



# New data on the paleobiology of the Gravettian individual L2A from Cussac cave (Dordogne, France) through a virtual approach

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**TITLE:** New data on the paleobiology of the Gravettian individual L2A from Cussac cave (Dordogne, France) through a virtual approach

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**ABSTRACT:** One of several elements making Cussac cave an exceptional site is the preservation of many prehistoric human remains lying on the ground, including an individual in a bear nest (Locus 2) in ventral decubitus, subject L2A. The protected status of the site does not allow for excavations or direct manipulation of the remains, at least for the near future. Thus, the tools of virtual anthropology were employed to further study this individual, after preliminary analyses *in situ* in 2014 raised several questions on its biological characteristics. A high-resolution 3D photogrammetric record of Locus 2 allowed for the virtual reconstruction of the *ossa coxarum* and cranium to be measured in TIVMI. Metric data from the *ossa coxarum* were used to apply the DSP, which indicated a male sex assessment for the left side. The linear variables and log shape ratios extracted from the cranium were compared to a reference sample composed of 46 Upper Paleolithic (UP) subjects. The cranial morphology of L2A is closer to the male variability for the UP, but displays an unusual pattern, with a short cranial height and a wide splanchnocranium. The biological peculiarities of this subject are discussed with regard to Gravettian funerary practices and the depositional context of Cussac cave.

**KEYWORDS:** Virtual Anthropology; Photogrammetry; Sexual dimorphism; Probabilistic sex diagnosis; Coxal bone; Skull; Upper Paleolithic

## 1. Introduction

Since 2010, Cussac cave (Dordogne, France) underwent several extensive research campaigns that focused on several non-invasive archaeological and anthropological investigations (Ferrier, et al., 2016, Henry-Gambier, et al., 2013, Ledoux, et al., 2016, Villotte, et al., 2015). The cave hosts a unique combination of parietal art and human remains dating to the Gravettian (31,000 – 22,000 BP). The striking artistic elements consist of more than 150 engravings, mostly animal and human depictions, which represents one the richest corpora of European parietal art for the Gravettian (Aujoulat, et al., 2001, Jaubert, et al., 2016). Similarly, human skeletal remains from this site significantly enriched the fossil record of the Upper Paleolithic of Europe, a period for which well-preserved human skeletons are relatively rare (Henry-Gambier, 2005). Several hundred human remains (fragments or complete bones) are scattered on the surface of the cave in at least three different *loci*.

One of the *loci*, Locus 2, consists of a well-represented skeleton – partially covered by clay - contained in a bear nest. Given the absence of duplicate elements, all the bones are attributed to the same individual, subject L2A. The current arrangement of the bones in the *locus* follows a logical anatomical pattern (Figure 1), indicating that the individual was deposited in *ventral decubitus* (Henry-Gambier, et al., 2013, Villotte, et al., 2015). The other *loci* contain commingled human remains from several individuals. The consistency between the artistic style of the parietal engravings and two  $^{14}\text{C}$  dates suggests that the human activity in the cave spans between 29,000 and 28,000 cal BP (Jaubert, et al., 2016).

Due to its unique characteristics, the Cussac cave is now protected under the national heritage status. The site is closed to the public, and even the scientific team (*Programme Commun de Recherche*, PCR Cussac) has a relatively short window of time for intervention each year due to the high concentration of  $\text{CO}_2$  in the cave between spring and fall. Moreover, to ensure the protection of the preserved floor, no excavations nor samplings are planned in the near future. Given these limitations, the bioanthropological studies focus on non-invasive analyses, consisting, to date, of *in situ* observations and measurements of the visible elements. Using these methods, a preliminary study of L2A had been performed from a metallic walkway specially extended above the Locus 2 (Villotte, et al., 2015). Before and after this study, the locus was virtually documented via 3D photogrammetry, allowing for additional research on these human remains.

Based on the characteristics of the auricular surface (Schmitt, 2005), the first evaluation of L2A estimated an age-at-death between 20 to 49 years (Villotte, et al., 2015). The sex determination was done through visual scoring of the visible morphology of the *os coxae* (Brůžek, 2002), and from measurements computed in a probabilistic tool for sexual diagnosis, DSP (Murail, et al., 2005). These morphometric methods applied to the left *os coxae* gave a male diagnosis. However, the presence of shared sexual traits in the morphoscopic evaluation, as well as a very low stature for this individual (outside the Gravettian range) called for further investigation into the sex of L2A (Villotte, et al., 2015).

Moreover, the body proportions of this individual raised the question of a possible developmental anomaly (Villotte, et al., 2015), an occurrence which appears to be abnormally frequent in the late Pleistocene sample (Wu, et al., 2013). In addition, L2A was laid in a unique context for an Upper Paleolithic burial (a bear nest), and in *ventral decubitus*, a very

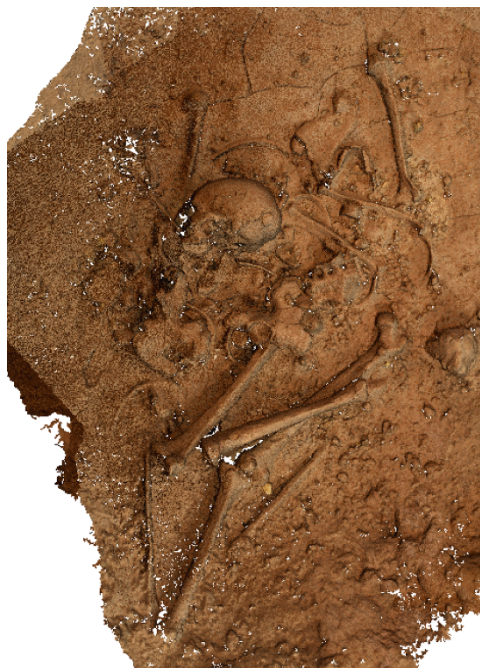
uncommon position for the Gravettian period (Henry-Gambier, 2008). A new analysis of this individual will therefore contribute to the debate on possible specific burial treatments of pathological individuals during the Upper Paleolithic (Formicola, 2007, Formicola, et al., 1990, Formicola, et al., 2001, Mallegni and Fabbri, 1995, Pettitt, 2013, Sparacello, et al., n.d., Villotte, et al., 2017).

To this end, we employed a high-resolution photogrammetric tridimensional (3D) reconstruction to obtain virtual models of L2A's bones, and applied the now commonly used methods of virtual anthropology (Weber and Bookstein, 2011). We present in this report a new analysis of the L2A pelvis with the DSP method, as well as an analysis of its cranial morphology in comparison with a sample from the Upper Paleolithic.

## **2. Material and Methods**

### *2.1 The 3D photogrammetric model*

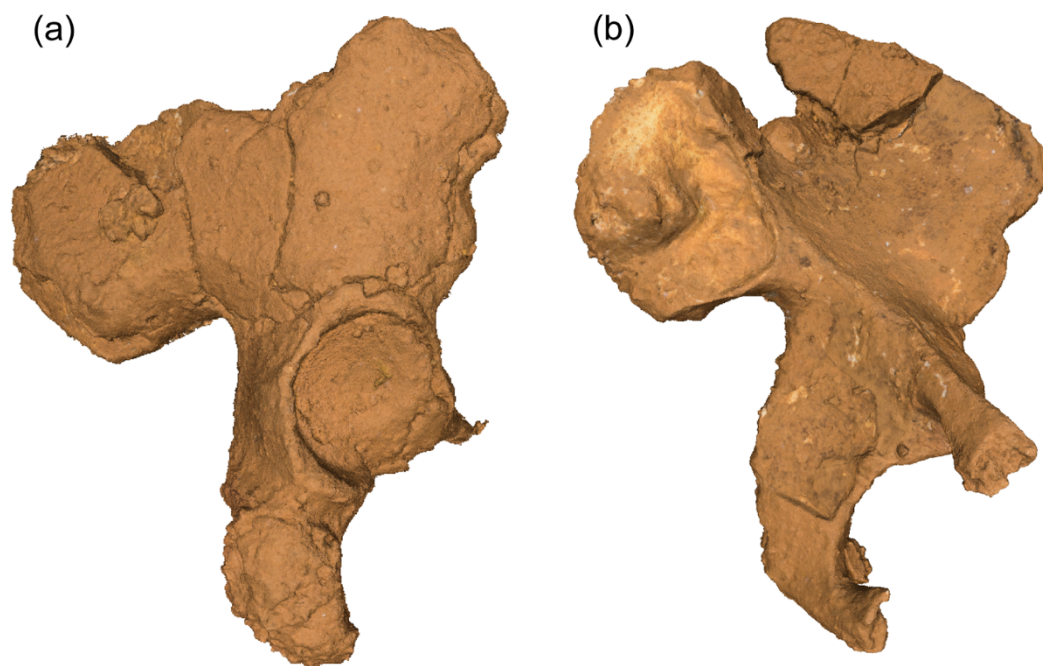
Several photogrammetric acquisitions of the Cussac cave areas that include human remains were performed between 2012 and 2015, with global views and close-ups of the visible osseous elements. This allows for a 3D modelling and isolation of the different bones; the resulting 3D model of Locus 2 is displayed in Figure 1. More than 700 photographs were processed with a Nikon d700 (zoom 24–70 2.8 used at 24 mm) during three different campaigns using Photoscan (Agisoft©) and PMVS (Furukawa and Ponce, 2010) software. This resulted in several 3D point clouds with a spatial resolution ranging from 1 to 0.5 mm. Points clouds were meshed and scaled using local physical scales and topographic points (with x, y, z coordinates, acquired by a Leica© total station).



**Figure 1.** Visualization of the global 3D photogrammetric record of the Locus 2 with textures (in MeshLab©, ISTI, v.1.3.4)

## 2.2 Methodology for the ossa coxarum analysis

The 3D photogrammetric models of the *ossa coxarum* of L2A were extracted from the global model to allow more accurate measurements (Figure 2). In order to reveal key anatomical areas for age and sex estimation, a layer of clay was removed from the left *os coxae* during one of the campaigns (Villotte, et al., 2015). Figure 2 displays the 3D models of the bones after cleaning (i.e. posterior to the record in Figure 1). The *ossa coxarum* were isolated with the Geomagic® Wrap 2014 software.



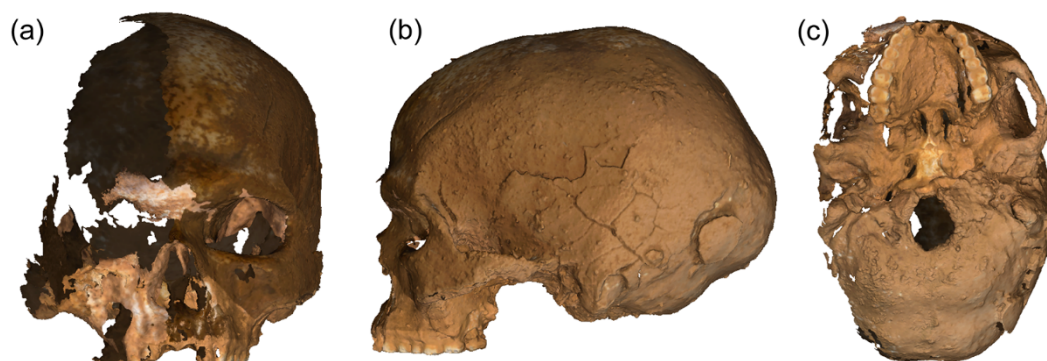
**Figure 2.** Visualization of the isolated 3D models of the *ossa coxarum* of L2A with textures (in MeshLab®, ISTI, v.1.3.4): (a) right *os coxae* in lateral view; (b) left *os coxae* in medial view.

One of the most objective and reliable morphometric methods to assess the sex from the pelvic region is DSP (Murail, et al., 2005). DSP has been used in the preliminary *in situ* study of Cussac L2A, and resulted in a male assessment from direct measurements of the left *os coxae* (Villotte, et al., 2015). As this method was already validated for use in a virtual approach (Chapman, et al., 2014), measurements were recorded for this study on the virtual model of the *ossa coxarum* in TIVMI software (Dutailly, 2016) to confirm the results previously obtained with traditional measures (Villotte et al., 2015).

## 2.3 Methodology of analysis for the cranial morphology

The refined photogrammetric acquisition of the cranium (Figure 3) was also cropped in Geomagic® Wrap 2014 for virtual processing. A layer of clay deposit covers most of the human remains in Locus 2, with a variable thickness; the teeth and spheno-occipital suture were cleaned during the *in situ* analysis for age estimation purposes (Villotte et al., 2015). The

mandible, although present, was not included in the present study, as it would require an extensive reconstruction of the non-visible parts (this element lies on its inferior surface and is partly covered by clay).



**Figure 3.** Visualization of the 3D model of L2A cranium with textures (in MeshLab©, ISTI, v.1.3.4): (a) isolated cranium in frontal view; (b) cranium in left lateral view; (c) cranium in inferior view.

The cranium of L2A is lying on its right side, thus several anatomical parts are non-visible on the model (Figure 3a). Consequently, the available landmarks on the left side were mirrored in TIVMI, using the sagittal plane as a reference (passing through the landmarks *nasion*, *prosthion* and *bregma*), to obtain the corresponding right points and ensure the collection of sufficient craniometrics data (see Table 2). The linear measurements were extracted in TIVMI through the *Segment3D* plugin, or using projections on planes when necessary (Guyomarc’h, et al., 2014). The landmarks that were covered by a layer of clay were manually corrected to account for this layer, or were not collected when the thickness of the sediment could not be evaluated. At this stage of the analysis, this correction can only be an estimation based on comparisons with the areas not showing clay deposits (i.e. 1 to 2 mm thickness on the left lateral vault).

From the list of variables defined by Martin (Bräuer, 1988), a subsample of measurements were selected following their availability on L2A and their representation in the comparative sample. Table 1 lists the codes, measurements, and corresponding landmarks of the 30 retained variables, along with 18 cranial indices.

Code (Bräuer, 1988)	Variable	Landmarks/measurements	L2A	Code (Bräuer, 1988)	Variable	Landmarks/measurements	L2A
M1	Maximum cranial length	Glabella – Opisthocranium	191.1	M54	Nasal breadth	Apertion L – Apertion R	27.7
M2	Glabella-inion length	Glabella – Inion	179.7	M55	Nasal height	Nasospinale - Nasion	42.3
M3	Glabella-lambda length	Glabella - Lambda	179.9	M60	Maxillo-alveolar length	Prosthion – Alveolare	52.7
M5	Length of the skull base	Basion – Nasion	98.6	M61	Maxillo-alveolar breadth	Ectomolare L – Ectomolare R*	70.2



M8	Maximum cranial width	Euryon L – Euryon R*	140.5	M62	Internal palate length	Inner distance between each R and L canine/premolar alveolar border	45.9
M9	Least frontal breadth	Frontotemporale L – Frontotemporale R*	98.2	M63	Internal palate breadth	Endomolare L – Endomolare R	39.0
M10	Maximum frontal breadth	Coronale L – Coronale R*	125.9	I1	Cranial index	M8/M1*100	73.5
M17	Basibregmatic height	Basion – Bregma	129.1	I2	Vertical index	M17/M1*100	67.5
M20	Auriculo-bregmatic height	Porion L – Bregma (in projection)	108.0	I3	Transversal vertical index	M17/M8*100	91.9
M23	Horizontal circumference	Glabella – Opisthocranium - Glabella	552.3	I4	Auricular vertical index	M20/M1*100	56.5
M24	Transverse Arc	Porion R* – Bregma – Porion L	154.9	I5	Vault height index	M20/M8*100	76.9
M26	Frontal sagittal arc	Nasion – Bregma (outline)	129.5	I12	Transversal frontal index	M9/M10*100	78.0
M27	Parietal sagittal arc	Bregma – Lambda (outline)	127.1	I13	Transversal fronto-parietal index	M9/M8*100	69.9
M28	Occipital sagittal arc	Lambda – Opisthion (outline)	131.0	I16	Sagittal fronto-parietal index	M27/M26*100	98.2
M29	Frontal chord	Nasion – Bregma	109.6	I17	Sagittal fronto-occipital index	M28/M26*100	101.2
M30	Parietal chord	Bregma – Lambda	114.5	I18	Sagittal parieto-occipital index	M28/M27*100	103.1
M31	Occipital chord	Lambda - Opisthion	100.6	I22	Sagittal frontal index	M29/M26*100	84.7
M40	Basion-prosthion length	Basion – Prosthion	99.5	I24	Sagittal parietal index	M30/M27*100	90.1
M44b	Bi-orbital breadth	Ectoconchion L – Ectoconchion R*	105.1	I39	Superior facial index	M48/M45*100	43.1
M45	Bi-zygomatic breadth	Zygion L – Zygion R*	139.9	I42	Orbital index	M52/M51*100	63.1
M46b	Bi-maxillary breadth	Zygomaxillare L – Zygomaxillare R*	97.4	I42(1)	Orbito-facial transversal index	M51/M45*100	29.9
M48	Naso-alveolar height	Prosthion - Nasion	60.3	I42(2)	Orbito-facial vertical index	M52/M45*100	43.8
M51	Orbital breadth	Maxillofrontale – Ectoconchion (R* and L mean)	41.9	I48	Nasal index	M54/M55*100	65.4
M52	Orbital height	Projected distance between the Orbitale and Supraconchion (R* and L mean)	26.4	I54	Maxillo-alveolar index	M61/M60*100	133.2

**Table 1.** Variables used in the study and raw data for L2A (in mm). \* indicates the missing landmarks estimated for L2A.

## 2.4 Cranial comparative sample

Data on the comparative sample were mainly collected from the literature from specimens with relatively well-preserved crania, with a known context of discovery, and available direct dating if possible. All the selected individuals date to a period covering the Middle-Upper Paleolithic (MUP) and the Late Upper Paleolithic (LUP). Some of these remains have recently been tested genetically (see Fu, et al. (2016) for V1, O1, DV13, DV14, B1; Tarsi, et al. (2006) for AC5), and the sex of most subjects was identified from their *ossa coxarum*

morphology (CM1, AP1, BT2, BC1, BG1, BG5, GE5, PG25, DV3, DV16, PV1, S1, R6, AC2, AC4, AC3, AC12, IA, L1, LB4, LP5, SG1, ST1, OK1, OK2, S1). Additional specimen are used in the general comparison analyses, but are not included in the sex-related test (CM2, CM3, DV15, P3, P4, P9, P10, S5, B2, B3, R4, R6, AC12, C, RR1, CB). Table 2 lists the 46 subjects of the comparative sample with their source publications and the acronyms used in this study.

<b>Site</b>	<b>Specimen (Sex)</b>	<b>Localization</b>	<b>Period</b>	<b>Data source</b>	<b>Sex diagnosis</b>
Cro-Magnon	CM1 (M), CM2*, CM3*	France (SW)	MUP	(Vallois and Billy, 1965)	(Gambier, et al., 2006)
Abri Pataud	AP1 (F)	France (SW)	MUP	(Billy, 1975)	(Villotte, 2009)
Dolní Věstonice and Pavlov	DV3 (F), DV13 (M), DV14 (M), DV15*, DV16 (M), PV1 (M)	Czech Republic	MUP	(Sládek, et al., 2000)	(Fu, et al., 2016, Trinkaus and Svoboda, 2006)
Předmostí	P3*, P4*, P9*, P10*	Czech Republic	MUP	(Velemínská and Brůžek, 2008)	-
Sunghir	S1 (M), S5*	Russia	MUP	(Trinkaus, et al., 2014)	(Villotte, 2009)
Ostuni	O1 (F)	Italy (S)	MUP	(Coppola, 2013)	(Villotte, 2009)
Paglicci	PG25 (F)	Italy (S)	MUP	(Coppola, 2013)	(Villotte, 2009)
Brno	B2 (I), B3 (I)	Czech Republic	MUP	(Coppola, 2013)	-
Grotte des Enfants	GE5 (F)	Italy (N)	MUP	(Coppola, 2013)	(Villotte, et al., 2011)
Barma del Caviglione	BC1 (F)	Italy (N)	MUP	(De Lumley, 2016, Guipert, et al., 2014)	(De Lumley, 2016)
Barma Grande	BG1 (M), BG5 (M)	Italy (N)	MUP	(De Lumley, 2016, Graziosi, 1942)	(De Lumley, 2016, Villotte, et al., 2011)
Baoussou da Torre	BT2 (M)	Italy (N)	MUP	(Villotte, et al., 2017)	(Villotte, et al., 2011)
Romito	R6 (F), R4*, R6*	Italy (S)	LUP	(Mallegni and Fabbri, 1995)	(Villotte, 2009)
Arene Candide	AC2 (M), AC3 (M), AC4 (M), AC5 (M), AC12 (M)	Italy (N)	LUP	(Paoli, et al., 1980, Sergi, et al., 1974)	(Tarsi, et al., 2006, Villotte, 2009)
Le Bichon	B1 (M)	Switzerland	LUP	(Chauvière, 2008)	(Villotte, 2009)
Les Iboussières	IA (M)	France (S)	LUP	Personal observation	Personal observation
Chancelade	C*	France (SW)	LUP	Personal observation	-
Rochereil 1	RR1*	France (SW)	LUP	Personal observation	-
Cap Blanc	CB*	France (SW)	LUP	(von Bonin, 1935)	-
Lafaye	L1 (F)	France (SW)	LUP	Personal observation	(Villotte, 2009)
Laugerie-Basse	LB4 (M)	France (SW)	LUP	Personal observation	(Villotte, 2009)
Le Peyrat	LP5 (M)	France (S)	LUP	(Samsel, et al., 2016)	(Samsel, et al., 2016)
Saint Germain la Rivière	SG1 (F)	France (SW)	LUP	Personal observation	(Henry-Gambier, et al., 2002)
San Teodoro	ST1 (F)	Sicily	LUP	Personal observation	Personal observation
Villabruna	V1 (M)	Italy (N)	LUP	(Vercellotti, et al., 2008)	(Fu, et al., 2016, Villotte, 2009)
Oberkassel	OK1 (M), OK2 (F)	Allemagne	LUP	Personal observation	(Trinkaus, 2015)

**Table 2.** Reference material: code, sex, localization, period, data source and sex source of the specimens. \* indicates the specimen is considered as of undetermined sex.



To summarize, the MUP subsample includes 10 males, 6 females and 9 undetermined sex individuals; the LUP group is composed of 10 males, 5 females, and 6 undetermined sex individuals. The 15 subjects without assessed sex were not used in the sex-related tests.

## 2.5 Statistical analysis of the cranium

The morphometric variations in terms of size are related to sexual dimorphism, but the morphology also contains variations in shape that may be related to sex: applying a log correction to linear variables is a method commonly used to extract shape information (e.g. Churchill, et al. (1999)). We use size-adjusted measurements following the ratio for shape analysis (Jungers, et al., 1995), as proposed by Darroch and Mosimann (1985) to obtain the log shape ratios of the linear measurements. Including the linear variables, the indices, and the log shape ratios, a total of 78 variables are used to assess the position of L2A among the Upper Paleolithic (UP). As some variables do not follow a normal distribution, the non-parametric test was used (Wilcoxon-Mann-Whitney) to assess the cranial differences between groups on the measurements, indices, and log shape ratios. Principal Component Analyses (PCA) allow for a synthetization of the variables and help with the interpretation of the positioning of the L2A specimen within the comparative samples. Instead of replacing the missing values with the mean of variables (the default option in most software), we use the *missMDA* R package to perform more specific estimations of these unknown values following the subject's pattern (Josse and Husson, 2013). Additionally, probabilistic distances, or adjusted Z-scores (Maureille, et al., 2001), calculated between the means of the UP, MUP, and LUP samples and the variables from L2A will provide a visual assessment of its position relative to the comparative sample. Non-parametric tests were performed in Statistica© (v. 7.1, StatSoft©, Tulsa, OK), and PCA with R (R Core Team, 2016).

## 3. Results

### 3.1 DSP results

The virtual analysis of the *ossa coxarum* allowed for the collection of additional data compared to the *in situ* preliminary study (one variable on the left *os coxae* and three new measurements on the right *os coxae*). The DSP results are displayed in Table 3.

Os Coxae	Observation	PUM	SPU	DCOX	IIMT	ISMM	SCOX	SS	SA	SIS	VEAC	PF	PM	Sex
Left	Villotte et al. 2015, obs 1	n/o	28.7	214.0	37.0	n/o	n/o	75.6	76.4	n/o	n/o	0.018	0.982	Male
	Villotte et al. 2015, obs 2	n/o	30.3	216.0	38.2	n/o	n/o	75.1	78.2	n/o	n/o	0.012	0.988	Male
	3D photogrammetry	n/o	29.4	216.9	38.4	n/o	152.1	75.1	76.0	n/o	n/o	0.001	0.999	Male
Right	Villotte et al. 2015, obs 1	n/o	n/o	n/o	n/o	100.0	n/o	n/o	n/o	38.8	47.6	n/a	n/a	n/a
	Villotte et al. 2015, obs 2	n/o	n/o	n/o	n/o	103.5	n/o	n/o	n/o	37.2	52.5	n/a	n/a	n/a
	3D photogrammetry	n/o	n/o	n/o	39.4	106.7	155.9	74.8	n/o	37.2	51.3	0.386	0.614	ND

**Table 3.** DSP input and results for the left and right *ossa coxarum*, including the measurements collected *in situ* by two observers (Villotte, et al., 2015), and the measurements

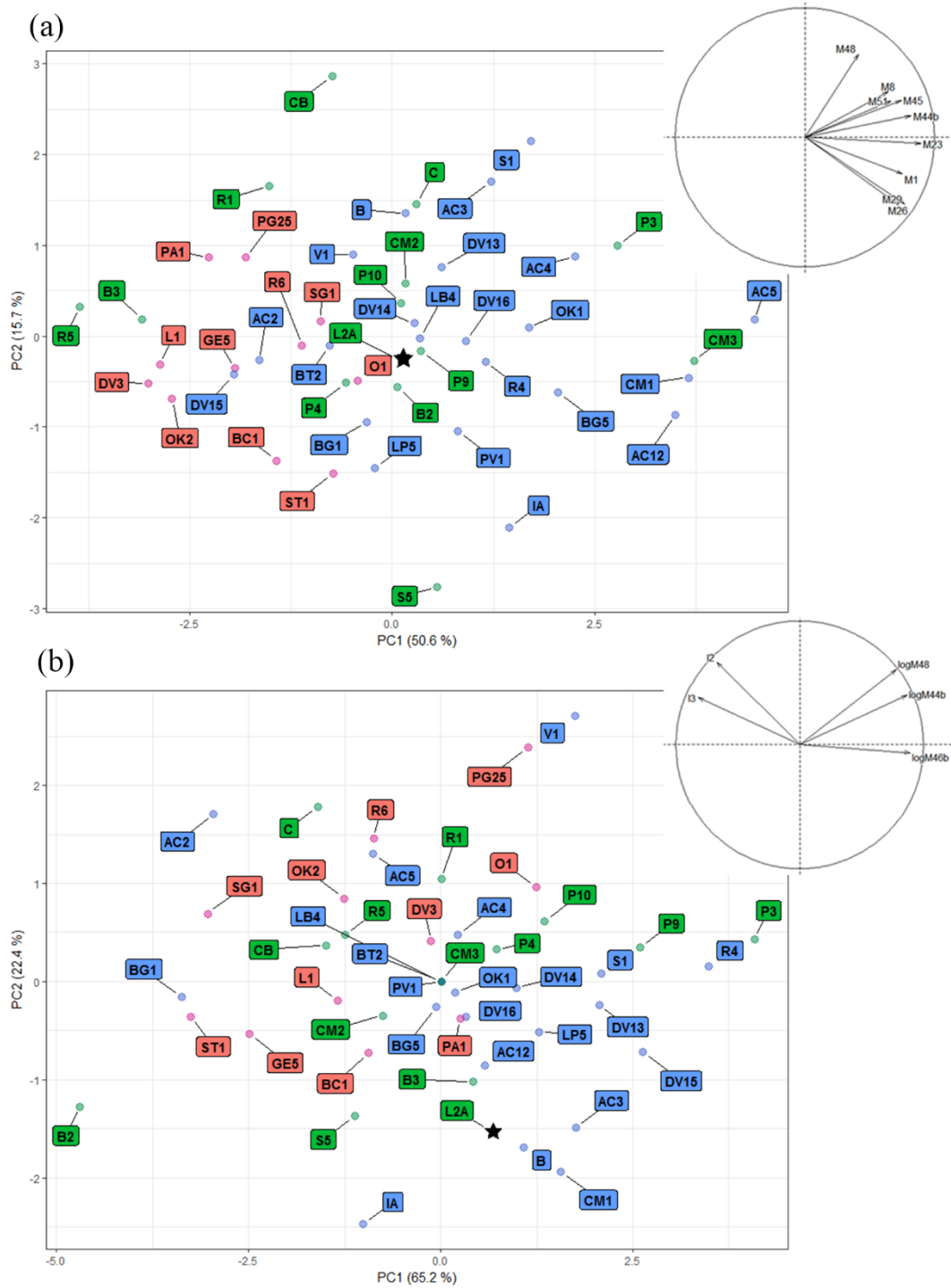
collected on the 3D photogrammetric records in TIVMI; n/o = not observable, n/a = not applicable; PF = probability of female sex; PM = probability of male sex. See Murail, et al. (2005) for measurements abbreviations.

The negligible differences between the *in situ* and photogrammetric measurements confirm the validity of the virtual application of the DSP method, with an average difference in the measurements of 2.4 % (sd: 2.2 %, min: 0.01 %, max: 7.9 %). The result on the left *os coxae* is similar to the conclusions of Villotte, et al. (2015), but the DSP failed to attribute a sex using the dimensions of the right *os coxae*. Any combination of four available measurements provides a higher probability for the male sex, but never above the acceptable threshold of 0.95.

### 3.2 Craniometric results

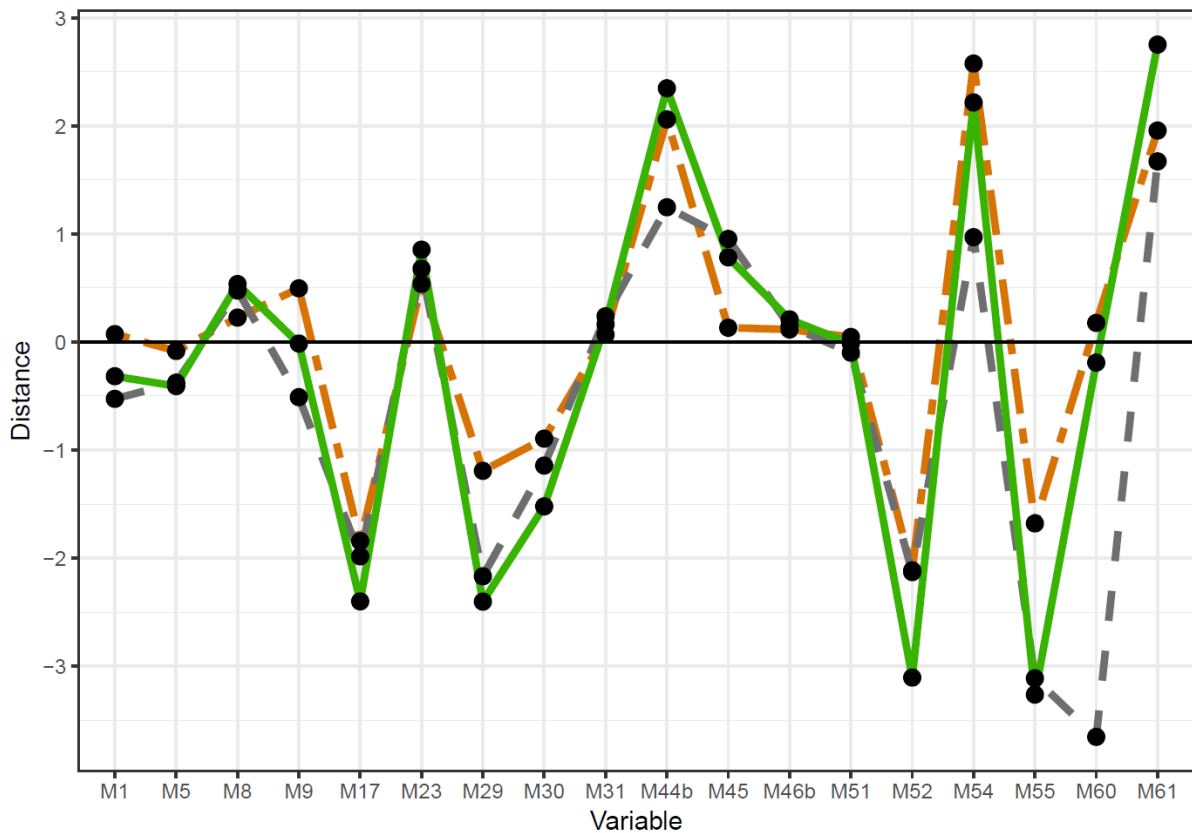
The visible cranial morphology of L2A is not particularly indicative of its sex, with some masculine (no frontal or parietal eminences, square orbits) and some feminine (V-shaped palate, smooth nuchal crests, small occipital condyles) traits displayed. The other commonly used features are either moderately expressed (mastoid process, supraorbital ridge) or not observable. A morphometric analysis was thus performed.

The 78 cranial variables were tested for significant differences between males and females with the Wilcoxon-Mann-Whitney test. Eleven variables show a significant sexual dimorphism in the UP sample (Supplementary Table 1), with males consistently displaying larger values than females. Overall, the values for L2A tend to indicate a relatively small size. This is illustrated by the PCA on the sexually dimorphic size variables (Figure 4). The first principal component (PC) of the size PCA (50.6%) allows for a distinctive separation between sexes, and L2A is within the male variability (positive values), but also close to the female group (negative values). Regarding the PCA on sexually dimorphic shape variables, the first PC (65.2%) shows a stronger overlap of the groups, and L2A is closer to the male variability (positive values) than the female one (negative values). A linear discriminant analysis computed on the sexually dimorphic variables (size and shape) classified L2A as male with a posterior probability of 0.97 (see Supplementary Data for details on the analysis).



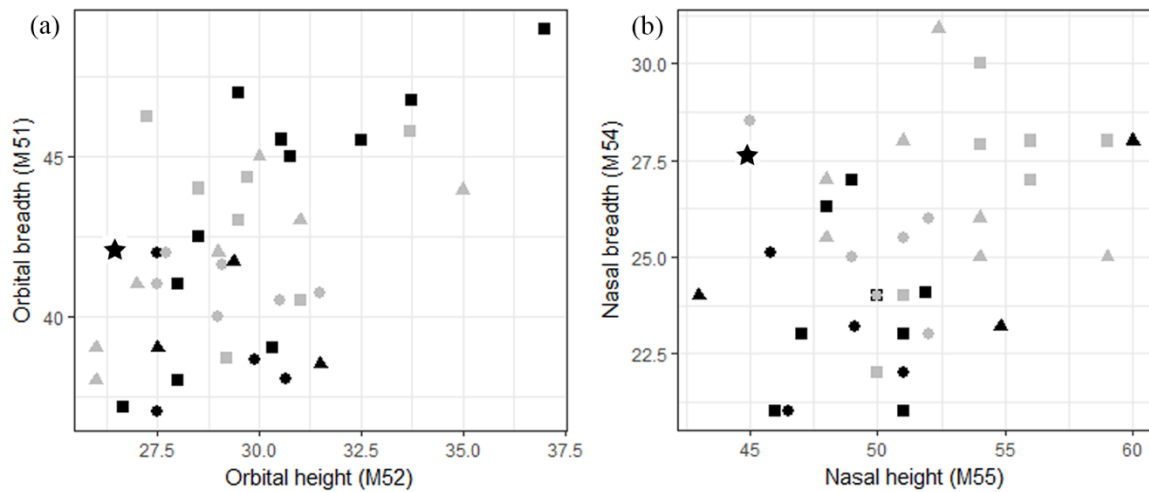
**Figure 4.** PCAs on sexually dimorphic size (a) and shape (b) variables (blue = males, red = females, undetermined sex = green). L2A is indicated with a star. Dimorphic variables used are M1, M8, M23, M26, M45, M48 and M51 for size morphology, and I2, I3, logM44b, logM46b and logM48 for shape morphology.

When considering the main cranial variables for which no sexual dimorphism was detected in the UP sample, L2A shows some very low (M17, M29, M52, M55) and very high (M44b, M54, M61) values, which are outside the range of variation known for the UP (Figure 5).

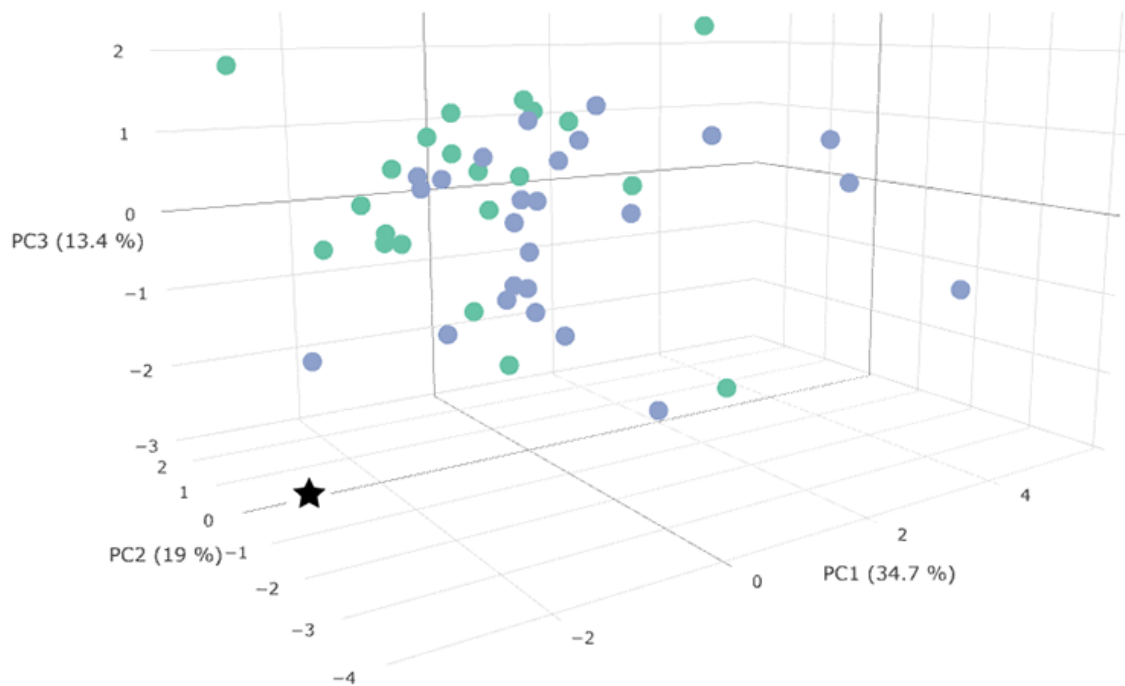


**Figure 5.** Adjusted Z-scores between L2A, and the UP (green line), MUP (gray dashed line), and LUP (orange double-dashed line) comparative samples, computed on main cranial variables. The values -1 and 1 on the y axis represent 95% of the group variabilities; the position of the groups is relative to the L2A measurements.

L2A thus presents a very peculiar morphology, with a relatively flattened cranium, a wide face, a wide and short nasal aperture, a wide palate, and low orbital height (e.g. Figure 6). To illustrate this peculiar cranial shape, a selection of indices was processed in a PCA (I1, I4, I5, I12, I13, I18, I39, I42, I48, I54); because the results displayed a wide variability, the three first PCs are presented in Figure 7. On PC1 and PC3, L2A appears relatively separated from the UP sample, although cannot be considered a clear outlier.



**Figure 6.** Bivariate plots for orbital (a) and nasal (b) height and breadth (in mm) in the UP sample (MUP = gray, LUP = black, male = square, female = circle, indeterminate = triangle, L2A = star).



**Figure 7.** 3D scatterplot of PC1, PC2 and PC3 of the PCA performed on 10 cranial indices (MUP = blue, LUP = green, L2A = star).

#### 4. Discussion and conclusions

The extensive photogrammetric record of Cussac cave allowed for the reconstruction of 3D models that could be used for new bioanthropological study, while minimizing the manipulation of those protected human remains. New metric data were generated for the

Gravettian individual L2A, allowing for further evaluation of the cranial and pelvic remains through a virtual anthropology approach (Weber and Bookstein, 2011).

Although this kind of virtual analysis cannot fully replace the traditional study of the remains (i.e. we have no access to the whole surface of the bones or their internal structures), our research confirmed a male sex diagnosis for L2A. Despite his relatively small-sized cranium, the presence of some female non-metric cranial features, and a short stature relative to other Upper Palaeolithic individuals, the pelvis clearly indicates a male sex. Several Upper Palaeolithic fossils were traditionally diagnosed solely from the cranial morphology (Gambier, et al., 2006, Villotte, et al., 2011), and following this method L2A may have been wrongly sexed as a female. The example of L2A highlights the risk of obtaining the wrong sex diagnosis using non-pelvic traits.

L2A's stature is well below the range of variation seen for Gravettian males, and its body proportions are uncommon for the Middle Upper Palaeolithic, with the femur being rather long compared to the humerus and tibia (Villotte, et al., 2015). The peculiarity of this individuals is confirmed by the results of the present analysis, which show an unusual cranial morphology. L2A body proportions and cranial morphological peculiarities may be related to a growth delay, or a pathology. Congenital disorders are common in the Late Pleistocene human fossil record, and this has been interpreted as a possible indicator of high levels of inbreeding (Sparacello, et al., n.d., Wu, et al., 2013). L2A may be another case in support of this hypothesis. No definitive conclusion can be drawn without excavating the remains; however current evidence on cranial morphology and body proportions suggests that L2A can be considered as an outlier among the Gravettian variability.

The joint analysis of the biological profile of buried individuals and of their depositional context is essential for a proper interpretation of Paleolithic funerary behaviors (Mitnik, et al., 2016, Trinkaus and Svoboda, 2006). L2A's biological characteristics, in the specific context of Cussac, raise the question of the social status of this male individual. L2A is one of the few Upper Paleolithic subjects from the southwest of France discovered in relative anatomical connection (Henry-Gambier 2005, 2008), and although several flooding episodes are attested to the layer of clay covering most of its bones, their position strongly advocates for a primary deposit in *ventral decubitus* (Jaubert, et al., 2016), a very rare position for the Gravettian. Indeed, out of ca. 33 attested Gravettian burials (with ca. 100 individuals), only three other subjects are in a ventral position (BT3, GE5 in the Grotte des Enfants double burial, and DV14 in the triple burial of Dolní Věstonice) (Henry-Gambier, 2008, Riel-Salvatore and Gravel-Miguel, 2013). Moreover, very few Paleolithic human remains were found in a decorated cave or shelter (Bartolomei, et al., 1974, Foucher, et al., 2012, Henry-Gambier, et al., 2007, Mallegni and Fabbri, 1995, Mussi, et al., 2008). The body position of L2A, the fact that the body was deposited in a decorated cave, and its peculiar morphology echo with other UP burials displaying an association between a specific funerary treatment and marked osseous modifications, i.e. the burials of Dolní Věstonice, Sunghir, Arene Candide, and Romito sites (Formicola, 2007, Formicola, et al., 2001, Mallegni and Fabbri, 1995, Sparacello, et al., n.d., Trinkaus, et al., 2014).

The continuation of the biological analyses of the Cussac human remains – in particular the infracranial skeleton of L2A in the event of new excavation of the Locus 2 in the near future – as well as their integration with data from other scientific disciplines, will deepen our understanding of the Gravettian funerary practices in the southwest of France. The analysis (and reanalysis) of the other skeletal remains from this region will also be necessary. A laboratory study of these remains is essential to bridge the gaps in our knowledge about the biological variability during the Gravettian, and its possible relations with funerary behavior, which is still poorly documented.



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## Supplementary Data

The following Supplementary Table 1 contains the descriptive statistics of the comparative sample (n=46) and the raw values for the subject L2A.

	MUP			LUP			Males			Females			p (sex)	L2A
	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd		
M1	25	193.3	7.1	21	190.8	8.1	22	194.1	7.7	11	188.5	6.9	<b>0.05</b>	191.1
M2	16	188.6	8.1	17	182.7	7.2	19	187.0	8.3	7	182.0	6.2	0.09	179.7
M3	20	187.3	7.0	11	183.6	4.2	12	189.2	5.7	8	183.2	5.2	0.07	179.9
M5	8	108.1	18.6	19	100.3	7.4	16	102.7	15.0	7	100.9	4.6	0.87	98.6
M8	25	138.9	5.7	20	139.8	4.7	21	140.7	4.5	11	135.8	4.4	<b>0.01</b>	140.5
M9	24	99.7	5.0	21	96.5	5.2	21	99.5	5.4	11	96.0	3.6	0.05	98.2
M10	22	120.2	5.9	18	115.9	5.4	19	119.5	5.8	10	116.3	4.0	0.15	125.9
M17	14	133.2	2.5	18	136.7	5.9	15	134.9	5.8	9	134.8	4.6	0.86	129.1
M20	17	118.6	7.6	18	114.2	4.3	17	117.3	7.2	9	115.2	4.3	0.43	108.0
M23	8	538.8	16.9	17	543.4	22.7	12	553.4	20.5	7	529.3	11.5	<b>0.01</b>	552.3
M24	8	319.6	11.7	9	309.4	15.9	7	318.6	11.0	6	314.8	11.2	0.37	154.9
M26	19	135.6	8.6	17	132.3	8.0	20	136.7	6.5	8	129.8	3.9	<b>0.02</b>	129.5
M27	19	131.8	8.9	16	137.2	10.1	19	134.7	10.4	8	135.4	9.6	0.70	127.1
M28	11	123.0	5.2	14	118.6	10.9	14	121.4	8.3	7	121.5	11.4	0.86	131.0
M29	19	117.6	6.2	17	113.6	6.0	20	117.7	4.7	8	111.4	5.0	<b>0.01</b>	109.6
M30	23	120.0	7.9	16	120.2	8.5	19	121.4	7.9	8	119.3	6.6	0.77	114.5
M31	10	99.7	3.8	13	100.1	8.6	14	100.1	7.6	7	99.6	6.6	0.86	100.6
M40	8	103.1	4.1	15	96.2	6.9	14	97.9	7.6	5	97.6	7.1	1.00	99.5
M44b	13	100.2	4.6	16	95.5	6.2	16	100.9	4.3	8	92.6	5.7	<b>&lt;0.01</b>	105.1
M45	15	134.2	7.7	15	139.1	7.5	13	142.4	5.0	9	130.1	5.1	<b>&lt;0.01</b>	139.9
M46b	11	96.3	7.7	8	96.1	9.0	10	99.0	5.3	6	89.4	9.7	0.07	97.4
M48	20	67.5	4.8	17	67.3	4.5	17	68.0	3.8	10	64.5	2.1	<b>&lt;0.01</b>	60.3
M51	20	42.0	2.4	18	41.7	3.9	18	43.3	3.5	10	40.2	1.7	<b>0.02</b>	41.9
M52	22	29.7	2.4	20	30.4	2.8	20	30.3	2.5	11	29.7	2.5	0.38	26.4
M54	21	26.3	2.2	18	23.8	2.2	17	24.9	2.8	11	24.6	2.2	0.78	27.7
M55	20	52.3	3.6	19	49.3	3.9	18	50.9	3.8	11	49.1	2.4	0.28	42.3
M60	8	55.8	0.7	14	51.9	5.7	14	54.6	3.9	6	51.5	6.8	0.78	52.7
M61	11	62.0	5.1	16	61.5	5.9	16	62.1	6.0	8	61.4	5.0	0.53	70.2
M62	3	48.3	2.9	11	44.3	4.9	8	45.0	3.3	4	47.8	6.2	0.46	45.9
M63	11	36.7	3.7	14	37.3	1.6	14	37.8	2.6	7	36.1	3.1	0.22	39.0
I1	25	71.9	3.4	20	73.4	2.8	21	72.6	3.1	11	72.1	3.5	0.70	73.5
I2	14	69.2	2.2	18	71.6	3.2	15	69.5	3.2	9	71.8	1.7	<b>0.01</b>	67.5
I3	14	95.7	4.4	17	97.9	5.0	14	94.5	4.8	9	99.9	3.2	<b>0.01</b>	91.9
I4	17	61.7	3.0	18	59.8	2.3	17	60.4	3.4	9	61.1	2.2	0.29	56.5
I5	17	86.0	6.5	17	81.8	3.5	16	83.1	6.1	9	84.8	4.4	0.12	76.9
I12	22	82.7	3.0	18	83.5	3.6	19	83.6	3.1	10	82.8	3.0	0.46	78.0
I13	24	71.8	3.9	20	69.0	3.5	20	70.7	4.4	11	70.7	2.6	0.70	69.9
I16	19	97.5	7.6	16	104.7	9.4	19	99.2	9.5	8	104.3	6.9	0.12	98.2
I17	11	90.9	6.7	14	90.6	8.2	14	89.5	6.4	7	93.9	8.4	0.40	101.2
I18	11	94.9	5.4	14	86.5	10.7	14	90.7	9.2	7	90.6	12.6	0.86	103.1
I22	19	86.8	2.8	17	86.0	3.5	20	86.2	2.9	8	85.9	4.4	0.86	84.7
I24	19	91.6	2.9	16	87.7	3.6	19	90.3	2.8	8	88.2	3.8	0.39	90.1
I39	15	50.7	2.7	14	48.2	3.6	13	48.1	3.4	9	50.0	2.2	0.21	43.1
I42	20	70.1	5.1	18	72.0	5.2	18	70.0	5.1	10	72.6	5.3	0.29	63.1
I42(1)	14	31.3	2.4	13	30.2	2.5	12	30.8	2.4	8	31.4	2.1	0.73	29.9
I42(2)	20	43.8	4.7	16	45.6	4.5	17	44.6	3.6	10	46.0	4.6	0.54	43.8
I48	20	50.5	5.3	17	48.2	5.0	16	48.3	4.2	11	50.2	5.9	0.48	65.4
I54	8	111.5	9.3	13	121.0	21.9	13	115.4	16.6	6	122.2	25.2	0.90	133.2
logM1	25	0.29	0.07	21	0.3	0.05	22	0.29	0.06	11	0.31	0.04	0.61	0.30
logM2	16	0.25	0.08	17	0.27	0.05	19	0.27	0.06	7	0.29	0.03	0.82	0.27
logM3	20	0.28	0.07	11	0.26	0.05	12	0.27	0.06	8	0.28	0.03	0.97	0.28
logM5	8	0.03	0.05	19	0.03	0.04	16	0.02	0.04	7	0.04	0.03	0.72	0.01
logM8	25	0.15	0.08	20	0.16	0.05	21	0.15	0.07	11	0.17	0.05	0.94	0.17
logM9	24	0.01	0.08	21	0.00	0.05	21	0.01	0.06	11	0.02	0.05	0.97	0.01

logM10	22	0.09	0.07	18	0.07	0.05	19	0.08	0.05	10	0.1	0.06	0.84	0.12
logM17	14	0.16	0.04	18	0.16	0.04	15	0.16	0.04	9	0.17	0.04	0.38	0.13
logM20	17	0.07	0.06	18	0.08	0.05	17	0.06	0.07	9	0.09	0.05	0.43	0.05
logM23	8	0.69	0.07	17	0.74	0.05	12	0.74	0.06	7	0.73	0.03	0.54	0.76
logM24	8	0.49	0.03	9	0.48	0.05	7	0.47	0.05	6	0.5	0.02	0.45	0.21
logM26	19	0.11	0.07	17	0.13	0.05	20	0.13	0.06	8	0.13	0.03	0.67	0.13
logM27	19	0.10	0.08	16	0.14	0.06	19	0.12	0.07	8	0.15	0.05	0.58	0.12
logM28	11	0.10	0.04	14	0.08	0.05	14	0.09	0.04	7	0.1	0.04	0.69	0.14
logM29	19	0.05	0.07	17	0.06	0.05	20	0.06	0.06	8	0.06	0.02	0.41	0.06
logM30	23	0.08	0.08	16	0.08	0.06	19	0.08	0.07	8	0.09	0.04	0.98	0.08
logM31	10	0.01	0.04	13	0.01	0.05	14	0.01	0.05	7	0.02	0.03	0.64	0.02
logM40	8	0.04	0.04	15	0.00	0.04	14	0.02	0.04	5	0.01	0.05	1.00	0.02
logM44b	13	0.01	0.05	16	0.01	0.04	16	0.02	0.03	8	-0.01	0.04	0.07	0.04
logM45	15	0.16	0.05	15	0.17	0.05	13	0.18	0.04	9	0.15	0.06	0.32	0.17
logM46b	11	0.00	0.03	8	-0.01	0.05	10	0.01	0.03	6	-0.03	0.04	0.09	0.01
logM48	20	-0.14	0.05	17	-0.15	0.05	17	-0.14	0.05	10	-0.16	0.05	0.22	-0.20
logM51	20	-0.35	0.04	18	-0.35	0.06	18	-0.34	0.06	10	-0.36	0.05	0.31	-0.36
logM52	22	-0.5	0.05	20	-0.5	0.05	20	-0.5	0.06	11	-0.49	0.05	0.79	-0.56
logM54	21	-0.55	0.05	18	-0.6	0.06	17	-0.58	0.06	11	-0.57	0.06	0.78	-0.54
logM55	20	-0.25	0.05	19	-0.28	0.05	18	-0.26	0.05	11	-0.27	0.06	0.61	-0.35
logM60	8	-0.23	0.03	14	-0.27	0.08	14	-0.24	0.07	6	-0.27	0.08	0.72	-0.26
logM61	11	-0.19	0.04	16	-0.18	0.04	16	-0.18	0.04	8	-0.18	0.03	0.83	-0.13
logM62	3	-0.29	0.05	11	-0.33	0.04	8	-0.32	0.02	4	-0.29	0.06	0.81	-0.32
logM63	11	-0.42	0.05	14	-0.41	0.04	14	-0.4	0.04	7	-0.42	0.03	0.40	-0.39

**Supplementary Table 1.** Descriptive statistics for the MUP and LUP groups and results of the Wilcoxon-Mann-Whitney test on linear distances, indices, and log shape ratios (log) with mean, standard deviations (sd), and sample size (n). The adjusted p level is reported with a significant level inferior to 0.05 (in bold). The raw values (mm for the linear variables) of Cussac L2A are reported for comparison.

The Supplementary Table 2 presents the specificities of a Linear Discriminant Analysis (LDA) based on dimorphic size and shape variables.

	LDA
Wilk's lambda	0.28
Classification for males (at pp > 0,50)	100% (22/22)
Classification for females (at pp > 0,50)	100% (11/11)
Classification for males (at pp > 0,90)	(19/22) (no misclassification)
Classification for females (at pp > 0,90)	(9/11) (no misclassification)

**Supplementary Table 2.** Results of the LDA. Prior probabilities are equal for each group. Missing values were replaced by MDA.

Using this model, individuals with an undetermined sex were classified as male for P10, P3, C, and CM3; were classified as female RR1, R5, and B3; six subjects remained undetermined under the posterior probability of 0.90: CM2, P3, P4, B2, S5, and CB. These results indicate a trend in the morphology of this sub-sample of MUP individual, and are globally consistent with the sexual diagnosis based on the cranial remains of these individuals. However, due to the small sample size and the varying sexual dimorphism of the skull, such model cannot be considered *per se* as a reliable sex determination method.

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