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***Acinonyx pardinensis* (Croizet et Jobert) remains from the Middle Villafranchian locality of Varshets (Bulgaria) and the Plio-Pleistocene history of the cheetahs in Eurasia**

Restos de Acinonyx pardinensis (Croizet et Jobert) del Villafranchiense Medio de Varshets (Bulgaria) y la historia de los guepardos en Eurasia durante el Plio-Pleistoceno

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ABSTRACT

The article describes and discusses remains of late Pliocene (middle Villafranchian) cheetah, *Acinonyx pardinensis* (Croizet et Jobert) from Varshets, N.-W. Bulgaria. It is accepted that three chronofoms *A. pardinensis pardinensis*, *A. p. pleistocaenicus* and *A. p. intermedius* succeed in Europe from the Early Villafranchian (Etouaires, approx. 2.6 Ma) till the Middle Pleistocene. Remains are scarce and at this level of knowledge we could accept the recently proposed subspecific status of all these forms but their taxonomical relations could be rather more complicate. The remains from Varshets correspond to the earliest form *A. pardinensis pardinensis* which inhabited Eurasia during the late Early and the Middle Villafranchian and the beginning of the Pleistocene. Other European remains of *A. p. pardinensis* are known only from Spain, France, Italy and the Azov region of Southern Russia. It seems that then the species occupied only the southern part of the European continent (the Mediterranean-Balkan-Northern peri-Pontic area), and from there it probably spread till Central Asia (Tajikistan). Such a distribution supports the concept of the faunal entity of South Europe in Villafranchian time as well as the theory for the Central Asian influence of this fauna mainly through the Balkans by two ways: via Bosphorus and via the peri-Pontic area. According to the paleontological data the fossil *Acinonyx* does not reach Central Europe (Austria and Germany) before the Epivillafranchian, possibly after new waves of dispersal of another, Early Pleistocene form of Central Asia. The relationship of the Middle Villafranchian *A. pardinensis* with the rather contemporaneous forms from China (Hezheng) "*Sivapanthera linxiaensis*" and *A. kurteni* and from Siwaliks is not clear, but the Chinese forms must represent taxa different from *A. pardinensis*. *Acinonyx* s. str. is characterized by strongly domed and enlarged frontal area, shortened skull and downwards inclined neurocranium. The new data argue the supposition of its Eurasian origin at the end of the Ruscinian/ beginning of the Villafranchian.

Keywords: *Acinonyx pardinensis*, fossil cheetahs, Villafranchian fauna, Bulgaria

RESUMEN

Se describen y discuten restos de guepardo, *Acinonyx pardinensis* (Croizet & Jobert) del Plioceno final (Villafranchiense medio) de Varshets, NW de Bulgaria. Se acepta la existencia de tres cronofomas *A. pardinensis pardinensis*, *A. p. pleistocaenicus* y *A. p. intermedius* que se suceden en Europa desde el comienzo del Villafranchiense (Etouaires, ca. 2,6 Ma) hasta el Pleistoceno medio. Aunque los restos fósiles son escasos podemos aceptar la reciente propuesta de un estatus subspecífico para todas estas formas, pero sus relaciones taxonómicas son bastante complejas. Los fósiles de Varshets corresponden a la primera forma *A. pardinensis pardinensis* que habitó Eurasia durante el Villafranchiense inferior y medio hasta el comienzo del Pleistoceno. Otros restos europeos de *A. pardinensis pardinensis* son conocidos sólo en España, Francia, Italia y la región de Azov en el sur de Rusia. Parece que la especie

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sólo ocupó la parte sur del continente europeo (áreas Mediterránea-Balcanes-Norte del Ponto), y desde allí probablemente se expandió al Asia central (Tajikistán). Tal distribución apoya el concepto de entidad faunística del sur de Europa durante el Villafranchiense, tanto como la teoría de una influencia centro asiática en esta fauna, principalmente a través de los Balcanes por dos rutas, el Bósforo o el área Peri-pónica. De acuerdo a los datos paleontológicos los *Acinonyx* fósiles no alcanzaron Europa central (Alemania y Austria) antes del Epivillafranchiense, posiblemente después de una nueva dispersión de otras formas del Pleistoceno inferior del Asia central. La relación de *A. pardinensis* del Villafranchiense medio con las formas casi contemporáneas de China (Hezheng) "*Sivapanthera linxiaensis* y *A. kurteni* y con las de los Siwaliks no es clara, pero las formas chinas pueden representar diferentes taxones de *A. pardinensis*. *Acinonyx sensu stricto* está caracterizado por el área frontal ensanchada con acusada forma de domo, cráneo acortado y neurocráneo inclinado hacia abajo. Los nuevos datos argumentan la suposición de su origen Eurasiático hacia el final del Rusciniense o comienzos del Villafranchiense.

Palabras clave: *Acinonyx pardinensis*, guepardos fósiles, fauna Villafranchiense, Bulgaria

Introduction

The well known Middle Villafranchian locality of Varshets, N-W Bulgaria, has yielded more than 150 vertebrate species: about 20 amphibian and reptile species (M. Böhme, N. Tzankov pers. comm.), 74 bird species (BOEV, 1999, 2000), 37 species Micro-mammalia (POPOV, 2001) and 21 species Macro-mammalia (Spassov, 2000 and additional pers. data). This is evidently the richest Pliocene locality of vertebrate fauna in Europe. The mammal megafauna of this locality demonstrates an apparent similarity with localities typical for the late Pliocene – Middle Villafranchian, such as Saint-Vallier and Chillhac (France), La Puebla de Valverde (Spain), etc. Varshets is placed, after its macromammal fauna, in the first half of the NMQ17, between Rocaneyra (possibly close to) and St. Vallier. The appearance of the fauna of Varshets shows great similarity to that of the European-Mediterranean localities but unlike most of the well known Mediterranean faunas, that of Varshets also shows a connection with the faunal associations of Middle- and E-Europe. The relationship with the Middle East is evidently strong, too. A tendency of prevalence of taxa with S-European and Middle East distribution emerges. This, in fact, appears to be quite logical bearing in mind the geographical position of the locality and the clear indications of an influence of Asian elements (SPASSOV, 2000; 2003). The distribution of the macromammalian species from Varshets in different habitats shows that the physiognomy of the landscape is determined chiefly by forest-steppe/mosaic biotopes or open forests. The open forests (park-like forests) and shrubs prevail. The analysis of the micromammalian species leads to similar conclusions for a temperate, mild climate and a mosaic landscape

with forests and meadows prevailing over typical steppe vegetation (POPOV, 2001). The data from the analysis of the ornithofauna are similar. The birds of the open spaces are 63 % of the number of the forest birds, but dominant are the birds of the mixed (mosaic) environments, especially the phasianids (BOEV, 1999).

Till now *Acinonyx pardinensis* Croizet et Jobert is only mentioned in the check-list of Varshets (Spassov, 1997; 2000; 2003). The fossil remains of cheetah in Europe are still rare, that determines the importance of the description of the *Acinonyx* remains from Varshets.

Abbreviations:

MHNL : Muséum d'Histoire Naturelle, Lyon

MNHNP : Museum National d'Histoire Naturelle, Paris

NMNH: National Museum of Natural History, Sofia

SI-NMNH" Smithsonian Institution National Museum of Natural History, Washington D.C.

Systematics

Order Carnivora Bowdich, 1821

Family Felidae Fischer de Waldheim, 1817

Genus *Acinonyx* Brookes, 1828

Acinonyx pardinensis (Croizet et Jobert, 1828)

"*Felis*" *pardinensis* Croizet et Jobert, 1828

(?) *Felis arvernensis* Croizet et Jobert, 1828

"*Felis*" *elata* (Brav.): Gervais, 1859

(?) *Felis* (?) *Cynaelurus* *brachygnathus* Lydekker, 1884

(?) *Leopardus arvernensis* (Croizet et Jobert) : Del Campana, 1915

- Cynailurus etruscus* Del Campana, 1915
 (?) *Cynailurus pleistocaenicus* Zdansky, 1925
 (?) *Sivapanthera lydekkeri* Kretzoi, 1929
 (?) *Sivafelis brachygnathus* (Lydekker) : Pilgrim, 1932
Cynaëlurus elatus (Bravard): Schaub, 1939
Schaubia vireti: Schaub, 1942
Acinonyx pardinensis (Croizet et Jobert): Schaub, 1949
Sivapanthera arvernensis (Croizet et Jobert): Villata, 1952
Acinonyx pardinensis (Croizet et Jobert): Viret, 1954
 (?) *Acinonyx intermedius* Thenius, 1954
Acinonyx pamiroalayensis Sharapov, 1986
 (?) *Acinonyx pardinensis pleistocaenicus*: Hemmer, 2001
 (?) *Acinonyx pardinensis* (s. lato) *intermedius*: Hemmer et al., 2008

Material

(Coll. Of the NMNHS): Upper canines (FM 849; FM 851), upper carnassials – P4 (FM 953; 954; 955, all are possibly from three female individuals), astragalus FM 873; calcaneus FM 878 (the astragalus and calcaneus are most probably from one and the same ind.); I phalanx FM876 (Fig.1).

We could refer to this species also the following remains: metapodials (FM 870; 879); II phalanxes (FM 874; 875; 877); III phalanx (FM 983) and two bones of a juvenile individual: a symphysis fragment (FM 862) and a calcaneus (FM868).

The remains from Varshets, belonging to at least 4 individuals, make the cheetah the most numerous carnivore species in the taphocoenosis of the locality.

Description and comparison

The canines (FM 849; 851) have the characteristic cheetah-like crown shape: relatively short and thick. The typical felid longitudinal furrows are visible on the labial surface. Normally these furrows are absent on the *A. jubatus* canines. The aforementioned furrows are also not visible on the specimens from the Epivillafranchian cheetah from Untermassfeld (Hemmer, 2001), but exist, weakly marked on the canines of the specimens from St. Vallier, as well as in the lower canines of *A. pardinensis* from the MNQ18 of Fonelas (Spain) (Garrido, 2008). Unlike most felids however, those furrows on the Varshets canines are relatively weak and short. Probably this felid character disappears secondary in cheetah and could be more frequently manifested in the larger teeth of the older populations of the genus. The canines correspond in their size to the compared specimens of *A. pardinensis* from St. Vallier (MNQ17) (table1).

Upper P4s are characterized by a strong reduction of the protocone which shapes no point and is very slightly protruding in

lingual direction. It looks more like a prolongation of the lingual root of the tooth at the crown level. The root itself is closely pressed to the main body of the tooth. Such morphology is typical for cheetahs (Teilhard De Chardin & Leroy, 1945; Viret, 1954; Sotnikova, 1989). In this respect, the P4 differs clearly from the P4 of the recently described species from the Late Pliocene of China, named *Acinonyx kurteni* (see below). The size of the varshets P4 is statistically larger than the Recent *A. jubatus*. The preparastyle of the Varshets specimens is only vestigial, clearly less developed than in the recent form, which explains why the mesial paracone border is more oblique than in the recent species. The protocone of the Recent species is slightly more distally displaced. In the position of the protocone (displaced mesially), the Varshets specimens also correspond to another specialized form that is close to *Acinonyx* and mainly to *Puma* – the North American *Miracinonyx inexpectatus* (= *M. studei*) (JWT 563-420664 - cast, col. SI-NMNH). The size and morphology of the Varshets P4s completely correspond to *A. pardinensis* from the Middle Villafranchian of Saint-Vallier (France). Both the MNQ17 samples, the sample from St.-Vallier and the one from Varshets do not reach the dimensions of the Untermassfeld (Germany) *A. p. pleistocaenicus* teeth (see Hemmer, 2001). The maximum dimensions of the Late Pliocene N. African *A. aicha* (Geraads, 1997) are also larger. At the same time, the European cheetahs from St. Vallier and Varshets have slightly thicker upper P4s than the mentioned primitive African species (Table 2).

The calcaneus (FM 878) is typically felid (see Gromova, 1960), its size is rather larger than a jaguar and much smaller than a male lion. The sustentacular (inner astragalus) facet is obviously rounded, rounder than in a jaguar or leopard for example. Its articular surface is in a single plane. Plantary from the sustentaculum there is a very strong furrow which usually is not that deep in the noted species of genus *Panthera*. In the proximal end, on the lateral surface, there is a pronounced elongated fossa. In proximal direction it reaches the proximal edge of the bone (i. e. the edge of the cuboid facet). This fossa is practically missing in lions and jaguars. The bone is larger than the calcaneus of *Megantereon* and lacks its strong convexity on the lateral surface of the proximal end. Although of approximately the same total length, the Varshets calcaneus differs strongly from *Homotherium*: it is much more slender, and its distal portion is quite elongated; it lacks also the navicular facet typical of *Homotherium* (Ballesio, 1963). Significantly larger than the calcaneus of a Recent cheetah (60-78 mm after Gromova, 1960), the Varshets specimen fully corresponds in shape and size to the calcanei of *A. pardinensis* from Saint-Vallier stored in the MHNL (Table 3) but does not reach the values of the specimen from Untermassfeld.

The astragalus is typically felid. Compared to *Homotherium* (with length 48.3 mm and width 45.5 mm – coll. MNHNP, Lab. de Paléontologie) it is insignificantly longer but much narrower, with a narrower trochlea and differently situated caput. The caput of the astragalus looks “twisted” in ventral view, if compared to other large felids like leopard and jaguar: its maximal diameter is obliquely placed, compared to the noted species of genus *Panthera*. There is a strongly expressed drop-like fossa on the lateral surface of the caput's column, with its broader part ending ventrally on the edge of the articular surface of the caput. The elongated sharp end of the fossa touches the small facet for the calcaneus. A similar fossa is present on the astragalus referred by Kurten & Crusafont (1977) (see there

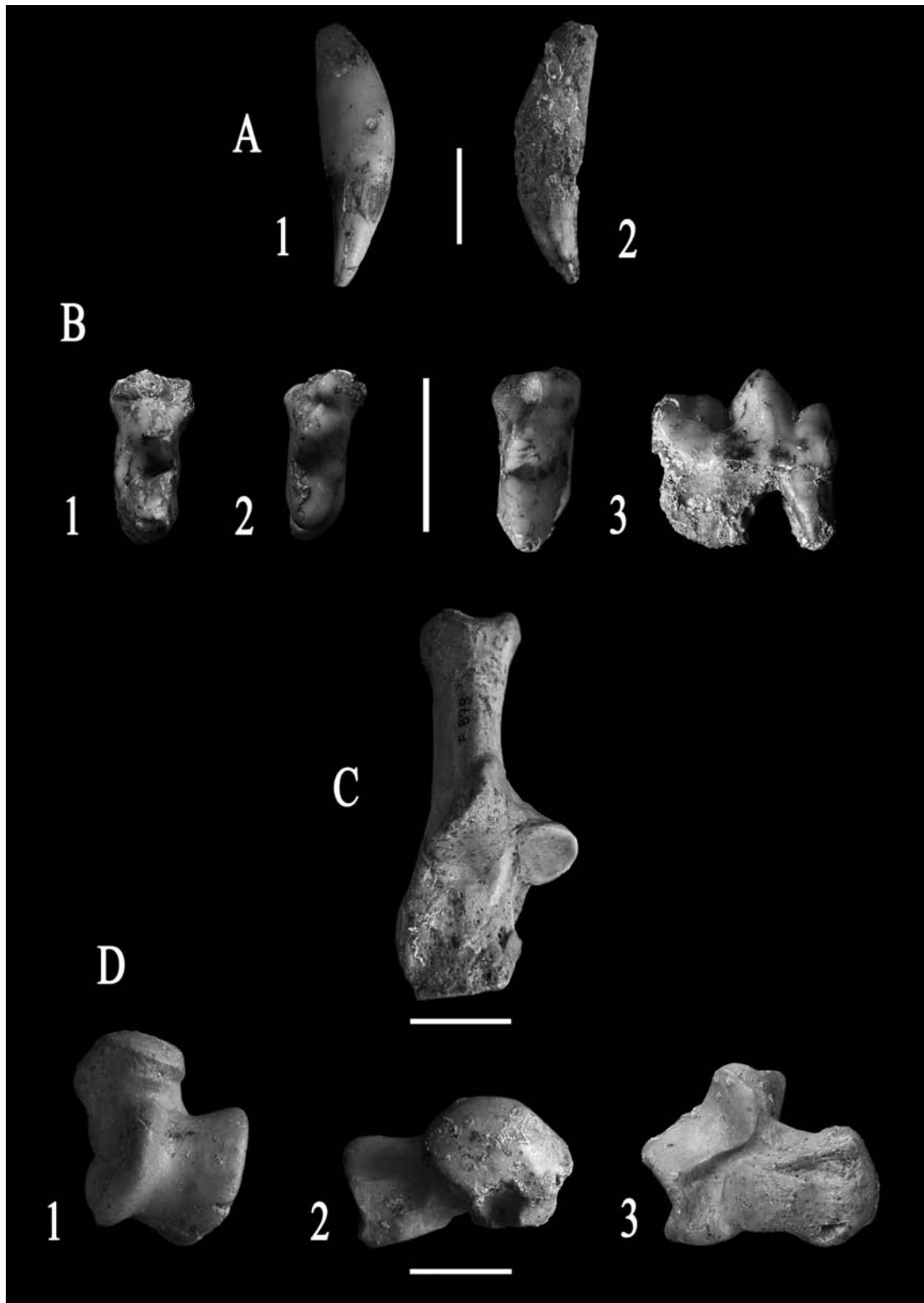


Fig. 1.—*Acinonyx pardinensis* remains from the middle Villafranchian locality of Varshets. A – upper canines in labial and lingual view: A1 – right C1 (FM 849); A2 – left C1 (FM 851). B – upper carnassials: B1 – right P4 (FM953) in occlusal view; B2 – left P4 (FM955) in occlusal view; B3 – left P4 (FM 954) in occlusal and labial views. C – calcaneus (FM 878) in dorsal view. D – astragalus (FM973) in dorsal view (D1), view of the distal surface (D2) and plantar view (D3).

the figured astragalus) to *A. pardinensis* from Puebla de Valverde. In all noted characters and in size (table 4.) the Varshets astragalus corresponds to the astragalus of *A. pardinensis* from St.-Vallier (Coll. MHNL) but it is smaller than the specimen from Untermassfeld.

The Varshets cheetah has morphological and morphometrical differences with the modern species. The postcranial remains are not only of larger size than the recent species, but also have more massive proportions. The fossil cheetah from Varshets was much larger than the Recent species and possibly not so fast. After the visual comparison of the astragalus and the calcaneus with these of different recent large cats with known weight, the body weight could be about 100-110 kg. The average weight of the recent male *A. jubatus* is somewhat more than 40 kg (Krausmann & Morales, 2005) and could reach no more than 65-70 kg. The upper P4 of the cheetah from Varshets has more oblique and elongated parastyle (as in “*Miracinonyx inexpectatus*”) than in the recent species. This puts their protocone in an even more anterior position than in recent cheetah – almost at one level with the parastyle. Those differences, despite the individual variations, show an obvious regularity. Having in mind the strong difference in body size (see below), the only statistically larger P4 of the Varshets form represents a rather plesiomorphic stage of the carnassial teeth in relation to the Recent species. Both morphological and morphometrical data show that the discussed fossils belong to large cheetahs, fully similar according the existent data to *Acinonyx pardinensis* (Croizet et Jobert) from the Early Villafranchian to the beginning of the Late Villafranchian of Europe. The morphological and metrical comparison of the fossil cheetahs is difficult because of the scarce material and the body weight comparison is only approximate. If the body mass of the Varshets cheetah (~ 100-110 kg after the postcranial remains) is comparable with the estimated weight of the Villafranchian *A. pardinensis* (probably males and females) from Les Etouaires (80-120 kg), St. Vallier (60-80 kg, calculated after tooth length, but *A. pardinensis* has smaller carnassials related to *A. jubatus*: see above), Olivola and Casa Frata (90-120 kg) and Dmanisi (around 100 kg), it would be smaller than the Epivillafranchian cheetah from Untermassfeld (110-140 kg) and larger than the Middle Pleistocene cheetah from Hundsheim and Mosbach (60-90 kg.) (see Hemmer, 2001; Hemmer *et al.*, 2008; Hemmer *et al.*, 2011).

Discussion. What is a cheetah? Problems of the taxonomy, the origin and the phylogeography of the cheetahs

The time and place of the origin of the genus *Acinonyx* are still debatable. Africa has been pointed out as one possibility (Sotnikova, 1989). Indeed, there are African finds referred to cheetahs, having a supposed absolute age ca. 4 Ma (Omo Mursi) and more than 3.5 Ma (Laetoli). Those remains, however, are very fragmentary, and their generic belong-

ing is not unequivocal (Turner, 1990). Turner (1990) supposed that cheetahs are immigrants into Africa. Recently, a new cheetah species with some plesiomorphic features compared to *A. Pardinensis*, such as a less convex and less specialized skull, was found in Africa (Geraads, 1997). The age of this form, *Acinonyx aicha* Geraads is about 2.5 Ma. In Africa, the oldest unequivocal fossil remains of genus *Acinonyx* s. str. are as old as 3 Ma (early MN16) and have been found both in Africa (Makapansgat 3) (Turner, 1990). In Europe the oldest *A. pardinensis* remains are from Perrier-Etouaire, from where comes the type specimen (a mandible: see Schaub, 1949) of the species *A. pardinensis* Croizet et Jobert. The age of Les Etouaires is not very clear but it is referred to MNQ16b (Steininger *et al.*, 1990) and could be at about 2.5 Ma (Guérrin, 2007) or most probably slightly older, close to the age of Montopoli (Aguirre *et al.*, 1997). The oldest known Asian remains (India – Pinjor, China) could be slightly younger. Recently a new species of cheetah with an estimated age of 2.2-2.5 Ma, that demonstrates a typical cheetah skull shape, but a rather plesiomorphic stage of the upper carnassials, was described in Hezheng area, China under the name of *A. kurteni* (Christiansen & Mazák, 2009). *A. kurteni* seems to be an *Acinonyx* s. str., characterized by advanced skull shape but plesiomorphic tooth morphology. Having in mind the features of this middle Villafranchian Asian specie and the co-existence of another species in Europe, we could suppose the presence of two parallel lineages of cheetahs in Eurasia from the Early Villafranchian: *A. kurteni* and *A. pardinensis*¹, and to imagine an Eurasian origin of the genus in Late Ruscinian/Early Villafranchian time. It is accepted that *Acinonyx* (and possibly *Uncia*) is a close relative of *Puma* (Salles, 1992; Van Valkenburgh *et al.* 1990) (The close affinities of the snow leopard with the *Acinonyx-Puma* group is contested by recent DNA investigations (Werdelin *et al.*, 2010)). The question of the place and time of the *Puma* origin is also still unclear. A form morphologically similar to cheetah, the American “cheetah” – *Miracinonyx* (Van Valkenburgh *et al.*, 1990), that was referred until recently to *Acinonyx* s. str., possibly shares a common ancestor with *Puma* from which both, *Puma* and *Miracinonyx* diverged, after some opinions, in N. America at about 3.2 Ma ago (Barnett *et al.*, 2005). As *Acin-*

¹ D. Geraads (CNRS UPR 2147, Paris) drew my attention to the fact that the well known domed skull of *A. pardinensis* from St. Vallier (NO. 821, coll. of the MHNL) is restored by plaster and its shape could be not so reliable. The second one (NO. 825) is crushed.

nonyx, *Puma* is also known in the Early Villafranchian of Eurasia with a form, that merits subgeneric separation as *P. (Viretailurus)*, having some skeletal and cranial differences from the recent form (personal observations). The oldest *Puma* localities known are Shamar, Mongolia and Kvabebi, Georgia but also Perrier-Etouaires, France (Hemmer *et al.*, 2004; Kurten & Crusafont (1977) and Red Crag, Great Britain, all of them with Early Villafranchian age. Hemmer *et al.* (2004) refer some African remains with an age of about 3.5–3 Ma to *Puma* and suppose an African origin of the genus.

Except from Varshets European fossil cheetah are known from about sixteen early Villafranchian to middle Pleistocene localities of France, Spain, Italy, Austria and Germany (See Garrido, 2008 and Hemmer *et al.*, 2008) as follows: Etouaires, Saint Vallier, Senèze, Le Vallonet, Saint-Estève (France); La Puebla de Valverde, Las Higuieruelas, Villarroya, Fonelas (Spain); Montopoli, Villafranca d’Asti, Olivola, Casa Frata (Italy); Untermassfeld and Mosbach (Germany); Hundsheim (Austria). A find from Liventsovka (Priazovian South Russia, NMQ17) noted as *Acinonyx* sp. (Titov, 2008) must represent the same species.

After the recent concept (Hemmer *et al.*, 2008) the European fossil cheetahs belong to a single and polymorphic large species or “macrospecies” - *A. pardinensis* (s. lato). The status of *Felis arvernensis* Cr. et Job., described, as well as *A. pardinensis* (Cr. et Job.) from Etouaires is still debatable. Some authors express the opinion that this cat has specific differences from *A. pardinensis* (see Heintz *et al.*, 1974; see also Hemmer *et al.*, 2008). It is difficult to decide from one hemimandible only if this is a separate taxon or an aberrant individual of *A. pardinensis* from Perrier - Etouaires. Possibly, however, Viret (1954) was right to consider this taxon a synonym of *A. pardinensis*, and this seems a more parsimonious hypothesis. Indeed, the type mandible has some atypical features such as the elongated distal part of P4, the shape of the paraconid (a specific occlusion) etc. At the same time, a number of characters such as the short massive canine, the short diastema, the rather massive symphysis and the position of P3 indicate cheetah affinities (Spassov, 1999). The history of cheetahs in Europe is still unclear, due to the scarce material. I will follow Hemmer (2001) and Hemmer *et al.*, (2008) who proposed a taxonomic concept according to which the fossil cheetahs of Europe could be dis-

tributed in three successive taxa with subspecific rank: *A. p. pardinensis* (Cr. Et Job.), for the Early Villafranchian till the Pleistocene beginning (Etouaires – Casa Frata), *A. p. pleistocaenicus* (Zdansky) for the Epivillafranchian form (Untermassfeld): a migrant from Asia) and *A. p. intermedius* (Thenius) for the Middle Pleistocene cheetah (Hundsheim and Mosbach). At the same time the Cheetah evolution could be much more complicated. Having in mind the considerable time span between the first and the last representative of the species on the continent we could suppose specific differences between the separate successive forms. Besides the probable size differences, some morphological differences support this supposition: Hemmer (2001) and Hemmer *et al.*, (2008) note some morphological differences in the mandibular symphysis between *A. pardinensis pardinensis* (the Etouaires – Olivola form) on one hand and the Epivillafranchian (Untermassfeld) and the Middle Pleistocene (Hundsheim, Mosbach) forms on another hand. If we judge after the recent carnivores, such kind of features that concern not only size and proportions but also the skull morphology could be regarded as criteria for specific distinction. After this second taxonomic possibility *A. pleistocaenicus* could be regarded as a separate Asian species, that invaded Europe during the strong aridification at the beginning of the Epivillafranchian.

The Varshets remains fill the knowledge gap on the dispersal of *A. pardinensis* (especially of “*A. p. pardinensis*” sensu Hemmer *et al.*, 2008) in the Villafranchian of Europe and show its presence not only in the Western Mediterranean but also in Southeastern Europe. We could conclude now, after the distribution of the known cheetah localities, that in the time interval between the Early Villafranchian and the beginning of the Pleistocene this cheetah occupied only the southern part of the European continent (the Mediterranean-Balkan area). From there, it was probably spread through the peri-Pontic area (South Russia - Liventsovka: Sotnikova, 1989 and Dmanisi - Georgia: Hemmer *et al.*, 2011) till Central Asia: Tajikistan (see Sotnikova, 1989) and in case that *Felis brachygnathus* Lydekker, 1884 (= *Sivafelis brachygnathus* (Lydekker) sensu Pilgrim, 1932) from Pinjor (Siwalik) represents the same species of cheetah, it could be spread also till India. Such a distribution supports the idea of the specific character of the South European fauna in Middle Villafranchian and of the strong Central Asian influence on this fauna through the Balkans

(Spassov, 2000; 2003). According the paleontological data the fossil cheetah does not reach Central Europe (Austria and Germany) before the Epivillafranchian and this is possibly related to a new wave of dispersal from the east, related to the continuation of the aridification.

The assignation of the scarce Indian (Pinjor) material to *A. pardinensis* is debatable. *Qiu et al.* (2004) are probably right to separate their new species *Sivapanthera linxiaensis* from *Acinonyx*. The skulls of this probably Middle Villafranchian taxon that is again (as *A. kurteni*) from Longdan, Hezheng area (China), figured in *Qiu et al.* (2004) differ from *Acinonyx* mostly by the less domed frontals, the large infraorbital foramen, the strong and elongated sagittal crest, the more elongated muzzle, the pinched caudal portion of the muzzle (the maxillary bones) on both side of the nasals. With all these features this new taxon shows similarities with *Puma* and could be regarded as a member of the *Acinonyx* stem-group. Its relations with *Miracinonyx* could represent certain interest. At the same time, the close affiliation of the later form “*Cynailurus*” *pleistocaenicus* Zdansky with *Sivapanthera linxiaensis* does not seem to be strongly supported by the paleontological facts and I will follow Hemmer *et al.* (2008) in the interpretation of this taxon as a trough cheetah, that migrated in the Epivillafranchian in Europe.

The recent fossil material described in Central Asia complicates the problem of the definition of the *Acinonyx* diagnosis: several forms of *Panthera*-sized cats with (1) short canines and (2) relatively developed frontal sinuses as well as with different degree of expression of the typical cheetah/cheetah-like facial and carnacial features have existed in a very large territory in the Early/ Middle Villafranchian:

1. forms with relatively flattened frontals; medium elongated/shortened skull; large (?) infraorbital foramen, but P4 protocone, with a cheetah-like trend to reduction (*Acinonyx aicha*, “*Sivapanthera*” *linxiaensis*; *Miracinonyx*);

2. forms with well to strongly domed and enlarged, cheetah-shaped frontal area and shortened skull; but with 2.1.: unreduced P4 protocone (*A. kurteni*)

or 2.2.: reduced protocone (*A. pardinensis*).

We could mention that the reduction of the P4 protocone is a feature that has appeared more than once in the felid evolution and this trend could appear in parallel especially in closely related forms.

Possibly the most peculiar features of the *Acinonyx* s. str. skull is the visibly bulged frontals, related to the strong development of the frontal sinuses. The development (to a different extent) of the frontal sinuses and the bulging of the frontal area represent synapomorphy of the closely related *Puma*, *Acinonyx* and *Uncia* but the extremal stage this development is reached in *Acinonyx*. The specific inclined position of the neurocranium of *Acinonyx* in respect to the palatal plane and the related more oblique position of foramen magnum, as well as the strong vertical elevation of the fronto-orbital region in this felid correspond to the important role of vision and are typical features of the cheetah. These features could be regarded as autapomorphies of *Acinonyx* as adaptation to a mode of life in open landscapes.

Post scriptum from the author

After this paper was in print Deng Tao’s publication (2011) came out. This paper revealed the news that the skull (type and single specimen) of this newly described species from China (Christiansen & Mazák, 2009) is a fossil forgery. Deng (2011) especially notes that the zygomatic arch, the occipital part, the sagittal crest, the basiooccipital area and parts of the parietal area (above all the posterior part of the skull) bear the traces of artificial modeling. It is possible that the cheetah-like domed shape of the skull roof has not been affected by the human interference (see the answer of Christiansen & Mazák cited in Deng Tao (2011), however we could not be sure in the natural appearance of the skull’s contour of this Chinese specimen (Deng Tao, pers. comm.). Neither the age, nor the location of the remains are clear; it could have been from Longdan (2.2-2.5 Ma), and neither is that sure. For this reason the shape of the skull and the name and age of the location cannot be used as firm arguments concerning some of the theses offered in my publication, and in particular:

- the existence of “two parallel lineages of cheetahs in Eurasia from the Early Villafranchian: *A. kurteni* and *A. pardinensis*”.

For this reason the probability, put forth in the paper that the cheetahs rather originated in Eurasia cannot be launched with priority before the version that they are African in their origins. The issue is still awaiting its solution.

The existence in the Middle Villafranchian of forms with strongly domed and enlarged, cheetah-

shaped frontal area and shorten skull, but with unreduced P4 protocone cannot be accepted for certain.

It is quite possible that the strongly domed skull was a relatively late apomorphy with cheetahs, dating as late as the Pleistocene.

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