

Systematic Palaeontology (Vertebrate Palaeontology)

Presence of *Hemitragus* aff. *cedrensis* (Mammalia, Bovidae) in the Iberian Peninsula: Biochronological and biogeographical implications of its discovery at Bolomor Cave (Valencia, Spain)

Florent Rivals^{a,*}, Ruth Blasco^b

^a ICREA and Institut Català de Paleoecologia Humana i Evolució Social (IPHES), Àrea de Prehistòria, Universitat Rovira i Virgili, Plaça Imperial Tàrraco 1, 43005 Tarragona, Spain

^b Institut Català de Paleoecologia Humana i Evolució Social (IPHES), Àrea de Prehistòria, Universitat Rovira i Virgili, Plaça Imperial Tàrraco 1, 43005 Tarragona, Spain

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Abstract

The discovery of new material in Late Pleistocene levels at Bolomor Cave (Valencia, Spain) raises some questions about the presence of the most ancient record of *Hemitragus cedrensis* in the peninsula, and its dispersal out of Provence. The morphology and dimensions of some lower teeth confirm the identification of *H.* aff. *cedrensis*. Moreover, it presents strong similarities, both morphological and metrical, with the specimens from Caune de l'Arago and bau de l'Aubesier (end of OIS 7 to OIS 5e) rather than with the population from the eponymous locality. The data suggest a dispersal event out of Provence towards the Iberian Peninsula during the Eemian. This dispersal was not stopped by natural barriers such as large rivers, or mountains. The results presented here confirm the biochronological interest of the genus *Hemitragus* for the Late Pleistocene in Mediterranean Europe. **To cite this article:** F. Rivals, R. Blasco, C. R. Palevol 7 (2008).

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Résumé

Présence d'*Hemitragus* aff. *cedrensis* (Mammalia, Bovidae) dans la péninsule Ibérique : implications biochronologiques et biogéographiques de sa découverte à la grotte de Bolomor (Valence, Espagne). La découverte de quelques fossiles dans les niveaux du Pléistocène supérieur de la grotte de Bolomor (Valence, Espagne) soulève quelques questions au sujet de la présence d'un tahr de petite taille (de type *Hemitragus cedrensis*) dans la péninsule (la plus ancienne à ce jour), et sa dispersion hors de Provence, sa région d'origine supposée. La morphologie et les dimensions des dents confirment l'identification d'une forme affine de cette espèce. De plus, elle présente de fortes similarités, morphologiques et métriques, avec les spécimens de la caune de l'Arago et du bau de l'Aubesier (fin du stade isotopique 7 jusqu'au stade 5e). Les résultats suggèrent une dispersion hors de Provence, en direction de la péninsule Ibérique au cours de l'Éémien. Cet événement de dispersion n'a pas été limité par des barrières naturelles telles que fleuves ou montagnes. Les résultats présentés ici confirment l'intérêt biochronologique du genre *Hemitragus* pour le

* Corresponding author.

E-mail address: florent.rivals@icrea.es (F. Rivals).

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Keywords: Caprinae; *Hemitragus*; Bolomor Cave; Dispersal; Local evolution; Late Pleistocene; Spain

Mots clés : Caprinae ; *Hemitragus* ; Grotte de Bolomor ; Dispersion ; Évolution locale ; Pléistocène supérieur ; Espagne

1. Introduction

The biochronological and biogeographical interest of the Caprinae is well evidenced in the Pleistocene, with various dispersal events and local evolutions [4,6,7,9,19,20]. Among the members of this family, some taxa revealed to be of particular interest for biochronology, like the species and sub-species of the *Capra* and *Hemitragus* genera [7,9,19]. The latter is composed of two species in the Middle and Late Pleistocene of Europe: *Hemitragus bonali* and *H. cedrensis*. Cèdres' tahr, *H. cedrensis* Crégut-Bonnoure 1989, was first described on the fossil remains from Les Cèdres, located in Var department, in southern France (Fig. 1), and whose stratigraphic sequence is related to OIS 6 [5,8]. The species was later identified in other French localities (Fig. 1): Rigabe (Var) and Saint-Marcel-d'Ardèche (Ardèche) by Crégut-Bonnoure [8], Bau de l'Aubesier (Vaucluse) by Fernandez [11], as

well in the Late Pleistocene levels at Caune de l'Arago (Pyrénées-Orientales) by Rivals [19]. All those localities confirm the presence of *H. cedrensis* in southern France (Provence and Roussillon) from the end of the Middle Pleistocene (end of OIS 7) to the beginning of the Upper Pleistocene (OIS 5) [5,8,10,20]. Moreover, some remains of a small form were briefly described and attributed to *Hemitragus* sp. in Spain at Cova Negra (Valencia) in levels from OIS 5c to 3 [18].

However, Crégut-Bonnoure (pers. comm.) estimates that the situation is certainly more complex. The size of *H. bonali* starts to decrease in the OIS 7 with a modification of the morphology tending to the morphotype *cedrensis*. Crégut-Bonnoure (pers. comm.) considers that the species *H. cedrensis* corresponds only to the populations located east of the Rhone River (Les Cèdres, Rigabe, Bau de l'Aubesier). What are the other populations located west of the Rhone, such as Saint-Marcel-d'Ardèche or Caune de l'Arago? Could they

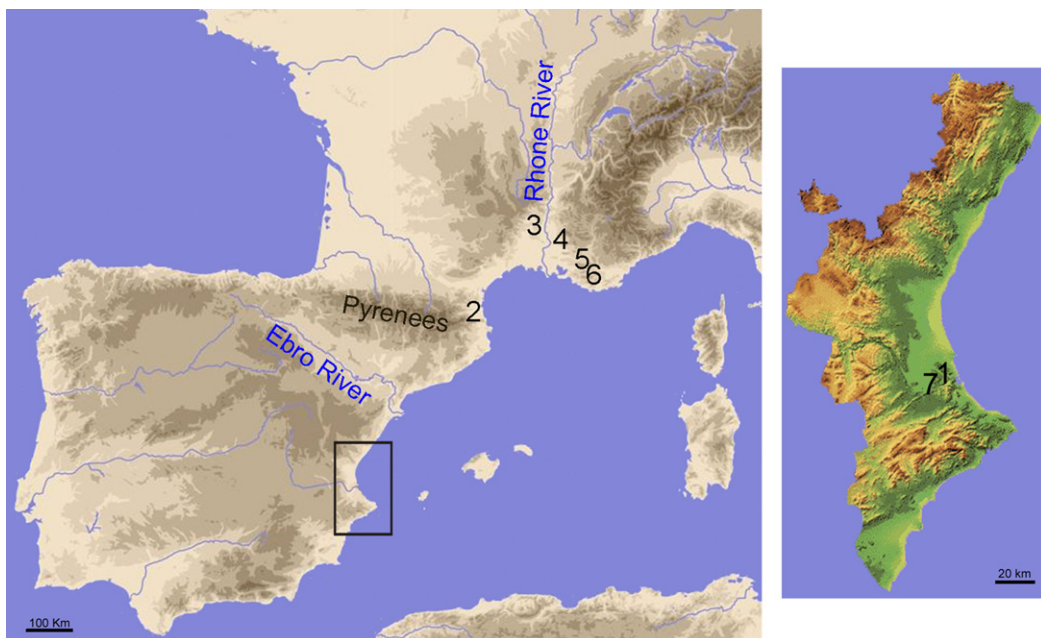


Fig. 1. Map showing the location of Bolomor Cave (1) and the reference localities (2–7). (1) Bolomor Cave, (2) Caune de l'Arago, (3) Saint-Marcel-d'Ardèche, (4) Bau de l'Aubesier, (5) Rigabe, (6) Cèdres, (7) Cova Negra.

Fig. 1. Carte de localisation de la grotte de Bolomor (1) et des sites de comparaison (2–7). (1) Grotte de Bolomor, (2) caune de l'Arago, (3) Saint-Marcel-d'Ardèche, (4) bau de l'Aubesier, (5) Rigabe, (6) Cèdres, (7) Cova Negra.

result from a size reduction and local evolution of *H. bonali* or are they phylogenetically related to *H. cedrensis*? Was the Rhone River, or other geographical features, a natural barrier to the dispersal of *H. cedrensis*?

To intend answering those questions we needed to find a locality that meets two criteria: (1) the presence of level(s) of the same chronology as the French localities where *H. cedrensis* have already been described, i.e. end of OIS 7 to the beginning of OIS 5, and (2) located west of the Rhone River, or west of other geographical barriers. We selected the material from level IV of Bolomor Cave in eastern Spain, because it meets the two criteria; previous studies already reported the presence of the genus *Hemitragus* at this locality [17].

2. Presentation of Bolomor Cave

Bolomor Cave is located on the southern slope of the Valldigna valley, approximately 2 km southeast of the town of Tavernes (Valencia, Spain). The cave is situated on the right bank of Bolomor Ravine, approximately 100 m above sea level. Northeast of the site, the coast runs almost perpendicular to the valley, the base of which, along which the Vaca River runs, is almost at sea level.

The sedimentary sequence of Bolomor Cave consists mainly of allochthonous material of colluvial origin that has been deposited via open channels on walls and ceiling. In addition to these deposits, there are other autochthonous ones of gravitational origin from the zenith subsidence, due to tectonics or weathering processes. Seventeen geoarchaeological levels have been identified [16]. Level IV consists of a sandy sediment with limestone clasts. The karstic deposit of Bolomor Cave has been dated by amino acid racemization (AR) and thermoluminescence (TL) to between OIS 9 and OIS 5e [12–14]. Several TL dates have been obtained: 121 ± 18 kyr for level II, and 233 ± 35 kyr, and 225 ± 34 kyr for level XIII. AR dates have also been made: 228 ± 53 kyr for level XIII and 525 ± 125 kyr for level XVII [12–14]. According to these results, level IV could correspond to the end of OIS 6 or the beginning of OIS 5.

At present, the lithic industry recovered from Bolomor Cave is classified as a Middle Palaeolithic techno-complex. All the stages of the *chaîne opératoire* are represented. The raw materials used consist of flint, limestone and quartzite, which come from marine, colluvial and fluvial stones from the immediate area around the site and from areas further afield up to 15 km from the site. Level-IV industry consists mainly of

small formats, predominantly scrapers, denticulate and retouching diversified [14].

The faunal analysis from Bolomor Cave by R. Martínez Valle, I. Sarrión, and more recent studies [2,3,15,17] have identified 17 species of macromammals. The biostratigraphic sequence is particularly characterized by the presence of tahr (*Hemitragus* sp.), horse (*Equus ferus*), red deer (*Cervus elaphus*) and fallow deer (*Dama* sp.), and by a more specific record at certain times of other species such as the giant deer (*Megaloceros giganteus*), wild boar (*Sus scrofa*), macaque (*Macaca sylvanus*), wild ass (*Equus hydruntinus*), aurochs (*Bos primigenius*), steppe rhino (*Stephanorhinus hemitoechus*), elephant (*Elephas (Palaeoloxodon) antiquus*), hippopotamus (*Hippopotamus amphibius*), and beaver (*Castor fiber*). The presence of carnivores in the cave is sporadic. Fossil remains of *Ursus arctos*, *Ursus thibetanus*, *Canis lupus* and *Lynx* sp. have been identified [2,3,15,17].

The investigations carried out to date at the site have yielded the remains of anthropogenic combustion structures in levels II, IV, XI and XIII. For this last level, there is a dating via AR on malacofauna, which gives a date of 228 ± 53 kyr. Therefore, at Bolomor Cave, there is the oldest recorded evidence for the controlled use of fire on the Iberian Peninsula. Human fossils have been recovered from Bolomor Cave: seven bone and dental pieces. Some of the remains come from the screening of removed sediments which were produced by the old quarrying work in the 1930s. But others have been recovered during the excavation and therefore have a clear stratigraphic location. According to Arsuaga et al. [1], the morphology of the human remains from Bolomor Cave is compatible with that of the European human fossils of the Middle Pleistocene.

3. Description of the material

A total of nine specimens were identified as *Hemitragus* at Bolomor Cave in level IV:

- two upper teeth: left M1 (CB'94 IV H2 C2 n° 16), and one fragment of molar (CB'94 IV B2 C2 cr-3);
- seven lower permanent teeth: three left premolars belonging to the same individual: p2 (CB'98 IV A2 C4 cr-24), p3 (CB'93 IV F2 C1 cr-175), and p4 (CB'97 IV F3 C4 No. 37), two fragments of molars (CB'94 IV J3 C2 cr-18 and CB'94 IV D4 C3 cr-3), and two permanent incisors or canines (CB'97 IV D2 C2 cr-86, a right i2 or i3, and CB'94 IV B3 C2 No. 42, a left i3 or canine).

The most significant specimens identified at Bolomor Cave (M1, p2, p3, and p4) were carefully described and metrically compared to all the other localities where *H. cedrensis* is already identified. Measurements correspond to the standards used for Caprinae by Crégut-Bonnoure [7,8]. However, because the sample size is very small, it is not possible to estimate the variability in the population, and thus our interpretations will be limited.

3.1. Upper teeth

3.1.1. Upper first molar (M1)

The M1 is heavily worn, and thus belong to an old individual. However, it is possible to describe the main features. The postero-lingual root of the M1 is more developed than in *Capra*, whereas the distal root is less extended. Moreover, the cemento-enamel line is relatively low. According to Crégut-Bonnoure [8], these two criteria are characteristic of the genus *Hemitragus*. Other features are specific to *H. cedrensis*: the parastyle is narrow, the paracone less dilated, and the folds of the paracone and metacone are narrower than in *H. bonali* (Fig. 2).

Metrical analysis (Table 1 and Fig. 3) shows strong similarities between the M1 from Bolomor and the data from Caune de l’Arago. However, because the tooth is heavy worn, some of the measurements (especially measurements 1 and 7, occlusal mesiodistal diameter and total buccolingual diameter, respectively) are smaller than in the other populations.

3.2. Lower teeth

3.2.1. Lower second permanent premolar (p2)

The morphology of the p2 is compared to the description made by Fernandez [11] on the population from Bau de l’Aubesier; the p2 is unknown in the Cèdres popula-

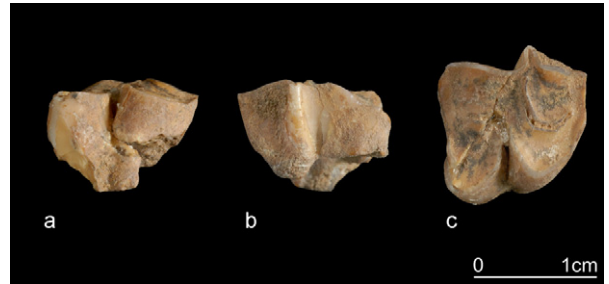


Fig. 2. *Hemitragus* aff. *cedrensis* left M1 from Bolomor Cave. Lingual (a), buccal (b), and occlusal (c) views. Specimen CB’94 IV H2 C2 No. 16.

Fig. 2. M1 supérieure gauche d’*Hemitragus* aff. *cedrensis* de la grotte de Bolomor. Vues linguale (a), labiale (b) et occlusale (c). Spécimen CB’94 IV H2 C2 No. 16.

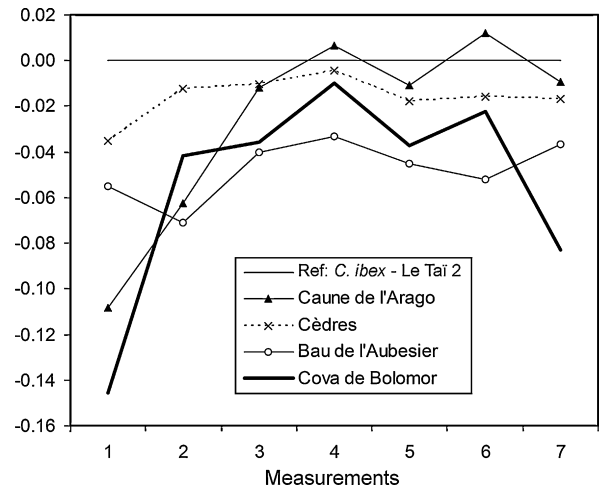


Fig. 3. Ratio diagram of M1 average measurements for *Hemitragus cedrensis* (standard base: *Capra ibex* from Le Tai 2 [9]). See Table 1 for measurements description.

Fig. 3. Diagramme des rapports des dimensions moyennes des M1 supérieures d’*Hemitragus cedrensis* (base de référence : *Capra ibex* – Le Tai 2 [9]). Voir le Tableau 1 pour la description des mesures.

Table 1

Hemitragus aff. *cedrensis* M1 measurements (in mm) from Bolomor Cave specimen and from other comparative sites

Tableau 1

Dimensions de la M1 d’*Hemitragus* aff. *cedrensis* (en mm) de la grotte de Bolomor et des sites de comparaison

Locality	n	DMD		DVL occlusal				DVL basal total	References
		occl. 1	basal 2	1st lobe		2nd lobe			
				total 3	median 4	total 5	median 6		
Cova de Bolomor	1	12.3	11.9	11.2	10.9	9.9	9.5	10.8	
Cèdres	8	15.9	12.7	11.9	11.0	10.4	9.6	12.5	[8]
Caune de l’Arago	4	13.4	11.3	11.8	11.3	10.5	10.3	12.7	[19]
Bau de l’Aubesier	23	15.2	11.1	11.1	10.3	9.7	8.9	12.0	[11]

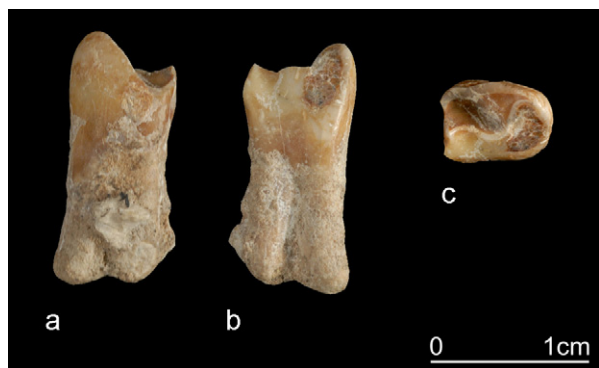


Fig. 4. *Hemitragus* aff. *cedrensis* left p2 from Bolomor Cave. Buccal (a), lingual (b), and occlusal (c) views. Specimen CB'98 IV A2 C4 cr-24.

Fig. 4. p2 gauche d'*Hemitragus* aff. *cedrensis* de la grotte de Bolomor. Vues labiale (a), linguale (b) et occlusale (c). Spécimen CB'98 IV A2 C4 cr-24.

tion. On the lingual side, the median denticle is well individualized and limited by two deep grooves (Fig. 4). The distal side is flattened and presents, on the buccal side, a small bulge at its base.

The dimensions for the p2 from Bolomor (Table 2 and Fig. 5) enter the range of variation of the measurements from Bau de l'Aubesier [11]. The p2 from these two populations are smaller than the reference sample of *H. bonali* from Caune de l'Arago.

3.2.2. Lower third permanent premolar (p3)

The various features to identify the p3 were described by Crégut-Bonnoure [8] and are mostly located on the lingual side of the tooth (Fig. 6). The lingual valley is well individualized on the mesial side only, not on both sides as in *H. cedrensis*. The metaconid, not strongly dilated, starts sub-vertical and then bends toward the front as in *H. bonali*, and is not straight as in *H. cedrensis*. On the buccal side, the inter-lobar groove is deep and the hypoconide is well expanded, as in *H. cedrensis* from Les Cèdres. The specimen from Bolomor presents a mosaic of primitive and derived features, corresponding to *H. bonali* and *H. cedrensis*, respectively.

Table 2
Hemitragus aff. *cedrensis* p2 measurements (in mm) from Bolomor Cave specimen and from other comparative sites

Tableau 2
Dimensions de la P2 inférieure d'*Hemitragus* aff. *cedrensis* (en mm) de la grotte de Bolomor et des sites de comparaison

Locality	n	DMD		DVL	References
		1	2		
Cova de Bolomor	1	9.46	6.1		
Bau de l'Aubesier	9	9.54	6.22	[11]	

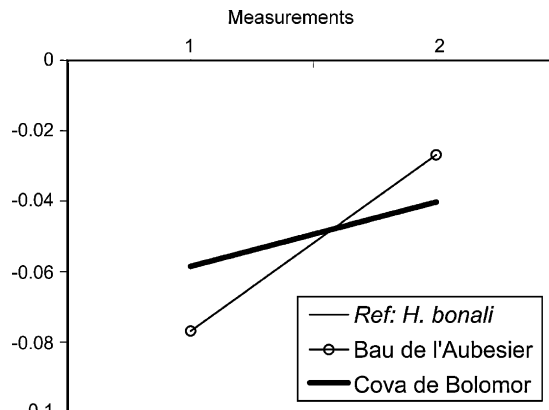


Fig. 5. Ratio diagram of p2 average measurements for *Hemitragus cedrensis* (standard base: *H. bonali* from Caune de l'Arago [19]). See Table 2 for measurements' description.

Fig. 5. Diagramme des rapports des dimensions moyennes des P2 inférieures d'*Hemitragus cedrensis* (base de référence: *H. bonali* de la caune de l'Arago [19]). Voir le Tableau 2 pour la description des mesures.

The measurements and the ratio diagram (Fig. 7 and Table 3) indicate a strong similarity with the tahr from Bau de l'Aubesier, Grotte des Cèdres, and Caune de l'Arago. It is however smaller than tahrs from those populations, especially since the three measurements of the buccolingual diameter indicate that the p3 of Bolomor is narrower. The specimen from Bolomor is extremely similar to the population from Bau de l'Aubesier, especially considering the length of the tooth (measurements 1 and 2).

Finally, a ratio is calculated, dividing the length of the lingual valley by the occlusal length [19]. This ratio is always higher than 0.5 in *Hemitragus*, compared to *Capra*, where this ratio is lower than 0.5 [19]. The

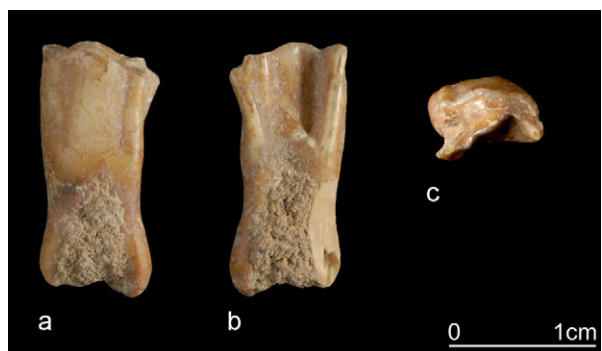


Fig. 6. *Hemitragus* aff. *cedrensis* left p3 from Bolomor Cave. Buccal (a), lingual (b), and occlusal (c) views. Specimen CB'93 IV F2 C1 cr-175.

Fig. 6. P3 inférieure gauche d'*Hemitragus* aff. *cedrensis* de la grotte de Bolomor. Vues labiale (a), linguale (b) et occlusale (c). Spécimen CB'93 IV F2 C1 cr-175.

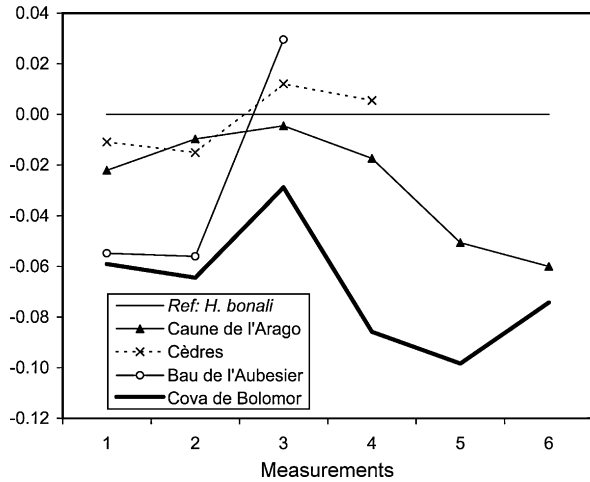


Fig. 7. Ratio diagram of p3 average measurements for *Hemitragus cedrensis* (standard base: *H. bonali* from Caune de l'Arago [19]). See Table 3 for measurements description.

Fig. 7. Diagramme des rapports des dimensions moyennes des P3 inférieures d'*Hemitragus cedrensis* (base de référence: *H. bonali* de la caune de l'Arago [19]). Voir le Tableau 3 pour la description des mesures.

specimen from Bolomor has a ratio of 0.56, similar to what is known in other populations of *H. cedrensis* (Table 3).

3.2.3. Lower fourth permanent premolar (p4)

The metaconid is not strongly dilated and, as described by Crégut-Bonnoure [8] and Fernandez [11], it is limited by shallow and large distal and mesial grooves (Fig. 8). However, the distal groove differs from the population from Les Cèdres. It is deeper and similar to what is known in *H. bonali* [8,19]. Such feature was also observed by Fernandez [11] on one specimen (out of 9) in the population from Bau de l'Aubesier. On the buccal side, the p4 presents a very deep interlobar groove. The stylides are not very prominent. The hypoconide is well developed and as large as in *H. bonali* from Caune de l'Arago. As already observed for the p3, the p4

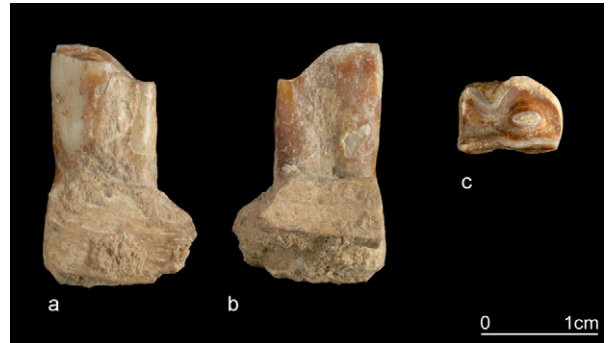


Fig. 8. *Hemitragus* aff. *cedrensis* left p4 from Bolomor Cave. Buccal (a), lingual (b), and occlusal (c) views. Specimen CB'97 IV F3 C4 No. 37.

Fig. 8. P4 inférieure gauche d'*Hemitragus* aff. *cedrensis* de la grotte de Bolomor. Vues labiale (a), linguale (b) et occlusale (c). Spécimen CB'97 IV F3 C4 No. 37.

from Bolomor presents a mosaic of primitive and derived features of both *H. bonali* and *H. cedrensis*.

Measurements of the p4 from Bolomor (Table 4 and Fig. 9) show a higher similarity with the population from Bau de l'Aubesier and Caune de l'Arago, than with the sample from Les Cèdres. These differences in dimensions and morphology suggest that the tahr from Bolomor is finally more similar to the population from Caune de l'Arago than the typical populations of Les Cèdres or Rigabe.

3.2.4. Synthesis

The morphology of the lower p3 and p4, the only characteristic teeth we have at Bolomor, display a mosaic of few primitive features from *H. bonali*, associated, on the same teeth, with the derived features characteristic of *H. cedrensis*. Such characters were also observed, east of the Rhone River, on a p4 from Bau de l'Aubesier 11 (p. 38)]. It is not exceptional to find such a mosaic of characters in *H. cedrensis*.

The tahr from Bolomor Cave presents strong similarities, both morphological and metrical, with the

Table 3

Hemitragus aff. *cedrensis* p3 measurements (in mm) from Bolomor Cave specimen and from other comparative sites

Tableau 3

Dimensions de la P3 inférieure d'*Hemitragus* aff. *cedrensis* (en mm) de la grotte de Bolomor et des sites de comparaison

Locality	n	DMD		DVL occlusal		DVL	Length of ling. valley	Ratio 6/1	References
		occl. 1	basal 2	1st lobe 3	2nd lobe 4	basal 5	6		
Cova de Bolomor	1	8.1	7.1	4.9	4.7	5.3	4.5	0.56	
Cèdres	4	9.05	8.00	5.35	5.85		5.45	0.56	[8]
Caune de l'Arago	2	8.82	8.10	5.15	5.55	5.92	4.65	0.53	[19]
Bau de l'Aubesier	17	8.18	7.28	5.57					[11]

Table 4

Hemitragus aff. *cedrensis* p4 measurements (in mm) from Bolomor Cave specimen and from other comparative sites

Tableau 4

Dimensions de la P4 inférieure d'*Hemitragus* aff. *cedrensis* (en mm) de la grotte de Bolomor et des sites de comparaison

Locality	n	DMD		DVL occlusal		DVL basal	References
		occl. 1	basal 2	1st lobe 3	2nd lobe 4	5	
Cova de Bolomor	1	9.46	8.92	6.1	5.2	6.23	
Cèdres	9	10.94	9.56	6.35	5.58	5.94	[8]
Caune de l' Arago	2	9.95	9.05	6.40	4.95	6.74	[19]
Bau de l' Aubesier	19	9.54	8.85	6.22	5.22	6.47	[11]

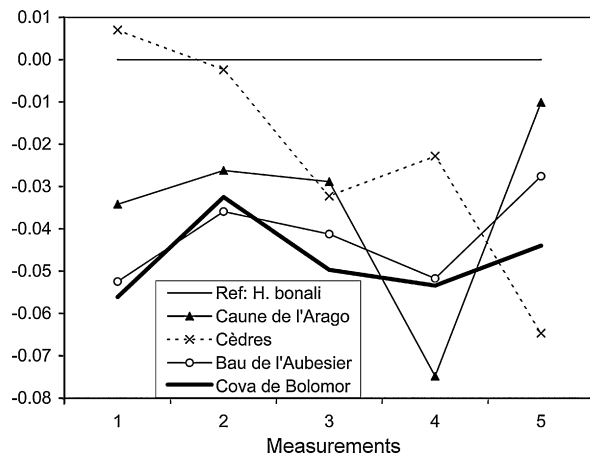


Fig. 9. Ratio diagram of p4 average measurements for *Hemitragus cedrensis* (standard base: *H. bonali* from Caune de l' Arago [19]). See Table 4 for measurements description.

Fig. 9. Diagramme des rapports des dimensions moyennes des P4 inférieures d'*Hemitragus cedrensis* (Base de référence: *H. bonali* de la caune de l' Arago [19]). Voir le Tableau 4 pour la description des mesures.

specimens from Caune de l' Arago (end of OIS 6 or OIS 5e) and bau de l' Aubesier (end of OIS 7 – beginning of OIS 6) rather than with the population from the eponymous locality. The material appears to be smaller than in other populations, especially the lower premolars, which seem to be shorter. However, the significance of these differences is difficult to interpret; they might be related to the small sample size.

What is the meaning of such differences? Is the population from Bolomor related to a dispersal of *H. cedrensis* out of Provence, or does it result from a local evolution *H. bonali*?

4. Discussion

H. cedrensis is known from five localities in France, whose sequences are related to the end of OIS 7, OIS 6,

and OIS 5e: Grotte des Cèdres, Rigabe, Saint-Marcel-d' Ardèche, Bau de l' Aubesier, and Caune de l' Arago. The tahr from Bolomor Cave is of smaller size than those from Les Cèdres and shows a resemblance in morphology and strong metrical similarities with the populations from Bau de l' Aubesier and Caune de l' Arago. These strong affinities are interesting. Caune de l' Arago is located in between the sites of Provence (Les Cèdres, Bau de l' Aubesier, and Rigabe) and Bolomor Cave. The similarities observed in Bolomor suggest some kind of phylogenetic relation of this population with the other two. It is unlikely that several convergent morphological features appear at the same time in three different regions, and are associated with the same size changes. However, because of the small size of the sample, we prefer to attribute it to *Hemitragus* aff. *cedrensis*.

In *H. bonali* as well as in *H. cedrensis*, the size decrease throughout the Pleistocene following the Bergmann's law [5]. This could explain the smaller size of the specimens from Bolomor, size reduction that has already been observed at Caune de l' Arago [20]. The morphological differences observed on the teeth, together with the decrease in size, suggest that the population from Bolomor Cave could be more evolved than the population from Les Cèdres. The population from Bolomor could be contemporary with or slightly more recent than those from Caune de l' Arago or Bau de l' Aubesier. Because no significant data is published on the small tahr from Cova Negra, it is not possible to include it in the comparisons. However, even if the sample size is too small to be significant on a chronological level, the tahr from Bolomor is, now, the oldest record of a small form similar to *H. cedrensis* in the Iberian Peninsula.

The presence of *H. aff. cedrensis* at Bolomor, and maybe at Cova Negra, confirms the hypothesis of a dispersal out of Provence during the Eemian (OIS 5e) or more probably slightly before. The presence of *H.*

cedrensis at Bolomor in level IV, dated from about 120 ka and related to the end of OIS 6 or the beginning of OIS 5, suggests a dispersal from the Provence region from where it originates, earlier than previously suggested by Rivals [20].

The similarity with the specimens from the French localities also reveal a rapid dispersal along the Mediterranean coast and bring evidence that the Rhone River, the Pyrenean Mountains, and the Ebro River were not important barriers for *Hemitragus*. The presence of other large mammals south of the Pyrenees, like *Rangifer*, identified in Mollet [21], confirm that the mountain range was not a natural barrier for those animals.

5. Conclusions

H. cedrensis is now identified in six localities whose stratigraphical sequences are related to the end of OIS 7, OIS 6 and OIS 5e; and maybe at Cova Negra with a more recent chronology (OIS 5c to 3). The data suggest a dispersal event out of Provence towards the Iberian Peninsula during the OIS 5e (Eemian), i.e. during a climatic warming. This dispersal was not stopped by natural barriers such as Rhone and Ebro Rivers, or the Pyrenean Mountains. The results presented here confirm the biochronological interest of *Hemitragus* for the Late Pleistocene in Mediterranean Europe.

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