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# Comment on two *Pachycrocuta brevirostris* (Aymard, 1846) mandibles from the Early Pleistocene in south-eastern France: Grosse Marguerite Cave (Aiguèze) and Trois Pigeons Swallow hole (Nîmes)

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authors also thank the reviewers, Ms Françoise Delpéch and Mr Jean-François Tournepiche, for their constructive comments.

## Introduction

- 1 During the European Pleistocene, three (or four) main genera and four species of Hyenids succeed each other or co-evolve.
- 2 Giant hyenas from the *Pachycrocuta Kretzoi* genus, 1938 (sometimes dissociated into two distinct *Pachycrocuta* and *Pliocrocuta* genera) including two species (*Pachycrocuta brevirostris* (Aymard, 1846) and *Pachycrocuta perrieri* or *Pliocrocuta perrieri* (Croizet, Jobert 1828)) develop between the end of the Pliocene and the Lower Pleistocene then make way about 600 000 years ago during the Middle Pleistocene for the last representative of the *P. brevirostris* genus (Turner, Antón 1996).
- 3 The striped fossil hyena (genus *Hyaena* Brünnich, 1771; the *Hyaena prisca* described by Serres, 1828) is sometimes described as a sub-species of the striped hyena: *Hyaena hyaena prisca*. This species evolves during the course of the Middle Pleistocene and disappears from our regions at the end of this same period. However, it lives on until recent phases of the Upper Pleistocene in refuge zones in Southern Europe (e.g., Furninha in Portugal in Cardoso 1996).
- 4 The spotted fossil hyena is issued from the genus *Crocuta* Kaup, 1828. The phylogeny of the Pleistocene members of this genus is still debated (multiple species or a single spotted hyena species; *Crocuta crocuta* (Erxleben, 1777) with many sub-specific forms). It appeared in Europe during the Middle Pleistocene (oldest traces around 800 000 years at Calsa Selce in Italy in Sardella; Petrucci 2012), it remains the most frequent hyena species and seems to disappear towards 25 000 BP (Werdelin, Solounias 1991; Discamps 2011). The cave hyena is present throughout Europe at many paleontological sites where it is the agent responsible for bone accumulations; Fourvel 2012). Proportionally, the other taxa of the *Pliocrocuta*, *Pachycrocuta* and *Hyaena* genera are much rarer. This is the case in particular for the earlier forms which are relatively poorly represented in spite of a wide geographic dispersal ranging from the Iberian Peninsula, with *P. brevirostris*, identified in the Lower Pleistocene site of Fonelas P-1 (Arribas, Garrido 2008), to the Far East with the *Pliohyaena* genus (Qiu 1987), which is synonymous with *Pliocrocuta* and *Pachycrocuta* (Werdelin, Solounias 1991).
- 5 In France, early forms of the *Pachycrocuta* and *Pliocrocuta* genera have only yielded a few remains (tab. 1). In particular, the giant hyena *Pachycrocuta brevirostris* has only been described at six sites. It seems to have been present during a relatively short lapse of time, between 0.9 and 1.2 Ma, during the formation of the MNQ 19 and MNQ 20 biozones.
- 6 The two mandibles from Grosse Marguerite Cave and Trois Pigeons Swallow hole, both in the Gard, belong to these early forms. The paleontological analysis of these objects and their specific determination thus add to our knowledge of these early Hyenids and their geochronological distribution in France.

## 1 – Geological setting and site presentation

- 7 Grosse Marguerite Cave and Trois Pigeons Swallow hole are both in the karstic domain of Eastern Languedoc, occupying an intermediary position between the Massif Central and the Cévennes, to the northwest and the west, the Rhône Valley to the east, and the Mediterranean coastal plain to the south (fig. 1). The structural context lies on a major network of faults linking Languedoc to the Northern Alps. This faulted network, modelled by Pyrenean-Alpine tectonics, gave rise to a karstic landscape, where exo- and endokarstic forms abound, with the presence of extensive and deep underground networks. These (Urgonian) limestone plateaus are carved up by a major hydrographic network (Ardèche, Cèze, Gardon, Vidourle) with entrenched gorges (Bourdier 1961; Debard 1988).

Table 1 - List of French paleontological sites with *Pliocrocuta perrieri* and *Pachycrocuta brevirostris* remains.

Site	Localisation	Chronologie	<i>P. perrieri</i>	<i>P. brevirostris</i>	Référence
Saint-Vallier	Drôme	MNQ17	NR=17 ; NMI=4		Argant 2004
Chagny	Saône-et-Loire	MNQ17	NR=1		Guérin 1980 ; Argant 1991
Sénezé	Haute-Loire	MNQ18	+		Stehlin 1923 ; Boeuf 1997
Blassac	Haute-Loire	MNQ19	NR=3		Beden et Guth 1970 ; Boeuf 1997
Ségries-Le Réservoir	Alpes-de-Haute-Provence	MNQ17	NR=6		Dubar <i>et al.</i> 1978
Cornillet 3	Alpes-de-Haute-Provence	MNQ17	NR=2		Dubar <i>et al.</i> 1978
Le Coupet	Haute-Loire	MNQ18	+		Crégut <i>in</i> Guérin et Patou 1996
Vialette	Haute-Loire	MNQ16a (3,1Ma)	NR=3		Lacombat <i>et al.</i> 2008 ; Guérin 2007
Perrier-Les Etouaires	Puy-de-Dôme	MNQ16b	+		Croizet et Jobert 1828 ; Guérin <i>et al.</i> 2007
Chilhac	Haute-Loire	MNQ17 (2,2Ma)	+		Boeuf 1997 ; Boivin <i>et al.</i> 2010
Sartanette	Gard	MNQ19		+	Bonnet 1980
Ceyssaguet	Haute-Loire	MNQ20-21 (0,9-1,2Ma)		NR=20 ; NMI=5	Tsoukala et Bonifay 2004
Sainzelles	Haute-Loire	MNQ20 (~1Ma)		Holotype	Boule 1893
Vallonnet	Alpes-Maritime	MNQ20 (0,9-1,0Ma)		NR=76	Moullé 1992 ; Moullé et Tréguier 2006
Escoffier	Ardèche	Pléist. inf. et moy.		cf. <i>P. brevirostris</i> NR=1	inédit
Bois-de-Riquet	Hérault	MNQ20-21 (1,1-1,3Ma)		+	Crochet <i>et al.</i> 2009 ; Bourguignon <i>et al.</i> 2015 accepté
Saint-Prest	Eure-et-Loire	MNQ20-21 (0,9-1,2Ma)		NR=2	Guérin <i>et al.</i> 2003

- 8 Grosse Marguerite Cave (Aiguèze) opens on the right bank of the Ardèche gorges, in the median part of the gorges, in a sector where the cliffs are particularly marked. The cave is part of a remarkable complex of about fifteen cavities on three stepped levels (Arbousiers Swallow hole, Bob Cave Swallow hole...) spread over a small surface. This density has yet to be explained but is clearly related to the underlying Castor source. A large northeast/southwest facing “keyhole” entrance leads into a large stepped network (fig. 2). The main part of the network is formed by an access gallery oriented like the entrance and opening onto a large, high and very concretionary chamber. No in-depth geological, geomorphological or archaeological studies have ever been conducted at Grosse Marguerite Cave. Nonetheless, this site seems to be an important protohistoric site, with an imposing pottery corpus and bronze pendants, curated at the Cité de la Préhistoire of Orgnac-l’Aven (Ardèche). The protohistoric pottery is currently being studied by J. Vital.
- 9 Trois Pigeons Swallow hole (Nîmes) opens about 1 km to the south of the Gardon gorges, at the base of a sinkhole. It is currently the deepest cavity known in the Gardon gorges. Access to the horizontal network, which develops along a northwest/southeast axis, is through a 20-metre-deep shaft (fig. 3). The cavity is made up of a series of

galleries leading onto two large chambers, in particular the Throne Chamber (la Salle du Trône), which contains a large hopper.

Figure 1 - Geographical location of sites. Map produced using D-maps.com (c) open-access site.

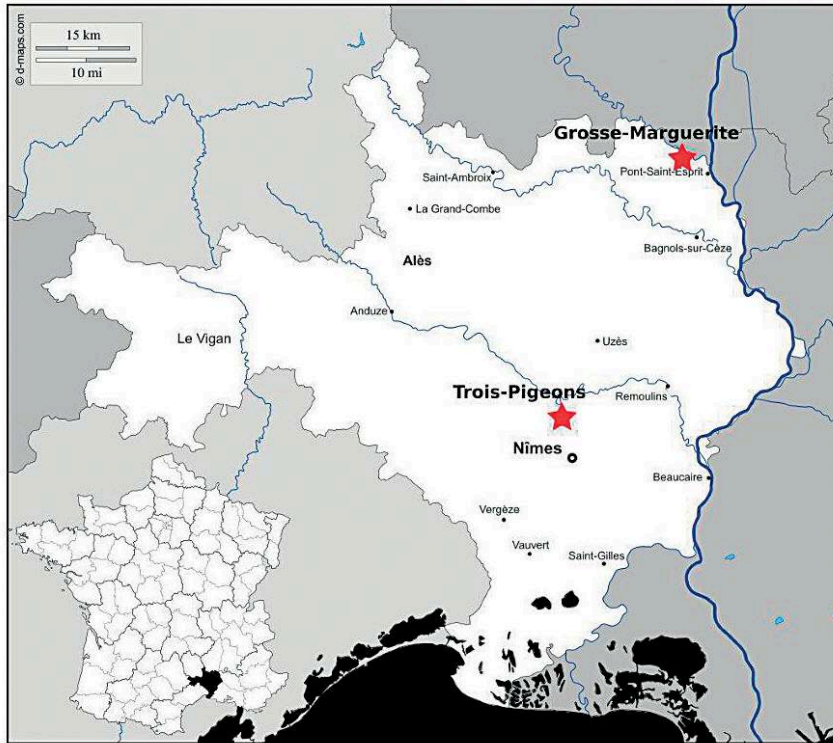
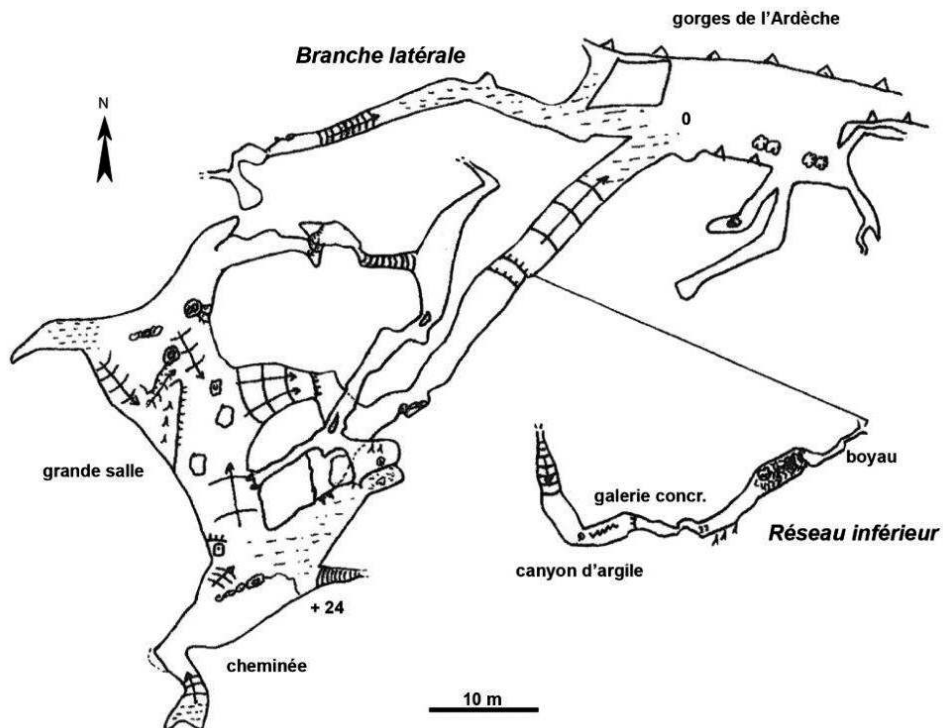


Figure 2 - Topography of Grosse-Marguerite Cave (Topography by T. Marchand and P. Harlez).



- 10 Apart from the hyenid mandible studied here, the Trois Pigeons swallow hole contained little paleontological material. A right horse pisiform and a cervical vertebra from a young carnivore were also discovered in the cavity.

## 2 - Material and method

- 11 The specimens from Grosse Marguerite Cave and Trois Pigeons Swallow hole are described from a morphological perspective using osteological and odontological terminology from the specialised paleontological (Argant 1991, 2004; Hillson 2005; Testu 2006) and veterinary literature (Barone 1979). Most of the osteometric and odontometric variables retained for this study are based on the different protocols of generalist (von den Driesch 1976) and specialized measurements in the study of Quaternary carnivores (Argant 1991; Testu 2006; Barycka 2008). The multiple observations from the morphological and osteo-odontometric description are compared to the different paleontological studies of Quaternary hyenids in order to give the specific attribution. The main works used focus on the early forms *Pliocrocuta perrieri* (Argant 2004; Baryshnikov, Tsoukala 2010) and *Pachycrocuta brevirostris* (Moullé 1992; Turner, Antón 1996; Turner 2001) and recent forms of the *Crocuta* genus (Bonifay 1971; Testu 2006; Barycka 2008; Fourvel 2012) and *Hyaena* (Bonifay 1971).

## 3 – Paleontological analysis

- 12 The following section presents a detailed description of the mandible specimens from Grosse Marguerite Cave and Trois Pigeons Swallow hole. The overall osteometric and odontometric values obtained are presented in table 2.

### 3.1 - The specimen from Grosse Marguerite Cave

- 13 This specimen corresponds to a left mandible portion discovered by Daniel Hussenot (Groupe Spéléologique de la Basse Ardèche); it was found recently among a protohistoric pottery assemblage, deposited in 2003 at the Cité de la Préhistoire d'Orgnac-l'Aven (Ardèche). Although there is no contextual information, this element can be clearly attributed to an early phase of the Pleistocene.

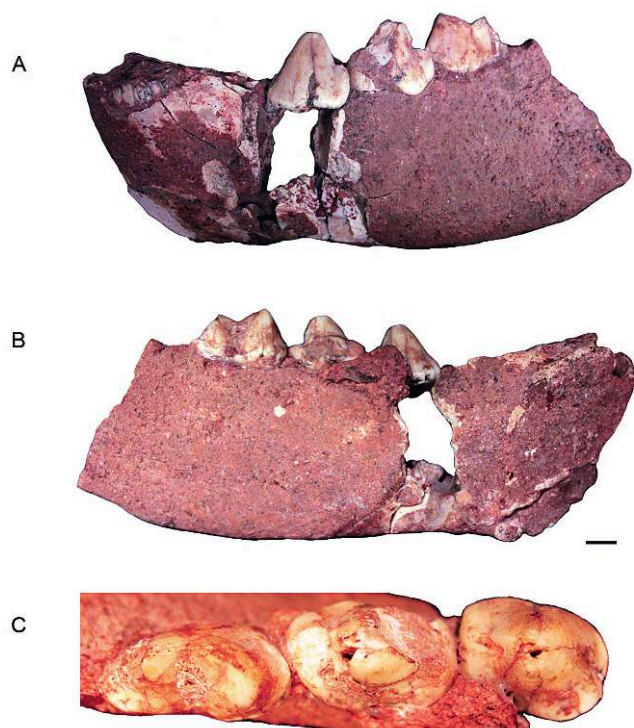
Table 2 - Osteometry of Grosse-Marguerite (3M) and Trois-Pigeons (3P) mandibles. Measurements in millimetres. (x) estimated measurements. \* Alveolar measurements. References: 1- This study; 2- Boule 1893; 3- Galobart et al. 2003; 4- Turner 2001; 5- Baryshnikov & Tsoukala 2010; 6- Fourvel 2012; 7- Fourvel, Philippe, Lateur, in progress.

Site	GM	3P	Sainzelles	Incarcal	Untermassfeld	Petralona	Artenac C10	Salomé
Espèce	n° 92,01	sans num	Pb	Pb	Pb	Pp	Ccs	Ccs
L jug.	89,5	93	100	96,1	91,7-94,0	83,7-85,0	82,0-88,0	87,8
L p	-	66,2	-	-	-	-	54,0-60,0	57,2
L c ant-m1	113,3	129	-	-	-	114,3-116,1	-	116
L c post-m1	94,4	108	-	-	-	-	-	99,6
H p2-p3	-	51,2	58	-	-	-	-	40
H p4-m1	51,8	56	71	55,6	-	-	32,0-45,0	47,3
H sous m1	-	57,4	-	-	-	-	39,5-50,0	53,5
H arr m1	57	59,3	64	-	48,7-53,8	-	-	57,2
L diast	6,2	15	10	-	-	-	-	9,9
Ep p2	23,8	27	-	-	-	-	-	21
Ep p3	22,8	26	-	-	22,4-26,5	-	-	21
Ep m1	20,3	18,5	-	-	-	-	-	16
Ep max	-	-	25	27,2	-	-	-	-
c DVL	-14,6	17	-	-	17,0-17,8	13,2-13,6	12,0-14,5	-
c DMD	-20,9	20,3	24	-	22,3-22,5	18,1-18,4	14,0-17,0	-
p2 DVL	11,9*	13,8	14,5	12,2	13,0-13,6	11,8-12,4	9,7-12,0	11
p2 DMD	16,2*	19	19,1	18,3	18,4-19,3	16,7-17,7	14,0-17,0	15
p3 DVL	17,1	18,2	19	17,6	17,6-18,0	14,6-16,0	14,0-17,0	16
p3 DMD	23,4	26	26	26,3	22,5-24,0	22,0-23,7	20,0-23,0	22
p4 DVL	16,7	-	17	16,1	15,7-17,4	14,5-15,1	13,0-15,3	14,7
p4 DMD	26,2	25,0*	28	27,1	26,4-28,0	23,8-24,5	21,0-24,0	23,2
m1 DVL	14,5	-14	15	15,2	14,5-15,9	12,8-13,3	11,0-14,3	13,6
m1 DMD	27,3	28	30	27,7	29,2-32,9	24,0-25,5	27,0-35,3	32,9
m1 para	13,8	13,2	-	-	-	-	14,0-17,4	15
m1 proto	11,6	-	-	-	-	-	11,0-15,0	11,8
m1 trig	23,6	-	25,5	23,8	23,8-26,8	20,1-20,8	24,0-29,0	27,9
Référence	1	1	2	3	4	5	6	7

- 14 This mandible presents all the Hyenid characteristics: reduced and specialized teeth, robust and conical premolars (fig. 4). It is a portion of the horizontal branch almost entirely covered with a fine layer of red concretionary clay with the third premolar, fourth premolar and the carnassial (the first molar). The wear of the jugal teeth points to a stage 4 or 5 adult individual (sensu Brugal, Fosse, Guadelli 1997).
- 15 Overall, the mandibular body is robust (thickness between 20.3 mm and 23.8 mm) and high (height between 51.8 mm, between the p4 and the m1, and 57 mm at the back of the carnassial tooth). The low variation in the height of the body gives the general impression that the upper and lower edges are parallel. The mandibular symphysis, observable at the canine level, in lingual view, is oval-shaped and relatively high (about 50 mm). In vestibular view, the mandibular foramen, situated mid-way up the mandibular body, under the second premolar, is large in size and presents a generally circular morphology; however concretionary deposits limit the description of this zone. At the back of the horizontal ramus, still in vestibular view, we observe the beginning of the masseteric fossa. The fossa is marked and deep suggesting a powerful muscular insertion. It begins behind, rather than under, the carnassial. The horizontal ramus is fractured behind the carnassial, at the level of the beginning of the masseteric fossa. The vertical ramus is missing and cannot be described.



Figure 4 - Mandible from Grosse-Marguerite Cave. A= vestibular view; B= lingual view; C= detailed occlusal view. Scale 10 mm. Photos J.-B. Fourvel.



- 16 The specimen still bears three (practically) complete jugal teeth as well as the base of the canine in its alveolus. The canine is fragmented at the base of the crown and can be succinctly described. This tooth presents a circular section. It appears to be clearly wider than the second premolar (observable through the alveoli), and nearly as wide as the third premolar; the odontometric values seem to back up these observations (tab. 2). The second premolar is not conserved. Only the roots of the tooth are still in the mandibular body and show that this tooth is bi-radicated with a wider mesial root than the distal root. The third premolar is typical of Hyenids: it is a robust tooth, with a high shape and generally conical (adapted to breaking hard, bony matter). The protoconid is high and wide, and covers most of the tooth surface. It is flanked by a relatively protuberant posterior denticle. In vestibular view, the base of the crown is marked by a slight cingulum, giving the tooth a relatively rectilinear base, unlike the *Crocuta* genus, which systematically bears a more sinuous crown base. This cingulum continues on the lingual face of the tooth. In occlusal view, we observe a transverse crest along the long axis of the tooth. Although this crest is visible, it is not as protuberant as the crest on the third lower premolars of the *Crocuta* genus (Fourvel 2012). The fourth premolar is a tri-cuspid tooth made up of a strong protoconid, anteriorly flanked by a well-developed paraconid, covering nearly a third of the length of the tooth. This paraconid is present in *Crocuta*, but is clearly less developed and less robust (Fourvel 2012). The protoconid lies on a well-developed posterior denticle (hypoconid). The tooth does not present a protruding cingulum on the lingual or the vestibular surface. The first molar is partially complete. The posterior half of the protoconid is missing. Overall, the tooth is short and massive, unlike the *Crocuta* carnassial tooth which is longer and transversally compressed. The paraconid is relatively high and goes beyond the



maximum height reached by the fourth premolar. The talonid is partially conserved, but does not seem to be prominent, as observed for *Hyaena*.

### 3.2 - The specimen from Trois Pigeons Swallow hole

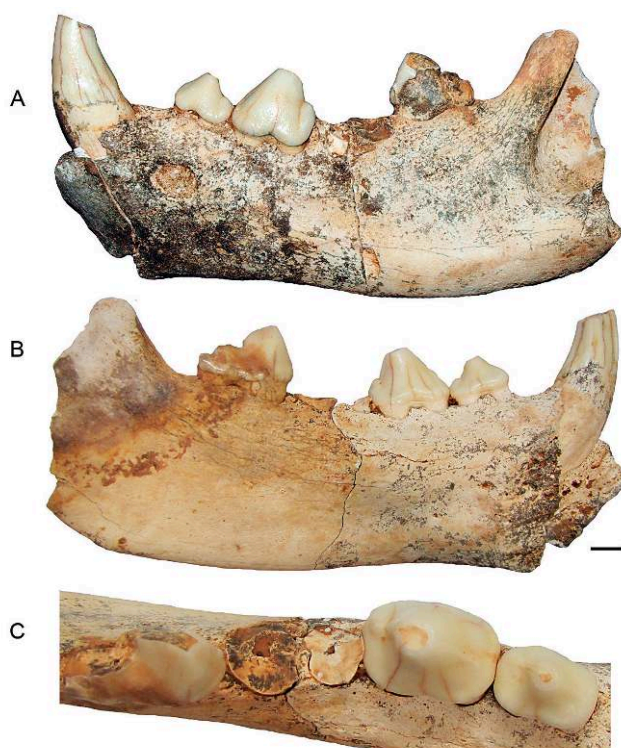
- 17 This specimen corresponds to a left mandible portion discovered in 2013 by Guillaume Grondin and Thierry Montesinos (Association spéléologique nîmoise) in the salle du Trône, during an exploratory study. It was lying in a sticky, light brown clayey level, corresponding to a residual sedimentary berm situated high up on the left wall. The first photographs that we saw enabled us to relate this remain to a carnivore from the Hyenid family. The material is currently conserved at the archaeological reserve of Saint-Césaire (Nîmes).
- 18 This left mandible portion still bears the canine, the second lower premolar, the third premolar and the first molar (fig. 5). The degree of wear of the jugal teeth indicates that this specimen corresponds to a stage 4 adult individual (sensu Brugal, Fosse, Guadelli 1997).
- 19 The horizontal ramus of the mandibular body presents the same characteristics as the mandible from Grosse Marguerite. The upper and lower edges are mainly sub-parallel. The branch is high (with a height varying between 51.2 mm between the p2 and the p3 to 59.3 mm at the back of the m1) and thick (varying from 18.5 mm at the m1 and 27 mm at the p2). In lingual view, in spite of the partial fragmentation of the anterior part of the mandible, we observe a high and wide symphysis as is the case on the specimen from Grosse Marguerite. In vestibular view, we observe at mid-height of the body and directly under the p2, a mandibular foramen with a circular morphology and a very large size. The horizontal ramus ends posteriorly in the masseteric fossa. The latter is very marked and deep. Like for the specimen from Grosse Marguerite, it clearly begins behind the carnassial. The ramus is not preserved.
- 20 Among the teeth, only the canine, the second and third premolars and the first molar have been conserved. The canine is robust, with a generally circular section. The crown is relatively high in spite of the fragmentation of the tip of the tooth. In lingual view, we observe that the wear facet, which is dissociated from the rest of the crown by two marked ridges, is rather short (active surface of 12 mm at the base of the crown between the ridges). The root is long and corpulent, oval-shaped with an almost globular aspect. The second premolar is a bi-radical tooth with a long and wide crown. This is made up of a marked protoconid covering most of the tooth and posteriorly flanked by an important denticle. This tooth differs from the second lower premolar of the *Crocuta* genus as the recurrent anterior denticle is absent in the latter. A salient ridge antero-posteriorly runs across the tooth. In lingual view, the base of the crown is bordered by a marked cingulum. The third premolar is similar to that of the specimen from Grosse Marguerite. The high and overlying protoconid is bordered by a major posterior denticle. This tooth can nonetheless be distinguished by a slight visible concavity in vestibular view, at the base of the crown directly below the tip of the protoconid. The fourth premolar has not been conserved. As for the first molar, although the total length is well-preserved, the protoconid did not resist. In spite of this, we observe that the carnassial tooth is short and wide. At the back of the protoconid, the tooth presents a marked but short talonid, which differentiates this

specimen from the *Hyaena* genus, in the same way as the specimen from Grosse Marguerite.

#### 4 – Specific attribution

- 21 Morphologically, both of the studied mandibles differ from the *Crocuta* genus. Indeed, the spotted hyena (both the Pleistocene form and its modern representative) presents a very different mandibular body. The upper and lower edges of the body are not parallel; the horizontal ramus is relatively low at the diastema and the p2, and the height of the body becomes progressively wider until reaching maximum height under the m1. At the Salomé network (Vallon-Pont-d'Arc, Ardèche; unpublished), the whole mandible of an adult cave hyena presents a difference of more than 15 mm between the p2 and the back of the m1 (tab. 2). In addition, the mandibular foramen is generally oval-shaped and smaller in size. The masseteric fossa begins beneath the protoconid of the m1, or even in extreme cases under the talonid, but never behind the carnassial. The jugal teeth are also very different: the *Crocuta* canine is less robust, the p2 is made up of three denticles, the anterior denticle of the p4 is poorly developed, and the very secant m1 is long and transversally compressed.

Figure 5 - Mandible from Trois-Pigeons Swallow hole. A= vestibular view; B= lingual view; C= detailed occlusal view. Scale 10 mm. Photos N. Lateur.

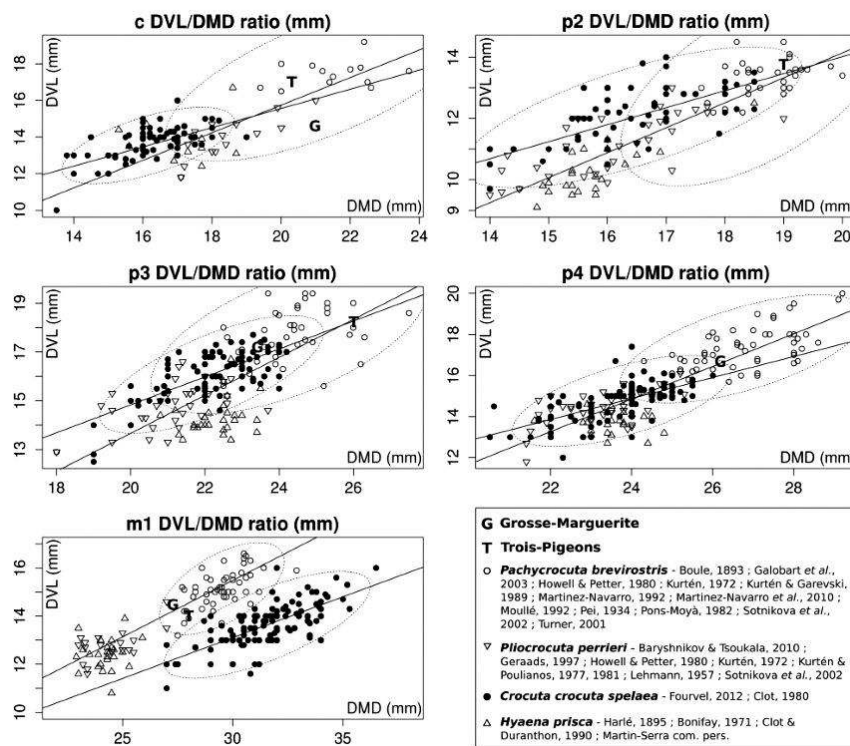


- 22 *Pliocrocuta perrieri* and *Hyaena prisca* (or its modern representative *Hyaena hyaena*) are morphologically more similar to the studied pieces. The lower and upper edges of the mandibular body are parallel. The masseteric fossa is behind the m1. The anterior denticle on the p2 is either absent, or very poorly developed. The mandibular foramen is rather small. The p3 presents a slight anterior denticle which is absent on our

specimens. All of the premolars bear marked prominences (secondary cuspids) and developed, well visible cingulums in lingual view. The carnassial systematically presents a strongly developed talonid and the protoconid is always flanked by a high and robust metaconid. Bonifay (1971) records all these criteria on the material from the Escale and Lunel-Viel caves. One of us (JBF) personally observed these characteristics on present-day striped hyena *H. hyaena* specimens (MNHN collection). In addition, the striped hyena from early (*P. perrieri*) or recent phases (*H. prisca* and *H. hyaena*) is generally smaller and more slender than the other Hyenids (tab. 2; fig. 6). Although the specimen from Grosse Marguerite corresponds to the field of variation recorded on the *Pliocrocuta* from Petralona, it does not match with the morphological criteria. As for the specimen from Trois-Pigeons, its morphology and greater dimensions differ from *Pliocrocuta*.

23 In his description of the holotype from Sainzelles, Boule (1893) stresses the difference in size of the *Hyaena brevirostris* teeth, which are more robust than those of the other hyenas. On the mandible from Sainzelles, the anterior denticles of the second and third premolars are reduced or non-existent, as observed by Boule. In the illustration, we observe a greater development of the p4 paraconid (Boule 1893 - plate 1, figure 1 and Boule underlines the absence of the metaconid at the back of the m1 protoconid and the thickset aspect of this tooth (“it is much longer than in the spotted hyena; and it is also more thickset” Boule 1893 - p. 92). In plate 1, we observe a comparable mandibular body morphology to the two studied pieces with sub-parallel upper and lower edges and a relatively rectilinear lower edge, a large mandibular foramen and a deep masseteric fossa clearly developed behind the m1.

Figure 6 - Bivariate plot of jugal teeth (c, p2, p3, p4, m1) length (DMD) / width (DVL) ratio. Confidence ellipses 95%. Measurements in millimetres.



- 24 In his study of the fauna from Vallonnet, Moullé (1992) describes different *P. brevirostris* specimens for which he notes that the mandible is large with a straight lower edge. The individual described by Moullé is juvenile, but it nonetheless presents comparable mandibular body heights (52 to 55 mm) and maximal thickness (23 mm) to Grosse Marguerite and Trois Pigeons. He notes the absence of the anterior denticle on the p3, and the p4 bears a well-developed anterior and posterior denticle, described as “cutting”. The m1 from Vallonnet are similar to the studied m1; they are short and wide and the talonid is present (although it is not as developed as on *Hyaena* and *Pliocrocuta*) and the metaconid is absent.
- 25 At Untermassfeld, Turner (2001) observed the regular presence of a slight anterior denticle on the p2. The p3 is characterized by a high protoconid and a strongly developed posterior denticle. On the p4, like at Vallonnet, Grosse Marguerite or Trois Pigeons, Turner mentions the presence of a very marked paraconid followed by a strong protoconid flanked by a prominent posterior denticle. The m1 presents a large talonid but no metaconid was clearly observed. The figures and plates present many similarities with the specimens described here: large mandibular foramen, sub-parallel edges and a deep masseteric fossa behind the m1 (Turner 2001 - figure 4a-b p. 684, figure 4c p. 685, plate 124). From a metric viewpoint, the Untermassfeld specimens are comparable with the material presented in this article (tab. 2)
- 26 The studied specimens thus concur well with descriptions of *Pachycrocuta brevirostris*. Moreover, the morphometric values are within the field of variation for this species. Lastly, the bivariate projections of the length and width ratios of the different jugal teeth systematically place the specimens from Grosse Marguerite and Trois Pigeons among large-sized Hyenids and more specifically among the different *P. brevirostris* populations (fig. 6). In this way, on the basis of morphological and metric characteristics, we can attribute these specimens from the Gard to the species *Pachycrocuta brevirostris* (Aymard, 1846).

## Conclusion

- 27 The specific attribution of the specimens from Grosse Marguerite and Trois Pigeons also has biochronological implications and emphasizes the early age of the deposits. In spite of many works focusing on early Hyenids and in particular on *Pachycrocuta brevirostris*, this species is relatively rare in Europe, and even more so in France. A rapid overview of the sites with paleontological remains highlights this rarity, as well as the short chronological time frame during which the carnivore seems to have developed in our regions. This time frame began about a million years ago (situation of the biozones MNQ19 and MNQ20). *Pachycrocuta brevirostris* had already been mentioned in the Gard (Sartanette in Bonnet 1980), but the present study is the first to clearly describe the paleontological material and to confirm the identification of this species in the department. The two specimens studied here thus shed a little more light on the presence of this species in France. The morphological description leaves no doubt as to the attribution of these pieces to the giant hyena and underlines the following characteristics:
- high and thick horizontal ramus with sub-parallel upper and lower edges;
  - high and covering symphysis and large circular mandibular foramen at mid-height of the body under the p2;

- marked masseteric fossa behind the m1;
  - general “crocutoid” morphology of the jugal teeth;
  - strong p2 and p3 with reduced prominences (absence of anterior denticle);
  - secant portion of the p4 amplified by the marked development of the paraconid;
  - short and wide m1 with a more or less developed talonid.
- 28 In addition, these remains enable us to underline the morphometric variability of the species as they include a large-sized individual (comparable to the specimens from Untermassfeld in Germany and Incarcál in Spain) and a more similar individual to the large Upper Pleistocene cave hyenas. The case of Trois Pigeons Swallow hole is interesting as the bones were gathered recently during a speleological excursion and the site may contain other remains. Forthcoming research could thus increase the sample and enable us to clarify the chronological position of the specimen.
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## ABSTRACTS

In the present paper, two hyenid mandibles, coming from two different sites in Gard, South-East France (Grosse Marguerite Cave at Aiguèze and Trois Pigeons Natural Trap at Nîmes) are describe. The palaeontological analysis, including morphological description and morphometric comparisons with other hyenid (genus *Pachycrocuta* Kretzoi, 1938 and *Pliocrocuta* Kretzoi, 1938 and genus *Crocuta* Kaup, 1828), allows us to relate these specimens to the Lower and Middle

Pleistocene Giant Hyena *Pachycrocuta brevirostris* (Aymard, 1846). Morphological features and metrical data are provide and allow us to describe morphometrical variability in this species. *Pachycrocuta brevirostris* is a rare species found in french pleistocene; consequently these specimens increase number a known sites which contain such ancient hyenids.

Deux mandibules de Hyénidés, issues de deux cavités du Gard (la grotte de la Grosse Marguerite, à Aiguèze et l'aven des Trois Pigeons, à Nîmes) sont décrites. À l'issue de l'analyse paléontologique, de la description morphologique de ces pièces et de la comparaison morphométrique avec d'autres spécimens de Hyénidés anciens (genres *Pachycrocuta* Kretzoi, 1938 et *Pliocrocuta* Kretzoi, 1938) et récents (genres *Crocuta* Kaup, 1828), nous pouvons attribuer ces pièces à l'espèce du Pléistocène inférieur et moyen *Pachycrocuta brevirostris* (Aymard, 1846). Ces vestiges paléontologiques nous permettent ainsi de mieux connaître les caractéristiques et les variabilités morphologiques et métriques des éléments dentaires et mandibulaires de cette espèce. Par ailleurs, ces pièces sont l'occasion de documenter deux nouveaux sites livrant des vestiges de Hyénidés anciens en France, *Pachycrocuta brevirostris* étant un taxon rare dans le Pléistocène français.

## INDEX

**Keywords:** Palaeontology, Carnivore, Hyenid, *Pachycrocuta*, Gard, South-East France

**Mots-clés:** Paléontologie, Carnivore, Hyénidé, *Pachycrocuta*, Gard, France

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