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1 **Wild or domestic? A 3D approach applied to crania to revisit the identification of**
2 **mummified canids from ancient Egypt**

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28
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31 determination

32

33 **1. Abstract**

34 Many of the million animals dedicated to the deities in Ancient Egypt were canids. In contrast
35 to the rare textual sources, the abundance of skeletal remains offers the opportunity to address
36 the question of rather wild or domestic canids were mummified. However, species
37 identification from osteological material remains problematic because it relies on a simple
38 qualitative appreciation or traditional biometric analyses with a low discriminatory power,
39 paired with incomplete comparative reference samples. Here we propose a new method of
40 identification based on cranial form using a 3D landmark based geometric morphometric
41 (GMM) approach. We built predictive methods using a large reference sample of numeric
42 models of crania of modern canids, including a variety of domestic breeds (N=69, 38 different
43 breeds) as well as feral dogs (N=31), and all species of wild canids present in Africa or the
44 Near East and likely to have been present in Ancient Egypt (N=157). We then applied these
45 methods to a sample of ancient canid remains (N=41). We compared the effectiveness of
46 multivariate discriminant analyses based on 3D GMM to that using traditional linear
47 morphometric measurements (LMM) commonly taken in the field. GMM provided much
48 better results than LMM, cross-validation percentages reaching over 97.5% when determining
49 the domestic/wild status, and 96.4% when determining the species among a reduced sample of
50 wild canids (versus 88.2% and 85.2 % in LMM). With 3D GMM we detected the presence of
51 dogs, but also African golden wolves and, for the first time, Near Eastern gray wolves among
52 the mummies.

53 **2. Introduction**

54 From the 1st millennium BC to the 4th century AD (Roman period), ancient Egyptians
55 mummified millions of animals, including ibises, owls, snakes, crocodiles, fish, cats, and dogs
56 (Murnane et al. 2000; Ikram 2013; Kitagawa 2016; Porcier et al. 2019). Some of these
57 animals had a special status, which implied that their bodies were treated for post-mortem
58 survival much like humans, yet most were classified as 'votive offerings' to gods and
59 goddesses by Egyptologists. Among those, millions of mummified canids have been
60 discovered throughout Egypt (Dunand et al. 2005, 2017; Ikram 2013; Kitagawa 2016). They
61 were dedicated to the deities of Anubis and Wepwawet (depicted as a canid or a human with a
62 canid head), which were associated with death and travel, recalling wild nocturnal canids (or
63 feral dogs) that roamed human cemeteries (Brixhe 2019).

64 The precise identity of these two canid deities remains uncertain, however: i.e. whether each
65 god depicts a wild canid or a domestic dog is still debated (Thiringer 2020). Numerous
66 authors have identified Wepwawet as a wolf (*Canis lupus*), perhaps because it was sometimes
67 depicted with a white or gray fur (Thiringer 2020), or because the ancient Greeks named
68 Asyut (one of the most well documented dog necropolises) “Lycopolis” (city of wolf) in its
69 honour. Others identify Wepwawet as a “jackal”, referring to depictions showing triangular
70 pointed ears, long bodies and straight bushy tails. However, these representations may be
71 somewhat misleading as the ancient Egyptians included symbolic codes in such depictions.
72 For example, when represented, jackals are completely black (which corresponds to no known
73 living species of jackal), likely because this color represented regeneration and was associated
74 with Anubis (Schenkel 1963, 2007; Thiringer 2020). The distinction between wild species
75 from art and text is therefore complex in ancient Egypt, where different perceptions of the
76 taxonomic diversity associated with such symbolism likely existed. In all cases, however, a
77 distinction between wild and domestic animals seemed important as they are frequently
78 represented in opposing positions. For example, in the Middle Kingdom and Second
79 Intermediate Period, the board game called ‘Hounds and Jackals’ was popular (Thiringer
80 2020).

81 This singular religious phenomenon, and the uncertainty surrounding the identity of the
82 deities, thus raises a simple question: which canids were used for mummification? Whether
83 wild canids or domestic dogs are represented in mummified offerings will provide insight into
84 e.g. supply strategies (animals bred on purpose, captured from the natural environment or
85 imported as exotics) and the relative importance of each in the religious practices of ancient
86 Egyptians.

87 Unfortunately, texts describing practices surrounding canid mummification are scarce, being
88 limited to rare and obscure epigraphic sources dating to the Greco-Roman period. For
89 example, the *Jumilhac papyrus* (332 to 30 BC) testifies that three kinds of canids were
90 protected, and that they were the subject of ambiguous considerations: a first type of tjesem
91 dogs (tjesem is the ancient Egyptian name for "hunting dog", and it is used to designate a type
92 of greyhound-like dogs) lived until an advanced age but suffered a rapid and premature death,
93 while the second type did not get a proper burial, did not reach religious status, and had its
94 body burned and its ba (i.e. soul, spirit) annihilated after death. A jackal (“ounech”) is also
95 described, and its death was the object of celebrations (because it was considered as an enemy
96 of Osiris) (Durisch Gauthier 2002; Bouvier-Closse 2003). Strabon, in his Geography,

97 indicates that "a cult and a gift of sacred food" existed for dogs at Cynopolis, which may have
98 been generalized to all of Egypt (Yoyotte et al. 1997). Yoyotte and Charvet even suggested
99 that pharaohs and some private persons had established agricultural domains whose income
100 ensured the feeding of sacred animals and the maintenance of the priestly personnel assigned
101 to their cults (Yoyotte et al. 1997, p. 152).

102 Given the scarcity of epigraphic documentation, and the diverse and ambiguous nature of
103 artistic representations, it appears that the zooarchaeological record offers us an alternative
104 way of addressing the question of what canids were mummified. Based on age-at-death data
105 (most canid remains are from very young animals) and the frequent dental anomalies and
106 pathologies observed on these remains, it has been proposed by both Egyptologists and
107 archaeologists alike that most canid mummies were likely domestic dogs, deliberately bred
108 for sacrifice by dedicated keepers (Dunand et al. 2005). Breeding dogs in captivity for
109 sacrifice would have secured a steady and reliable supply of specimens, affording
110 opportunities to satisfy high demand from pilgrims, and allowing such practices to operate at
111 a large scale. However, wild canids were also occasionally collected (yet not clear whether
112 after natural death or intentionally hunted), as attested by recovery of the bones of red or
113 Ruppel's fox (*Vulpes vulpes* and *V. rueppellii*, respectively) and "jackal" from previous
114 excavations (Kitagawa 2016; Brassard 2017; Dunand et al. 2017; Hartley 2017).

115 The identification of "jackal" in previous studies is somewhat problematic. A number of
116 jackal species are native to Egypt and the surrounding region, including the golden wolf
117 (*Canis lupaster*), the Ethiopian wolf (*Canis simensis*), the Side-Striped Jackal (*Lupulella*
118 *adustus*), the Black-Backed Jackal (*Lupulella mesomelas*), and the Near-Eastern golden jackal
119 (*C. aureus*). To date, conventional wisdom classified Egyptian jackals as a subspecies of the
120 golden jackal (*Canis aureus*; Wilson and Reeder 2005, pp. 574–575). However, recent
121 genetic studies have revealed that they most likely derive from another species altogether, one
122 more closely related to the grey wolf. Whilst studies first suggested that African specimens
123 belong to a cryptic subspecies of the grey wolf (*Canis lupus lupaster*; Rueness et al. 2011;
124 Viranta et al. 2017), others posited they are a completely distinct species (the African golden
125 wolf *Canis lupaster* also referred as *Canis anthus*), showing morphological convergence with
126 Eurasian golden jackals (Koepfli et al. 2015). More recent whole genome analyses have
127 suggested that it may well be a hybrid of the gray wolf and the 'Ethiopian wolf' (*Canis*
128 *simensis*; Gopalakrishnan et al. 2018). Given that Egypt is at the crossroads between Africa
129 and the Near East (where the golden jackal is present), it is possible that the Eurasian golden

130 jackal and the African golden wolf are both present in modern and ancient Egypt (Viranta et
131 al. 2017). Moreover, other species of jackals are also present in other geographically close
132 regions - for example the Side-Striped Jackal (*Lupulella adustus*), or the Black-Backed Jackal
133 (*Lupulella mesomelas*) and should, therefore, be considered when assessing species
134 identification from canid bones and mummies. Moreover, although there is no evidence that
135 they have ever lived in Egypt, gray wolves from the Near or Middle East (corresponding to *C.*
136 *l. pallipes* and *C. l. arabs* subspecies) may have been present among mummified canids, given
137 the geographic proximity with Egypt and the ability of these animals to travel long distances
138 (Castelló 2018) or be imported along well established trade routes. It is, therefore, important
139 to revisit conventions in how we determine and categorize “dog/jackal” from
140 zooarchaeological and mummified canids from Egypt, by including in our analyses
141 comparative specimens of all the species likely to be found in Egypt.

142 Finally, the extent to which imported ‘exotic’ canids may have been used is still unknown.
143 For example, though the African wild dog (*Lycaon pictus*) was unmistakably represented on
144 carved monumental palettes during the Predynastic period (and only rarely during the
145 Dynastic Period; Osborn and Osbornová 1998, p. 80), no osteological evidence supports its
146 presence anywhere in the Egyptian territory (Brémont 2021). It is thus possible that it was
147 imported from elsewhere in Africa. Indeed, animals were often represented in Egyptian art
148 despite not being indigenous (e.g. fallow deer, baboon or elephant; Brémont 2021).

149 The current methods of determination of bones are problematic for several reasons. To date,
150 the precise identification of canid species has relied on a macroscopic osteological
151 description of bones, mainly skulls, mostly based on qualitative criteria (see Lortet and
152 Gaillard 1903, 1907; Kitagawa 2016; Dunand et al. 2017; Hartley 2017). Measurements taken
153 with calipers are also common, yet the exploration of the trends in these metrics are often
154 limited to bivariate graphs or estimates of wither heights despite the availability of more
155 advanced multivariate analytical methods (Brassard et al., 2021; Callou in Dunand et al.,
156 2017). Moreover, all these previous studies unfortunately did not include all possible species
157 of modern canids present in Africa or the Near East. Therefore, it is possible that some wild
158 canids have remained undetected and that their prevalence in faunal assemblages of
159 mummified canids could be more important than previously thought. The present study is the
160 first to consider the full suite of wild and domestic canids likely present in the study region
161 and will help establish a methodology for separating domestic dogs from wild canids.

162 Unfortunately, studies of mummified Egyptian canids have not included an examination of
163 cranial size and shape using 3D geometric morphometrics (which consists in analyzing the 3D
164 coordinates of anatomical landmarks on the external surface of the object in order to describe
165 its size and shape). Yet, this approach allows for a more thorough description and statistical
166 analyses of shape and has proven its ability to differentiate wild and domestic canids in other
167 contexts (Drake et al. 2017; Ameen et al. 2019; Aurélie Manin 2020) or other taxonomically
168 close species of mammals such as sheep and goats (Evin et al. 2022; Jeanjean et al. 2022).
169 Advances in 3D data acquisition such as photogrammetry (which basic principle is to build a
170 3D model of the object from 2D photographs) allow easy and cheap data acquisition directly
171 in the field or on museum collections (Evin et al. 2016; Fau et al. 2016). This technique is
172 particularly promising for Egyptian zooarchaeological studies since transporting
173 archaeological remains from the site or between administrative territories within Egypt is
174 forbidden under cultural heritage laws, thus strongly limiting analytical techniques that cannot
175 be undertaken in the field. Photogrammetry in Egyptian archaeological contexts has been
176 limited to human mummies, artefacts, monuments and even sites (e.g. Lima et al. 2018; Prada
177 and Wordsworth 2018; Abdelaziz and Elsayed 2019; Vasilyev et al. 2019). This is the first
178 study to apply this technique to the examination of animal mummies.

179 In this study, we propose a novel 3D GMM based method for the identification of canid
180 species from mummified remains, and above all the domestic versus wild status of these
181 canids, based on cranial shape and size. We focus on complete crania (i.e. skull without the
182 mandible) which are abundant and often very well preserved in dog catacombs or Museum
183 collections. Moreover, their shape carries a strong phylogenetic signal (making it one of the
184 elements for which species diagnosis is easiest). First, we assess the ability of cranial shape
185 and size to distinguish between modern canids of known species, including a dataset of
186 domestic dogs incorporating dogs of known breeds as well as feral specimens. We further
187 sampled wild canid species present in Africa or the Near East and likely to have been present
188 or imported into Ancient Egypt. We then applied predictive methods on a small sample of
189 ancient canid remains from different dog catacombs found along the Nile valley and
190 maintained in the collections in the Musée des Confluences in Lyon (France). We used
191 multivariate statistics to optimize the exploitation of metric data, and compared the
192 effectiveness of discriminant analyses based on 3D geometric morphometrics with that based
193 on traditional morphometrics using linear measurements. To do so, we use morphometric
194 analyses commonly used in evolutionary biology or zooarchaeology allowing us to assess

195 morphological variation and to discriminate between species (e.g. see Claude 2013; Fabre et
196 al. 2014; Evin et al. 2020; Parés-Casanova et al. 2020; Jeanjean et al. 2022).

197 **3. Materials**

198 **3.1. Modern reference sample**

199 We investigated a total of 257 crania of modern canids collected from several institutions (the
200 detailed information about the origin and constitution of this sample is provided in SI 1). Wild
201 canids are represented by 157 specimens from 13 species of the genus *Canis*, *Lupulella*,
202 *Lycaon*, *Otocyon* and *Vulpes* (Table 1). Modern domestic dogs are represented by 100
203 specimens from a minimum of 38 different breeds (some pure, and others being crossbreeds).
204 Based on the assumption that ancient dogs may be similar in shape to medium-headed modern
205 dogs rather than breeds with highly specialised morphologies we included in this sample 26
206 modern feral dogs from Tunisia, Egypt, and Turkey, as well as 5 modern beagles, whose skull
207 shape is average among modern breeds (see Brassard et al. 2022). We also included long-
208 headed dogs (i.e. dolichocephalic dogs, such as Greyhounds, Afghan hounds) and short-
209 headed dogs (i.e. brachycephalic dogs, such as Bullmastiffs, Boxers) to account for a full
210 range of domestic variability within our analyses. We estimated how long or short-headed the
211 modern dogs are by calculating their cranial width (measure taken between the two zygomatic
212 arches which corresponds to measurement CR30 in fig. 1) and length ratios (CR1), which
213 corresponds to the cephalic index CI (Roberts et al. 2010). We arbitrary choose the cutoff
214 values, to obtain balanced groups: dogs with a $CI \geq 0.55$ were considered brachycephalic, dogs
215 with a $CI \leq 0.50$ were considered dolichocephalic and dogs with an intermediate CI were
216 considered mesocephalic.

217 We only considered young, subadult, and adult specimens, with permanent teeth fully erupted
218 (i.e. excluding the juveniles). This allows to limit ontogenetic variation since age is known to
219 have a significant impact on skull morphology, which is all the more important in sexually
220 immature canids (i.e. before 8-12 months, see Forbes-Harper et al. 2017; Brassard 2020).
221 Specimens were divided into categories depending the degree of closure of the cranial sutures
222 (Barone, 2010). We considered as subadults specimens with all the permanent teeth erupted
223 but a suture between the basisphenoid and the basioccipital (*Synchondrosis sphenoccipitalis*)
224 still open (between 6 and 8/10 months). Young specimens have the suture between the
225 basisphenoid and presphenoid not completely closed (between 10 months and 1-2 years old)
226 whereas it is completely closed in adult specimens (more than 1-2 years old). When the suture

227 between the basisphenoid and the presphenoid was not clearly visible, individuals were
 228 classified as ‘young/adult?’. Subadults are sexually immature specimens, but we chose to
 229 keep them in the analyses as we want to propose a method with the widest possible range of
 230 application (in terms of age).

231 Our aim is not to assess morphological differences between age and sex categories. However,
 232 we were careful to provide a reference sample that was as comprehensive and balanced as
 233 possible. As such, subadults are always much rarer in proportion, but their presence will help
 234 identify subadults in the archaeological sample.

235

236 Table 1. Constitution of the modern sample in terms of species, breed, sex, and age at death.
 237 Sex information, when available, is provided in brackets as follows (female/male).

Species	Breed	N	By age			
			Subadults	Young	Adults	Young/adults?
<i>Canis familiaris</i>	Total including	100 (32,34)	10 (5,3)	31(8,15)	35(14,10)	24(2,5)
	Feral	31(13,15)	6(6,3)	13(4,7)	8(6,2)	4(0,3)
	beagles	5 (3,2)	0	1(1,0)	4(2,2)	0
	brachycephalic	28	1	11	16	0
	mesocephalic	32	2	9	13	8
	dolichocephalic	40	7	12	14	7
<i>Canis lupus</i>		16	3 (1,1)	11(2,3)	0	2
<i>Canis lupaster</i>		17	1 (0,0)	10(4,4)	4(2,1)	2(1,1)
<i>Canis aureus</i>		2	0	2(0,1)	0	0
<i>Canis simensis</i>		9	1 (0,0)	8(2,2)	0	0
<i>Lycaon pictus</i>		13	1 (1,0)	6(2,2)	4(0,1)	2(0,1)
<i>Lupulella mesomelas</i>		20	4 (1,2)	10(1,1)	1(0,0)	5(2,2)
<i>Lupulella adustus</i>		8	0	4(4,0)	1(1,0)	3 (0,3)
<i>Vulpes vulpes</i>		23	3 (1,1)	8(3,2)	3(1,1)	7(1,3)
<i>Vulpes rueppellii</i>		15	1 (0,0)	2(1,0)	12(2,5)	0
<i>Vulpes pallida</i>		10	1 (0,1)	2(0,2)	4(2,2)	3(0,1)
<i>Vulpes chama</i>		4	0	0	2(0,0)	2(0,2)
<i>Vulpes zerda</i>		13	1 (1,0)	3(1,1)	4(1,0)	5(0,1)
<i>Otocyon megalotis</i>		7	0	0	4 (1,3)	3(1,2)
Modern sample		257	24 (10,7)	88 (28,30)	77 (26,24)	56 (7,21)
Ancient mummies		41	7	7(2,2)	14(1,0)	13 (1,1)

238

239 3.2. Archaeological specimens

240 We analyzed 41 archaeological crania from ancient canid mummies collected in dog
 241 catacombs along the Nile Valley by Louis Lortet, Claude Gaillard, and Gaston Maspéro in the
 242 early 20th century. No precise date is available for these specimens, but some other dog
 243 mummies from the collection were radiocarbon dated, and the oldest date to the 30th Dynasty,
 244 around 360 BC (Richardin et al. 2017; Porcier et al. 2019). Geographic provenance is known
 245 only for 26 specimens; these are from Assiout, Assouan, Rôda, Saqqara, Tehneh, and Thebes

246 (Louqsor; see SI 1). Some identifications were proposed by previous authors (Lortet and
247 Gaillard 1903, 1907), and are compared with the identification obtained in our study.

248 **4. Methods**

249 **4.1. Data acquisition**

250 *4.1.1. 3D modeling*

251 Scaled 3D models of the crania were obtained from different operators and by different
252 methods, including photogrammetry, surface scanning (Einscan), and medical CT scan
253 protocols (see SI 2 for details). The models were repaired, cleaned, simplified, and mirrored
254 where needed using © ‘Geomagic Wrap’ (version 2013.0.1.1206) and ‘MeshLab’ (v2016.12;
255 Cignoni et al. 2008).

256 *4.1.2. 3D Geometric morphometrics (GMM)*

257 Cranial shape was quantified from the 3D coordinates of landmarks placed by a single
258 operator (first author CB) on the numerical models using the software ‘IDAV Landmark’,
259 version 3.0.0.6 (©IDAV 2002-2005; Wiley et al. 2005). Forty-one unilateral landmarks were
260 placed on the left side of the cranium (Table 1, Fig. 1) and were then mirrored for further
261 visualizations, using function ‘mirrorfill’ from the package ‘paleomorph’ in R (R Core Team
262 2021). The resulting raw coordinates are available in the supplementary material (SI 3).

263 All following analyses were carried out in R, using mainly the packages ‘Morpho’ (Schlager
264 2017) and ‘Geomorph’ (Adams et al. 2016).

265 Mirrored landmarks coordinates were superimposed following a Generalized Procrustes
266 Analysis (GPA) using function ‘procSym’ (Rohlf and Slice 1990; Goodall 1991;
267 Mitteroecker and Gunz 2009; Dryden and Mardia 2016). During this procedure, the raw
268 coordinates undergo translation, scaling and rotation to standardise the relative positioning of
269 the specimens around their centroid to minimize the squared summed distances between
270 corresponding landmarks (Rohlf and Slice 1990). Centroid size (CS) is the square root of the
271 sum of squared distances of the landmarks from their centroid (Bookstein 1991) and measures
272 the dispersion of the landmarks around the centroid. This can be used as a univariate summary
273 of the overall size of the cranium. From this procedure we extracted the Procrustes
274 coordinates and the log₁₀-transformed centroid size, which are used to describe cranial shape
275 and size, respectively. The new set of shape coordinates obtained from the GPA – namely

276 Procrustes coordinates – together represent the total amount of shape variation in the entire
 277 sample. When the analyses focussed only on certain specimens, new GPAs were conducted
 278 separately for each separate dataset (corresponding to further analyses, e.g. when considering
 279 all species or just some of them).

280 For visualizations of shape variation, the 3D surface scan of the cranium of a feral dog was
 281 warped onto the consensus shape of the GPA, and then deformed using thin-plate spline using
 282 the function ‘tps3d’ (Bookstein 1989).

283 **Table 2.** Definition of the landmarks used in this study following the Nomina Anatomica
 284 Veterinaria nomenclature (NAV, 2017).

landmark	Definition
1	Most rostral point of Os incisivum, between incisor teeth I1 in dorsal view (Prosthion)
2	Most rostral point of Os nasale, on the midline (Sutura internasalis)
3	Most rostral point on Sutura nasoincisiva
4	Point at the junction of Os incisivum, Os nasale and Maxilla
5	Most caudal point of Os nasale, on the midline (Sutura internasalis) and at the junction with Os temporale (Nasion)
6	Most medial point at the postorbital constriction on the curvature corresponding to Linea temporalis
7	Most lateral point of the Processus zygomaticus of Os frontale
8	Processus frontalis of Os zygomaticum
9	Most rostral point of the curvature of the lower edge of the Fossa sacci lacrimalis
10	Bregmatic fontanel, most medial point of the Sutura coronalis, on the midline (Bregma)
11	Most rostral and medial point on the Sutura lambdoidea on the midline
12	Most posterior end of Os occipitale (Inion, called Akrokranion by von den Driesch)
13	Point at the extreme convex curvature of the Tuberculum nuchale
14	Point at the extreme convex curvature of the Crista supramastoidea
15	Most medial point of the Tuberculum articulare of Pars squamosa of Os temporale
16	Most rostral point of Maxilla in ventral view, on the midline
17	Most caudal point of Os palatinum, on the midline
18	Caudally to molar tooth M2, in the recess medial to Tuber maxillae of Os Maxilla (on the Facies pterygopalatine)
19	Most caudal point of the Synchondrosis sphenoccipitalis, on the midline
20	Most lateral point of the Synchondrosis sphenoccipitalis, rostrally to the Bulla tympanica
21	Most ventral point of Foramen magnum of Os occipitale, on the midline (Basion)
22	Most caudal point of the Condylus occipitalis of Os occipitale in ventral view
23	Point on the Canalis n. hypoglossi of Os occipitale in ventral view
24	Ventral tip of the Bulla tympanica
25	Tip of Processus paracondylaris
26	Most dorsal and caudal point of the Foramen alare caudale
27	Most ventral and posterior point at the junction of the Processus zygomaticus of Os temporale and Os zygomaticum, on the Arcus zygomaticus
28	Most caudal point at the junction between Maxilla and Os zygomaticum, under Arcus zygomaticus and near the Tuber faciale
29	Most cranial point of the alveolus of the canine tooth, on lateral side
30	Most caudal point of the alveolus of the canine tooth, on lateral side
31	Most cranial point of the alveolus of the upper carnassial tooth P4, on lateral side
32	Point between the alveolus of P4 and M1 teeth, on lateral side
33	Point between the alveolus of M1 and M2 teeth, on lateral side
34	Most caudal point of Maxilla behind tooth M2
35	Most dorsal point of the Foramen infraorbitale
36	Most ventral point of the Foramen infraorbitale
37	Most caudal point of curvature at the junction of Maxilla and Arcus zygomaticus of Os zygomaticum on lateral side

- 38 Most ventral and caudal point of the Foramen rotundum and alare rostrale
 39 Most rostral point of Meatus acusticus externus on lateral side
 40 Most caudal point of Meatus acusticus externus on lateral side
 41 Dorsal and caudal border of the Foramen magnum, on the midline (Opisthion)

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4.1.3. Linear morphometrics

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We chose 13 measurements following the nomenclature of Von den Driesch (1976) and

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commonly used by archaeologists and Egyptologists (Table 3, Fig. 1). To obtain these

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measurements, we calculated the Euclidean distance to the nearest 1 mm between

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corresponding 3D landmark coordinates recorded during the GMM acquisition (Table 3). We

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chose these measurements to represent the length, width and height of the cranium and avoid

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measurements that may carry redundant information. To disentangle size and shape from the

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LMM data (as done in GMM), we used the log-shape ratio method (Mosimann 1970).

294

Following this method, size was computed as the log₁₀ of the geometric mean of all

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measurements (i.e. isometric size), and shape as the log₁₀ of each measurement divided by

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the isometric size (shape ratios).

297

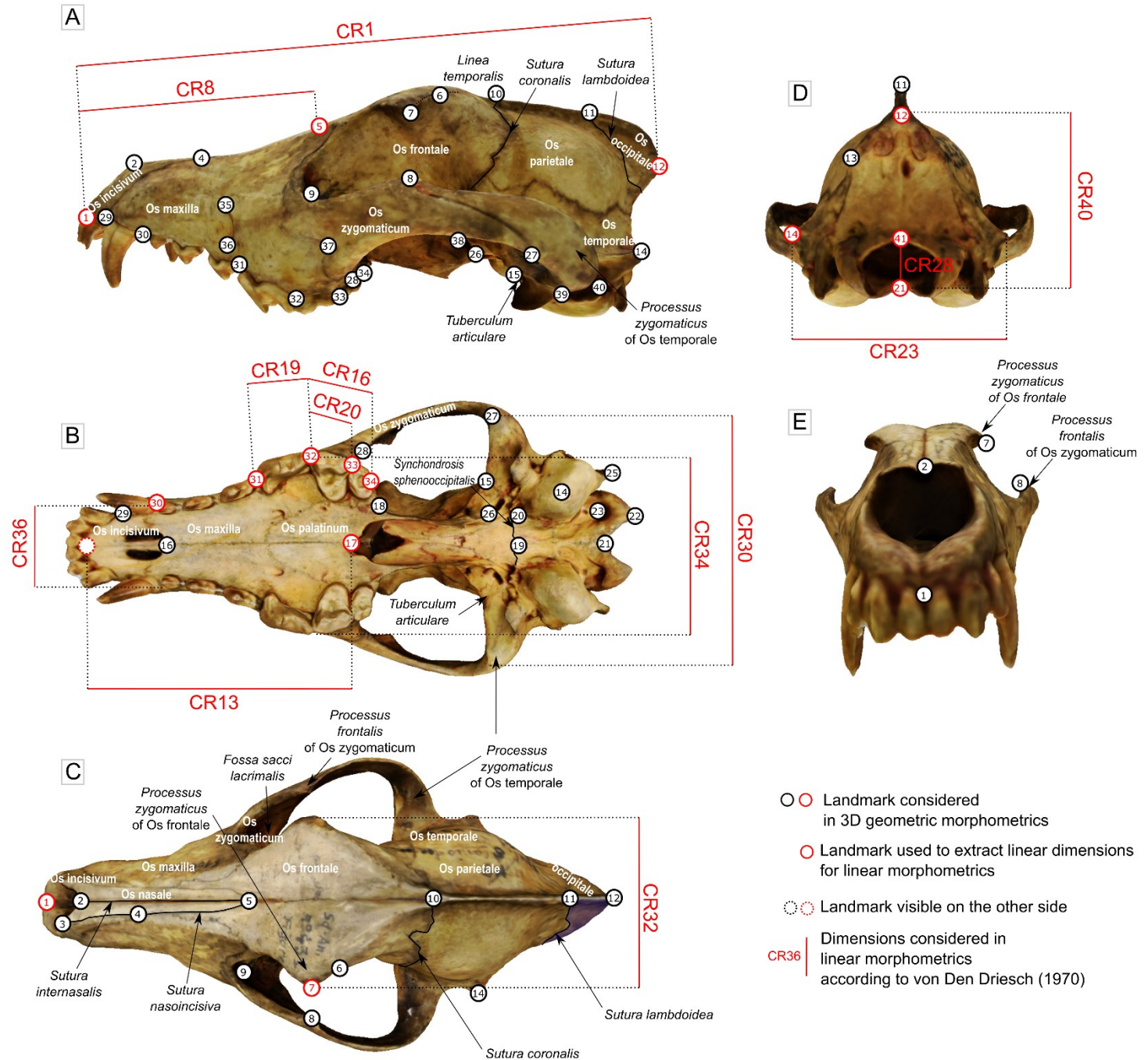
Table 3. Cranial measurements considered in this study following Von den Driesch (1976).

Measurement	Definition	Correspondance with landmarks
cr1	Prosthion-Akrokranion	1-12
cr8	Prosthion-Nasion	1-5
cr13	Median palatal length: staphylion prosthion	1-17
cr16	Length of the molar row (measured along the alveoli on the buccal side)	32-34
cr19	length of the carnassial alveolus	31-32
cr20	length of M1	
cr23	greatest mastoid breadth: greatest breadth of the occipital triangle: otion-otion	14-14'
cr28	height of the foramen magnum: basion-opisthion	21-41
cr30	zygomatic breadth: zygion - zygion	27-27'
cr32	Frontal breadth: Ectorbitale – Ectorbitale	7-48
cr34	greatest palatal breadth: measured across the outer borders of the alveoli	32-32'
cr36	Breadth at the canine alveoli	30-30'
cr40	height of the occipital triangle: akrokranion-basion	12-21

298

299

300 **Fig. 1.** Geometric and linear morphometric protocols: position of the landmarks captured on
 301 the cranium, and correspondence with the linear dimensions considered in our analyses
 302 according to Von den Driesch (1970). Landmark positions and linear measurement are
 303 described in Table 2 and 3, respectively. Anatomical features mentioned in Table 2 are
 304 indicated. A: lateral view; B: ventral view; C: dorsal view; D: caudal view; E: rostral view.



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309 4.2. Inter species comparison

310 To refine our form descriptions and our interpretations, we performed analyses on (log10
311 transformed) centroid size and shape separately. We did not perform analyses on allometry-
312 free shapes (allometry refers to size-related changes in shape; Klingenberg 2016).

313 Statistical analyses were performed following the same steps for 3D geometric (GMM) and
314 linear morphometrics (LMM). First, differences between modern species were visualized
315 using boxplots for size and principal component analysis (PCA) for shape (we used the
316 function ‘prcompfast’ and a similar code as the source code of function ‘procSym’ to obtain
317 the eigenvalues and scores). PCA reduces the dimensionality of shape data while preserving
318 as much as possible of the information contained in the original data. Thus, the first factorial
319 plane provides a representation of the overall variability in the dataset. The contribution of
320 linear dimensions to the first axes of the PCA in LMM was visualized using barplots. In
321 GMM, axes were interpreted based on visualizations and deformations from the consensus to
322 the theoretical shapes at the minimum and maximum of the PC axes (which were computed
323 using function ‘restoreShapes’). The morphological differences between group means were
324 visualized by deformations from the consensus to the mean shape of each species (SI 1). We
325 explored differences in shape variability between dogs and wild canids through disparity tests
326 (Foote 1997). Morphological disparity of each group was estimated as the Procrustes variance
327 (i.e. the sum of the diagonal elements of the group covariance matrix divided by the number
328 of observations in the group) using the residuals of a linear model fit (we used function
329 ‘morphol.disparity’ with 999 permutations with the formula $\text{shape} \sim 1$ to use the overall mean
330 rather than group means; (Zelditch et al. 2012). We performed analyses by grouping together
331 all the wild specimens of our study and then on all the species considered separately.

332 Differences in cranial size between species were tested using ANOVAs and post-hoc tests
333 (using functions ‘anova’ and ‘TukeyHSD’). Differences in cranial shape between wild versus
334 domestic groups, and then between species, were tested using MANOVAs (function
335 ‘manova’) followed by post-hoc tests (function ‘pairwise.perm.manova’ from package
336 ‘RVAideMemoire’) on the scores of the non-zero PC components from the PCA in LMM. In
337 GMM, we performed Procrustes ANOVA on Procrustes coordinates with a residual
338 randomization permutation procedure (using function ‘procD.lm’ with 999 iterations and
339 ‘RPPP=TRUE’; (Goodall 1991; Collyer et al. 2015) and post-hoc comparisons (function
340 ‘pairwise’ from package ‘RRPP’). We also performed Canonical Variate Analysis (CVA)

341 with 10,000 permutations, following a separate GPA fit for each analysis in GMM (Campbell
342 and Atchley 1981; Klingenberg and Monteiro 2005).

343 The discriminatory power of GMM and LMM was also assessed by linear discriminant
344 analyses (LDA) paired with a leave-one-out cross-validation procedure to determine
345 classification accuracy. Classification accuracy corresponds to the percentage of specimens
346 correctly re-assigned to their own group. The leave-one-out procedure removes one specimen
347 at a time, and predicts its classification into *a priori* defined reference groups using LDA
348 function computed on all the remaining specimens (Evin et al. 2013). The procedure is
349 repeated for each specimen in the sample, each in turn being treated as an unknown. This
350 avoids predicting a specimen on the basis of a function computed on data that includes the
351 specimen itself which would tend to spuriously inflate classification accuracy (Kovarovic et
352 al. 2011).

353 A weakness of this method is that it is sensitive to the number of variables, sample size, and
354 unbalanced design (see Mitteroecker and Bookstein 2011; Evin et al. 2013, 2015). The
355 sensitivity to class size is particularly important considering that some species have a low
356 occurrence in our primary dataset (e.g. *C. aureus* is only represented by two specimens, Table
357 1). Yet, large differences in sample size across groups may lead to the largest sample (i.e.
358 dogs) dominating the pattern of variance covariance in the data, resulting in a higher chance
359 of assigning ancient specimen to these larger groups leading to a possible misinterpretation of
360 classification accuracy (Kovarovic et al. 2011; Evin et al. 2013). To solve the problem due to
361 small sample size for some species, we first performed analyses to distinguish domestic dogs
362 (N=100) and wild canids (N=157) by grouping together all the wild specimens of our sample.
363 Then, we performed analyses on the wild candidate species that are closer to the
364 archaeological specimens which were classified as wild by the previous LDA and after
365 removing the species with the smallest sample sizes (e. g. *Canis aureus*).

366 To avoid the over-fitting of the data caused by the high number of variables and unbalanced
367 design we performed analyses after dimensionality reduction and homogenization of group
368 samples using the function 'mevolCVP' (from package 'mevolCVP'). This function allows to
369 determine the number of PCs needed in order to maximize the differences between groups.
370 We replaced the original shape variables (Procrustes coordinates or shape ratios) with the
371 scores of these first PCs (Baylac and Frieß 2005; Evin et al. 2013). In this procedure, perfectly
372 balanced groups are obtained by a random selection (repeated 1000 times) of a number of
373 specimens in the largest samples equal to the sample size of the smallest group. The outcomes

374 of this iterative resampling approach were summarized by the upper and lower 95th
375 percentiles of cross-validation percentage (CVP).

376 **4.3. Identification of archaeological specimens**

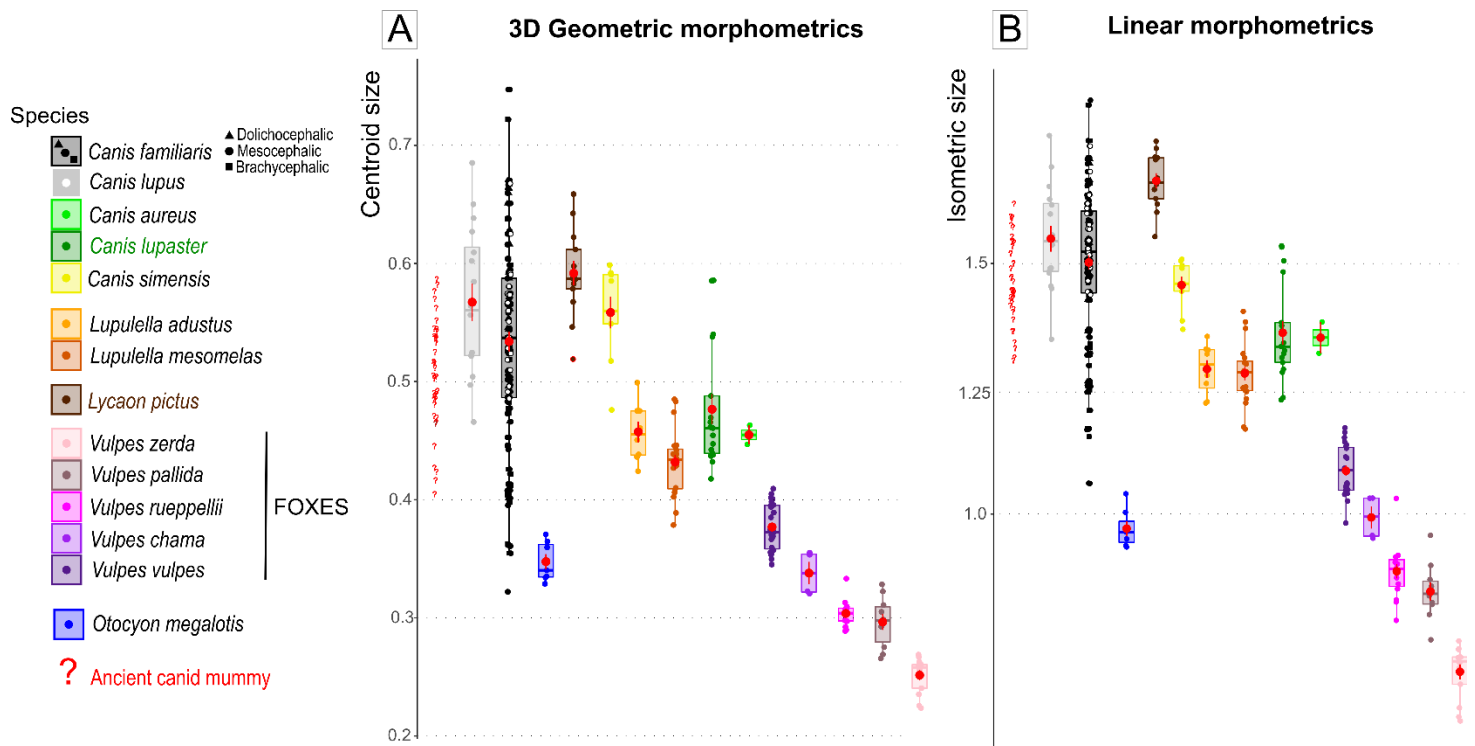
377 After Procrustes superimposition the archaeological specimens were projected on the PCA
378 with the modern specimens (using the same source code as in function ‘PCA’ from package
379 ‘FactoMineR’). The archaeological specimens were then assigned to the wild or domestic
380 group through predictive LDA. We performed analyses after homogenization of groups by
381 using the function ‘pldam’ from the package ‘mevolCVP’ following Evin et al. (2013). A
382 specimen can be assigned to a group with higher or lower confidence depending on its relative
383 distance to the group mean. The level of confidence is estimated by the posterior probabilities
384 of classification as described previously. The highest posterior probability (which relates with
385 the distance between the archaeological specimen and the mean of the groups) determines the
386 classification of the specimen.

387 Finally, a PCA was performed on the wild specimens only in order to establish the list of the
388 candidate species for further predictions of the wild canids among Egyptian mummies. We
389 considered the wild species that are closest to the archaeological specimens on the first
390 factorial plane of the PCA, and excluded the species with a low sample size (e.g. *Canis*
391 *aureus*). We then performed a new predictive LDA to classify the wild specimens.

392 **5. Results**

393 **5.1. Size differences between species**

394 Differences in the mean centroid size exist between many species ($P_{\text{AOV}} \ll 0.001$, $R^2 = 0.80$ in
395 both GMM; $P_{\text{AOV}} \ll 0.001$, $R^2 = 0.87$ and LMM; see supplementary material SI 4 for results of
396 the pairwise comparisons). However, dogs exhibit a large amount of variation in size and
397 strongly overlap with other canids for both GMM and LMM analyses (Fig. 2), making size
398 alone an insufficient criterion for species identification or the separation of wild from
399 domestic specimens.

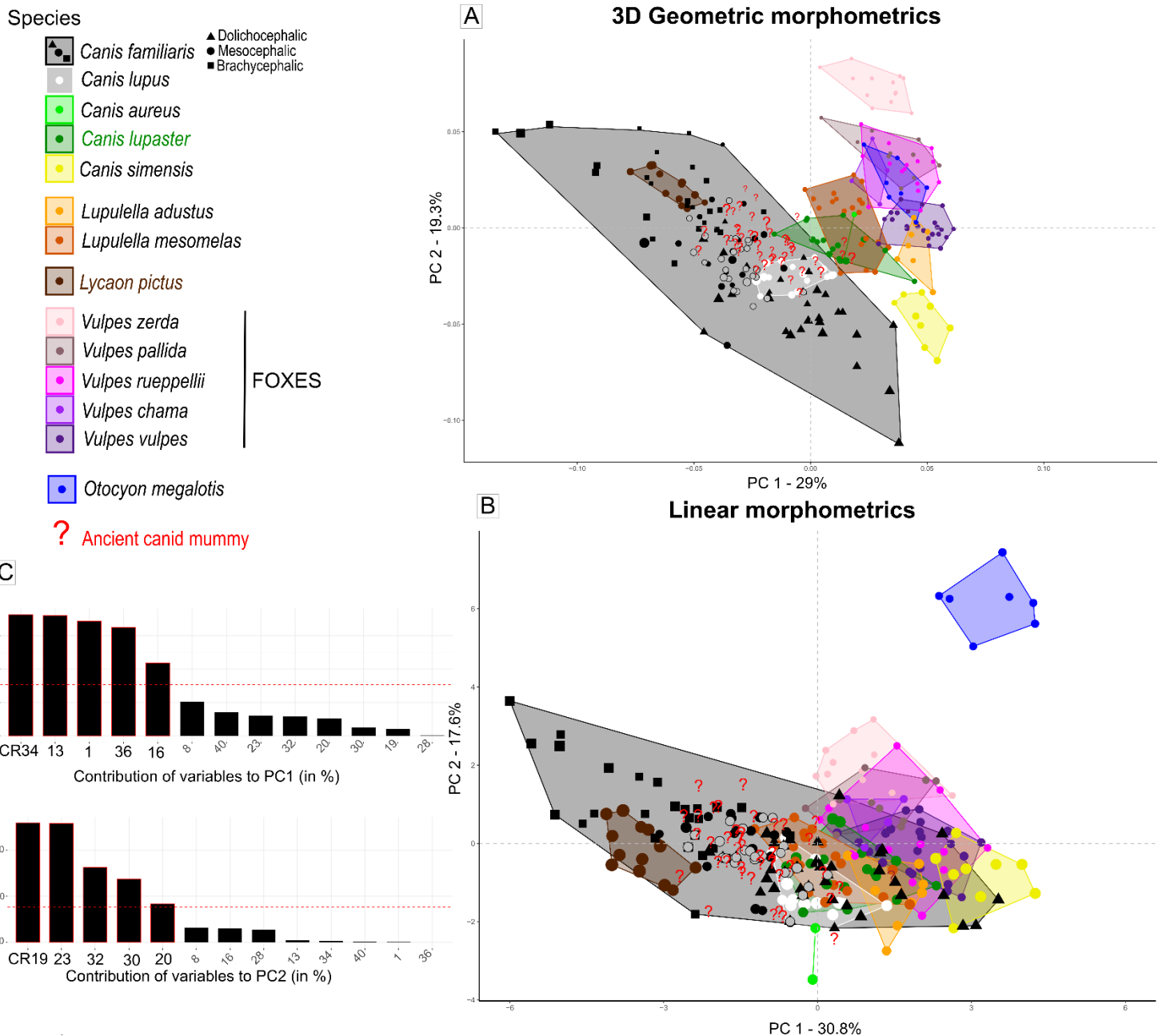


401 **Figure 2.** Visualization on boxplots of the variability in cranial size in ancient (N = 41)
 402 and modern (N = 100 dogs and 157 wild specimens) canids according to GMM (A) and LMM (B)
 403 analyses. Ancient dogs are represented by red question marks, and modern dogs are in black.
 404 Modern wild species are indicated in different colors. Point shape indicates the morphotype of
 405 modern dogs. See Table 1 and SI 2 for details about the sample. The red dots and red vertical
 406 lines indicate the mean and standard deviation for each group.

407 5.2. Shape differences between species

408 5.2.1. Variability in dogs compared to wild African canids

409 Dogs display as much intra-group variability in cranial shape as all the wild specimens in our
 410 study when grouped together, as observable on the two first PCs of the PCAs (Fig. 3) and
 411 demonstrated by the results of the disparity tests for both GMM and LMM analyses (GMM: P
 412 = 0.042, Procrustes variance = 0.0061 in 100 dogs and 0.0052 in the 157 wild canids; LMM:
 413 P = 0.4, Procrustes variance = 12.2 in dogs and 13.5 in wild canids). The GMM analyses even
 414 tend to suggest a greater disparity in dogs compared to *C. lupus*, *C. lupaster* and *L. mesomelas*
 415 (P < 0.003). Other comparisons are not significant when retaining a P value below 0.01 (see
 416 SI 4 for details).



418 **Figure 3.** Visualization of the variability in cranial shape on the first factorial plane of the
 419 PCA in ancient (N = 41) and modern (N = 100 dogs and 157 wild specimens) canids
 420 according to GMM (A) and LMM (B) analyses. Icon size is proportional to the log₁₀ of the
 421 centroid size. Ancient dogs are represented by red question marks, and modern dogs are in
 422 black. Modern wild species are indicated in different colors. Point shape indicates the
 423 morphotype of modern dogs. See Table 1 and SI 2 for details about the sample.

424 *5.2.2. Differences in shape between wild and domestic groups*

425 In both GMM and LMM analyses, highly significant differences are found in the mean cranial
 426 shape between domestic dogs and wild canids when grouped together (LMM: $P_{\text{MANOVA}} <$
 427 0.001 ; GMM: $P_{\text{Procrustes ANOVAs}} < 0.001$, $R^2 = 0.16$).

428 Based on raw Procrustes data, the CVA shows that each specimen can be correctly classified
429 between domestic and wild with an accuracy of 97.3% in GMM: only 5/100 dogs and 2/157
430 of the wild canids were not correctly assigned. Among the misidentified dogs, three are feral,
431 one is a borzoi, and another is a dachshund. The two misidentified wild canids are Near
432 Eastern wolves. When performing discriminant analyses on a balanced sample and a reduced
433 dataset (we kept only the first 12 PCs, which account for only 78.4% of the total variance but
434 are enough to discriminate species according to the results of the ‘mevolCVP’ function), we
435 obtain similar discrimination power and percentages (accuracy of **97.5% [95% confidence**
436 **interval: 97.46-97.59%]**). This confirms the robustness of the method.

437 LMM has less discriminatory power than GMM: the accuracy is lower, for both the CVA
438 (89.1% 13/100 dogs and 15/157 of the wild canids were not correctly assigned) and the
439 balanced LDA (performed on the first 8 PCs, which represents 93.7% of the total variance:
440 CVP = **88.2% [88.09-88.30%]**).

441 5.2.3. Differences in shape between all species

442 When performing analyses with all species considered as separate groups, we found that, in
443 GMM analyses, significant differences in the mean shape exist between all species except
444 between *V. pallida* and *V. rueppellii*, between *C. lupaster* and *L. mesomelas*, and between *C.*
445 *lupaster* and *C. lupus* ($P_{\text{Procrustes ANOVAs}} \ll 0.001$ see supplementary material SI 4 for results of
446 the pairwise comparisons). In LMM, although significant differences in shape are globally
447 found between species ($P_{\text{MANOVA}} < 0.001$, analyses performed on the 8th first PCs representing
448 93.7% of the total variance), the p-value in pairwise comparisons (when significant) is always
449 close to 0.05, suggesting more subtle differences compared to GMM (see SI 4). Additionally,
450 in LMM, the first factorial plane of the PCA is much less discriminating than for GMM (Fig.
451 3).

452 When considering species separately, the accuracy of the CVA is 94% in GMM, and 80.5% in
453 LMM. However, these accuracies need to be explored further using balanced LDA on a larger
454 and more robust sample. In GMM analyses, *L. adustus*, *L. pictus*, *C. simensis*, *V. vulpes*, *V.*
455 *zerda* and *O. megalotis* have a classification accuracy of 100% (SI 4). In LMM analyses, only
456 *L. pictus* and *O. megalotis* have a classification accuracy of 100%. In both GMM and LMM
457 analyses, there is less accuracy in separating dogs and *C. lupus* (97% of dogs and 81% wolves
458 are correctly assigned in GMM analyses, while the accuracy is of 91% for dogs and 50% for
459 wolves in LMM analyses), between *C. lupus*, *C. lupaster* and *L. mesomelas*, and between *V.*

460 *pallida* and *V. rueppelli* (see SI 4 for details). *Vulpes chama* seems rather similar to *V.*
461 *rueppellii* and *V. pallida*, while *C. aureus* is more similar to *C. lupaster* and *C. simensis*.
462 Wolves show frequent misclassification (43.7% of wolves are misclassified), as well as *V.*
463 *pallida*.

464 5.2.3. Differences in shape between *C. lupus*, *C. lupaster* and *L. mesomelas*

465 When considering only *C. lupus*, *C. lupaster* and *L. mesomelas* in our analyses, we evidence
466 strong differences in the mean cranial shape between the three species in both GMM and
467 LMM analyses (GMM: $P < 0.001$, $R^2 = 0.22$; LMM: $P < 0.002$). We also observe that *C.*
468 *lupaster* (Procrustes variance = 0.0017) is less variable in shape than both *C. lupus*
469 (Procrustes variance = 0.0024, $P=0.009$) and *L. mesomelas* (Procrustes variance = 0.0024, $P =$
470 0.008) in GMM analyses (results are not significant in LMM). We also obtain excellent
471 classification rates in GMM analyses: more than 96% for the CVA on Procrustes data, which
472 is confirmed by the high CVP in balanced LDA (**96.4 %** [96.3-96.5%]) performed on the first
473 7th PCs (representing 63% of the total variance). The accuracy is lower in LMM analyses
474 (81.1% for the CVA, **85.2 %** [84.9-85.6%] in the balanced LDA on the first 10 PCs).

475 5.3. Classification of ancient canid mummies

476 We observe that all ancient canids have cranial centroid sizes out of the range of *V. zerda*, *V.*
477 *pallida*, *V. chama*, *V. rueppellii* and *O. megalotis* in the GMM analyses, and even *V. vulpes* in
478 the LMM analyses (Figs 2 and 3, SI 5). Size thus helps with a preliminary exclusion of small
479 canid species. This first sorting is even more efficient for the LMM method.

480 The preliminary CVA performed on raw Procrustes shape data and considering all species
481 allowed to classify ancient canids into dogs ($n=32$), *C. lupaster* ($n=5$), and *C. lupus* ($n=4$; Table
482 4, SI 6). For the LMM analyses, the CVA classified canids into the same number of dogs
483 ($n=32$), but the distribution between wild canids is different (3 *C. lupaster*, 3 *L. mesomelas*, 2
484 *C. lupus* and even 1 *L. pictus*; Table 4, SI 6), although the size of the specimen identified as a
485 *L. pictus* is not compatible with this attribution.

486 The function ‘pldam’ identified 33 domestic dogs and 8 wild canids in both GMM and LMM
487 analyses. However, class assignment is different between GMM and LMM analyses for four
488 specimens (Fig. 4A, Table 4).

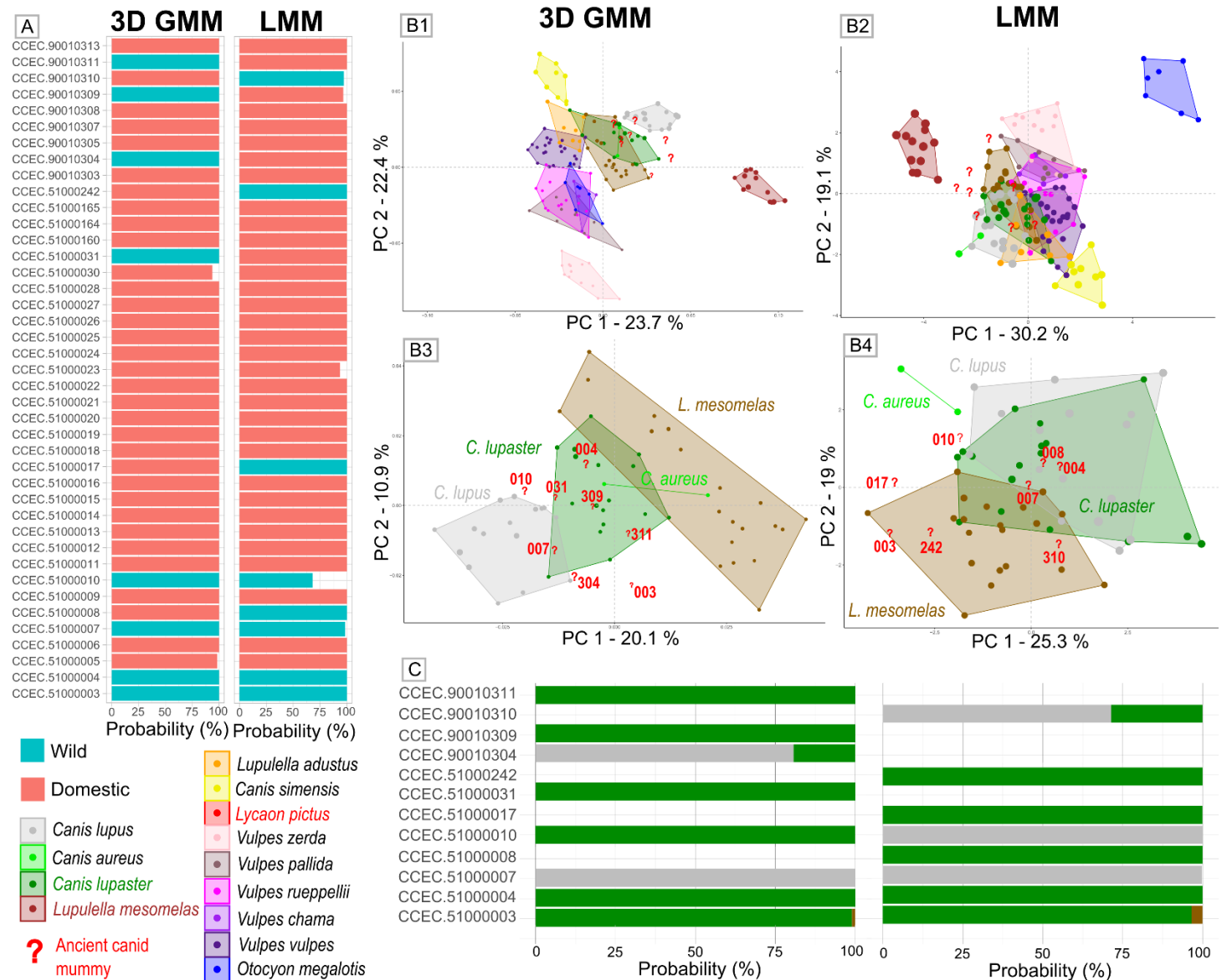
489 When these possible ancient wild canids are projected in the first factorial plane of the PCA
490 performed on shape data (GMM) of the modern wild specimens they position close to *C.*

491 *familiaris*, *C. lupus*, *C. lupaster*, *C. aureus*, and *C. mesomelas* (Fig. 4B1,B3), which allows to
492 refine the list of candidate species for further prediction analyses. When considering only *C.*
493 *lupus*, *C. lupaster* and *L. mesomelas* in the balanced LDA, the function ‘pldam’ identifies 2 *C.*
494 *lupus* and 6 *C. lupaster* among these canid mummies (Fig. 4C). For LMM analyses, there is
495 more overlap between species in the PCA (Fig. B2, B4), and the function ‘pldam’ identifies 5
496 *C. lupaster* and 3 *C. lupus*. Only three specimens are attributed to the same wild species in
497 GMM and LMM (2 *C. lupaster* and 1 *C. lupus*, Table 4).

498 Given the higher ability of GMM to distinguish between domestic and wild canids, and to
499 distinguish between *C. lupus*, *C. lupaster* and *L. mesomelas*, we consider the attributions
500 related to GMM analyses more reliable.

501 Accordingly, based on geometric morphometrics, we determine that the ancient canids present
502 in our sample are 6 *C. lupaster*, 2 *C. lupus* and 33 *C. familiaris* (with a probability over 75%
503 for all specimens; Fig. 4A, C). All these attributions are compatible with the range of centroid
504 size between species, considering that some specimens are relatively young (Table 4, Fig. 2).
505 One specimen identified as a *C. lupaster* has a rather large centroid (or isometric size)
506 compared to modern golden wolves (CCEC. 51000004), all the more it is a young specimen.

507



509 **Fig. 4.** Comparison of species predictions for archaeological dogs, in GMM versus LMM
 510 analyses. A: Classification between wild and domestic: posterior probabilities of the balanced
 511 LDA; B: Visualization of the variability in cranial shape on the first factorial plane of the
 512 PCA in all ancient (N = 8) and modern (N = 157) wild specimens (B1, B2) or on the PCA
 513 performed on the candidate species only (B3, B4) according to GMM (B1, B3) and LMM
 514 (B2, B4) analyses. C: Classification of the wild canid mummies: posterior probabilities of the
 515 balanced LDA.

516 In the PCAs, icon size is proportional to the log10 of the centroid size. Ancient dogs are
 517 represented by red question marks, and modern wild species are indicated in different colors.
 518 See Table 1 and SI 2 for details about the sample, and SI 6 for details about LDA attributions.

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523 **Table 4.** Determination of wild canids among ancient specimens based on Geometric (GMM)
 524 and Linear morphometrics (LMM) and confrontation with data about size (Csize), age,
 525 previous determination and provenance. See SI 6 for detailed attributions and probabilities.
 526 See SI 7 for photographs of the archaeological specimen. CS: Centroid size; IS: isometric
 527 size; DOG: *C. familiaris*; WOLF: *C. lupus*; LUPA: *C. lupaster*; MESO: *L. mesomelas*.
 528 Previous determination: identification made by Louis Lortet and Claude Gaillard or written on
 529 the cranium. Refer to Figure 2 for the distribution of centroid and isometric sizes in modern
 530 species. CCEC.51000004 is rather large for a *C. lupaster*.

ID	Age	GMM 96.4%		LMM 87.3%		Previous determination	Geographic provenance
		LDA	CS	LDA	IS		
CCEC.51000003	Subadult- juvenile	LUPA	0.43	LUPA	1.31	<i>Canis aureus</i>	?
CCEC.51000004	young	LUPA	0.57	LUPA	1.55	<i>Canis doederleini</i> (Lortet & Gaillard, 1909: fig. 202-203)	Assouan
CCEC.51000007	adult	WOLF	0.55	WOLF	1.55	stray dog (Lortet & Gaillard, 1905: fig.4)	Roda
CCEC.51000008	young	dog	0.51	LUPA	1.45	<i>Canis sacer</i> (Lortet & Gaillard, 1909: fig. 199-200)	Assouan
CCEC.51000010	Young /adult	LUPA	0.56	WOLF	1.58		Louqsor
CCEC.51000017	Young/adult	dog	0.54	LUPA	1.59	<i>Canis sp</i>	Tehneh
CCEC.51000031	adult	LUPA	0.49	dog	1.45	<i>Canis sp</i>	?
CCEC.51000242	adult	dog	0.49	LUPA	1.47	<i>Canis sp</i>	?
CCEC.90010304	Young/adult?	WOLF	0.59	dog	1.59	<i>Canis s</i>	Tehneh
CCEC.90010309	subadult	LUPA	0.46	dog	1.37	<i>Canis sp</i>	Roda
CCEC.90010310	Young/adult?	dog	0.51	WOLF	1.45	<i>Canis sp</i>	Roda
CCEC.90010311	subadult	LUPA	0.49	dog	1.41	<i>Canis sp</i>	?

531

532 6. Discussion

533 6.1. Domestic versus wild and identification of wild canids

534 In this study, we demonstrated that 3D geometric morphometrics is a very powerful method
 535 for determining whether ancient mummified canids were domestic dogs or wild canids. In
 536 addition, we found it is much more accurate (with a degree of confidence of over 97%) than
 537 linear morphometrics (88%). We also obtained very satisfying results when determining
 538 species among wild canids for a subset of taxa that more closely resembled the ancient
 539 specimens (*C. lupaster*, *C. lupus*, *L. mesomelas*).

540 When considering the full suite of species likely present in the study region, the determination
 541 of species is more challenging, even when using 3D GMM (though results are much better
 542 than for LMM analyses). In particular, the distinction between *C. lupus*, *C. lupaster* and *C.*
 543 *mesomelas* or between *V. pallida* and *V. rueppellii* remains difficult. Several factors may
 544 come into play here. First, recent changes in the classification (and the ongoing evolution of
 545 taxonomic considerations, as raised in the introduction) made the constitution of the reference
 546 sample challenging. Our modern sample (even if representative of all relevant species)

547 contains few individuals in each group so may not fully represent the variability within the
548 species, nor account for past variation not present in extant populations. Some species are
549 particularly difficult to find in collections. For example, we had only one specimen of *Vulpes*
550 *chama* (but as it is limited to the extreme south of Africa, it is unlikely to be found in ancient
551 mummies) and only two *Canis aureus* (for most specimens identified as golden jackal in the
552 collections, their location suggests that they were in fact *Canis lupaster*). Moreover, we did
553 not find any specimen of bat-eared foxes (*Vulpes cana*) to include it in our study. The native
554 range of this species along the Red Sea coastal mountains in eastern Egypt (as well as in the
555 south of the Arabian peninsula and Iran; Castelló 2018, p. 207) makes it a more likely
556 candidate for inclusion in mummified remains than foxes from more geographically distant
557 areas (e.g. the cape fox *Vulpes chama*). Previous studies suggest that the skull of *V. cana* can
558 be easily distinguished from that of *V. rueppellii* (with which it is sympatric throughout its
559 known African range) by its “smaller size, sharply pointed and relatively long snout” (Saleh et
560 al. 2018, p. 18). It is also larger than *V. zerda* (Castelló 2018, p. 207). Previous studies based
561 on linear morphometrics have shown clear differences between Eurasian golden jackals and
562 African golden wolves, yet morphometric comparisons of cranial shape between these species
563 are scarce. Further research is, therefore, needed before a full evaluation of their presence or
564 absence as mummified remains can be made.

565 Second, some wild canid species are very similar in shape (see SI 1) due to strong
566 morphological convergence, with specimens displaying remarkably similar phenotypes to the
567 point of being mistaken by trained biologists. This may explain our difficulties in
568 distinguishing between *C. lupus*, *C. lupaster* and *C. mesomelas* or between *V. pallida* and *V.*
569 *rueppelli*. Moreover, it is not impossible that some modern specimens from the collections
570 were originally misidentified, thus biasing the results of our predictive models. In our study,
571 *C. lupaster* occupies an intermediate and overlapping morphospace position (Figs 2, 4B)
572 between jackal-like forms and wolf-like forms, as found in previous studies (Machado and
573 Teta 2020). These morphological similarities are in line with previous GMM studies that
574 showed important variation within *Canis lupaster*, with some subspecies showing
575 morphological convergence with other species (e.g. between *C. l. soudanicus* and *L. adusta*,
576 or between *C. l. bea*, *L. mesomeleas* and *C. aureus*). A robust species determination can be
577 postulated by considering the species' current African or near Eastern distribution (when not
578 sympatric), but this cannot be definitive since it presumes that species ranges and distributions
579 have not changed over time.

580 A third significant challenge hinges on the fact that sympatric members of the
581 genus *Canis* can readily hybridize in the wild, and that some of those hybrids are viable and
582 able to form taxonomic complexes that are “ecologically and morphologically distinct from
583 their parent species” (Gopalakrishnan et al. 2018; Machado and Teta 2020). Past
584 hybridization and admixture between domestic and wild canids has been proven, for example,
585 between dogs and African golden wolf (Bahlk 2015; Mallil et al. 2020), golden jackals (Galov
586 et al. 2015) or Iranian wolves (*C. lupus pallipes*; Khosravi et al. 2013). The roaming of feral
587 dogs in ancient Egypt may have promoted this hybridization and could explain why some
588 ancient specimens were more difficult to classify between domestic and wild types. Other
589 studies have identified gene flow between Eurasian golden jackals from Israel and gray
590 wolves, dogs, and the African golden wolf (Koepfli et al. 2015), and between the Ethiopian
591 wolf (*C. simensis*) and the African golden wolf (Bahlk 2015). Some studies have even
592 suggested that the African golden wolf may originate from the hybridization between gray
593 and Ethiopian wolves (Gopalakrishnan et al. 2018).

594 None of these limitations regarding species identification necessarily represent a major
595 obstacle for studies of mummified canid remains. On the one hand ancient Egyptians had a
596 different concept of species classification than we do (Charron 2002). On the other, what also
597 interests us is to obtain information on the supply strategies/sourcing of the animals and
598 related insights into mummification practices in conjunction with religious beliefs. Therefore,
599 the most important classification to be made is between domestic and wild, and the method
600 we outline here is excellent at doing so.

601 **6.2. Statistical bias**

602 By considering large groups (i.e. domestic/wild and *C. lupus/C. lupaster/L. mesomelas*) in our
603 analyses and performing analyses on balanced samples and on the most discriminant PCs, we
604 reduced the number of predictors to below that of the number of individuals of the smallest
605 group and we ensured a satisfying number of specimens to define the reference groups in
606 balanced analyses (n=100 in analyses separating between domestic and wild, i.e. the number
607 of dogs; and n=16 in analyses on the candidate species only, i.e. number of *C. lupus*, Table 1).
608 We can thus consider that our results are robust (Kovarovic et al. 2011). This is all the more
609 important in the case of dogs, considering their tremendous diversity in cranial shape (which
610 is as important as all wild species combined. This result is in line with those of Drake and
611 Klingenberg (2010) who found that “the amount of shape variation among modern domestic
612 dogs [much of which being the result of 200 years of intensive breeding] far exceeds that in

613 modern wild species, and it is comparable to the disparity throughout the Carnivora”; Figs 2
614 and 3). However, a larger sample for each wild species would be needed to provide a more
615 accurate estimate of the precision of our method for wild canids.

616 Additionally, the metadata on the modern sample did not allow us to account for sex or age
617 differences. Due to the determinant role played by sexual dimorphism and ontogeny in cranial
618 shape (Younes and Fouad 2016; Brassard 2020; Machado and Teta 2020), more modern
619 specimens of known sex and age for each species are needed to build more accurate predictive
620 models for example to apply on different age categories of archaeological remains.

621 **6.3. Geometric versus linear morphometrics applied to archaeological remains**

622 To date, Egyptologists have identified cranial remains based on macroscopic criteria (e.g. the
623 relative size of the carnassial, which is unfortunately not always still present in the alveola, or
624 tympanic bubble). Metrics appears useful to classify mummified remains more objectively
625 and are necessary for the examination of large datasets. Linear morphometrics are not
626 sufficient, however, and (as we demonstrate here) 3D geometric methods undoubtedly brings
627 an additional refinement for the identification of species and for estimating wild/domestic
628 ratios in large assemblages.

629 Among the isolated crania of canid mummies from the Musée des Confluences, we identified
630 mainly dogs, but also eight wild canids, belonging to either Near Easter grey wolves or
631 African golden wolves. Ancient DNA analyses would be necessary, however, to confirm our
632 final determinations and thus assess the reliability of the 3D GMM method when applied to
633 ancient remains.

634 One of the mummified canids identified as an African golden wolf (*C. lupaster*) is from Roda,
635 others are from Assouan and Louqsor (Table 6). Those identified as gray wolves (*C. lupus*)
636 are from Roda and Tehneh. Unfortunately, due to the inconsistent recovery and curation
637 practises of the early 20th century, the specimens hosted in many museum collections are
638 rarely properly contextualized (the provenance is not even always known), limiting our
639 interpretations. It will thus be crucial to study specimens from the field to go beyond the
640 simple determination and description, and provide conclusions on the sourcing of the animals.
641 To our knowledge, this is the first study to consider the presence of Near Eastern wolves
642 among canid mummies. It will be necessary to enrich both our modern and archaeological
643 databases prior to questioning deeper the use of this species for mummification.

644 Although showing traits qualitatively indicating its identification as a dog (see SI 7), the
645 cranium of one mummy was clearly attributed to *C. lupaster* (with a probability over 90%,
646 CCEC.510000031, see SI 6). Surprisingly, it shows an advanced degree of dental wear and
647 many dental abnormalities. In particular, it shows signs of advanced periodontitis, with
648 osteolysis at the root of the molars and oronasal fistula (SI 8). Although this is most often
649 observed in domestic dogs or captive animals, Bertè (2017) has described similar traits in a
650 specimen of *C. lupaster* caught from the wild at the oasis of Giarabub (specimen MSNG
651 26228, collected in 1926-1927 by C. Confalonieri; Bertè 2017). The frontal bone of this canid
652 is deformed on both sides and its zygomatic process is very developed (somewhat
653 abnormally), which may bias our determination. This individual could also be a hybrid, or an
654 animal taken from the wild and then bred in captivity. Our identification for this specimen is
655 thus to be taken with caution pending further analysis of other available bones, such as the
656 mandible.

657 Although 3D GMM is efficient for species determination, this method should be seen as is
658 complementary to the qualitative/morphoscopic approach, since it only partially captures
659 shape compared to the human eye. Our own results may have been better had we used sliding
660 semi-landmarks on curves and surface landmarks (i.e. landmarks placed on the whole external
661 surface of the skull). However, this would have allowed us to capture only the skulls with an
662 intact surface, thus reducing our sample size. We instead considered only a limited number of
663 anatomical landmarks to be able to include also crania with a slightly damaged surface
664 (including crania which retained residues of mummified tissue; see example in SI 7).

665 Due to the special nature of the materials under study, we were fortunate enough to have
666 access to significant numbers of complete crania, an uncommon feature of most
667 zooarchaeological collections. Three-dimensional GMM methods can also be applied to
668 fragmented remains more efficiently than linear morphometrics, and we could easily adapt the
669 landmarking protocol to different fragmentation patterns to include more specimens in the
670 analyses, using a subset of the landmarks considered in this paper (for example see Brassard
671 et al. 2022). Moreover, we only analyzed isolated crania, but 3D models could be obtained
672 from medical scanners to access the data without the need to unwrap the mummy.

673 **7. Conclusions and future perspectives**

674 Geometric morphometrics provide a more efficient way of identifying crania in mummified
675 canids from Ancient Egypt compared to traditional linear morphometrics. Based on a sample

676 of 100 modern dogs and 157 modern specimens of 13 wild species from Africa and the Near
677 or Middle East, this study revealed clear differences between modern domestic dogs and wild
678 canids, based on the shape of their cranium. Results revealed that the majority of mummified
679 canids included in this dataset were the remains of domestic dogs. However, the reference
680 sample we used needs to be further expanded to ensure it better represents the full diversity of
681 shape in wild canids. Ancient DNA analyses could be deployed on the same specimens to
682 cross-validate the results with the predictions based on 3D GMM in order to assess the
683 reliability of our method. Once confirmed, the next step would be to apply this method to
684 specimens photographed *in situ* in dog catacombs to further explore the diversity in
685 mummified canids in contextualized sites. Moreover, once wild specimens are identified and
686 removed from the analyses, it will be possible to further explore the diversity of ancient dogs
687 to explore whether, for example, some particular morphologies were favoured over others, or
688 if assumptions can be made on their living condition (feral, captivity), thus opening new
689 perspectives pertaining to the source of canids used for mummification.

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711 **Data availability.** All data generated or analyzed during this study are included in this
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713 the crania are available in SI 9. Detailed information about the sample and methods are
714 provided in SI 2. Raw 3D coordinates of the landmarks considered in GMM analyses are in SI
715 3.

716 **Code availability.** The R code is available from C.B. on request.

717 **Authors' contributions.** C.B. conceptualized the project, set up the study, acquired data,
718 performed the statistical analyses and wrote the first draft of the manuscript. A.E., A.C., S.C.,
719 M.M. and D. T. provided 3D models for shape analyses. H.J. and C.G. collected part of the
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