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## How Does Masticatory Muscle Architecture Covary with Mandibular Shape in Domestic Dogs?

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18 **Abstract**

19 Despite the considerable scientific interest in the variability and patterns of integration in the  
20 dog skull, how these patterns impact or are driven by function remains largely unexplored.  
21 Since the mandible is directly involved in mastication, it can be expected to be directly related  
22 to the development of the adductor and abductor muscles. Here, we explore whether variation  
23 in the architecture and size of the masticatory muscles is associated with the variation in  
24 mandibular shape in dogs. We obtained muscle data from the dissection of 48 dogs from  
25 different breeds and morphotypes to explore the architecture of the muscles and used 3D  
26 geometric morphometric approaches to quantify the shape of the mandible. Covariations  
27 between the masticatory muscles and mandibular shape were explored using two-block partial  
28 least square analyses (2B-PLS). Our results show there is a strong covariation between  
29 mandibular shape and masticatory muscles mass (rPLS from 0.70 to 0.74 for the first axis  
30 representing more than 90% of the total covariance) and physiological cross-sectional area  
31 (rPLS from 0.64 to 0.73 for the first axis representing more than 80% of the total covariance),  
32 irrespective of whether size is taken into account or not. These results suggest muscle size and  
33 thus attachment area requirements for individual muscles are likely drivers of mandibular  
34 shape. Moreover, mandible shape is likely to be a good predictor of muscle force. Finally, it  
35 appears that domestication of dogs has not resulted in a disuse phenotype characterized by a  
36 decoupling between form and function.

37 **Key words:** dog; geometric morphometrics; jaw muscle; mandible; masticatory system

## 38 **Introduction**

39 As a consequence of several thousand years of artificial selection and inbreeding, the  
40 domestic dog has the highest variability in skull shape within the Carnivora (Drake and  
41 Klingenberg 2010; Selba et al. 2019) and encompasses over 400 breeds according to kennel  
42 clubs. The shapes extend beyond the variability of wild species (Drake and Klingenberg  
43 2010), varying from elongated and narrow skull shapes (dolichocephalic) to short and wide  
44 (brachycephalic) skulls. This diversification is the result of a slight relaxation of natural and  
45 functional selection pressures (Drake et al. 2015, 2017; Curth et al. 2017), but more  
46 importantly, depends on anthropogenic selection pressures driven by aesthetic considerations  
47 or the selection of animals for particular skills such as hunting or defense (Drake and  
48 Klingenberg 2008).

49 The genetic mechanisms underlying this diversity are well known (Fondon and Garner 2004;  
50 Bannasch et al. 2010; Boyko et al. 2010; Marchant et al. 2017). For example, the mutation of  
51 BMP3 has been shown to be involved in brachycephaly (Schoenebeck et al. 2012). Integration  
52 and modularity have also been extensively studied within the skull and even the mandible  
53 (Drake and Klingenberg 2010; Meloro et al. 2011; Curth et al. 2017; Curth 2018; Machado et  
54 al. 2018; Selba et al. 2019). However, the functional impact of this extraordinary variability in  
55 shape has received less attention in dogs (but see Ström et al. 1988; Endo et al. 1999; Koch et  
56 al. 2003; Ellis et al. 2008, 2009). Given that artificial selection can have indirect functional  
57 consequences in wild canids such as the red fox (Trut 1999; Trut et al. 2009; Dugatkin 2018),  
58 and since these selection pressures are strong, the resulting morphological changes may have  
59 occurred extremely rapidly (Johnston and Selander 1964; Reznick et al. 1997; Hendry and  
60 Kinnison 1999; Huey et al. 2000; Grant and Grant 2006; Trut et al. 2009; Dugatkin 2018). In  
61 most vertebrates species variation in the shape of the skull and the mandible is linked to  
62 variation in the jaw adductor muscles (Watt and Williams 1951; He and Kiliaridis 2003;  
63 Cornette et al. 2013; Cornette, Tresset, Houssin, et al. 2015; Fabre et al. 2018). Indeed, the  
64 jaw adductors and abductors and the skull and mandible are parts of the same functional unit  
65 with bones providing skeletal struts and levers that are moved by the forces generated by  
66 muscles (Frost and Schönau 2000; Herring et al. 2001; Frost 2003). In addition to the need for  
67 providing muscular attachment, bones are also modified due to the loads imposed by muscle  
68 contraction in addition to external forces such as bite and joint forces (Frost 2001, 2003;

69 Schoenau 2005; Sharir et al. 2011; Brotto and Bonewald 2015). For the jaw system to  
70 function, the muscles and bones need to be coordinated to achieve effective mastication and  
71 biting. As such the system can be expected to be functionally integrated (Olson and Miller  
72 1951; Van Valen 1965; Klingenberg 2014). The quantitative interplay between jaw muscles  
73 and the bones of the skull remains poorly described in domestic dogs (but see Liebman and  
74 Kussick, 1965), in contrast to other mammals (Crompton 1963; Weijs and Hillen 1986;  
75 Hylander et al. 1992, 1998; Herring et al. 2001; Lieberman et al. 2004; Ross and Metzger  
76 2004; Ross et al. 2005; Herring 2007; Ravosa et al. 2007, 2016; Bourke et al. 2008; Cornette  
77 et al. 2013; Cornette, Tresset, and Herrel 2015; Penrose et al. 2016; Fabre et al. 2018)  
78 rendering our understanding of the functional consequences of the tremendous morphological  
79 variation in the skull of domestic dogs limited.

80 Prior studies of *in vivo* bite forces and jaw-muscle electromyography in dogs (Lindner et al.  
81 1995; Ellis et al. 2008; Kim et al. 2018), as well as estimations obtained from the dry-skull  
82 method (Thomason 1991; Ellis et al. 2009) have suggested that differences in morphology are  
83 related to differences in bite force, mainly because of space constraints around the skull, and  
84 because of differences in the length of the in and out-levers of the masticatory apparatus.  
85 However, no study has focused on the architecture of the jaw muscles (fiber length, pennation  
86 angle or muscle mass) in domestic dogs rendering estimates of bite force difficult. In the dry  
87 skull method, the three-dimensional architecture of the jaw muscles is not incorporated  
88 (Schumacher 1961; Miller et al. 1965; Thomason 1991; Ellis et al. 2009), which can result in  
89 underestimates of maximal bite force.

90 The great morphological diversity present in the cranium of dogs provides a unique  
91 opportunity to understand the relationships between morphological variation and muscle  
92 development. Moreover, understanding these relationships would permit better inferences on  
93 the functional impact of selection in dogs. Here we focus on the mandible as this bone is  
94 implicated in a single function: mastication. We expect there to be a direct link between  
95 muscle attachment area and jaw shape, that means, in other words, significant covariations  
96 between jaw muscles architecture (mass and physiological cross-sectional area) and  
97 mandibular shape. However, as recent dog breeds have been selected largely for aesthetic  
98 reasons, we predict that these covariations are likely low. Finally, as the posterior part of the  
99 mandible both serves as the area for muscle insertion and is more strongly impacted by the

100 need for muscle attachment, we expect patterns of covariation to be stronger for the  
101 mandibular ramus.

## 102 **Materials and Methods**

### 103 *Specimens*

104 Specimens were obtained from the Veterinary School of Nantes (France), the Veterinary  
105 School of Maisons Alfort (France), and the laboratory of rabies and wildlife disease studies in  
106 Nancy – Anses (France). The dataset is composed of the mandibles of 59 dogs (*Canis lupus*  
107 *familiaris*) from various breeds (Table 1, see Supplementary material Table S1 for details).  
108 The breeds were estimated based on their similarity to existing standards, but crossbreeding is  
109 important and as such these animals may not represent ‘pure’ breeds. Because accurate ages  
110 were unknown, we estimated ages based on tooth wear, bone texture, and the aspect of the  
111 cranial sutures (degree of closure). The two dogs in the group ‘A’ (a beagle and a bull terrier)  
112 represent the youngest individuals with molars still erupting, a very porous mandible and  
113 unclosed cranial sutures (4-6 months according to Barone, 2010). The beagle in group ‘B’ has  
114 its sphenobasilar suture still open (<8-10 months for the dog according to Barone, 2010) and  
115 the mandible is still porous. The 22 individuals from the group ‘D’ are older, with a closed  
116 interfrontal suture and worn denture (>3-4 years). The 33 other dogs, from the group ‘C’, are  
117 intermediate adults (from 10 months to 3 years). We chose to keep the youngest individuals in  
118 our analyses to increase the morphological variability in the sample. There is no geriatric dog.

119

### 120 *Dissections*

121 Specimens were either dissected when still fresh or frozen and then defrosted (48 dogs). If  
122 preserved in formol, the head was not dissected but directly prepared for shape analyses (an  
123 additional 11 beagles). Dissection of the constituent bellies of the jaw adductor muscles were  
124 done in accordance with the description provided by Penrose et al. (2016), following the  
125 nomenclature of previous authors (Turnbull 1970; Ström et al. 1988; Tomo et al. 1993;  
126 Druzinsky et al. 2011). However the anterior and posterior parts of the  
127 zygomaticomandibularis were separated and the digastric was dissected as well. Since the  
128 lateral pterygoid is very small in carnivores (Turnbull 1970; Herring 2007; Penrose et al.  
129 2016), we considered medial and lateral pterygoids as one single muscle mass.

130 The following muscles were removed layer by layer: the digastric (Dig), the superficial  
131 masseter (MS), the deep masseter (MP), the anterior part of the zygomaticomandibularis

132 (ZMA), the posterior part of the zygomaticomandibularis (ZMP), the suprazygomatic part of  
133 the temporalis (SZ), the superficial temporalis (TS), the deep temporalis (TP), and the  
134 pterygoids (P). The origins and insertions of the nine muscle layers dissected are illustrated in  
135 Fig.1 and described in Supplementary material Table S2.

### 136 *Quantification of jaw muscles architecture*

137 After dissection, all muscle divisions were weighed using a digital scale (Mettler Toledo  
138 AE100). Fiber length and pennation angles were measured directly on the muscle after  
139 sectioning the muscles along their line of action. Several measurements were taken for each  
140 measurement at different location in the muscle, and we used the mean for our calculations.  
141 The reduced Physiological Cross-Section Area (PCSA), which represents a proxy of the  
142 intrinsic strength of the muscles, was calculated for each muscle muscle following the  
143 definition of Haxton (1944), and using a muscle density of 1,06 g/cm<sup>3</sup> (Méndez and Keys  
144 1960).

145 We used the following formula:  $PCSA = \frac{mass (g) * \cos(angle\ of\ pennation\ (rad))}{1,06 (g.cm^{-3}) * fiber\ length\ (cm)}$ .

### 146 *Photogrammetry*

147 After dissection, bones were cleaned and dried. One hundred photographs per right hemi-  
148 mandible were taken while turning around the specimen (Fau et al. 2016). Photos were taken  
149 using a Nikon D5500 Camera (24,2 effective megapixels) with a 60mm lense. The Agisoft  
150 PhotoScan software (© 2014 Agisoft LLC, 27 Gzhatskaya st., St. Petersburg, Russia) was  
151 used for the 3D reconstructions of the mandibles.

### 152 *Landmarking and geometric morphometrics*

153 Geometric morphometric analysis was used to quantify patterns of morphological variation.  
154 Twenty-five homologous anatomical landmarks and 190 sliding semilandmarks on curves  
155 were placed on each specimen using the software Landmark version 3.0.0.6 (© IDAV 2002-  
156 2005; Wiley et al. 2005). Landmark locations are provided in Fig. 2 and Table 2.

157 A template was also created following the method of Cornette et al. (2013) to patch 185  
158 sliding semilandmarks on the mandible surface of all specimens (Fig. 2). The  
159 three- dimensional coordinates for all sets of landmarks were then imported into R version  
160 3.6.0 (2019-04-26). The Morpho package (version 2.7) implemented in R (Schlager 2013)



161 was used for most of the following analyses. A 3D sliding semilandmark procedure  
162 (Bookstein 1997; Gunz et al. 2005) was performed. According to this iterative procedure,  
163 sliding semilandmarks on surfaces are projected from the template onto each specimen using  
164 a thin plate spline deformation (Klingenberg et al. 2002; Gunz et al. 2005; Schlager 2012,  
165 2013). Next, landmarks are slid iteratively while minimizing the bending energy. All sliding  
166 semilandmarks were constrained by homologous landmarks (Gunz et al. 2005) and allowed to  
167 slide along the predefined curves and surfaces. The sliding semilandmarks are consequently  
168 transformed into spatially homologous landmarks. Landmarks coordinates of all specimens  
169 can then be compared using traditional geometric morphometric methods.

#### 170 *Variability in mandibular shape and jaw muscles*

171 A Generalized Procrustes Analysis (GPA – Rohlf and Slice, 1990) was performed using the  
172 function `procSym` (Klingenberg et al. 2002; Gunz et al. 2005; Dryden and Mardia 2016). The  
173 importance and significance of the correlations between mandibular shape and centroid size  
174 and between muscle morphology (PCSA and mass) and centroid size were explored using the  
175 function “`cor.test`”. Allometry-free coordinates and visualisations were obtained using the  
176 functions “`CAC`” (Mitteroecker et al. 2004) and “`showPC`”. Allometry-free coordinates of  
177  $\text{Log}_{10}$ -transformed muscle data were calculated using the function “`lm`”. Principal Component  
178 Analyses (PCA) were performed using the function “`prcomp`” based on the coordinates of all  
179 aligned specimens, on allometry-free coordinates, on the PCSA of all muscles, on the scaled  
180 PCSA of all muscles, on muscle mass and, on scaled muscle mass. The deformation of the  
181 mandible of a beagle to the consensus of the GPA was used as a reference for all further  
182 visualisations. The beagle was chosen because it was the dog that was closest to center of the  
183 PCA describing variation in mandibular shape.

#### 184 *Covariations between mandible shape and jaw muscles*

185 To explore the patterns of covariation between the mandibular shape and the PCSA or mass of  
186 the jaw muscles, we performed a two-block partial least square analyses (2B-PLS) with the  
187 function “`pls2B`” (Rohlf and Corti, 2000). We did not consider phylogeny (Parker et al. 2004)  
188 in our analyses because we had no indication of pure race membership.

189 2B-PLS calculates singular values and creates new axes by looking for linear combinations in  
190 each block that maximise the covariance between blocks (the variation of PCSA or mass of all  
191 the muscles and mandibular shape). For each axis a PLS coefficient is generated (intensity of  
192 the covariation) and p-values are calculated by comparing the singular value to those obtained  
193 from 1000 permuted blocks (significance of the covariation).

194 The mandibular ramus is likely to be more closely associated with space constraints related to  
195 the volume of jaw muscles than the mandibular body. To test whether the covariation was  
196 higher between muscles and the ramus of the mandible only, we explored both covariations  
197 with the complete mandible shape, and with a subset of landmarks and sliding semilandmarks  
198 of curves representing the posterior part of the mandible only.

199 A total of twelve 2B-PLS analyses were conducted: mandibular shape – PCSA, mandibular  
200 shape – scaled PCSA, allometry-free mandibular shape – scaled PCSA, ramus shape – PCSA,  
201 ramus shape – scaled PCSA, allometry-free ramus shape – scaled PCSA, mandibular shape –  
202 mass, mandibular shape – scaled mass, allometry-free mandibular shape – scaled mass, ramus  
203 shape – mass, ramus shape – scaled mass, allometry-free ramus shape – scaled mass.

204 A Z-score was finally calculated to compare PLS coefficients with the function “compare.pls”  
205 from the package geomorph.

## 206 **Results**

### 207 *Variability in mandibular shape*

208 Results of the Principal Component Analyses and correlation tests for exploring allometries  
209 are detailed in Supplementary material Table S3.

210 The first two axes of the PCA represents 46.1% of the variability in mandibular shape. The  
211 next axes each represent a very small part of the total variability (8.9% for axis 3). Only the  
212 morphological variations related to axis 1 and axis 2 – that are the most informative – will  
213 therefore be described (Fig. 3). The mandibular shape varies greatly depending on the  
214 morphotype, and variation is also important within a single breed (beagles). Especially  
215 noticeable is the variation in robustness, the shape of the coronoid process, and the ventral  
216 curvature of the mandibular body. Along the first axis of the PCA, the  
217 molossoid/brachycephalic dogs are generally opposed to dolichocephalic/lupoid dogs. The  
218 first axis is mainly explained by differences in size ( $r=0.51$ ;  $P<0.001$ ) with the biggest  
219 mandibles being positioned to right of the scatterplot. Mesocephalic and dolichocephalic dogs  
220 are not clearly distinguishable and overlap towards the left part of the scatterplot. Most of  
221 these morphological changes are explained by size, since allometry is moderately strong  
222 ( $R^2=0.44$ ;  $P<0.001$ , Fig. S1). Molossoid dogs – which most often correspond to large  
223 mandible sizes – have shorter and more robust and laterally curved mandibles, with more  
224 developed coronoid, condylar, and angular processes. The rostral part of the mandible is more  
225 ventrally curved and the condyle tends to be at a straight angle to the sagittal plane in  
226 molossoid dogs (Figs 3A, S1). Variation along axis two is observed for dogs of the same  
227 breed, as is the case for the Beagle which occupies the entire upper left quadrant of the  
228 scatterplot. This variation is not related to size ( $P>0.05$ ) and describes the rostro-ventral  
229 curvature of the mandible and the orientation of the coronoid process. The two first axes are  
230 not correlated with the age of the dogs ( $P>0.05$ ). The PCA performed on allometry-free  
231 shapes (Fig. 3B) show that dolichocephalic and brachycephalic dogs oppose themselves along  
232 the first axis with the mesocephalic dogs at the very center. The variation along this axis  
233 involves the ventral and lateral curvature of the mandibular body, the width of the coronoid  
234 process and the relative size of the condyle and angular processes. The two youngest dogs are  
235 included in the same morphospace as the adults. Interestingly, the “juvenile” bull terrier is  
236 located in the same part of the scatterplot as the other molossoid dogs when analyses are

237 performed on allometry-free shapes (Fig. 3B). The “juvenile” Beagle remains positioned  
238 close to the adult Beagles.

### 239 *Variability in jaw muscle architecture*

240 Muscle data are given in Supplementary material Table S1 and the results of the statistical  
241 analyses (PCA and correlation tests exploring allometries) are detailed in Supplementary  
242 material Table S3.

243 The angles of pennation are around 0° in the digastric, 30-40° in the temporalis and masseter  
244 and 40° in the pterygoids. Muscles from the temporal complex have very long muscle fibers  
245 (up to 60 mm; mean around 30mm) compared to muscles from the masseteric and pterygoid  
246 complexes (up to 30mm; mean around 15-20mm). The temporal complex represents 64%  
247 (min=55%; max=71%) of the total volume and 50% (min=40%; max=61%) of the total PCSA  
248 of the adductor muscles. The masseteric complex represents 27% (min=22%; max=32%) of  
249 the total volume and 36% (min=29%; max=46%) of the total PCSA of the adductor muscles.  
250 The pterygoid complex represents only 9.6% (min=6%; max=13%) of the total volume and  
251 14% (min=6%; max=24%) of the total PCSA of the adductor muscles. The mass of the lateral  
252 pterygoid muscles represents only around 7% of the mass of the pterygoid complex in the  
253 domestic dog (min=2.5%; max=20.4%) and 0.67% of the total mass of the adductor muscles  
254 (min=0.20%; max=2.4%).

255 Whereas the mass and PCSA of jaw muscles vary greatly depending on breeds, significant  
256 variation is also observed among Beagles. Their morphological space stretches along axis 1,  
257 but mainly along axis 2. Since similar results were observed for mass and PCSA, only the  
258 PCA with muscle PCSAs will be described here (Fig. 4). The PCA with muscle masses is  
259 available in the supplementary material (Supplementary Fig. S2).

260 The first axis of the PCA performed on the raw or scaled PCSA (representing 76.5% or 51.3%  
261 of the total variation, respectively) or mass data (91.7% for raw mass and 71.8% for scaled  
262 mass) loads strongly with the temporalis and masseter muscles. The second axis of the same  
263 analyses explains only a small amount of the total variation (PCSA: 5.5% for raw data and  
264 10.5% for scaled data; mass: 2.3% for raw data and 7.5% for scaled data), and is driven by  
265 variation in the anterior part of the zygomaticomandibularis and the temporalis pars

266 suprazygomatica, for our analyses of PCSA, or by variation in the masseter group (above all  
267 the anterior part of the zygomaticomandibularis) for the PCA on mass.

268 The PCAs with raw muscle data reflect differences in the size of the head. Molossoid dogs –  
269 most often with larger heads – have more powerful jaw muscles than most of the other dogs.  
270 On the opposite, dogs from the Toy group (Chihuahua, Papillon) – characterized by very  
271 small heads – have the smaller and less forceful muscles. Statistical analyses showed that the  
272 variation in muscle volume and force is strongly correlated to variation in mandibular size  
273 (mass:  $r=0.89$ ,  $P<0.001$ ; PCSA:  $r=0.83$ ,  $P<0.001$ ).

274 The PCAs performed on scaled PCSA and scaled mass show that the dogs with biggest and  
275 strongest jaw muscles for their size are large molossoid dogs, represented by a Leonberg, an  
276 American Staffordshire, Mastiffs, a Cane corso, and more markedly the two Rottweillers, the  
277 Pitbull and the two Bulldogs. Surprisingly, the Chihuahua in our sample also has very strong  
278 and voluminous muscles for its size and is positioned close to the Cane Corso, the Rottweiler  
279 and the American stafforshire. The hunting and shepherds dogs (including the German  
280 Shepherd), the Papillon and the Boxers of our sample have medium to low muscle masses and  
281 rather weak muscles for their size. The Cavalier King Charles has masticatory muscle masses  
282 that are larger than the average of our sample when corrected for differences in size (close to  
283 the Cane Corso) but muscle strength is not impacted. Although the small sample size and the  
284 low intra-breed diversity of our sample does not allow us to draw conclusions about breed-  
285 specific diversity our results suggest that this would a fruitful avenue for further research.

### 286 *Covariation between mandibular shape and jaw muscle architecture*

287 A summary of the results of the 2B-PLS is given in Table 3. Detailed results are available in  
288 Supplementary material Table S4. Only the main results are detailed below.

289 The covariation between mandibular shape and the masticatory muscles is highly significant,  
290 whether size is taken into account or not (Table 3). The coefficients of covariation are high,  
291 and they do not significantly differ between muscle masses and muscle PCSAs, and between  
292 scaled and raw muscle data. The coefficients of covariation obtained for the shape of the  
293 ramus only are not higher than the ones for the complete mandible.

294 Here we focus on the covariations between mandibular shape and the scaled muscle data,  
295 since the centroid size is an important driver of covariation (but see supplementary material  
296 for further visualisations and results for the raw data: Figs S3 to S6). The covariation between  
297 scaled PCSA and mandibular shape was significant (Fig. 5), for the first PLS axis (PCSA:  
298 PLS1 88% of the covariance,  $r_{\text{PLS1}}=0.64$ ,  $P<0.001$ ). Similar results were observed for scaled  
299 masses (PLS-1 95% of the covariance,  $r_{\text{PLS1}}=0.70$ ,  $P<0.001$ ,  $Z_{\text{score}}=0.75$ ;  $P=0.23$ ,  
300 Supplementary Fig. S7). The first PLS axis (accounting for 88% of the covariance) shows that  
301 lupoid, graioid and bracioid dogs are situated at the positive part of the scatterplot and oppose  
302 molossoid breeds at the negative part of the scatterplot. All muscles strongly covary with  
303 mandibular shape. The positive part of the scatterplot corresponds to the breeds with a low  
304 PCSA of these muscles and a gracile mandible with a strait and flat body that curves outward,  
305 a higher ventral part of the ramus, a thin, reduced and slightly tilted outwards coronoid  
306 process with a shallow masseteric fossa, a small condyle and a small and straight angular  
307 process. Dogs at the negative part of the scatterplot have robust mandibles with a very  
308 ventrally curved and thick body, a lower ventral part of the ramus, a taller coronoid process  
309 with a deep masseteric fossa, and a large, medially and caudally extended and less medio-  
310 laterally oblique condyle.

311 The covariations between scaled muscle data and ramus shape are significant only on  
312 secondary axes, explaining less than 16% of the covariance. The 2B-PLS between the  
313 mandible ramus shape and the scaled masses of the jaw muscles (PLS-2 21% of covariation,  
314  $r_{\text{-PLS2}}=0.63$ ,  $P=0.006$ , Fig. 6) shows that dogs with more voluminous deep masseter muscles  
315 and less voluminous temporal muscles and superficial masseters for their size have a more  
316 curved coronoid process with a deeper masseteric fossa and a lower and less curved angular  
317 process (and *vice versa*). Similar results were observed for the third axis of the 2B-PLS  
318 between ramus shape and the scaled PCSA (Supplementary Fig. S8) and for the second axis  
319 of the 2B-PLS between allometry-free ramus shape and scaled masses (Supplementary Fig.  
320 S9).

321 Similar results were observed for allometry-free mandibular shape and scaled PCSA (Fig. 7)  
322 or scaled mass (Fig. S9). Changes in the body of the mandible along the first PLS axis are the  
323 same as those previously described except some more specific anatomical features for the  
324 coronoid process. For a given size of the coronoid process dogs with less forceful muscles

325 have a more caudally curved and narrower coronoid process (with a shallower masseteric  
326 fossa) contrary to dogs with stronger muscles which have a wider and thicker coronoid  
327 process (with a deeper masseteric fossa).

328 Significant covariations between allometry-free shape of the mandible ramus and scaled  
329 masses show that a more caudally curved coronoid process and a less pronounced and curved  
330 angular process are related to proportionally more developed deep masseter muscles and a  
331 proportionally less developed superficial masseter muscle (Fig. S10).

## 332 **Discussion**

### 333 *Variations in mandibular shape and masticatory muscles*

334 The general shape of the mandibular ramus and the relative importance of masticatory  
335 muscles in dogs reflects the specialization towards vertical movements as in other canids.  
336 Indeed, the condyle is cylinder-shaped, mediolaterally elongated, curved backwards, and at a  
337 right angle to the sagittal plane. Moreover, the temporal and masseteric complexes  
338 responsible for the vertical movements of the jaw are by far the most strongly developed in  
339 canids since they represent around 90% of the mass and intrinsic strength of the adductor  
340 muscles. This corroborates descriptions of previous authors (Schumacher 1961; Turnbull  
341 1970; Noble 1973; Ström et al. 1988). The pterygoid muscles – that have a more medio-lateral  
342 line of action – are small and the shape of the condyle permits only limited medio-lateral  
343 rotational movements that function to bring the blades of the carnassials into close contact  
344 (Ström et al. 1988; Ewer 1998). The lateral pterygoid is very small (it represents less than 3%  
345 of the of the total mass of the adductor muscles) and its role is ambiguous because it could be  
346 involved in both mandibular protraction and adduction (Turnbull 1970; Tomo et al. 1993;  
347 Evans and DeLahunta 2010).

348 The proportions in volume and PCSA of the different muscles were not the same. For  
349 example, even though the pterygoid complex always represents less than 13% of the total  
350 mass of the adductor muscles, it can represents up to 24% of the total intrinsic strength of the  
351 adductor muscles, indicating that these muscles are optimized for force production. This is  
352 because muscles with longer fibers (temporal) are in proportion ‘disadvantaged’ compared to  
353 muscles with shorter fibers (pterygoids or masseter). This reflects an architectural trade-off  
354 between PCSA and fiber length: a muscle cannot be optimized for both force production and  
355 contraction velocity (Gans and Bock 1965; Taylor and Vinyard 2013). The PCSA data  
356 provided here are further of interest as they may provide better estimations of bite force than  
357 estimations obtained from models using the ‘dry-skull’ method (Thomason 1991; Ellis et al.  
358 2009). However, muscle PCSAs are only general proxies of maximal intrinsic muscle force.  
359 Muscle loads on the mandible will also depend on the size and position of the attachment sites  
360 of the jaw muscles on the skull and mandible, on the unbalanced and uncomplete recruitment  
361 of the muscle during biting (Kim et al. 2018), and on the nature of the muscle fibers  
362 (Grünheid et al. 2009; Kim et al. 2018).



363 Extreme variation has already been demonstrated for the skull (Drake and Klingenberg 2010;  
364 Selba et al. 2019) and is generally considered to be the result of intensive dog breeding and  
365 artificial selection for aesthetic reasons. Our study demonstrates that the masticatory muscles  
366 and the shape of the mandible also show important variation related to variation in the size of  
367 the individuals and the type of breed. Breeds represented by several individuals, such as  
368 Beagles, also showed unexpected levels of variation. Although we had too few young  
369 individuals to assess the effect of ontogeny this is also likely to contribute to the overall  
370 diversity in both mandible shape and muscle architecture.

371 The different muscle layers show an important diversity in mass, but also in intrinsic muscle  
372 strength due to the great variation in fiber length and pennation angles (Supplementary  
373 material Table S1), making the architecture of the jaw muscles complex. Our results indicate  
374 that the masticatory muscles scale isometrically relative to mandibular size, which  
375 corroborates the results of Penrose et al. (2016). The molossoid dogs of our sample generally  
376 have the strongest and most voluminous muscles. On the contrary, the dogs from the Toy  
377 group of our sample (the Chihuahua, the King Charles and the Papillon) have very small  
378 muscles, logically resulting in a lower intrinsic force generation capacity. However our  
379 analyses suggest that some dogs of very small breeds such as the Chihuahua – the smallest  
380 breed recognized by kennel clubs – tend to have muscles that are as imposing and as powerful  
381 as those of some specimens of Cane Corso, Rottweiler or American Staffordshire when size  
382 is taken into account. However, the low intrabreed diversity in our sample does not allow us  
383 to explicitly test for differences between breeds. Future studies are needed to explore this  
384 further. In our study, the only German Shepherd is included within the variability of the other  
385 shepherd dogs in our sample, with less voluminous and powerful muscles irrespective of  
386 variation in size. As stated above, our sample does not allow to draw conclusions on breed-  
387 specific diversity but it would be interesting to test whether German Shepherd dogs are  
388 grouped with other shepherd dogs or with breeds dedicated to protection . Indeed, the German  
389 Shepherd is a very “multi-skilled” breed, that has been modified as an army or police dog but  
390 that was originally designed to be a working shepherder (Parker et al. 2004).

### 391 *Relations between mandibular shape and the development of masticatory muscles*

392 As predicted, we found significant covariation between the shape of the mandible and the  
393 development of the masticatory muscles irrespective of whether size is taken into account or

394 not. This study logically suggests that there is a strong association between muscle volume  
395 and mandibular form. The coefficient of covariation of the 2B-PLS with allometry-free shape  
396 and/or scaled muscle data is not different from the 2B-PLS on raw data and remains elevated.  
397 Therefore, size alone is not enough to explain the existing covariation. The dispersion of the  
398 individuals along the PLS axis for the 2B-PLS with scaled muscle data (Fig. 5-7,  
399 Supplementary Fig. S7-S10) shows, however, that similar mandibular morphologies can  
400 correspond to different relative muscle volumes or strength. For example, among the three  
401 dogs from the Toy group of our sample, the Chihuahua and the Papillon have very similar  
402 mandibular shapes but the Chihuahua dog has much more powerful and voluminous muscles  
403 than the Papillon when size is removed. This suggests significant differences in muscle  
404 architecture among dogs with similar morphotypes.

405 Morphological changes that appear directly related to muscle volume and strength involve  
406 areas of insertion of the masticatory muscles: the size and shape of the coronoid process, the  
407 depth of the masseteric fossa and the size and curvature of the angular process. This suggests  
408 that the attachment area requirements for individual muscles likely drive mandibular shape.  
409 Muscle volume and strength are also related to changes in general features, such as the  
410 robustness of the mandible, the ventral and lateral curvature of the body and the size of the  
411 condyle. Surprisingly, covariations are not significantly different when considering the  
412 posterior part of the mandible only relative to the entire mandible. This suggests that the  
413 curvature and thickness of the body where no muscles attach and which bears the dental  
414 alveoli, also covaries with the shape of the ramus. Indeed, the body and the ramus together  
415 form an integrated system adapted to the mechanical constraints of biting and chewing. The  
416 shape associated with low (scaled or not scaled) muscle masses and PCSAs is characterised  
417 by a relatively long and flat body, a small coronoid process curved at its posterior tip, a  
418 shallow masseteric fossa, and a small and ventromedial oblique condyle. On the contrary,  
419 shapes related to large and strong muscles correspond to robust mandibles with a relatively  
420 large, wide coronoid process with a deep masseteric fossa, a laterally and ventrally curved  
421 ramus, and a (medially) long and large condyle. All these changes can be explained by muscle  
422 volume, conditioning the space available for those muscles and responses to loading of the  
423 mandible at the teeth. Accordingly, for dogs with big and strong muscles (mainly large  
424 brachycephalic dogs), the mandible is more curved in the medio-lateral plane. This tempo-  
425 mandibular joint axis rotation has been described by Curth et al. (2017) and interpreted as a

426 result of reduced space availability in short-faced skulls. However, this could also be a  
427 mechanical adaptation to the volume occupied by the temporal and masseter muscles. An  
428 inclined mandible is more suited to allow large muscles to pass between the skull and the  
429 mandible and goes hand-in-hand with wider zygomatic arches in brachycephalic breeds. The  
430 slightly opposing orientations of the coronoid process and mandibular body (medially inclined  
431 condyle and body anteriorly curved outwards in dolichocephalic dogs) seem to reflect a  
432 compromise in shape to distribute the forces exerted on the mandible, allowing both muscle  
433 attachment and vertical opening/closing movements. Thus the change in the angle between  
434 the coronoid process and the condyle could be a mechanical response to the reaction forces  
435 and important for joint stabilisation.

436 All muscles covary together on the first axis of the 2B-PLS with the complete mandible  
437 (explaining more than 80% of the covariation; Figs 5, 7, S3, S4, S7, S9) but the secondary  
438 axis of the 2B-PLS performed with the mandible ramus only (explaining up to 20% of the  
439 covariation; Fig. 6, Supplementary Figs S5, S6, S8, S10) allowed us to describe more specific  
440 variations. We observed that the more the superficial masseter, the temporal complex and the  
441 pterygoid muscles were developed, the straighter the coronoid process was. On the opposite,  
442 the bigger the deep masseter and zygomaticomandibularis, the more caudally curved the  
443 coronoid process. Liebman and Kussick (1965) described variation in the morphology of the  
444 mandible depending on the removal of the temporal or masseter on one side of the head of a  
445 dog. They report that the variation in shape of the angular process is likely to be due to  
446 variation in both the pterygoid and masseter muscles. Indeed, the angular process tended to be  
447 straight rather than curved when the masseter muscle was removed. This description is  
448 consistent with our observations (Figs 6, S8, S10). For these authors, the shape of the  
449 coronoid process is more probably linked to the temporal muscle. They observed that the  
450 coronoid process tended to be straighter after removing the temporal muscle, whereas on the  
451 normal side the coronoid process was more caudally oriented. Our own observations,  
452 however, do not support these results (Figs 6, S8, S10). This could be due to a balance  
453 between the masseteric and temporal complexes. Liebman and Kussick (1965) completely  
454 removed one of the two complexes so their observations do not take these interactions into  
455 account. In our 2B-PLS showing opposing loadings (Figs 6, S8, S10), both complexes play a  
456 role in the construction of the PLS-1 axis. The less developed the temporal complex is, the  
457 more developed the deep masseter, including the zygomaticomandibularis. As the

458 zygomaticomandibularis anterior inserts mainly on the anterior part of the masseteric fossa to  
459 the tip of the coronoid process, a bigger muscle would involve a more important surface area.  
460 This could explain why we observed more caudally curved coronoid process in dogs with a  
461 relatively more imposing zygomaticomandibularis.

462 However, our study did not allow to explore the mechanical relations between mandible shape  
463 and muscle loading per se. Further investigations would be needed to explore the connection  
464 between bone resistance and muscle force through, for example, finite element analyses (e.g.  
465 Bourke et al. 2008; Kim et al. 2018; Penrose et al. *under review*). An interesting and  
466 complementary approach may be to investigate the link between mandible shape and bone  
467 cortical thickness and its degree of biomineralization to track functional variation according to  
468 load resistance (Ross et al. 2005; Kupczik et al. 2007; Rayfield 2007; Cox et al. 2015).  
469 Indeed, even though the shape of the mandible is the combined result of phylogeny and  
470 developmental constraints, its shape also depends on mechanical loading (Weijs and Hillen  
471 1986; Wolff 1986; Hannam and Wood 1989; Raadsheer et al. 1999; Currey 2002, 2003;  
472 Daegling and Hotzman 2003; Mavropoulos et al. 2004; Ravosa et al. 2007; Sharir et al. 2011;  
473 Slizewski et al. 2013). Furthermore, it has been shown that the relationship between bone  
474 morphology and muscle force is reciprocal, as the shape of a bone determines the load that it  
475 can tolerate (Weiner and Wagner 1998; Frost 2001). As a result, the mandible is plastic: it is  
476 constantly modeled throughout life to be able to resist the changes in the mechanical  
477 environment, that is the muscle forces and external forces exerted upon it during chewing  
478 (Frost 2001; Currey 2002; Fabre et al. 2018). Accordingly, it has been demonstrated that  
479 increased physical activity affects the geometry and composition of bones, whereas decreased  
480 loads due to enforced rest or muscle dysfunctions result in thinner bones (Schoenau 2005;  
481 Ward et al. 2006). Among other external constraints, diet is likely to play a significant role in  
482 mandible shape. We had no information about the diet of the individuals in our sample, but  
483 further studies exploring the influence of food texture on mandible shape and the mechanical  
484 properties of the cortical bone of the mandible would be of interest. Indeed, it has been  
485 demonstrated that food mechanical properties influence cortical bone modelling and  
486 remodelling (Bouvier and Hylander 1981, 1984; Lieberman et al. 2004; Ionova-Martin et al.  
487 2011; Scott et al. 2014a, 2014b; Ravosa et al. 2015, 2016). The study of Scott et al (2014a) on  
488 rabbits lead them to suggest that mammals may be very plastic even at late life-history stages.  
489 All these elements might explain the observed differences among the different dogs in our

490 study (Bouvier and Hylander 1981, 1984). Moreover it would be interesting to study how  
491 pathologies that impact muscle development (dysplasia and jaw locking) affect mandible  
492 shape (Robins and Grandage 1977; Johnson 1979; Thomas 1979; Hoppe and Svalastoga  
493 1980; Ström et al. 1988). Indeed, according to He and Kiliaridis (2003), the alteration of  
494 masticatory muscle function can affect the morphology of certain regions of the skull and face  
495 in ferrets. Additionnaly, we could not explore the role of ontogeny because we had too few  
496 juveniles to test for the effect of age. Future studies could explore the evolution of the  
497 interplay between bone and jaw muscles in dogs through postnatal development, as it has  
498 been done in other mammals (Swiderski and Zelditch 2013). Indeed, muscle  
499 provides growth factors for bone tissue throughout postnatal development independently of  
500 forces imparted to bones. This can significantly impact bone formation at attachment areas  
501 and might thus be a source of the observed patterns of covariation between muscle size and  
502 the shape of the mandibular ramus.

### 503 *Domestication and integration in the masticatory apparatus*

504 As predicted, jaw muscle architecture covaries with mandibular shape, but we did not expect  
505 such a strong covariation.

506 Integration is produced by the sharing of biological processes such as the same developmental  
507 origin or the implementation of the same function (Olson and Miller 1951, 1958, 1999). This  
508 strong integration makes sense given that bone is a living and plastically remodelled tissue,  
509 causing changes in the shape of the mandible in direct response to muscle and jaw loading.  
510 However we expected the extreme diversity in shapes due to artificial selection to interfere  
511 with this functional integration, as many domestic dogs are not under strong functional  
512 constraints for chewing or biting. This is even more surprinsing as a low integration has been  
513 documented in strepsirrhine primates, which are, on the contrary, subject to strong natural  
514 selection and dietary constraints (Fabre et al. 2018).

515 We suggest that this strong integration is perhaps determined by a strong interaction between  
516 genes responsible for the mandibular shape and genes responsible for the development of jaw  
517 muscles. Muscle development would therefore be intrinsically linked to bone development.  
518 Consequently, selection on morphology would therefore produce a correlated response in the  
519 functional abilities (Cheverud 1982; Klingenberg 2010, 2014). Muscles and bones indeed

520 share common genetic determinants (Karasik and Kiel 2008; Blank 2014) and cells derive  
521 from a common mesenchymal precursor. Multiple loci overlapping between the two traits and  
522 several genes with possible pleiotropic effects on both bones and muscles have been  
523 indentified (Kaji 2014). As a consequence, it is possible that some genes may trigger changes  
524 in bone anatomy, and as a result, affect muscle architecture (Karasik and Kiel 2008). It is also  
525 plausible that slight changes of systemic control factors occurs during development and  
526 impact both muscle and bone (e.g., small modulations of the growth hormone; Karasik and  
527 Kiel, 2008). Genetic muscle disorders provide an opportunity to learn how muscle and bone  
528 interact. For example, a myostatin deficiency (*growth differentiation factor 8* [*GDF8*]) is  
529 observed in the whippet dog breed (Mosher et al. 2007) and results in a ‘bully’ whippet, with  
530 an approximate doubling of muscle mass and resulting in more robust bones. Observed  
531 allometries in muscle data and covariations between muscle data and shape supports the  
532 genetic influence on both bone and muscle, as well as integration (Karasik and Kiel 2010).  
533 However, more investigations on the genetic and molecular interplay between jaw muscles  
534 and the mandible are needed to better understand the drivers of variation in the masticatory  
535 apparatus.

536 Moreover, our study seems to suggest that dogs show different patterns of integration  
537 according to their function. Breeds first selected for hunting or herding differ from the dogs  
538 that were first selected for human or herd protection. It seems that the selection for different  
539 biting abilities has resulted in different patterns of integration. Further studies focusing on a  
540 much larger sample are, however, needed to investigate whether dog breed selection is related  
541 to specialisations towards specific patterns of covariation between muscle and bones.

542 Our results raise the question of whether artificial selection produces a reorganization of the  
543 integration patterns in order to allow morphological traits to vary, as proposed by Hanot et al.  
544 (2018). Karasik and Kiel (2010) suggested that natural selection tends to favour alleles whose  
545 pleiotropic effects contribute to the attainment of appropriate proportions between muscles  
546 and bones, and the pattern of covariation is expected to evolve to match fitness demands. As a  
547 consequence, one would expect stronger integration among wild species since it responds to  
548 environmental selection pressures driving the jaw system towards an ‘optimum’  
549 corresponding to the ecological context, and resulting in less morphological variability,  
550 especially for the wolf (Curth et al. 2017). We had no wolves in our sample which would be

551 essential to test this hypothesis, but comparing our results with those non-domestic canids  
552 could help understand whether the phenotypic diversification of dogs is responsible for a  
553 change in integration pattern, and how integration may constrain changes in morphology or  
554 jaw muscle development.

## 555 **Conclusion**

556 Our study assessed the impact of the dramatic variation in mandible shape in domestic dogs  
557 on the development and architecture of the masticatory muscles. Our results suggest that jaw  
558 muscles and mandible shape form a highly integrated system in dogs. This could be the  
559 consequence of genes controlling both muscle and bone development, as well as epigenetic  
560 effects driving variation in muscles and bones (Inuma et al. 1991) or the interaction between  
561 genetic mechanisms and plasticity (Hanot et al. 2017). Our results provide a better  
562 understanding of jaw function in dogs which despite its general interest remains rather poorly  
563 understood (Ellis et al. 2008, 2009). To further test whether mandibular form is driven by  
564 attachment area requirements and/or load resistance, finite element approaches may be of  
565 interest. The strong integration of the lower jaw offers the possibility to infer the functional  
566 consequences of morphological changes in fossil or archaeological specimens. Despite this  
567 strong integration, the question remains whether integration is stronger in wild or commensal  
568 canids, and whether domestication has led to a disruption of the natural integration between  
569 form and function as suggested previously.

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## 581 **Conflict of interest**

582 The authors declare that they have no conflicts of interest.



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963 **Figure legends**

964 **Fig. 1**

965 Schematic illustration of the jaw muscles dissected in this study. Muscles in medial to  
966 mandible are rendered transparent.

967 **Fig. 2**

968 Position of the landmarks used in this study and mandible features following Budras (2007),  
969 Barone (2010), Evans and DeLahunta (2010). Anatomical landmarks are indicated in red,  
970 sliding semi-landmarks of curves are in blue and sliding semi-landmarks on the surface are in  
971 green. AM: angle of mandible; B: body of mandible; R : ramus of mandible; con: condyloid  
972 process; cor: coronoid process; ang: angular process; is: intermandibular suture; n: mandibular  
973 notch; he: head of mandible; ne: condylar neck; vb: ventral border; fos: masseteric fossa;  
974 conc: condyloid crest; corc: coronoid crest; manf: mandibular foramen; menf: main mental  
975 foramen; can: canine; car: carnassial (M1).

976 **Fig. 3**

977 First two axes of the PCA describing variation in: A) mandibular shape; B) allometry-free  
978 mandibular shape. The mesh of the consensus is represented in white. Illustrations represent  
979 the deformations from the consensus to the extreme of the axis in lateral, dorsal and caudal  
980 views for PC1 and in lateral view for PC2. Ages are indicated by colors. Beagles are in green  
981 and other breed names are indicated following Table 1.

982 **Fig. 4**

983 PCA describing variation in A) PCSA or B) scaled PCSA of the jaw muscles. Histograms  
984 represent the loadings of the original variables on the axes. Dig: Digastric; MS: masseter pars  
985 superficialis; MP: masseter pars profunda; ZMA: masseter pars zygomaticomandibularis  
986 anterior; ZMP: masseter pars zygomaticomandibularis posterior; SZ: temporalis pars  
987 suprazygomatica; TS: temporalis pars superficialis; TP: temporalis pars profunda; P:  
988 pterygoids. Ages are indicated by colors. Beagles are in green and other breed names are  
989 indicated following Table 1.

990 **Fig. 5**

991 2-Block Partial Least Square Analyses between mandibular shape and the scaled PCSA of jaw  
992 muscles, with muscle vectors and shapes at the minimum and maximum of the PLS axis.

993 Illustrations represent the deformations from the consensus to the extreme of the axis in  
994 lateral, dorsal and caudal views. Dig: Digastric; MS: masseter pars superficialis; MP:  
995 masseter pars profunda; ZMA: masseter pars zygomaticomandibularis anterior; ZMP:  
996 masseter pars zygomaticomandibularis posterior; SZ: temporalis pars suprazygomatica; TS:  
997 temporalis pars superficialis; TP: temporalis pars profunda; P: pterygoids. Ages are indicated  
998 by colors. Beagles are in green and other breed names are indicated following Table 1.

999 **Fig. 6**

1000 2-Block Partial Least Square Analyses between the shape of the ramus and the scaled mass of  
1001 jaw muscles, with muscle vectors and shapes at the minimum and maximum of the PLS axis.  
1002 Illustrations represent the deformations from the consensus to the extreme of the axis in  
1003 lateral, dorsal and caudal views. Dig: Digastric; MS: masseter pars superficialis; MP:  
1004 masseter pars profunda; ZMA: masseter pars zygomaticomandibularis anterior; ZMP:  
1005 masseter pars zygomaticomandibularis posterior; SZ: temporalis pars suprazygomatica; TS:  
1006 temporalis pars superficialis; TP: temporalis pars profunda; P: pterygoids. Ages are indicated  
1007 by colors. Beagles are in green and other breed names are indicated following Table 1.

1008 **Fig. 7**

1009 2-Block Partial Least Square Analyses between allometry-free mandibular shape and the  
1010 scaled PCSA of jaw muscles, with muscle vectors and shapes at the minimum and maximum  
1011 of the PLS axis. Illustrations represent the deformations from the consensus to the extreme of  
1012 the axis in lateral, dorsal and caudal views. Dig: Digastric; MS: masseter pars superficialis;  
1013 MP: masseter pars profunda; ZMA: masseter pars zygomaticomandibularis anterior; ZMP:  
1014 masseter pars zygomaticomandibularis posterior; SZ: temporalis pars suprazygomatica; TS:  
1015 temporalis pars superficialis; TP: temporalis pars profunda; P: pterygoids. Ages are indicated  
1016 by colors. Beagles are in green and other breed names are indicated following Table 1.

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1020 **Supplementary material**

1021 The online version of this article contains supplementary material, which is available to  
1022 authorized users.

1023 **Supplementary material Table S1**

1024 Details of the specimen used in this study including raw jaw muscles data and PCSAs.

1025 **Supplementary material Table S2**

1026 Origin and insertion of the jaw muscles dissected in this study, after a synthesis of  
1027 nomenclatures proposed by Schumacher (1961), Turnbull (1970), Ström et al. (1988), Tomo  
1028 et al. (1993), Christiansen and Adolfssen (2005), Budras (2007), Barone (2010), Evans and  
1029 DeLahunta (2010), Hung et al. (2010), Druzinsky et al. (2011), Hartstone-Rose et al. (2012),  
1030 Flahive (2015), Penrose et al. (2016).

1031 **Supplementary material Table S3**

1032 Results of the statistical analyses exploring allometries (sheet 1) and the variability (sheet 2)  
1033 in mandibular shape and muscle data.

1034 **Supplementary material Table S4**

1035 Results of the 2-Block Partial Least Square Analyses (sheet 1) and P-values and Z-scores of  
1036 the comparison tests (sheet 2). S: shape of the mandible; rS: shape of the ramus; a: allometry-  
1037 free (shape or shape of the ramus); M: mass; PCSA: PCSA; s: scaled (mass or PCSA).  
1038 Significant results ( $p$ -value  $< 0.05$ ) are indicated in bold.

1039 **Supplementary Fig. S1**

1040 Distribution of the specimens along the allometric slope with a visualisation of the differences  
1041 between large and small specimens relative to consensus shape. Ages are indicated by colors.  
1042 Beagles are in green and other breed names are indicated following Table 1.

1043 **Supplementary Fig. S2**

1044 PCA describing variation in A) mass or B) scaled mass of the jaw muscles. Histograms  
1045 represent the loadings of the original variables on the axes. Dig: Digastric; MS: masseter pars  
1046 superficialis; MP: masseter pars profunda; ZMA: masseter pars zygomaticomandibularis  
1047 anterior; ZMP: masseter pars zygomaticomandibularis posterior; SZ: temporalis pars  
1048 suprazygomatica; TS: temporalis pars superficialis; TP: temporalis pars profunda; P:

1049 pterygoids. Ages are indicated by colors. Beagles are in green and other breed names are  
1050 indicated following Table 1.

1051 **Supplementary Fig. S3**

1052 2-Block Partial Least Square Analyses between mandibular shape and the PCSA of jaw  
1053 muscles, with muscle vectors and shapes at the minimum and maximum of the PLS axis.  
1054 Illustrations represent the deformations from the consensus to the extreme of the axis in  
1055 lateral, dorsal and caudal views. Dig: Digastric; MS: masseter pars superficialis; MP:  
1056 masseter pars profunda; ZMA: masseter pars zygomaticomandibularis anterior; ZMP:  
1057 masseter pars zygomaticomandibularis posterior; SZ: temporalis pars suprazygomatica; TS:  
1058 temporalis pars superficialis; TP: temporalis pars profunda; P: pterygoids. Ages are indicated  
1059 by colors. Beagles are in green and other breed names are indicated following Table 1.

1060 **Supplementary Fig. S4**

1061 2-Block Partial Least Square Analyses between mandibular shape and the mass of jaw  
1062 muscles, with muscle vectors and shapes at the minimum and maximum of the PLS axis.  
1063 Illustrations represent the deformations from the consensus to the extreme of the axis in  
1064 lateral, dorsal and caudal views. Dig: Digastric; MS: masseter pars superficialis; MP:  
1065 masseter pars profunda; ZMA: masseter pars zygomaticomandibularis anterior; ZMP:  
1066 masseter pars zygomaticomandibularis posterior; SZ: temporalis pars suprazygomatica; TS:  
1067 temporalis pars superficialis; TP: temporalis pars profunda; P: pterygoids. Ages are indicated  
1068 by colors. Beagles are in green and other breed names are indicated following Table 1.

1069 **Supplementary Fig. S5**

1070 2-Block Partial Least Square Analyses between the shape of the ramus and the PCSA of jaw  
1071 muscles, with muscle vectors and shapes at the minimum and maximum of the PLS axis.  
1072 Illustrations represent the deformations from the consensus to the extreme of the axis in  
1073 lateral, dorsal and caudal views. Dig: Digastric; MS: masseter pars superficialis; MP:  
1074 masseter pars profunda; ZMA: masseter pars zygomaticomandibularis anterior; ZMP:  
1075 masseter pars zygomaticomandibularis posterior; SZ: temporalis pars suprazygomatica; TS:  
1076 temporalis pars superficialis; TP: temporalis pars profunda; P: pterygoids. Ages are indicated  
1077 by colors. Beagles are in green and other breed names are indicated following Table 1.

1078 **Supplementary Fig. S6**

1079 2-Block Partial Least Square Analyses between the shape of the ramus and the mass of jaw  
1080 muscles, with muscle vectors and shapes at the minimum and maximum of the PLS axis.  
1081 Illustrations represent the deformations from the consensus to the extreme of the axis in  
1082 lateral, dorsal and caudal views. Dig: Digastric; MS: masseter pars superficialis; MP:  
1083 masseter pars profunda; ZMA: masseter pars zygomaticomandibularis anterior; ZMP:  
1084 masseter pars zygomaticomandibularis posterior; SZ: temporalis pars suprazygomatica; TS:  
1085 temporalis pars superficialis; TP: temporalis pars profunda; P: pterygoids. Ages are indicated  
1086 by colors. Beagles are in green and other breed names are indicated following Table 1.

### 1087 **Supplementary Fig. S7**

1088 2-Block Partial Least Square Analyses between mandibular shape and the scaled mass of jaw  
1089 muscles, with muscle vectors and shapes at the minimum and maximum of the PLS axis.  
1090 Illustrations represent the deformations from the consensus to the extreme of the axis in  
1091 lateral, dorsal and caudal views. Dig: Digastric; MS: masseter pars superficialis; MP:  
1092 masseter pars profunda; ZMA: masseter pars zygomaticomandibularis anterior; ZMP:  
1093 masseter pars zygomaticomandibularis posterior; SZ: temporalis pars suprazygomatica; TS:  
1094 temporalis pars superficialis; TP: temporalis pars profunda; P: pterygoids. Ages are indicated  
1095 by colors. Beagles are in green and other breed names are indicated following Table 1.

### 1096 **Supplementary Fig. S8**

1097 2-Block Partial Least Square Analyses between the shape of the ramus and the scaled PCSA  
1098 of jaw muscles, with muscle vectors and shapes at the minimum and maximum of the PLS  
1099 axis. Illustrations represent the deformations from the consensus to the extreme of the axis in  
1100 lateral, dorsal and caudal views. Dig: Digastric; MS: masseter pars superficialis; MP:  
1101 masseter pars profunda; ZMA: masseter pars zygomaticomandibularis anterior; ZMP:  
1102 masseter pars zygomaticomandibularis posterior; SZ: temporalis pars suprazygomatica; TS:  
1103 temporalis pars superficialis; TP: temporalis pars profunda; P: pterygoids. Ages are indicated  
1104 by colors. Beagles are in green and other breed names are indicated following Table 1.

### 1105 **Supplementary Fig. S9**

1106 2-Block Partial Least Square Analyses between between allometry-free mandibular shape and  
1107 the scaled mass of jaw muscles, with muscle vectors and shapes at the minimum and  
1108 maximum of the PLS axis. Illustrations represent the deformations from the consensus to the  
1109 extreme of the axis in lateral, dorsal and caudal views. Dig: Digastric; MS: masseter pars

1110 superficialis; MP: masseter pars profunda; ZMA: masseter pars zygomaticomandibularis  
1111 anterior; ZMP: masseter pars zygomaticomandibularis posterior; SZ: temporalis pars  
1112 suprazygomatica; TS: temporalis pars superficialis; TP: temporalis pars profunda; P:  
1113 pterygoids. Ages are indicated by colors. Beagles are in green and other breed names are  
1114 indicated following Table 1.

1115 **Supplementary Fig. S10**

1116 2-Block Partial Least Square Analyses between the allometry-free shape of the ramus and the  
1117 scaled mass of jaw muscles, with muscle vectors and shapes at the minimum and maximum of  
1118 the PLS axis. Illustrations represent the deformations from the consensus to the extreme of the  
1119 axis in lateral, dorsal and caudal views. Dig: Digastric; MS: masseter pars superficialis; MP:  
1120 masseter pars profunda; ZMA: masseter pars zygomaticomandibularis anterior; ZMP:  
1121 masseter pars zygomaticomandibularis posterior; SZ: temporalis pars suprazygomatica; TS:  
1122 temporalis pars superficialis; TP: temporalis pars profunda; P: pterygoids. Ages are indicated  
1123 by colors. Beagles are in green and other breed names are indicated following Table 1.