



# An intriguing find of an early Middle Pleistocene European snow leopard, *Panthera uncia pyrenaica* ssp. nov. (Mammalia, Carnivora, Felidae), from the Arago cave (Tautavel, Pyrénées-Orientales, France)

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## Abstract

A complete mandible of a leopard-sized cat from the early Middle Pleistocene Arago cave MIS 14 level (Tautavel, France) was at first assigned to the snow leopard, *Panthera uncia*. A subsequent comprehensive description and analysis found the mandibular corpus snow leopard-like, but interpreted the dentition more like the leopard, *Panthera pardus*. Thus, this cat was classified as *P. pardus*. The re-study given in this paper presents the key to its real evolutionary place. The extant snow leopard is characterised by an autapomorphic excessively large dentition, not found in any other *Panthera* species. The Arago specimen represents the symplesiomorphic small-tooth type. Subtracting this character leaves diagnostic uncertainty, when only looking at the teeth, but provides an unambiguous *P. uncia* assignment when looking for the unique factor combination of the mandibular corpus. We deal with an ancestral snow leopard who demonstrates that the later large dentition was not yet evolved in the early Middle Pleistocene. An abstract heading in a symposium program book proposed the name *Panthera pardus tautavelensis* nov. ssp., not available by the International Code of Zoological Nomenclature. Therefore, the Arago snow leopard is named *Panthera uncia pyrenaica* ssp. nov. A single *Panthera uncia* record in the Eurasian late Middle Pleistocene from Zhoukoudian Locality 3 (China) perfectly bridges the difference between the Arago cat and the extant snow leopard. The early Middle Pleistocene European history of leopard-sized cats was originally understood as a more or less uniform development within the species *P. pardus*. This turns out to be a repeated replacement of different species and subspecies, involving *Puma pardoides*, *Panthera pardus* and *Panthera uncia*. It cannot even be excluded that snow leopards returned in each intense cold period of the Middle and Late Pleistocene from their Central Asian home to Europe.

**Keywords** *Panthera uncia* · *Panthera pardus* · Arago cave · Tautavel · Middle Pleistocene

## Introduction

A serial cast of a complete large cat mandible found in the early Middle Pleistocene MIS 14 lower levels of the Arago cave (Tautavel, France) and brought from a visit in the Tautavel Museum by R.-D. Kahlke (Weimar) provided the first contact the present author had with a European snow leopard. The first look suggested that this specimen is not a leopard, *Panthera pardus* (Linnaeus, 1758). A subsequent comparison with leopard, snow leopard and

puma mandibles stored in the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt revealed its true nature as a large and somewhat aberrant snow leopard, *Panthera uncia* (Schreber, 1778). As the author had at that time a publication in-press on the Pleistocene cats of Europe, he included a first, short note on the Arago cat, mentioned its large size and weak dentition, and referred to an at that time pending detailed study of this fossil (Hemmer 2003). The fossil was next cited in a public lecture at the 18<sup>th</sup> International Senckenberg Conference/VI International Palaeontological Colloquium in Weimar, 2004, published 2007 (Hemmer 2007). In connection with this lecture, the author had the opportunity to ask A.-M. Moigne (Tautavel) for a good cast for further research. In between, Testu (2006) presented as part of her thesis on the Felidae and Hyaenidae of Mediterranean Europe a comprehensive description and an extensive analysis of the fossil in

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question. She found the mandibular corpus snow leopard-like, but interpreted the dentition to be leopard-like. This contradictory finding hindered an unambiguous classification. Consequently, the Arago mandible was called *Panthera* sp., which encouraged later authors to also leave the issue open (Cardoso and Regala 2006; Madurell-Malapeira et al. 2010). Subsequently, a new leopard subspecies, *P. pardus tautavelensis*, was proposed for the Arago

cat in the Program/Guide book of excursions of the 16<sup>th</sup> International Cave Bear and Lion Symposium, Azé, 2010 (Testu et al. 2010). Finally, the results of Testu's thesis were condensed in the symposium publication, the mandible now interpreted as that of a leopard, but without the act of nomenclature announced in the program book (Testu et al. 2011). Meanwhile, H. de Lumley sent the cast requested and it forms the base of this study (Fig. 1), its



**Fig. 1** The Arago snow leopard mandible, *Panthera uncia pyrenaica* ssp. nov., buccal views (photos taken from cast). Scale bar: 50 mm

excellent quality confirmed by measurements of the single teeth, which deviate only within the 1/10-mm range from those taken from the original (Testu 2006; Testu et al. 2011) (Table 1).

## Materials

The author recorded morphometric and morphognostic data for 16 *P. uncia* and a large number of *P. pardus* skulls in the years 1963 and 1964 in the collections of the Zoölogisch Museum Amsterdam (4), Museum Alexander Koenig Bonn (4), Senckenberg Forschungsinstitut und Naturmuseum Frankfurt/M. (2), Rijksmuseum van Natuurlijke Historie Leiden (2), Zoologische Staatssammlung München (3) and Naturhistorisches Museum Wien (1) (in parentheses number of skulls), providing an important basis for this comparative study. With the cast of the Arago mandible, the author re-visited the material housed in the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt and the Naturhistorisches Museum Basel (3 further skulls).

## Comparative study

### Mandibular corpus

The lateral view of the Arago mandible (Fig. 1) shows a steep front profile of the symphysis, which is combined with a gently convex lower border of the mandibular corpus. This shape is typical for *P. uncia* (Fig. 2), but not for *P. pardus* (Testu et al. 2011). Only slightly less steep profiles can be found, though, in some Late Pleistocene European leopards (Koenigswald et al. 2006; Spassov and Raychev 1997). There are three mental foramina with different arrangement on the left and the right sides. This morphognostic feature provides no diagnostic value, as the number of foramina varies in the snow leopard as well as in the leopard. A clear difference is found for the masseteric fossa. It terminates with a shallow anterior border below the tip of the  $M_1$  protoconid. Its lower edge limits the deep masseteric hollow all the way up to its end at the outer point of the condylar process. This is the morphology as found in the snow leopard. In contrast, the ventral margin of the leopard's masseteric fossa mostly looks like an inclined, caudoventrally expanded platform (Fig. 3), forming a lateral widening in dorsal view. The profile of the coronoid process is evenly rounded at its summit, runs caudally at first in a quite straight line downwards and finally bends in a concave line to the condylar process. This shape is exactly reproduced by some snow leopards, but there is an enormous

variability in *P. uncia* even to the impression that the caudal border would have been vertically cut off (see the specimen in Fig. 2).

The inner view (Fig. 4) of the mandibular ramus reveals two additional diagnostic highlights of the Arago specimen. The first is the strikingly rostral location of the mandibular foramen. The ratio of the shortest distance from the most anterior point of the mandibular foramen to the  $M_1$  alveole to the shortest distance from the same point at the foramen to the coronoid process is 65.5 and 61.9 in the Arago cat. The range of this ratio in snow leopards was found as 66.2–89.0 ( $n=9$ ), whereas a few leopard measurements, including the Late Pleistocene hemimandible from Geinsheim (Upper Rhine valley, Germany: Koenigswald et al. 2006), gave ratios of 89.8–103.7 ( $n=5$ ), which show the Arago mandible near the snow leopard, but not the leopard. The second conspicuous character in inner view concerns the pterygoid fossa. Unlike *P. pardus*, but comparable to *P. uncia*, the insertion of the pterygoid muscle is marked around the clearly hollowed fossa by a strong relief of the mandibular corpus surface (Fig. 4). Altogether, there are four striking mandibular features, mainly morphognostic ones and differing in snow leopard and leopard, all of them undoubtedly displaying the snow leopard nature of the clearly very robust Arago cat's mandible.

### Relative tooth size

The snow leopard is distinguished from all other *Panthera* species by its extraordinary large dentition (Fig. 2), mostly represented by the lower carnassial related to the mandible length (Christiansen 2008, fig. 1 (i); Hemmer 1973, fig. 2). The length of the Arago mandible (Table 1) falls in the broad variability of *P. pardus* mandibles (112–158 mm in a large series of leopards from a single East African regional population in the collection of the Zoologische Staatssammlung München), but is just over the maximum of *P. uncia* (Testu 2006, table 10; 112–133 mm in 16 mandibles measured by the author). In contrast, the length of the Arago molar also falls in the leopard variability (14.9–21.0 mm), but is just a little less than the snow leopard minimum (17.2 mm; see also Fig. 8). Consequently, this diagnostically important feature excludes the extant population of *P. uncia* for the Arago cat, without assigning it strictly to *P. pardus*, as the relatively small dentition is also typical for all other *Panthera* species. The extremely large teeth of the snow leopard also determine two other ratios than the  $M_1$  length to mandible length ratio alone, i.e. the ratio mandibular depth behind  $M_1$  to  $M_1$  length and the ratio diastema ( $C_{inf.}-P_3$ ) length to  $P_3-M_1$  length. Listed like separate characters, these ratios suggest more than just the single difference caused by the extraordinary size of the *P. uncia*



**Fig. 2** Extant snow leopard mandible (above) compared to the Arago mandible (cast, below), both brought to the same size. Bars: lengths of both tooth rows  $P_3$ - $M_1$

dentition. This applies also for multivariate analyses where this pure size feature is involved in one way or another, as used with principal component analysis by Testu (Testu 2006; Testu et al. 2011) to advocate for a leopard nature of the Arago mandible.

$C_{inf}$ .

The most distinct feature of the snow leopard's dentition to be seen even in the living animal is the canine which has a more circular cross-section, whereas it is oval in all other



**Fig. 3** The Arago snow leopard mandible (cast, above) compared to a Late Pleistocene leopard mandible (Geinsheim, Germany; cast). The oblique view from above illustrates the contrast of the masseteric fossa ventral margin of *P. uncia* and *P. pardus*

large cats (Schmid 1971). This is not only true for the upper canine, but also expressed by the ratio largest width to largest length in the lower canine. In the Arago mandible, this ratio amounts 81.7 and 82.4%. The maximum ratio of the largest published series of *P. pardus* lower canines ( $n = 88$ ) is 79.2, mean 72.5 (Schmid 1940). The canine thus supports a *P. uncia* diagnosis.

### P<sub>3</sub>

In morphognostic terms, the Arago right third premolar (the left one is damaged at the rear) best fits in buccal view a *P. uncia* P<sub>3</sub> (compare Fig. 5 and Hemmer 1966, plate VII). In occlusal view, it is characterised by a slightly convex inner boundary line and an even less convex buccal margin, giving

the tooth a somewhat oval shape. Such a form is typical for *P. uncia*, whereas the leopard shows at least a little waisting of the inner and outer contours (Schmid 1940). There is no paraconid in front of the Arago cat's P<sub>3</sub> (Testu et al. 2011), whereas the snow leopard's premolar has a paraconid (Schmid 1940; Testu et al. l.c.). Both morphotypes occur in the leopard, 29.6% without and 70.3% with paraconid (Schmid 1940). Thus the Arago P<sub>3</sub> matches the leopard. Main morphometric differences between *P. pardus* and *P. uncia* third premolars are expressed by three ratios, protoconid height in % tooth length, protoconid length in % protoconid height and anterior width in % tooth length (Schmid 1940). The first of them does not separate the Arago P<sub>3</sub> from the leopard nor from the snow leopard. The second excludes by its extremely small values *P. pardus* completely (large, representative series of 85 teeth), but ranges within the *P. uncia* variability, respectively, fall partially even below the latter in the case of the measurements taken by Testu (Testu et al. 2011). The third ratio fails to differentiate for the Arago specimen between the two species in question. The length, height and width ratios are, however, the subject of allometries in *Panthera* species. These were first analysed for *P. onca gombaszoegensis* (Hemmer et al. 2003), subsequently also for *P. leo* and *P. tigris* (Hemmer et al. 2010). It holds true for *P. pardus* and *P. uncia*, too (Figs. 6 and 7). The relative protoconid length of the P<sub>3</sub> in question falls outside the 99% confidence limits of the leopard, but within the 95% limits of the snow leopard (Fig. 6). The protoconid height, related to the protoconid length [cf. the ratio P<sub>3</sub> protoconid length in % protoconid height of Schmid (1940)], falls for the right tooth outside the leopard's upper 95% confidence limit, the left tooth is located near that limit (Fig. 7). Altogether, four out of five morphognostic and morphometric characters point to a *P. uncia* diagnosis for the Arago mandible's third premolar.

### P<sub>4</sub>

The Arago fourth premolar is placed well below the allometric line of *P. pardus*, when plotted in a scatter diagram P<sub>4</sub>/M<sub>1</sub> (Fig. 8). The larger teeth of *P. uncia* scatter around the same distance to the leopard line. An unquestionable species diagnosis is, however, not possible with this result, as *P. pardus* shows an enormous variability, which includes the Arago as well as all *P. uncia* values (Fig. 8). Nevertheless, the P<sub>4</sub> of the mandible in question is short, when its length is related to the M<sub>1</sub> length (and also the P<sub>3</sub> length), as are the snow leopard's fourth premolars (Aristov and Baryshnikov 2001). The protoconid of this tooth (Fig. 5) is asymmetric in lateral view and thus looks somewhat inclined backwards. Such a shape is typical for the leopard (Hemmer and Heidtke 2013; Schmid 1940; Testu et al. 2011), whereas the snow leopard usually has a symmetric form. The lingual contour of the Arago P<sub>4</sub> is moderately



**Fig. 4** The Arago snow leopard mandible (cast) in oblique view from above, to illustrate the morphognostic characters around the mandibular foramen and the pterygoid fossa

convex, its buccal margin is nearly rectilinear, gently concave under the protoconid in occlusal view (Fig. 6). This shape is found in *P. uncia* beside a more leopard-like form, whereas the *P. pardus* tooth is always more or less waisted.

There are three metrical characters which partially separate snow leopard and leopard fourth premolars, i.e. the ratios protoconid length in % protoconid height, median width in % tooth length and anterior width in % median width (Schmid 1940). The first is not really measurable in both  $P_4$ . With the necessary completion of the slightly damaged height of the left one, it would fall within the variability of both species. The large width of the Arago premolar excludes the snow leopard, but fits the leopard's variability with the second ratio. In principle, this is also true for the third ratio, which is based on the same measurement as the former; here, reaching the snow leopard's minimum depends just on the measuring error. Thus, two of three morphognostic and morphometric characters of the fourth premolar support a *P. pardus* diagnosis.

#### $M_1$

The molar of the Arago mandible has no metaconid, not even a vestigial one, above the talonid at the protoconid's distal edge (Fig. 4). Testu et al. (2011) therefore definitely exclude a *P. uncia* diagnosis for the carnassial, claiming that the snow leopard would always be characterised by the presence of such a cusplet (four skulls studied). By contrast, Schmid (1940, p. 17) emphasises for the  $M_1$  of the snow leopard the lack of a metaconid as a typical feature (16 skulls studied). The author of this present study also noted only two rudimentary metaconids in 19 snow leopard skulls (probably including five of Schmid's study). This unbridgeable difference proves that both forms, presence and lack of a metaconid, are found in *P. uncia*. The existence of a metaconid seems not to be an absolute diagnostic criterion in any *Panthera* species. For example, everybody who is familiar with the leopard dentition would agree that leopards have no metaconid at their  $M_1$ . But, there are four skulls out of

**Table 1** *Panthera uncia pyrenaica* ssp. nov. measurements of the holotype mandible (mm); taken from a cast, in brackets taken from the original (Testu et al. 2011)

	Arago E14-EFNI-1000 sin	Arago E14-EFNI-1001 dex
Mandible length Infradentale-Condylion mediale	c.134 [137.7]	c.134 [137.2]
Mandible length Infradentale-Proc. coronoideus	c.132.5 [129.6]	c.132.5 [129.8]
Mandible height Gonion ventrale-Coronion	64.7 [63.5]	63.3 [62.5]
Depth behind M <sub>1</sub>	30.0 [28.2]	28.3 [28.3]
Depth in front of P <sub>3</sub>	27.2 [27.4]	27.2 [26.9]
Thickness below P <sub>4</sub> /M <sub>1</sub>	14.7 [14.7]	13.9 [15.0]
Alveolar length P <sub>3</sub> -M <sub>1</sub>	43.2 [43.2]	43.2 [42.9]
Diastema length	c.14 [14.2]	16.4 [16.4]
C <sub>inf.</sub> length	12.0	11.9
width	9.8	9.8
height	24+	-
P <sub>3</sub> length	- [9.9]	10.6 [10.7]
greatest width	5.6 [5.8]	5.8 [5.8]
anterior width	5.0 [4.9]	5.0 [5.1]
protoconid length	5.6 [5.4]	5.5 [5.3]
protoconid height	6.9 [7.2]	7.0 [6.9]
P <sub>4</sub> length	15.1 [15.2]	15.3 [15.4]
greatest width	7.7 [7.6]	7.6 [7.8]
anterior width	6.5 [6.4]	6.6 [6.6]
protoconid length	8.0 [8.0]	8.0 [7.9]
protoconid height	- [9.6]	10+ [10.0]
M <sub>1</sub> length	16.9 [17.0]	16.9 [16.9]
greatest width	8.0 [8.0]	7.9 [7.6]
protoconid length	10.7 [10.6]	10.8 [10.5]
paraconid length	8.4 [8.4]	8.4 [8.4]
protoconid height	10.9+ [10.8]	10.9+ [10.8]
paraconid height	10.2+ [9.0]	10.2+ [9.6]
notch height	5.0 [4.9]	5.1 [4.5]

seven originating in Angola and seen by the author in 1965 in the collection of the Museum of Zoology Hamburg (no. 4679–4685), which present just this cusplet, well developed or at least rudimentary. So there are leopards with some accumulation of an otherwise nonexistent character in a regional population. Consequently, this feature also has no diagnostic value at all for the Arago mandible.

The M<sub>1</sub> talonid is small and low as in the leopard, not extending in height at least to about one-third of the rear protoconid edge as in the snow leopard. On the other hand, the back edge of the protoconid is not formed as a sharp mini-crista up to the tip, as in the leopard, but this sharp edge does not reach the tip, as in the snow leopard (Schmid 1940; Spassov and Raychev 1997). The snow leopard molar is characterised in occlusal view by a bulge opposite to the pit between paraconid and protoconid. This is only faintly indicated at the Arago M<sub>1</sub>, nearer to the shape usually found in leopards, but not really leopard-like. Neither of the ratios described to best differentiate the snow leopard and leopard molars (paraconid length and notch height in % length,

notch height in % width) (Aristov and Baryshnikov 2001; Schmid 1940) allows a definite diagnosis for the Arago cat. The relative short paraconid length falls in the first quarter of *P. pardus*, but near the mean of *P. uncia*. There are deviating measurements of the height at the notch between protoconid and paraconid, when taken from the cast or the original (Table 1). Related as well to the tooth length as to the width, the measurements taken by Testu (Testu 2006; Testu et al. 2011) allow no decision between the two species; taken from the cast they point to the leopard. Thus, the carnassial cannot be attributed to either *P. uncia* or to *P. pardus* with certainty.

## Discussion and conclusions

The key to understanding the evolutionary position and thus the classification of the Arago cat is the excessively large dentition of the extant snow leopard. Undoubtedly, this is an autapomorphic feature, which characterises the Holocene species, not found in any other extant or extinct



**Fig. 5** P<sub>3</sub>-M<sub>1</sub> of the Arago snow leopard (cast) in occlusal (above) and buccal view (below)

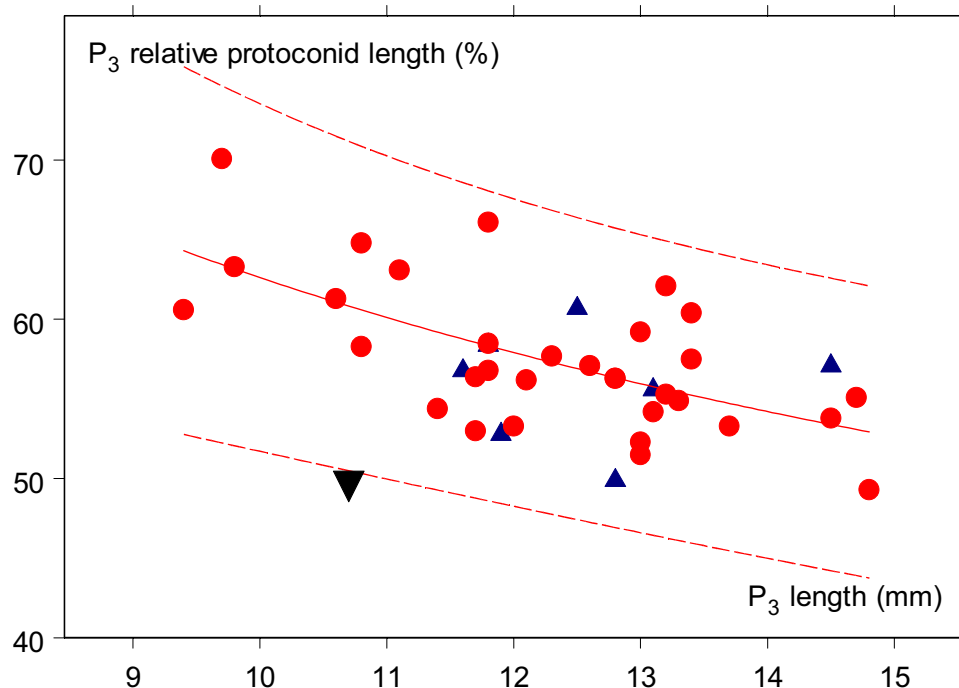
*Panthera* species. It is not per se clear when it evolved in the phylogenetic history of *P. uncia* on its way between the basal node with the tiger, the sister species of the snow leopard (Davis et al. 2010; Figueiró et al. 2017; Johnson et al. 2006), and its Holocene Central Asian population. Subtracting this major not snow leopard-like character of the Arago mandible leaves a more or less open diagnostic result, though focused on the snow leopard (seven out of 11 features are snow-leopard-like, four are leopard-like), for the decision between *P. uncia* and *P. pardus*, when looking at the teeth, but provides an unambiguous snow leopard assignment when looking for the unique factor combination of the mandibular corpus. Therefore, this early Middle Pleistocene fossil, dated at 0.57–0.53 Ma (Testu et al. 2011), is an unequivocal early representative of *P. uncia*. It demonstrates that the excessively large dentition of the extant species was not yet evolved at that time.

There is only a single other record of a snow leopard in the Eurasian Middle Pleistocene, a hemimandible from Locality 3 of the famous North Chinese site of Zhoukoudian

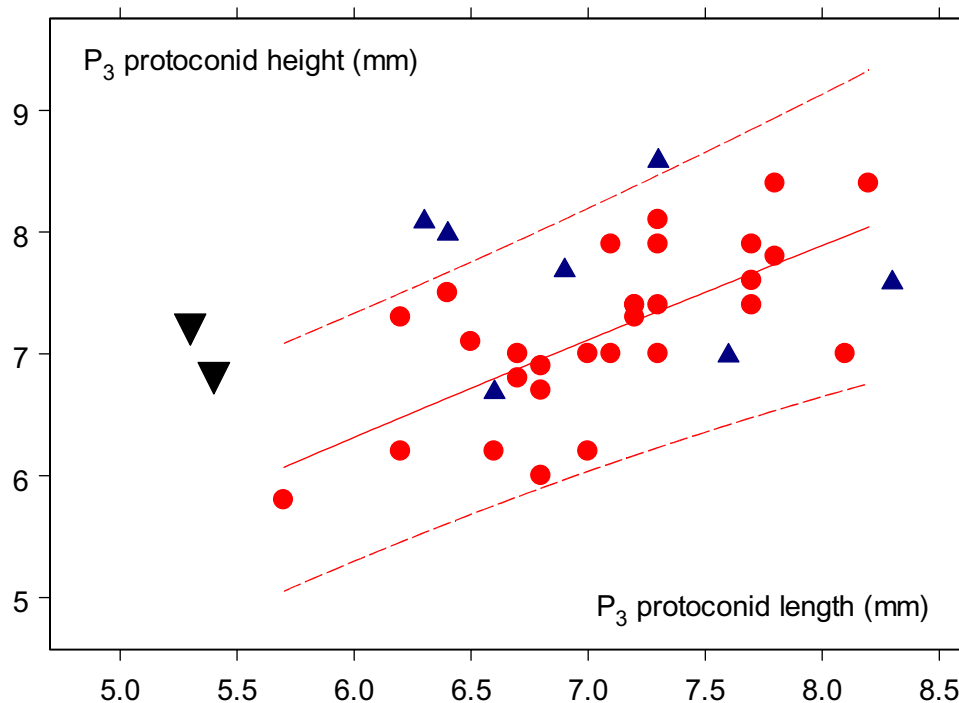
(Pei 1936). This specimen was tentatively referred to the leopard, leaving open the possibility of its alternative attribution to the snow leopard (Pei 1936). The Locality 3 fauna had been geochronologically correlated with the European Saale glaciation of the late Middle Pleistocene (Kurtén 1960). This locality was found probably coeval with Locality 4, placed by uranium series dates at 0.175–0.135 Ma. Localities 15 and 4 were also found to be coeval. The artifact-bearing layers at Locality 15 were placed in a time span between 0.140 and 0.110 Ma (compilation by Gao 2000). U-series dating of Locality 15 provided an age between 0.284 and 0.155 Ma (Shen et al. 2004). In summary, the mandible from Zhoukoudian Locality 3, diagnosed by Kurtén (1960) as *P. uncia*, is reliably dated in the later part of the late Middle Pleistocene.

This mandible (drawings in Pei l. c., fig. 29; re-drawn in Thenius 1969, fig. 2) has the same size (mandible length 137.5, Pei l. c.) as the Arago one, but in combination with the large dentition typical for the extant *P. uncia* (alveolar length P<sub>3</sub>-M<sub>1</sub> 48.0 vs. 43.2 in the Arago specimen, P<sub>3</sub> 13.0

**Fig. 6** Scatter diagram of  $P_3$  relative protoconid length (RPL = % of  $P_3$  length) and  $P_3$  length (L) of Holocene and Pleistocene leopards (*P. pardus*, red circle), Holocene snow leopards (*P. uncia*, blue up-pointing triangle) and the Arago cat (black down-pointing triangle). Allometric line (power curve fit) with 99% confidence limits for leopards:  $RPL = 168.2 \times L^{-0.429}$ ;  $n = 33$ ;  $r = -0.63$ ;  $p < 0.001$ . Mean RPL for  $L = 10.0$  mm: 62.6 (%), for  $L = 15.0$  mm: 52.6 (%). All measurements taken by Testu (2006, table 13)



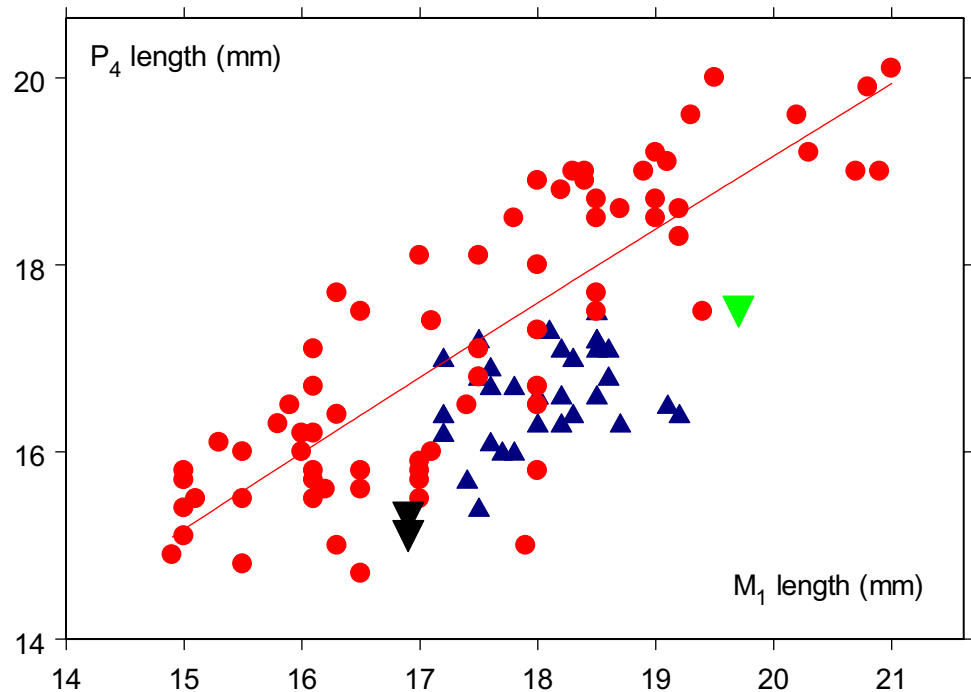
**Fig. 7** Scatter diagram of  $P_3$  protoconid height (PH) and  $P_3$  protoconid length (PL) of Holocene and Pleistocene leopards (*P. pardus*, red circle), Holocene snow leopards (*P. uncia*, blue up-pointing triangle) and the Arago cat (black down-pointing triangle). Allometric line (power curve fit) with 95% confidence limits for leopards:  $PH = 1.579 \times PL^{0.774}$ ;  $n = 29$ ;  $r = 0.67$ ;  $p < 0.001$ . All measurements taken by Testu (2006, table 13)



vs. 10.6,  $P_4$  17.5 vs. 15.1/15.3,  $M_1$  19.7 vs. 16.9). The crucial morphology of the mandibular corpus is the same as in the French fossil, with the same symphyseal part, the same deep masseteric hollow with the same shape of its ventral margin, the same rostral position of the mandibular foramen and the same strong relief around the pterygoid fossa. The carnassial also shows no metaconid and has

also only a small talonid and the same shape of the rear edge of the protoconid, but a slightly larger lingual bulge in occlusal view. The two premolars are characterised by comparable buccal and lingual contours, but the  $P_3$  has a small paraconid and a slightly larger posterior cusp. The evidence indicates that the Zhoukoudian mandible perfectly bridges the difference between the Arago cat and

**Fig. 8** Scatter diagram of  $P_4$  length and  $M_1$  length of East African leopards (*P. pardus*, red circle), snow leopards (*P. uncia*, blue up-pointing triangle), the Zhoukoudian snow leopard (green down-pointing triangle) and the Arago cat (black down-pointing triangle). Allometric line (power curve fit):  $P_4 = 1.687 \times M_1^{0.8113}$ ,  $n = 75$ ,  $r = 0.841$ ,  $p < 0.001$



the extant snow leopard, just as does its geochronological assignment.

Some material from Early Pleistocene upper Siwalik Pinjor stage deposits of northern Pakistan, dated to 1.4–1.2 Ma, has been claimed possibly to represent snow leopards (Turner and Antón 1997). The fragmented specimens from locality 73 are from leopard-sized cats. Their lower deciduous carnassial lacks a posterior fourth cusp. This feature was used to classify the felid in question as a *Panthera* species (Dennell et al. 2005). Actually, this character could exclude a snow leopard diagnosis and allow an attribution to *P. pardus*, but also to the genus *Puma* on the other hand. The  $DP_4$  of *P. uncia* has a metaconid-talonid complex. Consequently, there is not yet clear fossil evidence of Early Pleistocene snow leopards. There are also no Pliocene ones. “*Panthera*” *blytheae* Tseng, Wang, Slater, Takeuchi, Li, Liu and Xie, 2014, from Late Miocene-Early Pliocene sites in the Tibetan Himalaya, claimed to represent a sister species of *P. uncia*, is not a member of the genus *Panthera* (Geraads and Peigné 2017).

Therefore, there are only two mandibles of snow leopards known from the Eurasian Early and Middle Pleistocene. Both of them, the early Middle Pleistocene Arago specimen and the late Middle Pleistocene Zhoukoutian fossil, represent the species *P. uncia*. Nevertheless, they differ from one another in a key character. The Chinese cat by the autapomorphic excessive size of its dentition links to the Holocene type. The geochronologically older French cat has the symplesiomorphic tooth proportions of all other *Panthera* species. This calls for a taxonomic action. Hence, the Arago snow leopard is separated from the extant one

with own subspecific status. Based on the idea it would be a leopard, Testu et al. (2010) named it *P. pardus tautavelensis* nov. ssp. in the title of their abstract in the Azé cave bear and lion symposium program book. By article 9.10. of the International Code of Zoological Nomenclature (fourth edition with effect from 31 December 1999, and amendments with effects from 1 January 2012), this does not constitute published work available for zoological nomenclature; the condition of article 16.4. (explicit fixation of name-bearing types) is also not fulfilled in that abstract. So the early Middle Pleistocene European snow leopard subspecies has to be named corresponding to the International Code of Zoological Nomenclature as a new one (ssp. nov.), but not as a new replacement name (nom. nov.; Article 16.1, Recommendation 16A, Glossary).

2003 *Uncia uncia* Hemmer, p. 11.

2004 *Panthera* cf. *pardus* Moigne et al., p. 175.

2006 *Panthera* sp. Testu, p. 206.

2010 *Panthera pardus tautavelensis* nov. ssp. Testu et al., p. 64.

2011 *Panthera pardus* Testu et al., p. 271.

*Panthera uncia pyrenaica* ssp. nov.

**Holotype:** Mandible, stored in the Muséum National d’Histoire Naturelle, Département de Préhistoire, Tautavel (France); Arago E14-EFNI-1000 (left hemimandible) + Arago E14-EFNI-1001 (right hemimandible). For photos of the original specimen, see Testu et al. (2011).

**Etymology:** *pyrenaica*—latin, coming from the Pyrenees region.

**Type locality:** Arago cave, Tautavel (Pyrénées-Orientales, France).

**Geological age:** Marine Isotope Stage 14, early Middle Pleistocene, 0.57–0.53 Ma

**Diagnosis:** In contrast to the extant snow leopard (*P. uncia uncia*) with extraordinary large dentition, *P. uncia pyrenaica* is characterised by comparatively small teeth as in all other *Panthera* species. For other differences, see text.

The extant snow leopard has an extremely low autosomal heterozygosity, compared to the other *Panthera* species (Barnett et al. 2020, fig. 3). Molecular genetics revealed population reductions in all *Panthera* species ca. 100,000 to 300,000 years ago, resulting in loss of genetic diversity (Figueiró et al. 2017). This bottlenecking seems roughly to have coincided in *P. uncia* with the geochronological existence of the Zhoukoudian specimen. So the reduction of heterozygosity looks like the evolutionary booster for the subsequent successful spreading of the new big-tooth character.

We can only speculate about the selective forces that may have driven that unique enlargement of the dentition. Nearly all specific characters of the modern snow leopard are to be understood as functions of its high mountain habitat adaptation (Hemmer 1972; Kitchener et al. 2016). So this should also be true for the oversized teeth, functionally involved in feeding. At first glance, there seems to be no indication for any selective need for substantial strengthening of the carnassials compared to all other *Panthera* species. Nevertheless, there may exist a very simple reason. The Middle Pleistocene snow leopards were as large as the maximum of the extant conspecifics. This means a body mass of at least 50–55 kg (compilation for extant *P. uncia*: Nowell and Jackson 1996). Needing a daily meat supply of 3 kg (calculated by a body mass–based predictor equation: Hemmer 2004, 2007), the cat should repeatedly return to a kill of a larger ungulate. In the high mountain region, this could mean feeding on deep-frozen meat in winter. Particular carnassial strength would be very helpful in such a case.

These large carnassials are paired in *P. uncia* with a predicted bite force that is in accordance with a general felid bite force—body mass allometry, when bite force output from the mandible adductor muscles is estimated based on temporalis and masseter muscle cross-sectional areas (Christiansen 2007: table 1, fig. 2). The snow leopard greatly differs from the other *Panthera* species in view of the mean ratio of the estimated moment arms of the temporalis (MAT) and the masseter (MAM) muscles as measured from the mandibular condyle to the coronoid and the angular processes, respectively. The MAT to MAM ratio varies from 1.56 to 1.62 in *P. leo*, *P. pardus*, *P. onca* and *P. tigris*, but amounts to 1.87 in *P. uncia*, which falls within the hyaenid variability (1.77–1.89) (Van Valkenburgh and

Ruff 1987, calculated from data in table 1 and appendix 2). This differentiation of the jaw muscular forces underlines the importance of the enlarged dentition for the Holocene snow leopard.

At all events, the highly specific and complex pattern of functional adaptation in the extant snow leopard was obviously not complete before the end of the late Middle Pleistocene. The early Middle Pleistocene *P. uncia pyrenaica* may be understood as an ancestral form, whose ecological adaptation was not yet the same as in the later *P. uncia uncia*. When the cat, whose mandible was found in the Arago cave, lived at the foot of the Pyrenees near the Mediterranean, the climate was cool and dry (Testu et al. 2011). It may be speculated that this was then the preferred condition for an animal, which finally reached a close functional morphological adaptation (Haltenorth 1937; Hemmer 1972) to very cold, dry or semi-dry habitats with steep rocky slopes. This development ecologically trapped the snow leopard in the warmer Holocene within the Central Asian high mountains.

Leopard-sized cats were represented in Europe in the Early Pleistocene by the Eurasian puma, *Puma pardoides* (Hemmer 2001; Madurell-Malapeira et al. 2010). Just after the Matuyama/Brunhes magnetochron reversal at around 0.78 Ma, approximately in the time period MIS 19 to 18/17 (compilation by Kahlke et al. 2011), pumas were still present at the Czech locality of Stránská skála (Moravia). Two mandibular fragments of leopard-sized cats from different layers of that site were at first attributed to leopards, then compared with snow leopards (Thenius 1969), again ascribed to leopards (Hemmer 1971), but finally diagnosed as pumas (Hemmer 2001). The chronologically next dentition remains of the size in question are two upper carnassials from Gombaseg (Slovakia), described and figured by Kretzoi (1938). These two teeth show none of the features which characterise the leopard P<sup>4</sup> from Mauer (Heidelberg, Germany) and rather resemble extant leopards (Schütt 1969), although Gombaseg might possibly date from the earlier MIS 17 period (Maul and Parfitt 2010).

The leopard remains from the *Homo heidelbergensis* site of Mauer, including a P<sup>4</sup> and a mandibular fragment with P<sub>3</sub>, P<sub>4</sub> and M<sub>1</sub>, show unique morphognostic and morphometric characters and were attributed to a subspecies of their own, *P. pardus sickenbergi* Schütt, 1969. The fauna of this locality suggests referral to an interglacial equivalent to MIS 15, therefore to an age of ca. 0.60 Ma, and indicates a temperate climate with a mosaic of forest and open habitat (Schreiber et al. 2007; Wagner et al. 2011). Relying on the few fossils of this single site, this leopard has no clear affinity to other *P. pardus* subspecies (Schütt 1969). A mandibular fragment from the lower level of the Petralona cave (Greece), tentatively equated with the Mauer and Mosbach sites (Kurtén and Poulianos 1981), seems to be comparable with *P. pardus sickenbergi*, so far the only published length

and width measurements of the two premolars allow any diagnosis.

The faunal assemblages of Mosbach 2 (Germany) and Hundsheim (Austria) are slightly younger than the Mauer assemblage and can be placed in the MIS 15 or MIS 13 stage (Hemmer et al. 2008; Kahlke et al. 2011). These sites supplied no comparatively useable materials. Leopard-sized large cat remains from Mosbach 2, originally considered as leopards, turned out to be jaguars and cheetahs (Hemmer et al. 2003, 2008). A P<sup>3</sup> from Hundsheim (Freudenberg 1914) cannot be attributed to any of the extant leopard subspecies (Schütt 1969). Central European leopard tooth morphology changed anew in the late Middle Pleistocene. Leopards from Lunel-Viel (Hérault, France), *P. pardus lunellensis* (Bonifay, 1971), are distinct from the Mauer conspecifics (Bonifay 1971). This Western European Mediterranean site is dated at around 0.38 Ma; its faunal assemblage indicates a mosaic-like landscape with temperate conditions (Kahlke et al. 2011).

What was presented as a more or less uniform development within the single species *P. pardus* (Testu et al. 2011) turns now to a repeated replacement of different species and subspecies of leopard-sized cats during the European early Middle Pleistocene, following the extreme alternation between very different landscapes by the oscillation between intense cold and warm periods (Kahlke et al. 2011). Initially, the puma has been displaced by the leopard. This takeover of the corresponding ecological niche by *P. pardus* in Europe was interrupted by the dispersal of an ancestral snow leopard, *P. uncia pyrenaica*, to Western Eurasia in the cold and dry MIS 14 period, before new leopards came back in the following temperate MIS 15 period.

The diversification process in early European leopards might not have been exclusively intraspecific evolution. There is evidence of multiple post-speciation introgression in the genomes of all extant *Panthera* species (Figueiró et al. 2017). The X-chromosome of the leopard “is deeply divergent from the remaining species, a striking result most likely caused by ancient admixture between the leopard and an extinct lineage closely related to *Panthera*” (Figueiró et al. l.c., p. 3). It may not be wrong to look for that unknown extinct cat to *Puma pardoides* (sensu lato, including the African Plio-Pleistocene pumas: Hemmer et al. 2004), which was replaced by *P. pardus* in Africa already in the late Early Pleistocene. Hybrids of *Puma concolor* and *P. pardus* were born in captivity (Gray 1972; Hemmer 1966) and establish the possibility of a successful mating between members of these two genera.

Possible introgression in the genomes of snow leopards as well as of leopards could also have played some role in the European Late Pleistocene. A complete skull including the mandible found together with postcranial remains in the Manga Larga cave (Santó Antonio Plateau, Porto

de Mós, Portugal) shows predominant snow leopard characters, so far photos, graphic presentations and measurements allow a preliminary diagnosis. This specimen was attributed to *P. pardus*. Unfortunately, it proved to be outside the range of radiocarbon dating; nevertheless, an age of only 20–35 Ky has been estimated (Cardoso and Regala 2006). A re-study of this skull is greatly desirable, morphologically and by molecular genetic methods. South-eastern European leopards, *P. pardus vraonensis*, from 7–25-Ky-old layers of the Vraona cave (Attica, Greece), have some *P. uncia*-like features, especially in the paws. This could be but is not necessarily a case of parallel adaptation to a similar habitat (Nagel 1999). With the current state of the art, it cannot be excluded that snow leopards returned in each intense cold period of the Middle to Late Pleistocene climatic cycles from their Central Asian home to European rocky and dry landscapes.

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## Declarations

**Conflict of interest** The author declares that he has no conflict of interest.

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