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1 **A shared pattern of midfacial bone modelling in hominids suggests deep evolutionary roots**
2 **for human facial morphogenesis**

3
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33 **Abstract**

34 Midfacial morphology varies between hominoids, in particular between great apes and humans for which
35 the face is small and retracted. The underlying developmental processes for these morphological
36 differences are still largely unknown. Here we investigate the cellular mechanism of maxillary
37 development (bone modelling), and how potential changes in this process may have shaped facial
38 evolution. We analysed cross-sectional developmental series of gibbons, orangutans, gorillas,
39 chimpanzees and present-day humans (N=183). Individuals were organized into five age groups according
40 to their dental development. To visualize each species' bone modelling pattern and corresponding
41 morphology during ontogeny, maps based on microscopic data were mapped onto species-specific age
42 group average shapes obtained using geometric morphometrics. The amount of bone resorption was
43 quantified and compared between species. Great apes share a highly similar bone modelling pattern,
44 whereas gibbons had distinctive resorption patterns. This suggests a change in cellular activity on the
45 hominid branch. Humans possess most of the great ape pattern, but bone resorption is high in the canine
46 area from birth on, suggesting a key role of canine reduction in facial evolution. We also observed that
47 humans have high levels of bone resorption during childhood, a feature not shared with other apes.

48 Key words: facial evolution – ontogeny – bone formation – bone resorption – geometric morphometrics

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65 1. Introduction

66
67 Hominoids show large variation in facial shape and size [1]. Orangutans possess upwardly oriented faces
68 in relation to the basicranium, a condition called airorhynch [2]. In contrast, African great apes are
69 klinorhynch, with the midface rotated ventrally and posteriorly [2]. The short and retracted face of humans
70 is distinct from the long, forwardly projecting faces of non-human great apes. Similarly, in gibbons the
71 midface is also less prognathic than in other hominoids [3–5]. The morphology of the dental arcade is U-
72 shaped in apes and parabolic in humans [6]. Additionally, human evolution is marked by smaller canine
73 teeth and less difference in size between males and females [7,8]. However, the underlying ontogenetic
74 mechanisms explaining variation in hominoid facial morphology remain unclear.

75 A way to study the ontogeny of morphological features, is by looking at the microscopic
76 development of the bone. Bone modelling is the cellular process of bone growth and development. Along
77 with sutural growth, it is the key mechanism that participates in bone morphogenesis. During the
78 development of skeletal features, the two opposite cellular activities of bone formation and resorption
79 work in concert in order to model and increase the size of the bones. Donald Enlow was the first to propose
80 a link between the cellular activity and the shape of bone [9]. Later, it was noticed that bone formation
81 and resorption both leave specific marks on dry bone's periosteal surface, which can be visualized with
82 non-invasive microscopic techniques [10]. Among primates, the human facial bone modelling pattern has
83 been investigated the most [11–17]. The human pattern is described as unique and derived, characterized
84 by high levels of bone resorption in the maxilla in relation to the small human face [18,19]. However, when
85 this change in the cellular pattern occurred in the course of human evolution remains elusive. The study
86 of bone modelling in extant hominoids can thus shed light on major evolutionary events regarding facial
87 morphogenesis.

88 Studies focusing on other primate species and fossil hominins are scarce. Previous work proposed
89 that patterns of bone modelling are variable, but species-specific. Contrary to humans, bone resorption is
90 less present in gorillas and chimpanzees who display larger amounts of bone formation in the face [19,20].
91 Previous work on early hominins suggested that *Australopithecus* and *Paranthropus* possess opposite
92 patterns of bone modelling, with *Australopithecus* showing no bone resorption and projecting faces, and
93 *Paranthropus* showing resorption in the premaxilla associated to more vertical faces [21,22]. However, as
94 most previous studies suffered from a lack of quantitative data, there is no consensus about how variable
95 bone modelling is in great apes, which limits our ability to study bone modelling in fossils. Moreover, a

96 shared ancestral pattern in all hominids has also been suggested (38, 40, 43), such as similarities in bone
97 modelling between gorillas and chimpanzees [20], as well as between chimpanzee and humans [19]. To
98 verify the hypothesis of a shared pattern, we compare maxillary development in several hominoid species
99 (gibbons, orangutans, gorillas, chimpanzees and humans). We investigate the development of facial
100 prognathism, and aim to identify key ontogenetic events that led to changes in facial morphology. We use
101 an integrative approach that combines techniques of geometric morphometrics to quantify and visualise
102 the shape changes on the macroscopic scale, as well as surface histology, to quantify and visualise the
103 cellular changes on the microscopic scale.

104

105 **2. Materials and methods**

106

107 (a) Sample

108 The number of individuals varied depending on the analysis (bone modelling (BM) surface analysis, and
109 geometric morphometric (GM) shape analysis). We studied cross-sectional ontogenetic series of gibbons
110 (represented by several species: *Hylobates lar*, *H. muelleri*, *H. agilis* and *H. molloch*; BM: N=24, GM: N=18;
111 Naturkunde Museum, Berlin, Germany), orangutans (*Pongo pygmaeus*; BM: N=31, GM: N=38; Naturkunde
112 Museum, Berlin; Phyletisches Museum, Jena, Germany), gorillas (*Gorilla gorilla*; BM: N=24, GM: N=37;
113 Naturkunde Museum, Berlin, Germany; Phyletisches Museum, Jena, Germany), chimpanzees (*Pan*
114 *troglydytes*; N=33 in both BM and GM analyses; Tai anatomical collection from the Max Planck Institute
115 for Evolutionary Anthropology, Leipzig, Germany) and present-day humans (BM, GM: N=57 in both BM
116 and GM analyses; Anatomical collection of Strasbourg, France; Anatomical Institute of the University of
117 Leipzig, Germany; Coimbra Anthropological collection, Portugal). Individuals were organized into five age
118 groups (AG) according to maxillary dental development such as in [23]: no teeth erupted (AG 1), deciduous
119 dentition (AG 2), first permanent molar (M1) erupted (AG 3), second permanent molar (M2) erupted (AG
120 4), and third permanent molar (M3) erupted (AG 5). Individuals with apparent pathologies or
121 taphonomically altered surfaces were not studied.

122 Imprints of the maxillary surface were generated using a low viscosity silicone (President Plus Light
123 body, Coltène) directly applied onto the bone following [24]. Positive replicas were then created using a
124 transparent epoxy resin (Araldite 2020, Escil). Computed tomographic (CT) images were used to generate
125 three-dimensional models of each individual. The resolution of the scans ranged between 0.03 and 0.4
126 mm. Surface models were generated using Avizo (Thermo Fisher Scientific).

127

128 (b) Analyses

129 (i) Geometric morphometrics

130 Using the software Viewbox 4 (dHAL software; Kifissia), we digitized 249 landmarks and semilandmarks
131 (Table 1) on the right maxilla of each individual. Estimation of missing landmarks was carried out with a
132 thin-plate spline (TPS) interpolation [25] using the package Morpho in R [26]. We performed the sliding of
133 all the semilandmarks, minimizing the bending energy, in order to assure geometric homology between all
134 individuals [27]. Finally, to standardize the position, orientation and scaling to a unit centroid size, a
135 generalized Procrustes analysis was performed [28]. We computed principal component analyses (PCA) of
136 the morphological data in shape space and Procrustes form (size and shape) space [29].

137 To visualize the patterns of shape changes within one species throughout ontogeny, heat maps
138 were computed to show the shape differences between subsequent age group means [30]. Only the
139 differences between AG 1 and 3, and AG 3 and 5 were computed so as to enhance the visualization of the
140 results. As AG 1 is missing in our gibbon and gorilla samples, the shape changes between AG 2 and 3 were
141 computed instead. Results are shown using the surface model of the youngest age group (i.e., 1 and 3).
142 Warm colours indicate positive differences between the two meshes, while cold colours indicate negative
143 differences. This can be interpreted as forward and backward displacements from the youngest to the
144 oldest age group, respectively [16,20]. Because of inter specific variation in the amount of shape change,
145 maps were computed at different scales for each species to optimize the visualization of the colours. Only
146 the surface in relation to the template shows informative data, which excludes the teeth.

147

148 (ii) Surface histology

149 Surface histology was employed to analyse the bone modelling patterns in each species [16,31]. Pictures
150 of the bone surface were taken with a confocal microscope (Sensofar S neox) using a 5x lens. Only one of
151 the two sides (right or left) was chosen depending on the surface preservation. A grid of 5x5 mm was
152 drawn directly on the positive replicas and divided into sub-squares of 2.5x2.5 mm in areas of interest (i.e.,
153 where both bone formation and resorption can be found). The pictures taken in each 2.5x2.5 mm square
154 were then analysed in the software ImageJ [31]. Areas of bone resorption were manually selected on the
155 pictures and transformed into percentages for each square of the grid.

156 To visualise and compare the bone modelling pattern of each species/individual, digital maps were
157 created in R Studio based on the calculated percentages [16]. A colour code is used to represent the

158 amount of bone resorption. Cold tones indicate high percentages of bone resorption while warm tones
159 indicate low percentages of bone resorption. A percentage of zero indicates bone formation. Bone
160 formation can either be represented by areas of intensively newly added bone, or areas where bone is
161 almost quiescent. As individuals of different ages (and thus, sizes) are represented in our sample, each
162 map was standardized to a given grid size (in this case, 8x8 squares; see [16] for a description of the
163 method). This standardization step allows for the comparison of all individuals' bone modeling pattern in
164 our analyses.

165 To visualise the average changes in bone modelling throughout ontogeny, mean bone modelling
166 maps were calculated at each age group and for each taxon. These were projected directly onto their
167 respective mean forms (i.e., the shape retaining the individual maxillary size measured as centroid size)
168 using Geomagic Studio (3D Systems, Research Triangle Park).

169 To quantify the changes in the amount of bone resorption throughout ontogeny on the periosteal
170 surface of the maxilla, a total percentage of bone resorption (%BR) was calculated for each individual using
171 the calculated amount of bone resorption corrected by the total area of the bone. As this is not indicative
172 of local changes of bone resorption on the maxilla, the percentage of bone resorption was computed and
173 compared for each of the 51 squares of the mean grid, at each age group and for each species.

174 A principal component analysis (PCA) was performed on the bone modelling data (represented as
175 the percentages of bone resorption at each square) to investigate the variation in bone resorption within
176 and between species, and a PERMANOVA (1,000 permutations) was conducted on the percentages of bone
177 resorption to test for significant differences between species using a Bonferroni correction.

178

179 **3. Results**

180

181 (a) Shape analysis

182 Principal component analyses in shape (figure 1A) and form space (electronic supplementary material,
183 figure S1) were performed on the maxilla. The PCA in shape space highlighted differences between species
184 in maxillary development. The first PC (PC1) accounts for 53.1% of the total shape variation and PC2
185 accounts for 15.7%. While the ontogenetic trajectory in all non-human apes occurs in a similar direction in
186 young age groups (from AG 1 to 3), this differs in late stages during which each species' trajectory diverges
187 (in AG 4 and 5). The human trajectory diverges in direction from birth on, although it shows a pattern of

188 shape change similar to that of the great apes from AG 1 to AG 3. Results of the permutation test
189 performed on the scores of the first three principal components indicate that humans and gibbons are
190 significantly different from the non-human great apes. Gorillas and orangutans also significantly differ
191 (Table 2). The morphological changes associated to PC1 (from negative to positive values) relate to a
192 vertical elongation of the bone, and enlargement as well as a forward development of the premaxilla
193 (figure 1B). Changes associated to PC2 (from negative to positive values) relate to an enlargement of the
194 frontal process, as well as the forward development of the premaxilla.

195 Figure 2 shows the shape changes between subsequent age groups (AG 1 and 3, and AG 3 and 5)
196 in each species. Both orangutans and chimpanzees show warm colours in the canine region (indicative of
197 a positive distance, i.e., a forward displacement of this area) while humans show cold colours in this area
198 (indicative of a negative distance, or a backward displacement). In gibbons, such as in orangutans and
199 chimpanzees, the canine region again shows warm colours indicative of a positive difference. Shape
200 changes in the gorilla are more homogeneous across the whole maxilla (i.e., showing green colour
201 indicative of subtle changes), with negative distances found in the frontal process. For all species, the
202 differences between AG 3 and 5 were computed. All species, apart from humans and gorillas, show positive
203 values in the canine and canine pillar regions. In gorillas, shape changes are again more homogeneous
204 across the bone, with slightly warmer colours in the premaxilla and zygomatic regions and colder colours
205 in the post canine region. Similarly, humans show less contrasted colours in the heatmap, with cold colours
206 in the canine area.

207 (b) Surface analysis

208 Principal component analyses were performed on the bone modelling data of the whole sample (figure 3,
209 electronic supplementary material, figure S2). The first two PCs represent 49.6% of the total variation (PC1:
210 38.3%; PC2: 11.3%; figure 3A). Although a large overlap is observed (especially between humans and great
211 apes), the majority of the humans plot in the positive values (see 75% ellipse) while the other species plot
212 in the negative values on PC1. They were the only one to show significant different scores with all the other
213 species on PC 1 and 2 (Tables 3 and 4). The gibbons all plot in the non-human great ape range of variation.
214 Changes associated to PC1 relate to the increase in bone resorption in the whole bone from the negative
215 to the positive values. Changes associated to PC2 relate to a slight increase in bone resorption in the frontal
216 process and the zygomatico-maxillary suture area from the negative to the positive values.

217 The first and third PCs represent 46% of the total variation (figure 3B). Gibbons distinguish
218 themselves from the other apes on PC3 (7.7%), with the major axis of the ellipse showing a similar direction

219 to the humans. Table 5 shows the results of the permutation test on PC3 scores. Significant p -values are
220 found between gibbons and chimpanzees, gibbons and orangutans, as well as between humans and
221 orangutans. Changes associated to PC3 relate to an increase in bone resorption in the maxillary arcade and
222 frontal process from the negative to the positive values.

223 (i) The gibbon bone modelling pattern

224 We analysed for the first time the maxillary bone modelling pattern of the gibbons (figure 4). The gibbon
225 maxilla shows predominant bone formation in the frontal process and in the nasal area. Bone resorption
226 was only found near the zygomatico-maxillary suture and post canine regions, with some areas close to
227 the canine. This pattern is repeated from AG 2 to adulthood.

228 (ii) The great ape bone modelling pattern

229 The computation of the great apes' mean bone modelling maps highlighted different points (figure 4). In
230 all species for which data on individuals at birth were not missing (orangutans, chimpanzees and humans),
231 AG 1 is the ontogenetic stage that diverges the most from the other age groups regarding where bone
232 resorption is found on the bone. Humans already show more bone resorption at birth in the maxillary
233 arcade, with higher percentages of bone resorption located on the canine bulb and near the fronto-
234 maxillary suture. In both of the non-human great apes (orangutans and chimpanzees), resorption is found
235 in the premaxilla.

236 From AG 2, bone resorption appears in the following areas in all great apes: the premaxilla, the
237 zygomatic process, the top of the frontal process, as well as along the alveolar process and in the post
238 canine area. Humans also possess bone resorption in these regions; however, bone resorption covers the
239 entire maxillary arcade, joining the premaxilla and the post canine regions. This pattern is repeated from
240 AG 2 to AG 5.

241 (iii) Changes in the total amount of bone resorption throughout ontogeny

242 The variation in the total amount of bone resorption for each individual highlighted species' specific
243 differences in how bone resorption is expressed throughout ontogeny (figure 5). In comparison to the
244 great apes, gibbons show lower amounts of bone resorption throughout life (between 0 and 25%), with a
245 small increase between AG3 and AG4. The non-human great apes show a larger range of variation
246 (between 0 and 40%). Each species shows a different pattern, with chimpanzees expressing a peak in bone

247 resorption in AG2, while gorillas express a peak in AG3. Orangutans show the most homogeneous pattern
248 throughout life among non-human primates.

249 Humans express high amounts of bone resorption already from birth, with particularly high
250 amounts expressed in AG2 and 3. A progressive decrease is observed between AG 3 and 4, and between
251 AG 4 and 5. This pattern is unique to that species.

252 (iv) Local differences in bone resorption

253 To quantify the local variation of bone resorption we plotted the percentage of bone resorption in each
254 square of the mean grid at each age group (figure 6). When considered locally, bone resorption can be
255 expressed in either high or low amounts, depending on the area, age group and species considered (i.e.,
256 the pattern of expression of bone resorption changes with time and between species). For example, in AG
257 2, the square 86 expresses high %BR in humans and orangutans (respectively 44 and 51.5%), while low
258 percentages in chimpanzees (19.9%) and gorillas (1.1%). Resorption is absent from this square in gibbons.
259 This pattern changes in AG 3, in which bone resorption is at 0% in chimpanzees and gibbons, 32.5% in
260 gorillas, 42.5% in orangutans and 16.42% in humans.

261 Moreover, this analysis highlighted that some squares possess consistently higher values in
262 humans than in the other apes. When plotting these squares on a grid, we observed that a large majority
263 of them is located in the canine area (electronic supplementary material, figure S3).

264

265 **4. Discussion**

266

267 This study investigated for the first time the patterns of maxillary bone modelling of almost all extant apes,
268 and sheds new light on the underlying cellular mechanisms that have acted on the evolution of facial
269 morphology.

270

271 (a) A change in the cellular pattern on the hominid lineage

272

273 In this study we identify areas of bone resorption in great apes that were not previously described in
274 bone modelling studies of Afro-Asian monkeys [32,33], such as the presence of bone resorption in the

275 premaxilla (Fig. 4). It has been shown that a first step in the evolution of the hominoid face lies in the
276 reduction of facial prognathism [34–36], and that compared to Afro-Asian monkeys, great apes possess a
277 shorter facial length [37]. Our results suggest that this change in facial morphology could relate to a change
278 in the cellular pattern on at least two different levels: firstly, the appearance of new resorptive areas such
279 as discussed above; and secondly, the increase in the amount of bone resorption on the hominid lineage
280 (figures 4 and 5), a process that was previously only attributed to *Homo sapiens* due to the large resorptive
281 area found in this species [38]. To test for a correlation between changes in facial size and bone modelling
282 between the gibbons and the non-human great apes, a multiple multivariate regression was performed
283 between the percentages of bone resorption and the logarithm of the centroid size of each individual. We
284 found a significant but weak correlation between size and bone modelling, indicating that size only played
285 a partial role in the appearance of new resorbing areas in non-human great apes (electronic supplementary
286 material, table S1).

287 Surprisingly, we found that the gibbon pattern differs the most from our hominoid sample, with areas
288 of bone resorption located mostly in the post canine region (figure 4). We would expect to find more bone
289 resorption in their maxilla, since it is often proposed that prognathism is reduced in gibbons [3]. In this
290 respect, the gibbon maxillary bone modelling pattern is more similar to what is currently known for Afro-
291 Asian monkeys who show bone resorption near the zygomatico-maxillary suture [32,33,39]. Midfacial
292 ontogeny in gibbons may thus imply other mechanisms not quantifiable in this study, such as a differential
293 sutural growth that would play a role in their less prognathic face.

294

295 (b) A shared bone modelling pattern between non-human great apes

296

297 This study identified that most areas of bone resorption are shared between great apes (figure 4), although
298 shape differences exist between them from birth on (electronic supplementary material, figure S4), as well
299 as differences in facial orientations, projection and diets [40,41]. Thus, the patterns of bone modelling that
300 were observed at the surface of the bone do not seem related to facial orientation, as orangutans possess
301 similar patterns to chimpanzees and gorillas. Rather, sutural growth might be the main process involved
302 in determining facial prognathism [42,43]. Moreover, the high similarities that we found in the location of
303 bone resorption suggest a major influence of genetic factors in determining the cellular pattern of bone
304 growth, as the cellular development appears constrained despite maxillary shape differences. Based on
305 these results, it is likely that early hominins share this “ape-like” pattern, although differences in bone
306 modelling between *Australopithecus* and *Paranthropus* have been discussed in previous studies [21,22].

307 *Paranthropus* is less prognathic than *Australopithecus*, and similar to the great apes, shows areas of bone
308 resorption in the premaxilla that have not been found in *Australopithecus*. Considering the strong
309 preservation of the location of bone resorption highlighted by this study, it is likely that *Australopithecus*
310 also express bone resorption in this area. However, it could be expressed on a lesser degree, such as
311 suggested by a previous study [44].

312 Although the cellular pattern is similar in hominids, shape differences exist. We found that
313 although bone resorption is present in similar areas, its expression varies depending on the species and
314 age group considered (figures 5 and 6). This differential expression of bone resorption throughout
315 ontogeny suggests that differences in timings and rates of the cellular activities are the main cause for
316 morphological variation. Differences in cellular proliferation rates could also explain the differences in
317 morphology observed in our sample, as discussed in other species [45]. On the genetic level, this indicates
318 a differential regulation of genes throughout ontogeny, along with a shared pattern in all species. It was
319 found that while most genes are similar between humans and chimpanzees, the genetic expression (i.e.,
320 regulatory patterns) of stem cells differentiated into osteogenic cells differ between the two species [46].

321

322 (c) Human specificities in midfacial development

323

324 In humans, facial size is reduced, and the maxilla is retracted, showing high percentages of bone resorption
325 from birth on. When looking at the changes in the amount of bone resorption through time in the entire
326 maxilla (figure 5), humans distinguish themselves from the other apes by maintaining high amounts of
327 bone resorption during childhood (AG 2 and 3), while it is more constant in all other species. Whether this
328 change is due to a higher number of osteoclast precursors and/or osteoclasts (i.e., differences in cellular
329 differentiation and/or division), or more active resorbing cells, is still unknown. This denotes a change in
330 the cellular expression within the human lineage, possibly already occurring in early phases of embryonic
331 development as studies have suggested that a reduction in the number of neural crest cells reduces the
332 size of the jaws [47–49]. The results of this study highlight parts of the mechanisms behind facial
333 gracilization in present-day humans: high amounts of bone resorption that are maintained throughout
334 childhood, followed by a progressive decrease in the cellular activity towards adolescence, which
335 corresponds to a truncated growth (electronic supplementary material, figure S5). This could be related to
336 a change in the hormonal expression pattern, as such pattern (a reduced activity towards adolescence)
337 has also been observed in the expression of the thyroid-stimulated hormones [50,51].

338 Finally, a noticeable difference between humans and great apes is found in the canine area, in
339 which humans possess uniquely high percentages of bone resorption (figure 6). The analysis of the pattern
340 of shape change (figure 2) showed that canine development is the main difference maintained throughout
341 ontogeny between humans and the other apes. From birth on, resorption is found on the canine bulb in
342 humans, while it is present in the premaxilla in great apes (figure 4). This early stage difference in the
343 human bone modelling pattern in comparison to the non-human great apes strongly supports the
344 hypothesis of a selection towards the reduction of the canine on the hominin lineage [7].

345

346 **5. Conclusion**

347

348 This study highlighted key periods during hominid facial evolution and ontogeny. First, we found a change
349 in cellular activity in the hominid lineage. Resorption increases slightly and appears in new areas, such as
350 in the premaxilla. This denotes a fundamental change in the cellular pattern of the hominid maxillary
351 development, that has been described as less prognathic than Afro-Asian monkeys. Secondly, this pattern
352 is similar between hominids, as bone resorption is found in similar areas. This denotes strong
353 developmental canalization of the hominid midface. However, this pattern is differently expressed,
354 suggesting differences in cellular differentiation and proliferation, as well as in genetic regulation. Finally,
355 we found two unique features in humans. One is the high percentage of bone resorption that is maintained
356 during a longer period (corresponding to childhood (AG 2 and 3) in our sample) that suggests an extended
357 period of osteoclastic activity. Secondly, resorption is uniquely high in the canine, and present from birth
358 on. Thus, selection for canine reduction represented a major step for midfacial evolution in the human
359 lineage. Our study highlights the importance of bone resorption in shaping the facial skeleton and how
360 selection of this process acted to generate new morphologies. Altogether, these results help to better
361 understand the underlying mechanisms for morphological variability, and will represent a solid framework
362 for future bone modelling studies of fossil remains.

363

364 **Data accessibility**

365 Data and code are available from Dryad:
366 <https://doi.org/10.5061/dryad.000000094>

367

368 **Authors' contributions**

369 A.S.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project
370 administration, resources, software, visualization, writing—original draft, writing—review and editing;
371 Y.H.: conceptualization, resources, software, project administration, writing—review and editing; P.G.:
372 data curation, methodology, writing—review and editing; M.B.: resources, writing—review and editing;
373 C.N.S.: data curation; J.-J.H.: resources, software, data curation, funding acquisition; S.F.:
374 conceptualization, methodology, writing—review and editing.

375

376 **Competing interests**

377 The authors declare no competing interests.

378

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396

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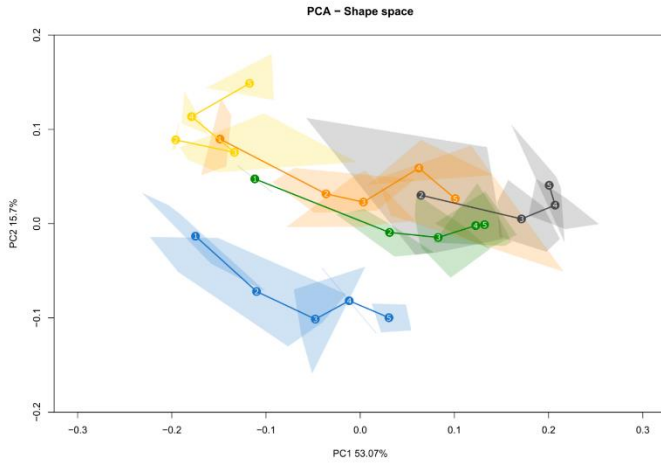
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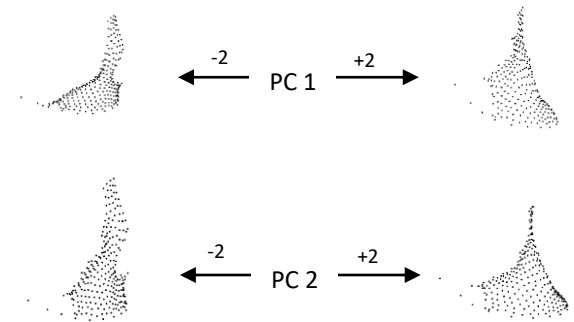
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538 **Figures**



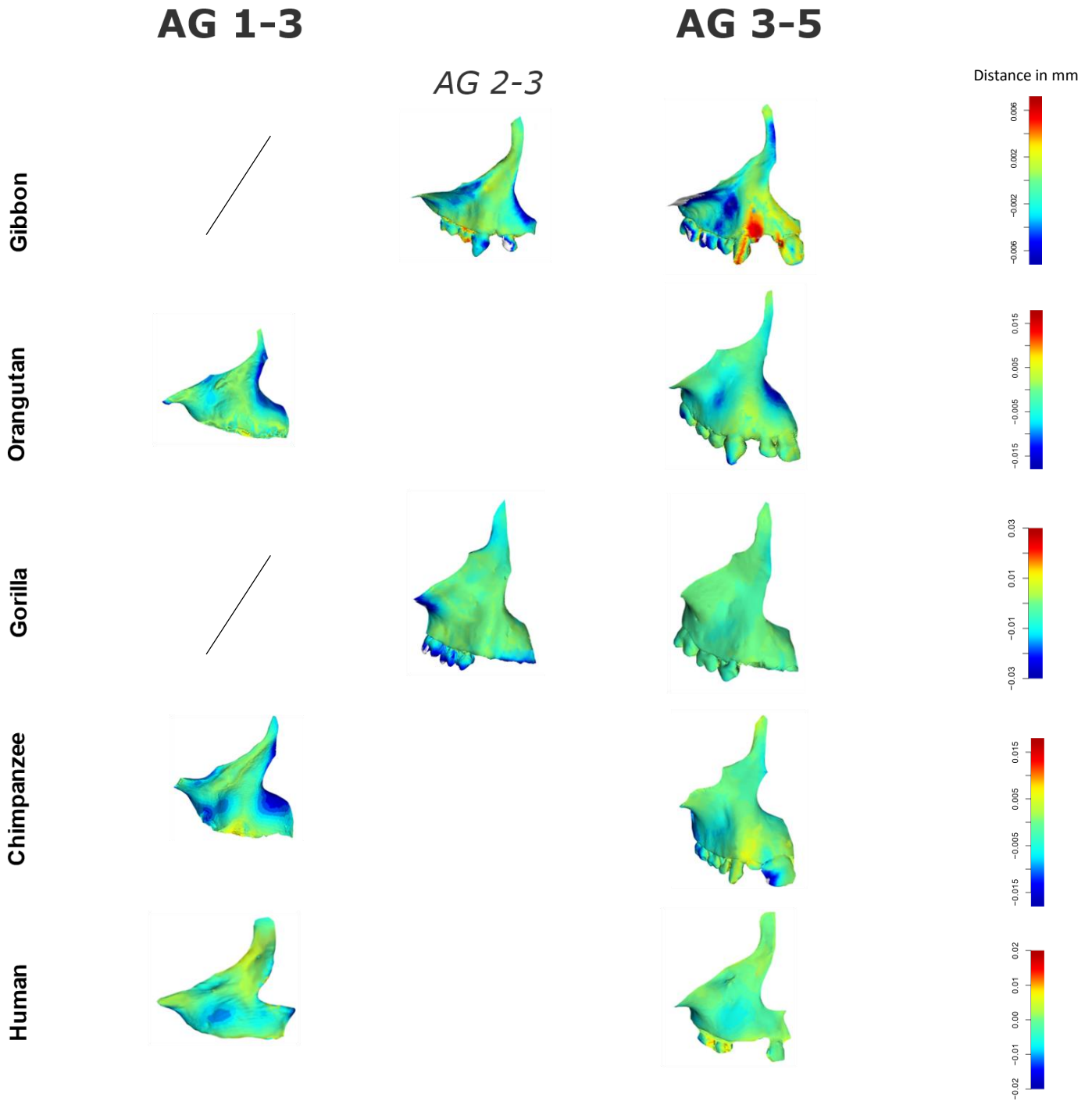
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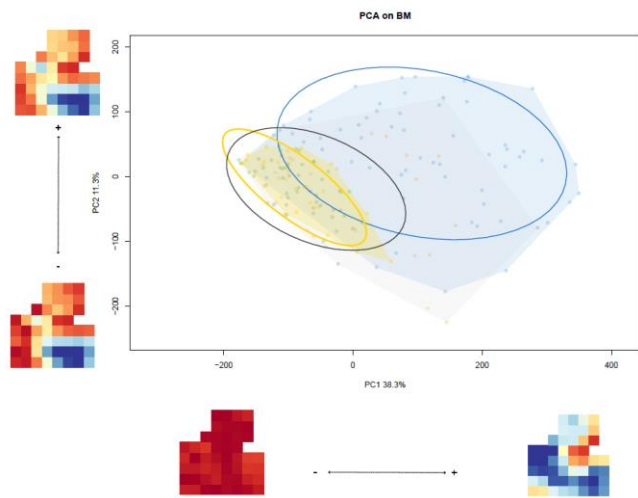
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540 **Figure 1** A) Principal component analysis (PCA) in shape space. Developmental trajectories are
541 represented as solid lines linking each age group's mean shape (shown as large dots and numbers). Blue:
542 humans; green: chimpanzees; orange: orangutans; black: gorillas; yellow: gibbons. B) Landmark
543 configurations representing the extreme shapes at each PC with plus/minus 2 standard deviations from
544 the sample mean.

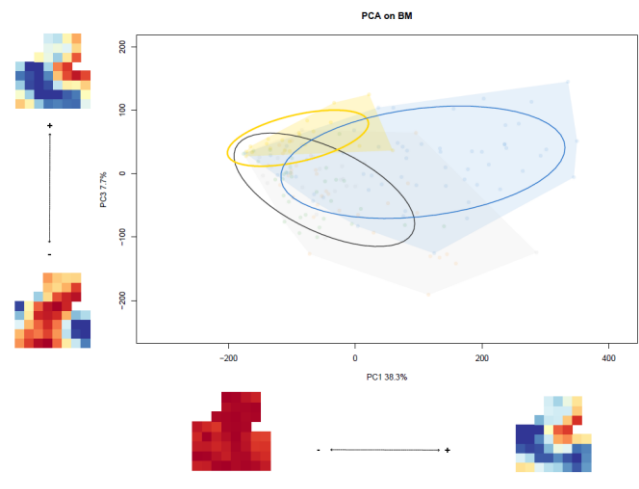


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546 **Figure 2** Shape changes between subsequent age groups within species, visualized as heatmaps on
547 the surface of the youngest age group. For better visualization, the changes were computed between AG
548 1 and 3, and AG 3 and 5. As AG 1 is missing in gibbons and gorillas, shape differences were computed
549 between AG 2 and 3 instead. The heatmaps were computed with a different color scale for each species
550 in order to improve the visualization. Only the surface in relation to the template shows informative data,
551 which excludes the teeth.



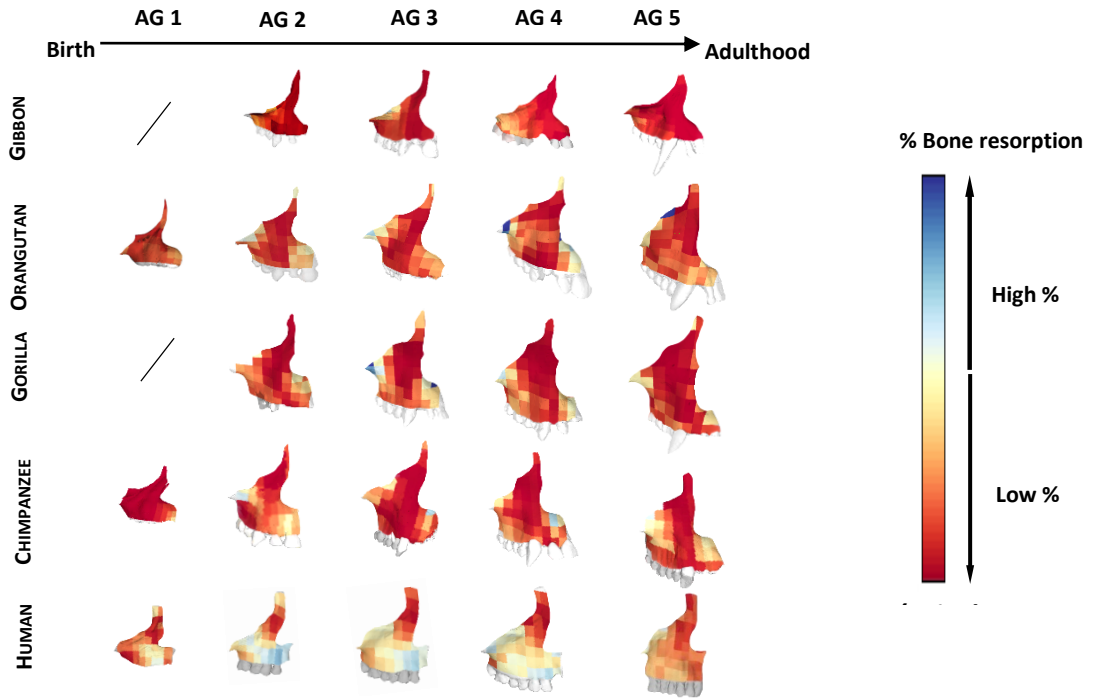
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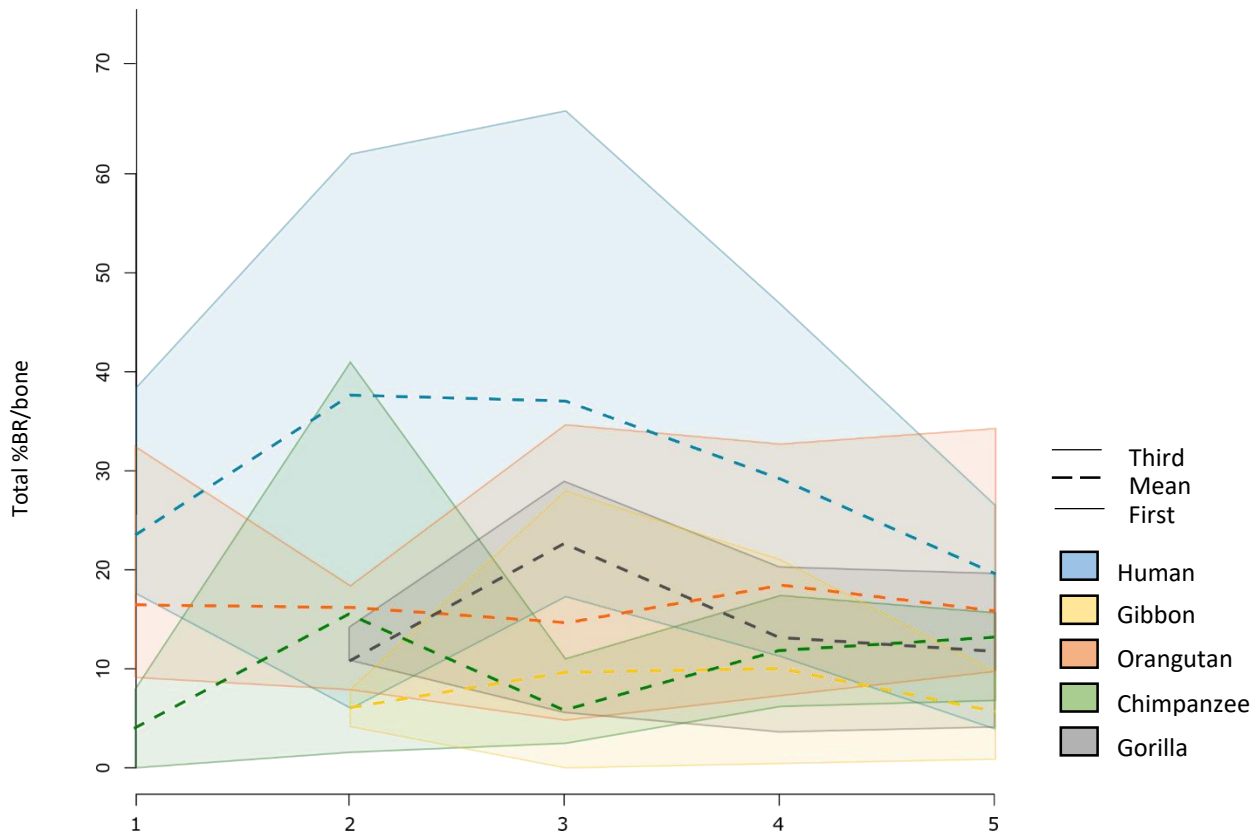
552

553 **Figure 3** Principal component analysis (PCA) of the bone modeling data. A: PC 1 against PC 2; B: PC
 554 1 against PC 3. Humans are shown in blue, the non-human great apes (gorillas, chimpanzees and
 555 orangutans) in grey, and gibbons in yellow. Ellipses encompass 75% of the total variation.

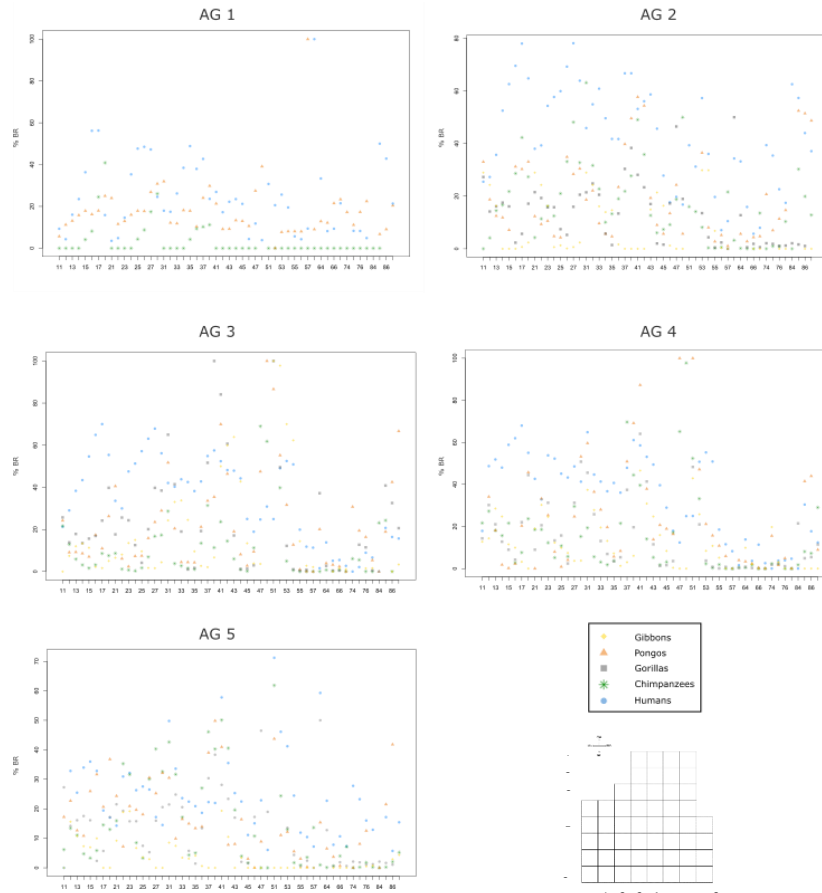


557 **Figure 4** Mean bone modeling maps representing the bone modeling pattern of each age group
558 and species. High percentages of bone resorption are represented in cold tones while low percentages of
559 bone resorption are represented in warm tones. A percentage of 0 indicates bone formation.

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574 **Figure 5** Variation in the total amount of bone resorption in the maxilla throughout ontogeny in all
 575 species. Blue: humans; green: chimpanzees; orange: orangutans; black: gorillas; yellow: gibbons. Dashed
 576 lines: mean, solid lines: first and third quartiles.



577
 578 **Figure 6** Plots representing the percentages of bone resorption at each square of the grid. X axis:
 579 square number; Y axis: percentage of bone resorption. Blue dots: humans; green stars: chimpanzees; grey
 580 squares: gorillas; orange triangles: orangutans; yellow diamonds: gibbons. A grid is represented to show
 581 the location of each square.

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583

584 **Tables**

585

586 **Table 1** Landmarks and semilandmarks numbers and definition (total: 249).

587

Landmarks	Label
<i>Fixed landmarks</i>	sln

Superolateral nasion	
Dacryon	d
Zygoorbitale	zyo
Inferolateral rhinion	ilr
Anterior nasal spine	ans
Alveolare (infradentale superius)	ids
Zygomaxillare	zm
Malar root origin	mro
Maxillo-palatine suture	mps

Curve semilandmarks

Number - definition

Fronto-maxillary suture	FMS	2 – superolateral nasion to dacryon
Naso-maxillary suture	NMS	6 – superolateral nasion to inferolateral rhinion
Inferior orbital margin	IOM	6 – dacryon to zygoorbitale
Nasal aperture outline	NA	6 – inferolateral rhinion to anterior nasal spine
Subnasal outline	SO	3 – nasal spine to alveolar
Zygomatiko-maxillary suture	ZMS	5 – zygoorbitale to zygomaxillare
Maxillary contour	MC	4 – zygomaxillare to malar root origin
Alveolar outline	AO	8 – alveolare to maxillo-palatine suture

Surface semilandmarks

200 – covering the whole surface of the bone

588

589

590 **Table 2** Permutation test performed on the scores of the first three principal components of the shape
591 data (figure 1). Significant *p*-values are highlighted in bold.

	Chimpanzees	Gibbons	Gorillas	Humans
Gibbons	0.01			
Gorillas	0.25	0.01		
Humans	0.01	0.01	0.01	
Orangutans	0.38	0.01	0.01	0.01

592

593 **Table 3** Permutation test performed on the scores of the first principal component (PC1) of the bone
594 modelling data (figure 2). Significant p -values are highlighted in bold.

	Chimpanzees	Gibbons	Gorillas	Humans
Gibbons	1.00			
Gorillas	1.00	1.00		
Humans	0.01	0.01	0.01	
Orangutans	1.00	1.00	1.00	0.01

595
596 **Table 4** Permutation test performed on the scores of the third principal component (PC2) of the bone
597 modelling data (figure 2). Significant p -values are highlighted in bold.

	Chimpanzees	Gibbons	Gorillas	Humans
Gibbons	1.00			
Gorillas	1.00	1.00		
Humans	0.38	0.29	0.01	
Orangutans	1.00	1.00	1.00	0.01

598
599 **Table 5** Permutation test performed on the scores of the third principal component (PC3) of the bone
600 modelling data (figure 2). Significant p -values are highlighted in bold.

	Chimpanzees	Gibbons	Gorillas	Humans
Gibbons	0.01			
Gorillas	1.00	0.17		
Humans	0.17	1.00	1.00	
Orangutans	1.00	0.01	1.00	0.01

601