jaguars; Kurtén, 1965, 1973). The Dmanisi measurement falls outside the lower 95% confidence limit of jaguars (width to length scatter), as do extant cheetahs and the *Acinonyx* humerus of Étouaires. In contrast, the Dmanisi humerus compares well with the humerus of the late Early Pleistocene (Irvingtonian) Hamilton Cave *Miracinonyx inexpectatus* skeleton. In total, the *Miracinonyx*/Puma-group (data by Van Valkenburgh et al., 1990) ranges just around the lower 95% confidence limit of *Panthera onca*, but above the cheetahs.

The distal part of a cheetah humerus is characterised by a weak entepicondylus, resulting in an unusually large trochlear transverse diameter when related to the distal width. The trochlea is also comparatively high and thick. Its upper margin to the fossa olecrani runs nearly horizontal; the fossa olecrani itself is formed like a high pointed arch. The posterior entrance of the foramen entepicondylodeum is positioned high at the shaft (Schütt, 1970). Indices, which allow morphometric expression of these specific characters, demonstrate that the humerus of the Dmanisi cat significantly differs from that of *Panthera* humeri, but is affiliated to those of



Fig. 2. *Acinonyx pardinensis* (Croizet et Jobert, 1828) s.l., Dmanisi, Humerus sin. (D2000), from left to right: anterior, external, posterior and internal views. Scale bar 1 cm.

Table 1

Dimensions of humerus, radius, ulna and metacarpalia of the cheetah (*Acinonyx pardinensis* s.l.) from Dmanisi (Georgia): TD – transverse diameter, APD – antero-posterior diameter (measurements in mm).

Humerus		Radius		
Greatest length	281.5	Maximal length	271.4	
Length from caput	273.0	Maximal proximal TD	30.9	
Maximal proximal TD	58.5	Maximal proximal APD	21.4	
Maximal proximal APD	73.5	Minimal shaft TD	21.8	
Minimal shaft TD	24.5	Maximal distal TD	47.3	
Maximal distal TD	60.2	Maximal distal APD	31.0	
Maximal distal APD	43.4			
Trochlear TD	45.5			
Trochlear minimal thickness	22.8			
Trochlear minimal height	20.1	Ulna		
Fossa olecrani maximal width	27.5	Cavitas sigmoides major height	26.5	
Foramen entepicondyloideum distance to medial trochlear keel	c.47	Olecranon maximal width	c.35.5	
Foramen entepicondyloideum maximal length	c.15	Minimal shaft TD	12.2	
		Maximal distal TD	13.8	
Metacarpalia	MC II	MC III	MC IV	MC V
Greatest length	95.3	109.2	106.9	86.3
Maximal proximal TD	19.8	22.0	13.7	15.5
Maximal proximal APD	23.5	20.5	20.4	18.2
Minimal shaft TD	10.7	12.8	11.3	9.8
Maximal distal TD	16.7	17.8	16.8	16.5
Maximal distal APD	16.6	19.0	18.6	16.6

Acinonyx. The relative width of the trochlea distinguishes it from those of the *Miracinonyx*/*Puma*-group (Table 2).

In conclusion (and despite of some similarities to the Nearctic *Miracinonyx inexpectatus*), the Dmanisi humerus discussed here has been attributed to the genus *Acinonyx*. This element represents the largest humerus of an extinct or extant cheetah on record, and is clearly stouter than the insignificantly shorter humerus from Étouaires. The latter fossil is not presented in Table 2, as the published distal transverse diameter measurements are contradictory: 44 mm in Croizet and Jobert (1828; the humerus is listed here as belonging to a dirktooth cat), but c. 41.3 mm in Van Valkenburgh (1990). Moreover, the drawing given by Croizet and Jobert (l.c.) indicates some breakage at the entepicondylus.

4.2.2. Radius

The distal transverse diameter to radius length scatter places the slender Dmanisi radius (Fig. 3) far outside the variability recorded for extinct and extant American *Panthera onca*, and even places it outside an extrapolation of the 99% confidence limits. Only specimens of *Acinonyx* and *Miracinonyx* range this far outside of the jaguars' variation. Nearest to the range for the Dmanisi radius are those of the Étouaires specimen, which is even more slender than the Dmanisi element. *Miracinonyx* radii show comparable proportions, but are much shorter.

Van Valkenburgh et al. (1990) highlighted some diagnostic characteristics which enable discrimination between the extant cheetah and the *Puma*/*Miracinonyx*-group. Proximally, the proximal length of the biceps tuberosity of *Puma*, *Miracinonyx* and *Acinonyx pardinensis* (Étouaires) has about twice the extension (near to 10% of the radius length) of that measured in *Acinonyx jubatus* (about 5%). The Dmanisi fossil fits the former group. Distally, in *Puma* and *Miracinonyx* the articular facet for the ulna is elliptical, with its long axis oriented perpendicular to the shaft, rather than in line with the shaft as seen in Old World cheetahs. In the Dmanisi specimen this facet appears to be nearly circular. Overall, the morphology of the Dmanisi radius matches closest to that of the Étouaires *Acinonyx* radius, though the latter looks slightly more advanced towards that of the extant cheetah.

4.2.3. Ulna

The ulna of the Dmanisi cat (Fig. 4) is not completely preserved, a large part of the olecranon is missing. Thus, important measurements such as the greatest length and some olecranon diameters cannot be taken. Diagnostic characters of the distal part of the ulna, as comparatively shown by Van Valkenburgh et al. (1990) for *Acinonyx jubatus*, *Miracinonyx inexpectatus* and *Miracinonyx trumani*, in addition to *Puma concolor*, exclude the extant cheetah, puma and ancient *M. inexpectatus* – contemporaneous with the Dmanisi specimen – as possible candidates. The styloid process of the latter resembles *Acinonyx* from Étouaires (Croizet and Jobert, 1828; *Felis*, Plate 1, Figs. 4 and 5).

4.2.4. Metacarpalia

The metacarpals II–V (Figs. 5–8) look very slender in comparison with the same elements from both extinct and extant jaguars. The most diagnostic MC V ratio diagram shows that the Dmanisi measurement even falls outside of the jaguar's lower 99% confidence limit. In contrast, the Dmanisi values fit well with the allometric lines recorded for cheetah metacarpals from Pliocene through to extant specimens (Fig. 9). Measurements of *Puma* and *Miracinonyx* scatter slightly above the *Acinonyx* allometric lines. A safe morphometric discrimination of the Dmanisi metacarpals from those of the similar-sized *Miracinonyx inexpectatus* is not possible.

4.3. Body mass estimation

The availability of a nearly complete leg of the Dmanisi cheetah permits an attempt to estimate its body mass. The most accurate results are most likely to be obtained using an approach based on the long bone shaft diameters, which are load-related and therefore provide a direct functional relationship to body mass (Hemmer, 2001, 2004, 2007a). So far, body mass prediction based on felid foreleg elements has been restricted to the smallest humerus shaft transversal diameter (Hemmer, 2001). In order to increase the likelihood of obtaining a reliable body mass estimation for the Dmanisi cat, new prediction equations were calculated for MC II to

Table 2

Distal humerus morphometric diagnosis of *Acinonyx*, *Miracinonyx*, *Puma* and *Panthera*: indices after Schütt (1970) (Index values given to the nearest 0.5%). The indices of the Dmanisi *A. pardinensis* s.l. differ from the combined *Panthera* means by 2.6–4.4 standard deviations.

	Distal transverse diameter (distTD, mm)	Trochlear transverse diameter in % distTD	Trochlear minimal thickness in % distTD	Trochlear minimal height in % distTD	Distance foramen entepicondylodeum to medial trochlear keel in % distTD	Source of data
<i>Acinonyx</i>						
<i>A. pardinensis</i> s.l.						
Dmanisi (Georgia), c.1.77 Ma	60.2	75.5	38	33.5	78	this paper
<i>A. pardinensis arvernensis</i>						
Villafranca d'Asti (Italy), >3.0 Ma	53+	75.5–	38.5–	c.33–	–	this paper
<i>A. pardinensis pardinensis</i>						
Saint Vallier (France), c.2.0 Ma	52	74	41	36.5	88	this paper
	52	74	40.5	38.5	88	
<i>A. pardinensis intermedius</i> ,						
Mosbach (Germany), c.0.6–0.5 Ma	48.5	75	41.5	39	91.5	Schütt 1970
<i>A. jubatus</i>						
extant	38.3	74	40	37	92.5	Schütt 1970
	31	74	41.5	35.5	93.5	
<i>A. jubatus</i>						
extant, mean (n = 6)	37.4	73	–	–	–	Van Valkenburgh et al., 1990
<i>Miracinonyx</i> , <i>Puma</i>						
<i>M. inexpectatus</i>						
Santa Clara (CA, USA), c.2.4–2.0 Ma	58	67	–	–	–	Van Valkenburgh et al., 1990
Hamilton Cave (VA, USA), 0.85–0.82 Ma	59.5	72	–	–	–	
<i>M. trumani</i> , mean (n = 8)						
Natural Trap Cave (WY, USA), 13–11 ka	52.7	69	–	–	–	Van Valkenburgh et al., 1990
<i>P. pardoides</i>						
Untermaßfeld (Germany), c.1.05 Ma	47.0	68.5	31.5	28.5	58.5	this paper
<i>P. concolor</i>						
extant, mean (n = 9)	49.9	69.5	–	–	–	Van Valkenburgh et al., 1990
<i>Panthera</i>						
<i>P. onca gombaszoegensis</i> ,						
Untermaßfeld (Germany), c.1.0 Ma;	78	68	32	–	63.5	Hemmer 2001
	76.5	67.5	32.5	–	65.5	
Le Vallonnet (France), c.1.0 Ma	81.4	c.72.5	–	–	–	De Lumley et al. 1988
Gombaseg (Slovakia), c.0.8–0.7 Ma	73.0	72.5	–	–	–	Kurtén 1969
Süßenborn (Germany) c.0.7–0.6 Ma	68.0	c.72	–	–	–	Kurtén 1969
<i>P. leo fossilis</i>						
Mosbach (Germany), c.0.6–0.5 Ma	85.6	68.5	30	25	71	Schütt 1970
<i>P. leo</i>						
extant	76.1	68.5	34	29	69	Schütt 1970
	81.2	71.5	31.5	26	63	
	98.0	70	30.5	28.5	61.5	
<i>P. pardus</i>						
extant	47.3	71.5	30	c.24.5	66	Schütt 1970

MC V shaft TDs, using various sets of published measurements (Table 3; see Section 2). We abstained from performing a similar calculation for the radius because the shaft transverse diameter is harder to define.

Calculations with the new equation set for the Dmanisi cat resulted in the following body mass raw data: humerus 126 kg, MC II 92 kg, MC III 98 kg, MC IV 102 kg, MC V 76 kg, and mean 99 kg. The retained body mass estimate, rounded to the nearest 10 kg as recommended by Hemmer (2001, 2004) to avoid inappropriate precision, amounts to 100 kg.

Overestimation of the body mass using the humerus diameter as well as underestimation by the MC V diameter requires interpretation. Generally, such differences in body mass estimation, based on different parts of a single skeleton, are not surprising, neither in felids nor in hominoids (Hemmer, 2001, 2007b). Morphometric analysis has shown that the Dmanisi humerus is substantially stouter than the (just insignificantly shorter)

humerus of the Étouaires cheetah (see Section 4.2.1). This may indicate a particularly robust development of this section of the foreleg. Compared to the other elements of the front paw, the MC V is more lightly built in modern cheetahs than in other felids, thus suggesting a too small body mass when calculating with the general felid equation. For example, the MC V of an average modern cheetah used by Thenius (1954) for comparison with a metacarpal from the early Middle Pleistocene Hundsheim site (Austria) points to a body mass of 34 kg, although the mean body mass for extant African cheetahs is 43.2 kg, with a minimum to maximum span between 21 and 65 kg (Marker and Dickman, 2003, compiled from a total of 220 East, Southwest and South African cheetahs). The MC V of a small West African cheetah referred by Thenius (1954), results in an obvious underestimation of the body mass of 20 kg only. Consequently, body mass calculations based on the MC V of extant and extinct cheetahs will lead to underestimations of around 20%.

Table 3

Prediction of body mass (BM, kg) by metacarpal shaft (minimum) transverse diameter (MCSTD, mm) in felids (log – log least-square regressions).

Metacarpal	r	Equation	Sample
MCI	0.991	$\log BM = 2.295 \log MCI_{STD} - 0.307$	7 species of the genera <i>Felis</i> , <i>Lynx</i> , <i>Puma</i> , <i>Panthera</i>
MCI	0.967	$\log BM = 2.093 \log MCI_{STD} - 0.326$	10 species of the genera <i>Felis</i> , <i>Lynx</i> , <i>Caracal</i> , <i>Acinonyx</i> , <i>Puma</i> , <i>Panthera</i>
MCI	0.995	$\log BM = 2.319 \log MCI_{STD} - 0.432$	7 species of the genera <i>Felis</i> , <i>Lynx</i> , <i>Puma</i> , <i>Panthera</i>
MCI	0.962	$\log BM = 2.334 \log MCI_{STD} - 0.435$	12 species of the genera <i>Felis</i> , <i>Lynx</i> , <i>Caracal</i> , <i>Acinonyx</i> , <i>Puma</i> , <i>Panthera</i>

5. Discussion

5.1. Taxonomic affiliation of the Dmanisi cheetah

The morphological analyses performed on the described Dmanisi cat remains (see Sections 4.1, 4.2.1–4.2.4) result in assignments to the genus *Acinonyx*. During the last four decades, Eurasian cheetahs of Late Pliocene and Early Pleistocene age (>3.0–0.8 Ma) were mostly attributed to one single species, *A. pardinensis* (Croizet et Jobert, 1828) (Schütt, 1970; Ficcarelli, 1984). Moreover, it has been suggested that the extant cheetah should be grouped together with all the Plio-Pleistocene specimens as representing one species (Turner and Antón, 1997). However, consideration of newly discovered fossils from the North African site of Ahl Al Oughlam (Morocco), dated to about 2.5 Ma (Geraads, 1997), alongside those from the East Asian loess deposits around Longdan (Gansu, North China) of 2.55 to 2.16 Ma (Qiu et al., 2004), may support the hypothesis that more than one cheetah taxon roamed the vast territories from North Africa to the Eurasian Far East during the Early Pleistocene. A decision based on reliable biological data, as to

whether correspondingly distinguishable forms – *Acinonyx aicha* Geraads, 1997 (from Ahl Al Oughlam) and *Acinonyx linxiaensis* (Qiu, Deng et Wang, 2004), in addition to *Acinonyx kurteni* Christiansen et Mazák, 2009 from Longdan – merit the species rank, or whether a subspecies rank might be more appropriate, should be postponed until the fossil record of cheetah evolution is more complete. In the meantime, it seems reasonable to unite the fossil cheetahs under the mutual name *A. pardinensis* in the widest sense (sensu lato), following a macrospecies concept established by Hemmer et al. (2008). The latter proposal omits extant *A. jubatus*, in light of its uncertain phylogenetic relationship to the described fossil forms, resulting from inadequate knowledge of Pleistocene sub-Saharan African cheetah evolution. DNA assessment of the recent subspecies has not helped to elucidate the early phylogeographic roots of *A. jubatus*, pointing to a population split of the extant Asian and African cheetahs no earlier than the Late Pleistocene (Charruau et al., 2011).

The elucidation of the history of European cheetahs has been hindered by the long-lasting confusion surrounding the type



Fig. 3. *Acinonyx pardinensis* (Croizet et Jobert, 1828) s.l., Dmanisi, Radius sin. (D2001), from left to right: anterior, external, posterior and internal views. Scale bar 1 cm.



Fig. 4. *Acinonyx pardinensis* (Croizet et Jobert, 1828) s.l., Dmanisi, Ulna sin. (D2001), from left to right: anterior, external, posterior and internal views. Scale bar 1 cm.

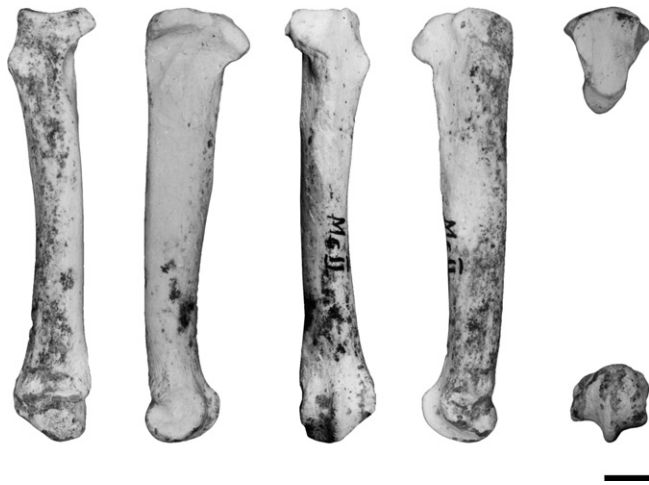


Fig. 5. *Acinonyx pardinensis* (Croizet et Jobert, 1828) s.l., Dmanisi, Os metacarpale secundum sin. (D2002a), from left to right: dorsal, external, palmar, internal, proximal and distal views. Scale bar 1 cm.

locality of the taxon *A. pardinensis* (Croizet et Jobert, 1828). Over the last 50 years, the type mandibular fragment has been attributed to the site of Étouaires (Schaub, 1949; Viret, 1954; Ficcarelli, 1984; Hemmer, 2001), alongside that of another important cheetah fossil, the type specimen of *A. pardinensis arvernensis* (Croizet et Jobert, 1828). This latter mandible differs so much from the *pardinensis* morphotype that in the first modern revision Schaub (1949) accepted their assignment as species of two different genera. Later, this *A. pardinensis arvernensis* jaw was considered to represent a very robust aged male cheetah individual, with a remarkably long molar (Viret, 1954 and later authors). However, the original authors explicitly stated that the *A. pardinensis pardinensis* type specimen was found at Ardé, about 1 km away from the Étouaires site (Croizet and Jobert, 1828, p. 208). Postcranial cheetah remains from the latter locality were originally misinterpreted as belonging to the genus *Megantereon* (revised by Schaub, 1939). In fact, they comprise the only other associated foreleg elements, besides the Dmanisi fossils described here. According to the provenance, the Étouaires



Fig. 6. *Acinonyx pardinensis* (Croizet et Jobert, 1828) s.l., Dmanisi, Os metacarpale tertium sin. (D2002b), from left to right: dorsal, external, palmar, internal, proximal and distal views. Scale bar 1 cm.

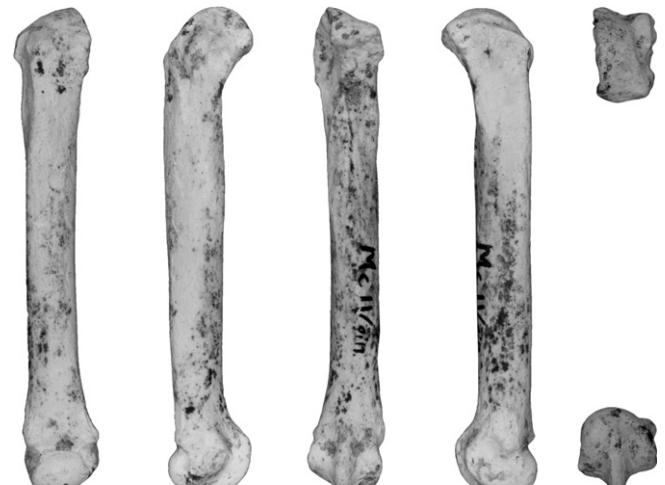


Fig. 7. *Acinonyx pardinensis* (Croizet et Jobert, 1828) s.l., Dmanisi, Os metacarpale quartum sin. (D2002c), from left to right: dorsal, external, palmar, internal, proximal and distal views. Scale bar 1 cm.

postcranial elements are part of the *A. pardinensis arvernensis* series, but are not that of *A. pardinensis pardinensis*. Chronostratigraphically, the Ardé sediments postdate the Étouaires (MN 16) type layer (Pastre, 2004). *A. pardinensis pardinensis*, best known by a cranial series from Saint Vallier of c. 2.0 Ma (MN 17; Guérin et al., 2004), was, therefore, a chronological successor of *A. pardinensis arvernensis* in Europe. The archaic level of cheetah evolution, as represented by the latter, may have persisted in eastern China until 2.0 Ma, as indicated by recent discoveries from the Tuozidong Cave near Nanjing (Jiangsu; Nanjing Museum and Institute of Archaeology, 2007).

Compared with the late Lower Villafranchian *A. pardinensis arvernensis* foreleg from Étouaires, the Dmanisi foreleg is differentiated by its noticeably more robust humerus and radius structure. The former appears to be more advanced, i.e. *A. jubatus*-like. In fact, this morphological shift may not have any taxonomic significance, but could be a result of sexual dimorphism, the Dmanisi cat being a very strong male and the Étouaires one a slender female. Such a sexual assignment is strongly supported by body mass estimations of only 70 kg for the Étouaires humerus,



Fig. 8. *Acinonyx pardinensis* (Croizet et Jobert, 1828) s.l., Dmanisi, Os metacarpale quintum sin. (D2002d), from left to right: dorsal, external, palmar, internal, proximal and distal views. Scale bar 1 cm.

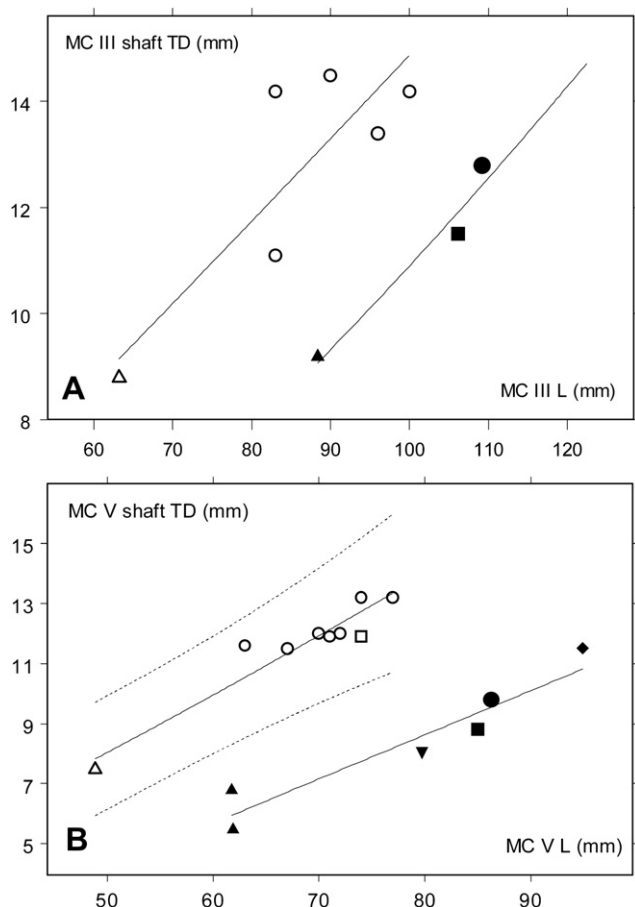


Fig. 9. Plot of MC III (A) and MC V (B) shaft transverse diameter against length. Solid symbols: *Acinonyx*, open symbols: *Panthera onca*; ● *A. pardinensis* s.l., Early Pleistocene (early Late Villafranchian), Dmanisi; ■ *A. pardinensis pardinensis*, Early Pleistocene (Middle Villafranchian), Saint Vallier, France (Argant, 2004); ◆ *Acinonyx pardinensis pleistocaenicus*, Early Pleistocene (Epivillafranchian), Untermaßfeld, Germany (Hemmer, 2001); ▼ *Acinonyx pardinensis intermedius*, early Middle Pleistocene, Hundsheim, Austria (Thenius, 1954); ▲ *Acinonyx jubatus*, extant (A: mean of $n = 2$, Van Valkenburgh et al., 1990; B: Thenius, 1954); ○ *Panthera onca augusta*, diverse localities, Pleistocene, USA (Kurtén, 1965, 1973); □ *Panthera onca gombaszoegensis*, early Middle Pleistocene, Chateau, France (Argant, 1991); △ *Panthera onca*, extant (Kurtén, 1965). Allometric lines (power function) for *Panthera onca* (in B with 99% confidence limits) and for *Acinonyx*.

using its shaft transverse diameter as measured by Van Valkenburgh et al. (1990). This is in contrast to a 120 kg result when based on the obviously large male (Viret, 1954) *A. pardinensis arvernensis* type mandible, using the M_1 predictor equation after Van Valkenburgh (1990). A MC IV found at the Early Villafranchian Las Higuieruelas site (Ciudad Real, Spain; Arribas and Anton, 1997) is less stout than that of the Dmanisi cat (3% longer, but 4% less shaft width), paralleling the situation of the Étouaires humerus. The corresponding body mass estimation results in 90 kg for this individual.

A similar comparison of the Dmanisi cheetah with the Middle Villafranchian *A. pardinensis pardinensis* is currently not possible, due to the shortage of suitable material. Two humeri from St. Vallier (France), which were assigned to *A. pardinensis* by Argant (2004), look to be attributable to *Puma pardoides*. A distal humerus fragment (NHMB St.V.265) is much less robust than that area of the Dmanisi humerus, but results in a body mass estimation of about 100 kg. Two metacarpals (MC III and V) from the same site appear to be a little more slender and somewhat shorter than those of the Dmanisi fossil, in all probability reflecting sexual dimorphism

rather than indicating differences of taxonomic relevance. Body mass estimations based on these metacarpals, which are thought to belong to the same small individual (Argant, 2004), result in 80 kg for the MC III and 60 kg for the MC V. As the MC V leads to an underestimation of body mass (see Section 4.3) the latter value fits with a possible female cheetah individual of around 80 kg. A distal humerus fragment from the early Middle Villafranchian (c. 2.4 Ma) locality of Liventsovka (Khapry Faunal Complex) near Rostov-on-Don (southern Russia) suggests a female of around 60 kg. In contrast, an upper carnassial from the similarly dated site of Morskaya, obviously belonged to a very large male individual (Sotnikova et al., 2002). These Khapry cheetahs may be assigned to *A. pardinensis pardinensis*, as should the Middle Villafranchian cheetah from Kuruksaj in Tajikistan, which was originally named *Acinonyx pamiroalayensis* Sharapov, 1986 (Hemmer, 2001; Hemmer et al., 2008). A 100 kg male as estimated for the Dmanisi cheetah, would be in accordance with *A. pardinensis pardinensis* male body masses of around 100 kg and corresponding female ones of 60–80 kg, but does not argue for its taxonomic affiliation.

Corresponding foreleg elements from Early Pleistocene northern Chinese cheetahs *A. pardinensis linxiaensis* (Qiu et al., 2004), its chronological successor *A. pardinensis pleistocaenicus*, and *A. pardinensis kurteni* (Christiansen and Mazák, 2009) have not yet been recorded.

A. pardinensis pleistocaenicus appeared in the western Eurasian 1.05 Ma old Epivillafranchian locality of Untermaßfeld in Germany (Hemmer, 2001; Kahlke, 2006), only slightly later than its youngest record in the east, at around 1.25 Ma (Qiu, 2006). Two metacarpals from that site, MC III and V (Hemmer, 2001), are much larger than those of the Dmanisi specimen and indicate a huge, surely male, cat. The MC III based body mass estimate is around 140 kg, matching an identical result based on a femur probably from the same individual (Hemmer, 2001). The MC V estimation of around 110 kg may be ~20% too low (see Section 4.3).

The lack of cranial cheetah remains from Georgia, along with the lack of sufficient comparable fore limb elements from other localities, prevent a more precise diagnostic affiliation of the Dmanisi cheetah within the genus *Acinonyx* than to that of *A. pardinensis*, the macrospecies proposed for all Plio- and Lower Pleistocene cheetahs.

5.2. The role of the cheetah in the Dmanisi palaeo-ecosystem

The discovery of such a powerful cheetah has helped to close an important ecological gap in the Dmanisi palaeo-ecosystem. This gap had resulted from the complete lack of evidence for a specialized hunter and carcass producer in the open palaeo-landscape around the site, where the existence of hyena (carcass destroyers) had already been established (see Section 3.2).

As *A. pardinensis* (s.l.) shows the exact same structural specialization as the extant *A. jubatus*, comparable functional use is assumed. This includes hunting as a sprinter in open landscapes, as well as suffocation killing by sustained jaw clench. Preference for this killing method is supported by a tooth-row characterised by rather short and blunt canines followed immediately by high-crowned premolars, which would have provided a steady row of sharp grasping points (Hemmer, 2001, 2004, 2007a).

Prey focus mass (PFM, kg) is defined as the modal class that constitutes the prey size preferred by a particular cat species, and is highly dependant on the body mass (BM, kg) of a felid species (method as described by Hemmer, 2004, 2007a; predictor equation: $\log \text{PFM} = 1.917 \text{ BM} - 1.71$; $r = 0.96$, $p < 0.001$). Testing the PFM method for the actual African cheetah reveals the peculiar situation of the highly specialized cat. Its mean body mass of 43.2 kg (Marker and Dickman, 2003, Table 2, 3) corresponds to a calculated prey mass value of 26.6 kg, i.e. the PFM class of 20 kg. The mean body

mass of the African cheetahs' preferred prey species, if calculated with three-quarters of mean female body mass in order to take account of calves and sub-adults eaten, was found to be 27.3 ± 4.8 kg (Hayward et al., 2006). This agrees well with the PFM predicted by the body mass. Analysis of the actual prey body mass shows that Namibian male cheetahs prefer to prey on the calves of large antelopes (c. 16 kg), while the females select the smaller antelopes (near 10 kg) (Marker et al., 2003). These figures are only around half of what has been estimated by a prey species age mix procedure and their mean fits the next lower size class (10 kg) on the PFM scale. This agrees with the observation that in addition to body mass, the size of canines also fundamentally influences prey size preference (Hemmer, 2004). Based on the upper canine length predictor equation, the PFM of Namibian cheetahs (Marker et al., 2003) can indeed be calculated to the 10 kg class.

In view of these results, the PFM method has been used for the Dmanisi cheetah. A body mass of 100 kg, as estimated for this specimen, in turn suggests that this cat would have focused on prey within the 100 kg class. Taking into account its typical cheetah specialization, this estimated prey body mass value probably indicates the upper limit for the Dmanisi cheetah, rather than its main focus. The 50 kg class of prey mass probably describe its prey target group more realistically.

Animals of appropriate body mass are well represented within the Dmanisi large mammalian assemblage, as calves and foals of larger sized species also need to be considered. Under these prerequisites, a considerably higher rate of hunting success compared to other species of the cat guild must be assumed for the Dmanisi cheetah, in parallel with the extant animal (for *A. jubatus* see Schaller, 1972; Kingdon, 1977; Nowell and Jackson, 1996). This would have qualified the Dmanisi cat to take its place as the top carcass producer within the carnivore community. Occasional loss of prey through encounters with predators ranking higher in the interspecific hierarchy, such as *Homotherium crenatidens*, *Megantereon cultridens* and *Panthera onca* (Hemmer, 2000, 2001, 2004), was presumably tolerable for this highly specialized species.

For the extant *A. jubatus*, Schaller (1972) analyzed 238 kills in the East African Serengeti and found a loss of 12%: twenty kills were taken by lions, eleven by hyenas, and one by a leopard before the cheetah was finished with the meal. The important role of kleptoparasitism has been widely discussed for the extant cheetah (Durant, 2000; Mills et al., 2004; Hayward et al., 2006). A female with cubs seven-eighths fully grown can even be dispersed from a carcass by a subadult spotted hyaena (*Crocuta crocuta*) (Caro, 1982), indicating the low rank of the cheetah within the extant carnivore guild, independent of the social behaviour of the dominant species. In the Dmanisi ecosystem, the cheetah would, therefore, also have been a principal target species for meat robbery.

The carnassial morphology of *A. pardinensis* in general points to its specialization on fresh meat, just like *A. jubatus*. Substantial parts of larger kills are left uneaten by cheetahs. The hunting activity of the 100 kg Dmanisi cheetah, focusing on 50–100 kg prey animals, whilst needing an average daily food intake of about 4.5 kg (for food intake prediction from body mass see Hemmer, 2004, 2007a), will have led to the involuntary supplying of other carnivorous competitors with fresh kills, or with carcasses in different stages of consumption. In addition, the Dmanisi cheetah will also have provided significant leftovers for carcass destroyers with bone-crushing capabilities. The following model calculation helps to illustrate the situation.

Extant solitary cheetahs make around 150 kills a year (compilation by Schaller, 1972). Using a minimal prey focus mass of 50 kg as the mean mass of an *A. pardinensis* kill, and assuming a similar kill frequency for the latter as estimated for *A. jubatus*, a total of around 7500 kg of prey a year, seems a realistic hunting estimation for the

Dmanisi cat. Cheetahs centre on fresh meat, heart and liver (Schaller, 1972). Taking the example of extant fallow deer (*Dama dama*), together, these parts of a carcass represent around 40% of live mass (calculated at the base of data compilation by Reinken, 1987). In a scenario involving a 100 kg solitary Dmanisi cheetah individual, around 3000 kg fresh meat of prey would have been produced in a year. Using an estimation of 4.5 kg for average daily food intake, the cheetah itself may have consumed at least 1500 kg, though less than 2000 kg, of this annual meat haul. Consequently, based on the cheetah's hunting activity, more than one ton of pure meat each year would have been available to other consumers, in addition to around 4.5 tons of leftovers, including bones, hide and intestines.

When considering the Dmanisi ecosystem as a whole, the cheetah must have been significantly more suited to the role of a potential prime fresh meat supplier than the dirktooth, the sabretooth or the jaguar, as it would have been a potential host for kleptoparasitism by other carnivorous mammals, which could dominate it in the interspecific hierarchy. By producing considerable amounts of fresh meat and other nutritious leftovers, the hunting success of *Acinonyx* would have benefited other meat consumers. Even for sympatric *Homo*, it might have been an occasional factor in their subsistence strategy. The available archaeological evidence indicates that Dmanisi *Homo* had to some extent early access to carcasses following a kill, and filleted the meat before any large carnivore was able to leave traces of consuming activities (Lordkipanidze et al., 2007, supplementary information; Tappen et al., 2007). This evidence fully agrees with the scenario of Dmanisi man as a potential hunter, as well as a potential confrontational scavenger, who was willing to drive off large felids from their fresh kills (Hemmer, 2000).

6. Conclusions

The detection of a large and stoutly built cheetah adds a new element to the extensive list of the Dmanisi palaeofauna. This felid would have successfully filled the ecological niche, previously thought to have been unoccupied, for a specialized hunter and carcass producer in the dry, open areas of the Dmanisi palaeo-landscape. The position and taxonomic affiliation of this large cat within the evolutionary history of the macrospecies *A. pardinensis* s.l. could not be ascertained in this study due to the lack of cranial elements. However, a shared range with *A. pardinensis pardinensis* might be possible. The existence of an approximately 100 kg cheetah at Dmanisi, with a hunting specialisation just like that of the much smaller extant *A. jubatus*, supports the idea of this species as having been a potential prime fresh meat supplier in Palaeo-archaic Early Pleistocene ecosystems, in preference to any other felid.

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