# The complete skeleton of the bear $n^{\circ} 2$ from the Galerie des Aiglons of the Azé Cave (Saône-et-Loire, France): Ursus spelaeus ladinicus 

# L'ours complet $\mathbf{N}^{\circ} \mathbf{2}$ de la Galerie des Aiglons de la grotte d'Azé 1 (Saône-et-Loire, France): Ursus spelaeus ladinicus 

Alain Argant ${ }^{1,2,5}$, Thierry Argant ${ }^{2,3}$, Lionel Barriquand ${ }^{2,4,5} \boldsymbol{\&}$ Jacqueline Argant ${ }^{1,2}$


#### Abstract

Between 1990 and 1997, excavations by R. Villeneuve in Azé 1 led to the discovery of the presence of a gallery parallel to the Azé 1 cave, the Galerie des Aiglons, as well as the complete skeletons of several bears in the gallery joining these two caves (Azé 1-6). It was possible to carry out a rather complete morphometric study of two of these bears, Bear $\mathrm{N}^{\circ} 2$, a female, and an adjacent bear cub, despite the extensive concretion of the remains requiring painstaking removal which nevertheless could only be partial. As a result, an individual of Ursus spelaeus ladinicus was identified, the most recent bear species found at Azé 1. The dating remains imprecise, but based on the general evolution of the cavity, it lies between the end of isotopic stage OIS. 6 and the upper limit of 14C-AMS (about 50 ka ), at the latest, stage OIS.4. The bear from Azé, which had previously provided a mtDNA analysis came from a group of remains in proximity to Bear $\mathrm{N}^{\circ} 2$. This bear belongs to haplogroup A, as does the sequence of bears at Conturines (Italy) which is precisely Ursus spelaeus ladinicus.


## Résumé

Entre 1990 et 1997, les fouilles de R. Villeneuve à Azé 1 ont permis de découvrir l'existence d'une galerie parallèle à la grotte d'Azé 1, la Galerie des Aiglons et le squelette complet de plusieurs ours dans la galerie de jonction (Azé 1-6). L'ours $\mathrm{N}^{\circ} 2$, une femelle, et un ourson, permettent une étude morphométrique assez complète malgré l'état très concrétionné des vestiges recueillis nécessitant un long travail de dégagement qui n'a pu être que partiel. Il est possible de déterminer un individu d'Ursus spelaeus ladinicus, sous-espèce d'ours la plus récente d'Azé 1. La datation en reste imprécise mais d'après le fonctionnement général de la cavité, elle se situe entre la fin du stade isotopique OIS. 6 et la limite supérieure du 14C-AMS (50000 ans environ), au plus tard au stade OIS.4. L'ours d'Azé ayant fourni auparavant une analyse d'ADN-mt correspond au stock en relation avec cet individu $\mathrm{N}^{\circ} 2$. Il appartient à l'haplogroupe A , comme la séquence de l'ours des Conturines (Italie) qui est justement Ursus spelaeus ladinicus.

Key-words: Ursus spelaeus ladinicus, Azé 1, single individual, morphometry, chronology.

Mots-clés: Ursus spelaeus ladinicus, Azé 1, unique individu, morphométrie, chronologie.

## 1. Introduction

From a geological, palaeontological and archaeological perspective, Azé is a very rich site (Fig. 1). Two main caves and six other much smaller ones open onto a south-facing cliff overlooking the valley of the Mouge. The upper cave, Azé 1, known as the "Prehistoric Cave", contains the famous palaeontological deposit of cave bear and lion remains (excavations A.J. Argant, 1982 to 1985) as well as the oldest prehistoric site in Burgundy (Lower Palaeolithic, excavations J. Combier, 1966 to 1970) (Fig. 2).

The removal of obstructions to enable tourist activities, followed by several scientific excavations, led to a good knowledge of the cave fillings, dating for the most part from the Middle Pleistocene. In 1990, a team led by René Villeneuve (specialist teacher in charge of a group of children with difficulties, the "Aiglons") began to empty out a small rounded recess, the Fosse Rotonde, on the eastern side of the main gallery of the tourist cave, about 30 metres from its entrance. In 1991, they discovered and very carefully removed two bears in anatomical connection. Then from 1991 to 1993 they emptied out the Boyau Ouest (= Connexion Galery, Junction Galery, Azé 1-6). In 1993, they reached, further below, the Salle des Pétoux, in reality the Galerie des Aiglons, which they proceeded to empty out until they reached the exterior on 16th August 1993, only a few metres below the entrance to the tourist gallery of Azé 1 .

The Galerie des Aiglons is parallel to Azé 1 in the general north-south axis of this karst-area. Its entrance had been hidden by slope deposits and was totally invisible until 1993. From 1998 to 2002, adding to the work done by R. Villeneuve, L. and J. Barriquand conducted four excavation campaigns during which they drew cross-section diagrams of all the sediments and carried out sedimentological studies (Barriquand et al., 2011). The fauna collected, identified by A. Argant, is much more diverse than in the rest of the cave and clearly indicates the presence of Crocuta spelaea, until then only known through a few remains in the upper gallery of Azé 1 . This fauna, at least in part, consists of a mixture of fossils from the upper gallery with those from the Galerie des Aiglons, which occurred because of drainage at a number of points, some known and probably many others unknown.

The Fosse Rotonde marks the beginning of a small gallery, the Boyau Ouest (Azé 1-6), which connects with the lower gallery about twenty metres from its exit at the cliff face. This connecting gallery
is narrow. It acted as a passageway and as a channel for the periodic evacuation of water from the upper gallery during times of flooding. It is probable that at such times there was a flushing action which drew into this channel the bodies of dead bears still connected by their ligaments, but the possibility of animals being trapped or killed in their place of hibernation cannot be completely ruled out. In any case, later water flows have removed nearly all the small bones such as carpal, tarsal and metapodial bones, phalanxes, sesamoids and incisors (the few exceptions being 1 calcaneus, 1 metapodial bone, 2 phalanxes and 1 incisor). The trampling of the skeleton by the passage of other bears has very probably contributed to its crushing and the severe cracking of the skull and long bones.



Fig. 2: Sketch of the Azé 1 cave and detail of Sectin 1 and of the Galerie des Aiglons. The connecting gallery Azé 1-6 and the location of Bear $\mathrm{N}^{\circ} 2$.
Fig. 2: Plan de la grotte d'Azé 1 et détail du tronçon $n^{\circ} 1$ et de la Galerie des Aiglons. Galerie de jonction Azé 1-6 et position de l'ours $\mathrm{N}^{\circ} 2$.

## 2. The complete bear $\mathbf{N}^{\circ} \mathbf{2}$

Bear $\mathrm{N}^{\circ} 1$, lying along the eastern wall at the beginning of the Fosse Rotonde, was the first individual found in anatomical connection, but in the same location were the scattered bones of several other individuals. The alignment of bones along the side indicates a "wall effect", a consequence of trampling by bears moving regularly through the passageway, pushing bones to the side. This is not the case for Bear $\mathrm{N}^{\circ} 2$ which affords us the certainty of a single individual, a female wedged across the gallery with the skull of a bear cub at its side (Fig. 3). These sorts of finds are too rare at Azé, as elsewhere, to not try to make use of their morphometric data. In order to be complete, the existence should be noted of other individuals in anatomical connection (at least partial) still in place to the south of Bear $\mathrm{N}^{\circ} 2$ in the connecting gallery (Azé 1-6) before it opens into the Galerie des Aiglons.


Fig. 3: Photo of Bear $\mathrm{N}^{\circ} 2$ in situ in the junction gallery Azé 1-6 (photo J. Argant)
Fig. 3: Photo de l'ours $\mathrm{N}^{\circ} 2$ en place dans la galerie de jonction Azé 1-6 (photo J. Argant).

Figure 3 shows the placement of the bones after their clearing by the Aiglons team. The bones are in anatomical connection, the animal lying on its side, head to the west, fore limbs towards the north, hind limbs towards the south, the spinal column in an arc across the gallery. The skeleton is in contact with the limestone wall on each side. It has been flattened horizontally but is clearly visible in the upper part of the filling of this small gallery a little more than a metre wide. All the bones are represented, but are in very poor condition for two main reasons. Firstly, after their trampling, the bones underwent a long stagnation in water which is the cause of the calcite concretions around most of them, requiring a lengthy period of removal and cleaning. A second reason relates to the in-situ exhibition to the public between 1991 and 2001 of two of the bears excavated by R. Villeneuve. This aggravated the cracking and splitting of the bones. In 2001, given the worrying state of the skeleton, the decision was taken to extract it. T. Argant was responsible for the extraction as part of the excavations of L. Barriquand (1998 - 2002). He mapped the area and plotted the spatial distribution of the remains (Fig. 4). He measured the pieces in situ in case they were damaged during extraction, numbered each of them and recorded their coordinates with a view to later study, then removed and archived them all.

In 2012, as part of a post-doctorate in the laboratory of M. Hofreiter at Oxford (England), C. Frischauf attempted a DNA analysis on a fragment of the femur of Bear $\mathrm{N}^{\circ} 2$ and a 14 C -AMS dating. Both attempts ended in failure because of a lack of collagen, emphasising the age of this bear, greater than the limits of these two methods.

## 3. Morphometric data

Advice to readers:
All the measurements in this study are in mm and this unit does not appear in the tables.
Abbreviations used:

* about (after a measure)
$\mathrm{APD}=$ antero-posterior diameter $=$ length or $\mathrm{DAP}=$ diamètre antéro-postérieur
Dentition: $\mathrm{I}=$ incisive; $\mathrm{C}=$ canine; $\mathrm{P}=$ premolar; $\mathrm{M}=$ molar
$\mathrm{DPD}=$ dorso-palmar or dorso-plantar diameter $=$ height
or $\mathrm{DDP}=$ diamètre dorso-palmaire ou
dorso-plantaire (= hauteur)
inf.; sup.; ant.; post.; med.; art.= inferior; superior; anterior; posterior; median; articular
L or $\mathrm{R}=$ left or right (= droit ou gauche)
$\mathrm{MD}=$ mesio-distal diameter $=$ length $($ for a tooth $)$
min., $\max .=$ minimum; maximum
$\mathrm{Mtt}=$ metatarsal bone; $\mathrm{Mtt} 3=3$ rd metatarsal bone
$\mathrm{P} / 2=$ second lower premolar
$\mathrm{P} 2 /=$ second upper premolar
PUEMA (Plan Ursidés d'Enregistrement Morphométrique Argant) = Plan Argant for morphometric record of Ursids.
prox.; ext. $=$ proximal extremity; dist. ext. $=$ distal extremity
$\mathrm{TD}=$ transverse diameter or $\mathrm{DT}=$ diamètre transverse
$\mathrm{TN}=$ transfer number (in a table, a figure, a caption)
$\mathrm{VL}=$ vestibulo-lingual diameter $=$ width (for a tooth) $\mathrm{HC}=$ heigtht of the crown

The state of the palaeontological material from Bear $\mathrm{N}^{\circ} 2$ did not allow the usual finesse of measurement according to the PUEMA plan for Ursids (Argant, 2010). Therefore, the measurements taken before dismantling played an essential role especially when later measurements could add to their
precision. It was not possible to remove the calcite encrustations from all the pieces, except in a few cases where painstaking removal using a diamond bur or acetic acid enabled key observations and measurements to be made. Most of the material consisted of fragments which in some cases could be glued back together. Nevertheless, it was possible to carry out a relatively complete morphometric study of Bear $\mathrm{N}^{\circ} 2$ in order to establish its characteristics.


Fig. 4: Sketch of the Bear $\mathrm{N}^{\circ} 2$ in situ in the connecting gallery Azé 1-6 (plan T. Argant).
Fig. 4: Plan de l'ours $\mathrm{N}^{\circ} 2$ en place dans la galerie de jonction Azé 1-6 (plan T. Argant).

### 3.1. The adult

This is a large bear, a female, given the relatively small dimensions of its long and thin canines and the slenderness of its mandible. Its long bones, though large, have neither the massiveness nor proportions of typiquely spelaean forms. Unfortunately, numerous identifying observations have not been possible because of the difficulties encountered in cleaning them.

- the cranium: it is unfortunately extremely fragmented. Only a few pieces are able to provide information. The very brechified incisor segment has however two upper canines in place, and part of the incisor bone is visible along with most of the empty alveoli of the incisors (Tab. 1). The complete upper left canine is long and has a relatively long and slender root. This confirms that the bear is indeed a female. On the left maxilla, also very concretionned, it was possible to clean the two upper molars, M1/ and M2/. The left P4/, also well-cleaned, was on a separate fragment (Fig. 5, Tab. 2).

| Bear N² - Ursus spelaeus ladinicus - Azé 1-6 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 튼 <br> 든 |  |  | 33 | Breadth of incisors row (at exterior of I3/) |  |  |  |  |  |  |  |  | 68 |
|  |  |  | 2 | Breadth min. of maxilla |  |  |  |  |  |  |  |  | 88 |
|  |  |  | 3 | Breadth of maxilla at the canines |  |  |  |  |  |  |  |  | 95,3* |
|  |  |  | 5 | Length, anterior of canine - posterior of the M2/ |  |  |  |  |  |  |  |  | 161 |
|  |  |  | 6 | Length, posterior of canine - posterior of M2/ |  |  |  |  |  |  |  |  | 138 |
|  |  |  | 7 | Length of the cheek teeth |  |  |  |  |  |  |  |  | 89 |
|  |  | - | 6 | Neuro-cranial length: Acrocranion-frontal medial (F) |  |  |  |  |  |  |  |  | 88 |
|  |  | 通 | 17 | Breadth max. of neurocranium Euryon-Euryon |  |  |  |  |  |  |  |  | 99 |
|  |  |  | 20 | Breadth max. of frontal Ectorbiital-Ectorbital |  |  |  |  |  |  |  |  | 78 |
|  |  |  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|  |  | L | 306,0 | - | - | - | - | - | - | - | - | - | - |
|  |  | R | 306,6 | 280 | - | - | - | - | 179 | 91,7 | - | 77 | 16 |
|  |  | $\stackrel{\sim}{\sim}$ | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 |
|  |  | L | - | - | - | - | 59,7 | - | - | - | - | 64.0 | 20.2 |
|  |  | $\mathrm{R}^{2}$ | 119,2 | 126,5* | - | - | - | 70,3 | 67,1 | 68,1 | 69 | - | - |
|  |  |  | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 |
|  |  | L | 90,8 | 40,6 | - | - | - | - | - | - | - | - | - |
|  |  | R | - | - | - | - | 151 | - | 91,7* | 180 | - | - | - |



Tab. 1: Bear $\mathrm{N}^{\circ} 2$, Azé 1-6, Ursus spelaeus ladinicus, skull (PUEMA $10 \& 100$ ) and hemi-mandibles (PUEMA 20). Tab. 1: Ours $\mathrm{N}^{\circ} 2$, Azé 1-6, Ursus spelaeus ladinicus, crâne (PUEMA $10 \& 100$ ) et hémi-mandibules (PUEMA 20).

- P4/: the crown of this premolar is simple, with three well-individualized cusps dominated by the paracone. The metacone has a slight bulge at the rear. The deuterocone, simple and small in size, stands out on the internal edge of the crown a little towards the rear of the tooth.


Fig. 5: Bear $\mathrm{N}^{\circ} 2$, Azé 1-6, Ursus spelaeus ladinicus, left cheek teeth, lingual (a) and occlusal (b) views. Fig. 5: Ours $\mathrm{N}^{\circ} 2$, Azé 1-6, Ursus spelaeus ladinicus, dents jugales supérieures gauches, vues linguale (a) et occlusale (b).

A slight cingulum lies below this edge essentially in its anteromedial part. The two crests of the paracone and metacone are not aligned but form between them an angle of about $150^{\circ}$ (Fig. 5).

- M1/: on the crown the metacone slightly dominates the metacone. These cusps are simple, with smooth sides and no significant grooves. The occlusal surface is also smooth, without furrows or ridges. A small parastyle lies at the front of the molar. The metastyle stands out more prominently at the rear. The internal edge of the crown is well developped and has a relatively low gradient (Fig. 5). - M2/: this is a large, long and simple tooth with a flat occlusal surface and parallel and relatively narrow edges. The paracone clearly dominates the metacone. These two cusps are simple, with smooth sides and a relatively low volume. The talon is slightly granular. On the lingual edge a small cingulum extends as far as the talon. The anteromedial widening is marked but not very developed (Fig. 5).


## - the mandible: (Fig. 6)

The two hemimandibles lie flattened one upon the other, the right one above having pivoted $35^{\circ}$ under the weight of the skull. The point of the upper right canine is embedded in the hardened sediment surrounding the mandible below. These rest on a tangle of ribs, all in the same block. There is considerable mineralisation, and though very cracked, the bones have been consolidated by the varnish applied before extraction. All the cheek teeth are present, but only partially visible in lateral view, and impossible to remove in the available time because of their fragility and the hardness of the sediment. Only the incisors and the right $\mathrm{M} / 2$ are missing.
Both lower canines are embedded in sediment but only the right one is visible, in lateral view. It is long and slender. The dimensions are those of a large animal. The slender canines as well as the elongated form and not very massive body of the mandible indicate that this individual is female (Argant, 1991).


Fig. 6: Bear $\mathrm{N}^{\circ} 2$, Azé 1-6, Ursus spelaeus ladinicus, concretionary hemi mandibles connected with ribs. Fig. 6: Ours $\mathrm{N}^{\circ} 2$, Azé 1-6, Ursus spelaeus ladinicus, hémi mandibules concrétionnées et soudées à des côtes.

- post-cranial skeleton (Tab. 3, 4, 5; Fig. 7)

The right tibia has been entirely reconstitued and has provided the usual dimensions (Fig. 7, Tab. 4). It is relatively elongated and not as massive as typical of Ursus spelaeus. The index of massivity is 24.2, which is even close to that of Ursus deningeroides ( $=$ U. spelaeus deningeroides MotтL, 1964) from Repolusthöhle (Austria) (Kavcik \& Rabeder, 2004, Fig.8)

### 3.2. The bear cub

Four pieces from a young bear cub - two fragments of the skull, a left mandible and a right ulna (Tab. 5) - were found wedged in the skeleton of Bear $\mathrm{N}^{\circ} 2$. Part of a calcite endocranial cast can be seen through an opening (Fig. 8). The fragment of the right maxilla holds the fully erupted M1/, not at all worn, as well as the partly erupted canine, only the tip of the crown appearing above the level of the maxillary bone (Fig. 9, Tab. 2). The M/3 has not emerged and the roots of the M/2 are visible through a break in the body of the right hemimandible.
They show that only the anterior part of the $\mathrm{M} / 2$ has emerged. The occlusal surfaces of these cheek teeth are not observable because of a covering of hardened sediment.
An age of 8 to 10 months can be attributed to this bear cub (Debeljak, 1996). It means that the cub died at the end of autumn, at the beginning of its second period of hibernation in the cave with its mother.

The dimensions and morphology of the first upper molar of the bear cub match perfectly those of the adult, but here the relief of the crown is clearly evident because of the complete absence of wear. The rather smooth appearance of the $\mathrm{M} / 1$ of the female is due to pronounced wear $(\mathrm{U}=3)$.
In contrast, the $\mathrm{M} / 1$ of the cub $(\mathrm{U}=0)$ has a noticeably granular functional surface (Fig. 9).

Is the female $\mathrm{N}^{\circ} 2$ the mother of this cub? The close association of the complete skeleton of the adult with the remains of a cub immediately makes us wonder about a filial relationship. The cub is not a foetus, but is at least 8 months old.

Bear N ${ }^{\circ}$ - Ursus spelaeus ladinicus - Azé 1-6

|  |  | Ref. | Lat. | Length | Width | HC | HT | Wearness | Paracone lenath | Metacone lenath |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | P4/ | TA. 06 | L | 17.3 | 12.5 | 10.7 | 32.8 | 1.0 | 11.4 |  |
|  | M1/ | TA. 06 | L | 25.0 | 19.0 | 10.0 | 31.5 | 1.5 | 9.7 | 9.6 |
|  | M2/ | TA. 06 | L | 48.2 | 24.5 | 11.1 | 36.6* | 1.5 | 15.3 | 11.9 |
|  | C | TA. 07 | R | 20.0* | - | 41.5* | - | 1.0 |  |  |
|  | P/4 | TA. 07 | L | 14.5 | - | - | - | - |  |  |
|  |  | TA. 07 | R | 14.9 | - | 9.0 | - | - |  |  |
|  | M/1 | TA. 07 | L | 25.4 | - | - | - | - |  |  |
|  |  | TA. 07 | R | 25.9 | - | - | - | - |  |  |
|  | M/2 | TA. 07 | L | - | - | 8.7 | - | - |  |  |
|  | M/3 | TA. 07 | R | 25.3 | 18.7 | 9.6 | - | 1.0 |  |  |
| Cub | M1/ | TA. 50 | R | 26.2 | 19.6 | 10.8 | 27.8 | 0.0 | 10.8 | 10.7 |

Tab. 2: Bear $\mathrm{N}^{\circ}$ 2, Azé 1-6, Ursus spelaeus ladinicus, upper and lower teeth.
Tab. 2: Ours $\mathrm{N}^{\circ} 2$, Azé 1-6, Ursus spelaeus ladinicus, dents supérieures et inférieures.

It would have been entering its second winter with its mother, hardly ever away from her, especially in a cave. The M1/, the only dental element usable, reveals a perfect morphometric correspondance between the two individuals.
Although it is not possible to be certain, the likelihood that the cub was lying close to its mother seems high and perhaps can be validly assumed.

### 3.3. How to determine the species of Bear $\mathrm{N}^{\circ} \mathbf{2}$ ?

Available evidence consists of morphometric comparison with bears from other loci in Azé 1 and the age of this bear which is beyond the limits of 14C dating. Right at the back of the cave ( 220 m from the entrance), Azé 1-4 delivered Ursus deningeri, as did Azé 1-3.
The latter was originally identified as Ursus spelaeus deningeroides Mottl, 1964 (Argant, 1991) in order to show its closeness to the ancestral form as well as its characteristics more recent than those of forms from the median Middle Pleistocene. Because of its morphological features, the skull of the cave lion contemporaneous with these bears belongs to the ancient form Panthera (Leo) spelaea fossilis (Sotnikova \& Nikolskyi, 2006, Argant \& Brugal, 2017).
The stalagmitic blockage of this part of the cave (terminal for bears) began at the end of OIS. 7 but mainly occurred during OIS.6.



Tab. 3: Bear $\mathrm{N}^{\circ}$ 2, Azé 1-6, Ursus spelaeus ladinicus, fore limb (PUEMA 50, $51 \& 52$ ).
Tab. 3: Ours $\mathrm{N}^{\circ}$ 2, Azé 1-6, Ursus spelaeus ladinicus, membre antérieur (PUEMA 50, 51 \& 52).

Tab. 4: Bear $\mathrm{N}^{\circ}$ 2, Azé 1-6, Ursus spelaens ladinicus, hind limb (PUEMA 60, $61 \& 62$ ).
Tab. 4: Ours $\mathrm{N}^{\circ}$ 2, Azé 1-6, Ursus spelaeus ladinicus, membre postérieur (PUEMA 60, $61 \& 62$ ).

The age of the bears from Azé 1-3 is consistent with this chronology and the determination Ursus deningeri must be retained. In the median part of the cave (from 90 to 100 m from the entrance), Azé 1-2 yielded a large collection of bear remains. These are more recent than Azé 1-3 based on a dental study (Argant, 1991, Fig.36) confirming the presence of two
different morphotypes for the $\mathrm{M} 2 /$, an important tooth for characterizing a species. The first morphotype is that of Ursus deningeroïdes, very similar to the photo of an M2/ from Repolusthöhle (Rabeder et al., 2016, Fig. 4-1). The second morphotype (for two M2/) is clearly different and corresponds to a short M2/ with parallel edges, but by its shortness it is different from that of Ursus spelaeus ladinicus. This collection from Azé 1-2 can be linked to the recent Middle Pleistocene because of the microfauna found above the remains, such as an Arvicola whose M/1 has the dental characteristics of Middle Pleistocene forms (Jeannet, 1980).
This is also confirmed by the presence of Paleoperdrix (Mourer-Chauvire, 1975).


Fig. 7: Bear $\mathrm{N}^{\circ} 2$, Azé 1-6,
Ursus spelaeus ladinicus, right tibia, posterior view.
Fig. 7: Ours $\mathrm{N}^{\circ}$ 2, Azé 1-6,
Ursus spelaeus ladinicus, tibia droit, vue postérieure.


Fig. 8: Cub, Bear Nº 2, Azé 1-6,
Ursus spelaeus ladinicus, skull, neurocranium with the opening showing the endocranium
partially casted by calcite.
Fig. 8: Ourson, Ours $\mathrm{N}^{\circ} 2$, Azé 1-6,
Ursus spelaeus ladinicus, crâne, neurocrâne avec ouverture montrant un moulage partiel de l'endocrâne par la calcite.

| Bear ${ }^{\circ} \mathbf{2}$ - Ursus spelaeus ladinicus - AZE 1-6 |  |  |  |  |  |  |  |  |  |  | Tab. 5: Bear $\mathrm{N}^{\circ} 2$, Azé 1-6, Ursus spelaeus ladinicus, post-cranial |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Vertebrae | Cervical vert. |  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |  |
|  |  |  | DPD | TD | APD | $\begin{aligned} & \text { art. } \\ & \text { cran. } \end{aligned}$ | caud. <br> Art. TD | max. APD | dors. <br> min. | vent. <br> min. | (diverse). |
|  |  | Atlas TA. 49 | 60,3 | 160,0* | - | - 77 | - | - | non | non | 1ab. 5: Ours N 2, Aze 1-6, |
|  |  |  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |  |
|  |  |  | cranial vert. body TD | cranial vert. body DPD | caud. vert. body TD | caud. vert. body DPD | max.ve <br> rt. body APD | Rank | Total length with apophysis |  |  |
|  |  | CV TA. 83 | 43.9 | 31.2 | - | 27.9 | 35.6 | 4 | - |  |  |
|  | Thoracic vert. | TA. 68 | - | - | 62.7 | 45.3 | 40.4 | 11 | 74.1* |  |  |
|  | Lombar vert. | TA. 60 | 61.9 | 39.9 | 61.4 | 61.6 | 45.0 | 6 | - |  |  |
| Scapula | left |  | 1 | 2 | 3 | 5 | 6 | 7 | 8 | 9 |  |
|  |  |  | L | max L. <br> (with <br> svina | APD | $\begin{array}{\|c\|} \hline \text { max. } \\ \text { prox. } \\ \hline \end{array}$ | $\begin{array}{\|c} \text { articula } \\ \text { r TD } \end{array}$ | articula <br> r DPD | APD neck | $\begin{array}{\|c\|} \hline \text { acromio } \\ \mathrm{n} \text { width } \\ \hline \end{array}$ |  |
|  |  | TA. 20 | 280.0 | 260.0 | 230.0 | 81.0 | 71.2 | 36.7 | 83.8 | 31.6 |  |
| Patella |  |  | L | 1 |  |  |  |  |  |  |  |
|  |  | TA. 47 | 61.0 | 45.0 |  |  |  |  |  |  |  |
|  | right |  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |  |
| Calcaneum |  |  | L | $\begin{array}{\|c\|} \hline \text { astr..art. } \\ \text { TD } \end{array}$ | $\begin{array}{\|c} \hline \text { tuber } \\ \text { calc. } \\ \text { TD } \\ \hline \end{array}$ | $\begin{array}{\|l\|} \hline \text { tuber } \\ \text { calc. } \\ \text { DPD } \\ \hline \end{array}$ | max. <br> prox. <br> TD | max. prox. DPD | min. diaphy sisTD | $\begin{array}{\|c\|} \hline \text { min. } \\ \text { diaphysi } \\ \text { s_APD } \\ \hline \end{array}$ |  |
|  |  | TA. 30 | 88.7 | 46.9 | 36.9 | 41.6 | 64.2 | 45.1 | 18.8* | 34.5* |  |
| Metatarsus |  |  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |  |
|  |  |  | L. | prox. TD | $\begin{aligned} & \text { prox. } \\ & \text { APD } \end{aligned}$ | med. TD | med. <br> APD | dist. TD | dist. APD | dist.art. TD |  |
|  | Mtt. 2 (left) | TA. 32 | 64.3 | 12.2* | 22.3 | 13.5 | 10.4 | 19.8 | 16.4 | 16.7 |  |
|  | Mtt. 3 (right) | TA. 59 | 72.5* | 19.8 | - | 13.6 | 13.3 | 22.1 | 19.3 | 19.4 |  |
| Phalanx 2 |  |  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |  |
|  |  |  | L. | prox. TD | $\begin{aligned} & \text { prox. } \\ & \text { APD } \end{aligned}$ | med. TD | med. <br> APD | dist. TD | $\begin{array}{\|c\|} \hline \text { dist.AP } \\ \mathbf{D} \end{array}$ | dist.art. TD |  |
|  |  | TA. 48 | 25.8 | 16.6 | 12.4* | 12.1 | 8.4 | 14.5 | 11.4 | 12.8 |  |

Festschrift zum 80. Geburtstag von emer. Univ.-Prof. Dr. Mag. Gernot Rabeder


Fig. 9: Bear $\mathrm{N}^{\circ} 2$, Azé 1-6, Ursus spelaeus ladinicus, fragment of the right maxilla with M1/ and C.
Fig. 9: Ourson, Ours $\mathrm{N}^{\circ} 2$, Azé 1-6,
Ursus spelaeus ladinicus, fragment du maxillaire droit avec M1/ et C.

It is interesting that the entrance chamber, Azé 1-1 (excavation J. Combier), has provided Ursus deningeri, a more ancient form than that of Azé 1-2, as well as very crude artefacts from the Lower Palaeolithic, evidence of the passage of prehistoric Man (Combier et al., 2000). Bear N ${ }^{\circ} 2$ from Azé 1-6 corresponds neither to Ursus deningeri nor to Ursus spelaeus deningeroïdes. It is a large bear, with a longer and less massive tibia, proportionally similar to that of Ursus deningeroïdes. The M2/ is very similar to the one in photography of the skull of Ursus spelaeus ladinicus from the Conturines (Italy) (Rabeder \& Kavcik, 2014). In the Galerie des Aiglons, just below the Fosse Rotonde, a group of two complete bear skulls was excavated. The southernmost, upside down, displayed a row of teeth morphologically very similar to those observed on Bear $\mathrm{N}^{\circ} 2$, with a right P3/ clearly visible, but with the corresponding left part of the maxilla hidden under encrustations. The presence of a P3/ is also encountered in Ursus spelaeus ladinicus (about 30\%, Rabeder et al., 2004) and is undoubtedly more frequent in ancient forms of this species. Here it is encountered chronologically well before the limit of 14C dating. In any case, Azé 1-6 (connecting gallery) and Azé1-5 (Galerie des Aiglons) contained the most recent of the bears found in Azé 1, which at this time could only reach the upper gallery of Azé 1 by passing through the Galerie des Aiglons and the connecting gallery.

## 4. Elements for dating

Most of the sedimentary filling still in place in the Azé 1 cave clearly dates to the Middle Pleistocene, principally characterised by important phases of concretion beginning during OIS 6. These phases partitioned the gallery into three sections, which then functioned separately but nevertheless also in ways that were determined by connection with the Galerie des Aiglons, including its parts still unknown. These concretions are probably linked to modifications of the surrounding limestone due to particularly strong erosion during OIS. 6 at the time of the second last glacial period. Indirect evidence is provided by the relative chronology of these events. The oldest corresponds to the stalagmitic system of the Salle du 14 Juillet blocking the Salle des Ours of Azé 1-3, and dated by U/Th at 190.7 $\mathrm{ka}, 158.1 \mathrm{ka}$ and 113.1 ka . It lies below the highest part of the Plateau de Rochebin. We can imagine maximum erosive action on the high part of the plateau during the severe cold of OIS. 6, dismantling the more impermeable upper layers of limestone. The stalagmitic blockage 60 m from the entrance occurred later. Nine U/Th datings: $134.6 \mathrm{ka} ; 114.6 \mathrm{ka} ; 63.4 \mathrm{ka} ; 58.9 \mathrm{ka} ; 53.5 \mathrm{ka}$ and four more recent ones relate it to OIS. 3 and then OIS.2. This blockage was clearly more to the south and lies below some of the large slope deposits which further down had closed the entrance to Aze 1. The dismantling of the surface in this location occurred later. Here the concretions began to form after the particularly severe stage OIS. 6, mostly during stage OIS. 4.

The second characteristic is the existence of the Galerie des Aiglons (Azé 1-5) a few meters below and to the east of Azé 1 and parallel to it. These two galleries are connected at a number of points. We had already become certain of the existence of a lower network during our excavations in Azé 1-2 (1978) and especially in Azé 1-3 (1982-1985) because of the presence of several drainage points in each of these cave sections where water which had accumulated over winter disappeared. Later in Azé 1-3, the dip of the bear and lion layer towards the north was confirmed (Argant et al., 2007), and explained a posteriori by the discovery of the drainage point at the "bayonet" in Azé 1-4 where a large number of bear remains had accumulated. Towards the entrance, the regular drainage of water from the filling of the Fosse Rotonde led to the discovery of a succession of parallel lines of bones directly below Bear $\mathrm{N}^{\circ} 1$, separated by sterile layers of clay. This clearly indicated that lines of bones originally in the same position as Bear $\mathrm{N}^{\circ} 1$ had gradually sunk against the west wall of the Fosse Rotonde (excavations L. Barriquand). Electric tomography carried out later by O. Kaufman clearly confirms the extension of the Galerie des Aiglons northwards, at least as far as the far end of Azé 3, as well as the presence of large voids upstream of the current terminal cross-section of the Galerie des Aiglons (Barriquand et al., 2016).

- The complete bears from the connecting gallery Azé 1-6 are geologically too old to be dated by 14C-AMS. Two separate attempts, one directly on Bear $\mathrm{N}^{\circ} 2$, ended with the same negative result,
"date beyond the limit of the method" (about 50 ka ). That left only two other dating methods that could be used, the sufficiently characteristic evolutionary stage of Bear $\mathrm{N}^{\circ} 2$, and dating based on the evolution and functioning of the connecting gallery between Azé 1 (tourist gallery) and the Galerie des Aiglons (Azé 1-5), using all available data.
- Section 1 of the front part of Azé 1 terminated at the stalagmitic blockage 60 m from its entrance. For a very long time this blockage was where the cave ended and it was broken through by speleologists only in 1963. It began to form during OIS.5e after the second last glaciation, ultimately preventing the arrival of any water from sections of the cave to the north. Running water in this part of the cave would have prevented or dismantled any deposit of calcite. Therefore, from this time, Section 1 of the cave functioned independently.
- The presence of prehistoric Man in Azé 1-1 (excavations J. Combier) indicates that he entered the front chamber of the cave directly from the outside and in daylight, but this occurred largely before OIS.6. The bear found here is Ursus deningeri. Later, the entrance of Azé 1 was blocked by slope deposits. The cave contained a body of water (permanent or temporary?) in which bones rolled along by the current were deposited by progradation (Argant, 2004). At a certain point in time, only the connecting gallery (Azé 1-6) allowed communication with the exterior through the Galerie des Aiglons (Azé 1-5). This explains the greater age and good preservation of the filling of the entrance chamber (Salle d'entrée, Azé 1-1).
- During major flooding, water could only enter Azé 1-1 from the lower Galerie des Aiglons via the connecting gallery, Azé 1-6, and other points of connection. In these conditions, rapid falls in the water level could have flushed Bear $\mathrm{N}^{\circ} 2$, still intact and attached by its ligaments, into the connecting gallery where it became jammed between the walls. Later, bears passed through this gallery and currents of water carried away smaller bones. Those left behind were covered by fine sediments and extensive concretions which protected them.
- The use of only Section 1 of the cave by bears to hibernate should be placed at the end of the recent Middle Pleistocene (OIS.6), at stage OIS.5, or at the latest, at stage OIS.4. Ursus spelaeus ladinicus is found neither in Azé 1-1, nor in Azé 1-3, nor in Azé 1-4. Azé 1-2 indicates the presence of Ursus spelaeus deningeroides which at that time could still reach Section 2 upstream of the stalagmitic blockage at 60 m which started at 134.6 ka and by OIS .5 was sufficiently developed to prevent the entry of large fauna. The use of the connecting gallery, Azé 1-6, as the only means of entering the upper gallery corresponds to this period. At this time Ursus spelaeus ladinicus was the only bear there. The bear from Azé which provided mtDNA comes from the palaeontological stock collected in Section 1, from near the Fosse Rotonde (Orlando et al., 2002, Fig.4). It is contemporaneous with Bear $\mathrm{N}^{\circ} 2$ and its location would indicate that its species is the most recent of those from Azé 1. The genetic
study shows that it belongs to haplogroup A, along with the sequences from Scladina (Belgium), Prélétang and les Merveilleuses (France), and Conturines (Italy). This constitutes a sound confirmation of the determination that Bear $\mathrm{N}^{\circ} 2$ is Ursus spelaeus ladinicus.
- The cave hyaena, Crocuta spelaea, is found in the Brèche de Château (Saône-et-Loire) at OIS. 6, and is not usually encountered in Burgundy before this stage. It has always been rare in Burgundy and only became more widespread from OIS. 4 until OIS.2. In Azé 1, a metapodial bone and some coprolites found in Azé 1-2 confirm its presence there but nothing has been found north of this locus. It is present in Section 1, downstream from the blockage at 60 m but in layers lower than the stalagmitic deposit which, because of their stratigraphic position, must correspond chronologically to those of Azé 1-2. It is represented there by several hemimandibles. The concretions at 60 m began to form at the very beginning of OIS. 5e, about 130 ka . Therefore, the presence of the cave hyaena in Azé 1 occurred before these concretions, during OIS.6, and was contemporaneous with Ursus spelaeus deningeroïdes and Ursus spelaeus ladinicus in Azé 1-2.
The excavation by L. Barriquand below the Fosse Rotonde encountered lines of bones directly below Bear $\mathrm{N}^{\circ} 1$, descending progressively from the upper gallery towards the Galerie des Aiglons. The fauna, still under study, is particularly diversified (Argant et al., 2011). Such diversity is
surprising at Azé 1 , which for a long time, had been only a bear den, with only the usual visites by cave lions. Classically, only two potential factors could explain such diversity, either man or cave hyaenas. Prehistoric man did indeed leave traces at Azé, very crude Clactonian type artefacts, much too ancient to be contemporary with Ursus spelaeus ladinicus. Evidence of the Middle Palaeolithic has not been found in Azé 1, although it has been found outside at Azé 2 (Combier \& Merle, 1999). Fragments of flint attributed to the Upper Palaeolithic were found in Azé 1 before the stalagmitic blockage at 60 m , and at the present end of the Galerie des Aiglons, proof of the possible penetration by Man at this time (Floss \& Hoyer, 2010).
But these rare indices are not sufficient to explain the abundance and the diversity of the fauna and they are more recent than the cave hyaena, Crocuta spelaea (OIS 6- OIS 5), which therefore remains as the only explanation for that.

Bears $\mathrm{N}^{\circ} 1$ and $\mathrm{N}^{\circ} 2$ in Azé 1-6 (connecting gallery) were situated above these lines of bones and had not time to be affected by the same subsidence towards the lower network. Chronologically, this places them after the activity of hyeanas began, and later than Azé 1-2, which took place before the stalagmitic blockage at 60 m .

- Previous searches for fossilized pollen in the Azé sediments had always been disappointing, hardly surprising given that the conditions for their deposit and preservation were far from favourable (Argant, 1990).

However, in the case of the connecting gallery it was worth a try. Pollen could have ended up embedded in sediment because it had been on the fur or in the digestive tracts of buried animals. In the case of Bear $\mathrm{N}^{\circ} 2$ and the cub, it appeared that conditions were favourable to the preservation of pollen because of the rapidity with which their bones were buried and then covered by concretions which would have protected them from the action of oxygen. Two samples of very compact concretions, one adhering to the skull of the bear $\mathrm{N}^{\circ} 2$ (TA.06), the other to the skull of the cub (TA.22) were chosen for pollen analysis.


Fig. 10: Bear $\mathrm{N}^{\circ} 2$, Azé 1-6, pollen grains from the samples of concretions in contact with the skulls (adult and cub).
1- Pinus ( $60 \mu \mathrm{~m}$ ); 2- Cedrus (damaged), ( $60 \mu \mathrm{~m}$ ); 3- Alnus ( $22 \mu \mathrm{~m}$ ); 4- Ulmus ( $24 \mu \mathrm{~m}$ ); 5-Quercus ( $20 \mu \mathrm{~m}$ ); 6- Poaceae ( $25 \mu \mathrm{~m}$ ) (Photos J. Argant).
Fig. 10: Ours $\mathrm{N}^{\circ}$ 2, Azé 1-6, grains de pollen des échantillons de concrétions en contact avec les crânes (adulte et ourson).
1- Pinus $(60 \mu \mathrm{~m})$; 2- Cedrus (abîmé), $(60 \mu \mathrm{~m})$; 3-Alnus $(22 \mu \mathrm{~m})$; 4- Ulmus $(24 \mu \mathrm{~m})$; 5- Quercus $(20 \mu \mathrm{~m})$; 6- Poaceae $(25 \mu \mathrm{~m})$ (Photos J. Argant).

They both provided pollen in very good condition and of a similar type, of which 34 were identifiable (Fig. 10, Tab. 6). They are essentially from trees, among them four types of conifers (pine, cedar, juniper and one undetermined), but the pollen grains of mesothermophilous broadleaved trees largely dominate: alder, hazelnut, deciduous oak, elm, hornbeam, ash. They indicate temperate conditions, and in the case of alder, water-logged soils essential for their growth.

| Azé 1-6. Bear N${ }^{\circ}$ 2 | TA-06 | TA-22 |
| :--- | :---: | :---: |
|  | Adult | Cub |
| Pinus | 1 |  |
| Cedrus | 1 | 1 |
| Undet. Conifer | 1 |  |
| Betula |  | 1 |
| Juniperus | 1 |  |
| Alnus | 3 | 2 |
| Corylus | 3 |  |
| Quercus | 3 |  |
| Ulmus | 1 | 1 |
| Carpinus | 5 | 1 |
| Fraxinus | 2 |  |
| Ranunculaceae | 1 |  |
| Poaceae |  | 1 |
| Brassicaceae | 5 |  |
| Chenopodiaceae |  |  |
| Undetermined | 32 | 7 |
|  | $\mathbf{1 9}$ | $\mathbf{5}$ |
| Total | $\mathbf{2}$ |  |
| AP |  |  |
| NAP |  |  |

Tab. 6: Bear $\mathrm{N}^{\circ} 2$, Azé 1-6,
Ursus spelaeus ladinicus, result of pollen analysis of the two samples.
Tab. 6: Ours $\mathrm{N}^{\circ} 2$, Azé 1-6,
Ursus spelaeus ladinicus, résultat de l'analyse pollinique des deux échantillons.

Though not enabling a reconstruction of the landscape, these results do however support the hypothesis that the bones were deposited and covered by concretions during a clearly temperate phase consistent with OIS.5, and rule out OIS. 4 which is considerably cold.

The Galerie des Aiglons is probably the major gallery of the karstic system of Azé 1. It has been active for a very long time, just as much as the upper tourist gallery, and continued to function long after the latter was closed by slope deposits.
A study of cryophilic microfauna by M. Jeannet indicates a glacial period dated by 14C-AMS at $15,945 \pm 65 \mathrm{BP}$ (OxA-12455).
A fragment of bear bone from the layer below this microfauna could not be dated because it was older than the limit of the method (Barriquand et al., 2011). A stalagmitic floor dated by U/Th at 8.1 ( $\pm 1.2$ ) ka BP sealed the filling. The entrance of the Aiglons therefore disappeared behind slope deposits at the latest in OIS.1, or even before the end of the Tardiglacial period, in OIS.2.
Finally, Bear $\mathrm{N}^{\circ} 2$ from Azé 1-6, Ursus spelaeus ladinicus, occurred between the end of OIS. 6 and at the latest OIS.4, in any case before the 50 -ka upper limit of the 14 C -AMS method. Pollen analysis indicates a warm temperate period attributable to OIS.5.

## 5. Conclusion

The complete skeleton of Bear $\mathrm{N}^{\circ} 2$ provides a reference point within a relatively precise chronological range in the evolution of cave bears in Burgundy (Tab. 7).


Tab. 7: Azé 1 chronological synthesis. Various chronological marks and position of the various bears following each other.

Tab. 7: Azé 1, synthèse chronologique. Différents repères chronologiques et position des différents ours s'y succédant.
Azé 1 establishes the direct and continuous links in the evolutionary stages and in the dynamics of the populations of bears in the course of time, from the form $U$. deningeri at the end of median Middle Pleistocene (since OIS. 9 or even before) in the entrance of Azé 1-1, in Azé 1-4, and at the end of Azé 1-3, then $U$. spelaeus deningeroides during the recent Middle Pleistocene (OIS.6) in Azé 1-2 (ArGANT, 1991).
Ursus spelaeus ladinicus form occurred later in Azé 1-5 and Azé 1-6, probably during OIS. 5, at the latest
during OIS.4, but in any case, before the limit of 14C. This latter subsisted until much later, for example in the Alps: Cuvée des Ours, Chapareillan (Isère, France), $1,641 \mathrm{~m}$ asl, $13,990 \pm 50 \mathrm{BP}, \mathrm{Ly}-2545$ (OxA) (ArGANT et al., 2018).
The site of Azé has been well studied in a wide range of fields (prehistory, palaeontology, history, dating, karstology, underground biology, botany).
Palaeontology provides elements of dating which can enable a better understanding of the evolution and functioning of this very particular karstic system, neither too large, nor too small, on the human scale of speleologists and scientists, and even of bears!

## 6. Acknowledgements

The authors would like to thank here all those who have worked to uncover the secrets of the site of Azé, as well as those who continue to do so, with passion and tenacity, even sometimes in very difficult conditions: R. Morel, M. Bonnefoy, A. Jeannet, J. Combier, R. Villeneuve and many others too numerous to name here. It is a source of great satisfaction to make a small contribution to that enterprise. G. Rabeder and C. Frischauf had the opportunity to see Bear $\mathrm{N}^{\circ} 2$ in its raw state when they visited the „Centre de Paléontologie de l'ARPA" in Château (Saône-et-Loire) in 2012. We are grateful to them for their wise observations on the material from Azé. We are also thankful to R. Norington (Canberra, Australia) who assisted with the translation into English and Leyla Seyfullah for correction.

## 7. References

Argant, A. (1991). Carnivores quaternaires de Bourgogne, Documents des Laboratoires de Géologie de Lyon, 115, 1- 309.
Argant, A. (2004). Rapports Hommes-Carnivores au Paléolithique inférieur d’Azé I-1 (Saône-etLoire, France). Revue de Paléobiologie, Genève, 23: 803-819.
Argant, A. (2010). Carnivores (Canidae, Felidae et Ursidae) de Romain-la-Roche (Doubs, France). Revue de Paléobiologie, Genève, 29: 495-601.
Argant, A., Argant, J., Barriquand, J., Barriquand, L., Bonnefoy, M., Guillot, L., Jeannet, M. (2011). Pleistocene Carnivores in the Mâconnais. Field-trip of the 16th International Cave bear and Lion Symposium (Azé, 2010). Quaternaire, hors série, 4: 27-37.
Argant, A., Barriquand, J., Barriquand, L., Guillot, L., Nykiel, C., Argant, J. (2007). Azé Cave (Saône-et-Loire, France). Azé 1-3 : bears, filling and dating data. Scripta fac. Sci. Nat. Univ. Masaryk. Brun, 35, Geology: 85-88.
Argant, A., Brugal, J.-P. (2017). The cave lion Panthera (Leo) spelaea and its evolution: Panthera spelaea intermedia nov. subspecies. Proceedings of the 22nd International Cave Bear Symposium,

Kletno, Poland, 22-23 September 2016, Acta Zoologica Cracoviensia, 60 (2): 59-104.
Argant, A., Griggo, C., Ersmark, E., Philippe, M., Bintz, P., Picavet, R., Fourgous, B., Tillet, T., Argant, J. (2018). Bilan du programme OURSALP - Exemple de l'ours fossile du Scialet de la Décroissance à Corrençon-en-Vercors (Isère, France). In Bintz P., Griggo C., Martin L., Picavet R. (coord.) L'Homme dans les Alpes, de la Pierre au Métal, Collection EDYTEM, 20: 31-49.

Argant J. (1990). Climat et environnement au Quaternaire dans le Bassin du Rhône d'après les données palynologiques. Documents du Laboratoire de Géologie de Lyon, 111: 1-199.
Barriquand, L., Barriquand, J., Argant, A., Floss, H., Gallay, A., Guerin, C., Guillot, L., Jeannet, M., Nykiel, C., Quinif, Y. (2011). Le site des grottes d'Azé. Quaternaire, hors série 4: 15-25.

Barriquand, L., Kaufman, O., Auboeuf, B., Blanchard, D., Deceuster, J., Dechamp, S., Guillot, L. (2016). Analyse par tomographie électrique du site et de la Grotte Préhistorique d'Azé (Saône-etLoire, France). Karstologia, 68: 39-48.
Combier J., Gaillard, C., Moncel, M.-H. (2000). L'industrie du Paléolithique inférieur de la Grotte d'Azé (Saône-et-Loire) - Azé I-1. Bulletin de la Société Préhistorique Française, 97, 3: 349-370.
Combier, J., Merle, C. (1999). Le site d'Azé 2, dépôt de pente moustérien. Travaux de l'Institut de Recherche du Val de Saône Mâconnais, 4: 35-50.
Debeljak, I. (1996). Ontogenetic development of dentition in the cave bear. Geologija, 39: 13-79.
Floss, H., Hoyer, C.(2010). Azé, a multifaceted Paleolithic cave and open-air site in Burgundy's south - In: Barriquand L. \& Barriquand J. (eds), Azé and the Mâconnais. 16th International Cave Bear and Lion Symposium, Azé, September 22nd-26th, 2010: 65-114.
Gamble, C. (1999). The Palaeolithic societies of Europe. Cambridge World Archaeology, Cambridge University Press: 505 p.
Jeannet, M. (1980). Les Rongeurs de quelques sites holocènes (Vallon-Pont-d'Arc et Foissac), würmiens (Gréolières, Casteljau et Bendorf) et rissien (Azé). Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon, 18, suppl.: 29-34.
Kavcik, N., Rabeder, G. (2004). Post-Cranial Skeletal Elements (excl. metapodial Bones) of Cave Bears from Potočka zijalka (Slovenia). In: Potočka Zijalka. Palaeontological and Archaeological Results of the Campaigns 1997-2000. Mitteilungen der Kommission für Quartärforschung der Österreichischen Akademie der Wissenschaften, 13, Wien: 161-172.

Mourer-Chauvire, C. (1975). Les oiseaux du Pleistocène moyen et supérieur de France. Documents du Laboratoire de Géologie, Lyon, ${ }^{\circ} \mathbf{6 4}, 2$ fasc.: 624 p., 72 p.
Orlando, L., Bonjean, D., Bocherens, H., Thenot, T., Argant, A., Otte, M., Hänni, C. (2002). Ancient DNA and the population genetics of cave bears (Ursus spelaeus) through space and time. Molecular Biology and Evolution, 19: 1920-1933.
Rabeder, G., Hofreiter, M., Nagel, D., Withalm, G. (2004). New taxa of Alpine Cave Bears (Ursidae, Carnivora). Cahiers scientifiques - Département du Rhône - Muséum, Lyon, France, Hors série 2: 49-67.

Rabeder, G., Frischauf, C., Pacher, M. (2016). A new reference of Ursus deningeroides in Lower Austria. Cranium, Werkgroep Pleistocene Zoogdieren, 33,1: 8-13.
Rabeder, G., Kavcik, N. (Eds.) (2014). Abstracts and excursion-guide. XXth International Cave bear Symposium, Corvara (South Tyrol, Italy):45 p.
Sotnikova, M., Nikolskyi, P. (2006). Systematic position of the cave lion Panthera spelaea (Goldfuss) based on cranial and dental characters. Quaternary International, 142-143: 218-228.
(1) Aix Marseille Univ, CNRS, Minist Culture, LAMPEA, 5 rue du Château de l'Horloge, 13094 Aix-en-Provence, France.
(2) ARPA, Université Claude Bernard LYON 1, Bâtiment Géode R.1, 2 rue Raphaël Dubois, F-69622 VILLEURBANNE cedex.
(3) Éveha, - Études et valorisation archéologiques, 87 avenue des Bruyères, F- 69150 DÉCINES-CHARPIEU. Chercheur associé UMR ArAr 5138, thierry.argant @eveha.fr
(4) Université de Savoie, EDYTEM, UMR 5204, Bâtiment «Pôle Montagne», 5 Bd de la mer Caspienne, F- 73376 LE BOURGET-DU-LAC cedex.
(5) Association Culturelle du site d’Azé, Rizerolles, F-71260 AZE.

## ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database
Digitale Literatur/Digital Literature
Zeitschrift/Journal: Berichte der Geologischen Bundesanstalt
Jahr/Year: 2019
Band/Volume: 132
Autor(en)/Author(s): Argant Alain, Argant Thierry, Argant Jacqueline, Barriquand Lionel

Artikel/Article: The complete skeleton of the bear $n^{\circ} 2$ from the Galerie des Aiglons of the Azé Cave (Saône-et-Loire, France): Ursus spelaeus ladinicus 11-32

