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1 A comparative analysis of the vestibular apparatus in *Epipliopithecus vindobonensis*:  
2 Phylogenetic implications

3

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30

### 31 **Abstract**

32 Pliopithecoids are an extinct group of catarrhine primates from the Miocene of Eurasia.

33 More than fifty years ago, they were linked to hylobatids due to some morphological

34 similarities, but most subsequent studies have supported a stem catarrhine status, due to

35 the retention of multiple plesiomorphic features (e.g., the ectotympanic morphology)

36 relative to crown catarrhines. More recently, some morphological similarities to hominoids

37 have been noted, raising the question of whether they could be stem members of this

38 clade. To re-evaluate these competing hypotheses, we examine the morphology of the

39 semicircular canals of the bony labyrinth of the middle Miocene pliopithecoid *Epipliopithecus*

40 *vindobonensis*. The semicircular canals are suitable to test between these hypotheses

41 because: (1) they have been shown to embed strong phylogenetic signal and reliably

42 discriminate among major clades; (2) several potential hominoid synapomorphies have

43 been identified previously in the semicircular canals; and (3) semicircular canal

44 morphology has not been previously described for any pliopithecoid. We use a

45 deformation-based (landmark-free) three-dimensional geometric morphometric approach

46 to compare *Epipliopithecus* with a broad primate sample of extant and extinct anthropoids.

47 We quantify similarities in semicircular canal morphology using multivariate analyses,

48 reconstruct ancestral morphotypes by means of a phylomorphospace approach, and

49 identify catarrhine and hominoid synapomorphies based on discrete characters.

50 *Epipliopithecus* semicircular canal morphology most closely resembles that of platyrrhines

51 and *Aegyptopithecus* due to the retention of multiple anthropoid symplesiomorphies.

52 However, *Epipliopithecus* is most parsimoniously interpreted as a stem catarrhine more

53 derived than *Aegyptopithecus* due to the possession of a crown catarrhine synapomorphy  
54 (i.e., the rounded anterior canal), combined with the lack of other catarrhine and any  
55 hominoid synapomorphies. Some similarities with hylobatids and atelids are interpreted as  
56 homoplasies likely related to positional behavior. The semicircular canal morphology of  
57 *Epipliopithecus* thus supports the common view that pliopithecoids are stem catarrhines.

58

59 **Keywords:** Pliopithecidae; Catarrhini; Miocene; Inner ear; Phylogeny; Geometric  
60 morphometrics

61

## 62 **1. Introduction**

### 63 *1.1. The phylogenetic position of pliopithecoids*

64 Pliopithecoids are an extinct superfamily of catarrhine primates, recorded in Eurasia  
65 from the early to the late Miocene (Andrews et al., 1996; Begun, 2002, 2017; Harrison,  
66 2005, 2013). Their first occurrence, in the early Miocene of China (~18–17 Ma; Harrison  
67 and Gu, 1999; Begun, 2002; Harrison, 2013), slightly predates the oldest record of large-  
68 bodied apes in Eurasia (Heizmann and Begun, 2001; Casanovas-Vilar et al., 2011). In the  
69 absence of older (earliest Miocene) catarrhines in that continent, pliopithecoids are  
70 assumed to have an African origin (Harrison, 1987, 2013; Begun, 2017). Like apes,  
71 pliopithecoid ancestors probably dispersed into Eurasia before the Langhian  
72 transgression, which was possible due to the lowered sea level and tectonic events that  
73 led to the closure of the Tethys Seaway and the establishment of an intermittent terrestrial  
74 corridor beginning at ~19 Ma (Harzhauser et al., 2007; Harrison, 2013).

75 Decades ago, pliopithecoids were considered to be phylogenetically related to  
76 hylobatids due to some superficial resemblances in cranial morphology as well as body  
77 size and proportions (e.g., Hürzeler, 1954; Zapfe, 1958, 1960, 1961; Simons and Fleagle,  
78 1973). Currently, they are generally considered a clade of stem catarrhines—as supported

79 by the retention of several cranial and postcranial features that are plesiomorphic  
80 compared to the crown members of the group (Andrews, 1975; Ciochon and Corruccini,  
81 1977; Fleagle, 1984; Harrison, 1987, 2005, 2013; Andrews et al., 1996; Begun, 2002,  
82 2017). The divergence of pliopithecoids before the split of crown catarrhines is further  
83 supported by most recent cladistic analyses (Zalmout et al., 2010; Stevens et al., 2013;  
84 Nengo et al., 2017; Gilbert et al., 2020), implying a long ghost lineage of ca. 12–14 Myr for  
85 pliopithecoids (Begun, 2017). The exception is the cladistic analysis by Alba et al. (2015),  
86 which recovered pliopithecoids as a clade of stem hominoids—thereby eliminating the  
87 need to hypothesize a long gap in the pliopithecoid fossil record. Most recently, Almécija et  
88 al. (2019) further documented similarities in femoral morphology between pliopithecoids  
89 (*Epipliopithecus*) and extant hominoids, thereby casting additional doubts on the status of  
90 pliopithecoids as stem catarrhines. Further uncertainty in this regard stems from the fact  
91 that no tail vertebrae are known from pliopithecoids (Begun, 2017). Based on sacral  
92 morphology, Zapfe (1958, 1961) argued that no external tail would have been present, as  
93 in hominoids; although this has subsequently been rebutted (Ankel, 1965; Russo, 2016),  
94 available evidence in this regard remains uncertain.

95       There are multiple genera of pliopithecoids (Harrison and Gu, 1999; Moyà-Solà et al.,  
96 2001; Begun, 2002, 2017; Harrison, 2005, 2013; Alba et al., 2010; Alba and Moyà-Solà,  
97 2012; Alba and Berning, 2013; Sankhyan et al., 2017; Harrison et al., 2020), which,  
98 following Harrison et al. (2020), we provisionally group into four different families:  
99 dionysopithecids (*Dionysopithecus* and *Platodontopithecus*), krishnapithecids  
100 (*Krishnapithecus*), pliopithecids (*Pliopithecus* and *Epipliopithecus*), and crouzeliids  
101 (*Plesiopliopithecus*, *Barberapithecus*, *Anapithecus*, *Egarapithecus*, and *Laccopithecus*).  
102 However, it is noteworthy that the treatment of these genera at the family rank, and even  
103 the placing of some genera in one or another group, differs among authors (e.g., compare  
104 Alba and Moyà-Solà, 2012 with Begun, 2017). Such disagreements largely stem from the

105 fact that the internal phylogeny of pliopithecoids is still unclear and that their affinities with  
106 fossil catarrhines from Africa remain uncertain (e.g., Harrison, 2013).

107

## 108 1.2. Evidence from *Epipliopithecus*

109 Deciphering the phylogenetic relationships of most pliopithecoids is hampered by  
110 the fact that they are mostly known by fragmentary dentognathic remains, with the  
111 exception of *Epipliopithecus vindobonensis*, whose craniodental and postcranial  
112 morphology is well documented by several skeletons from the middle Miocene (MN6,  
113 ~14.85–13.45 Ma<sup>1</sup>) karstic infillings of Devínska Nová Ves, Slovakia (Zapfe, 1958, 1961;  
114 Andrews et al., 1996; Begun, 2002; Harrison, 2013). *Epipliopithecus* was originally  
115 established as a subgenus of *Pliopithecus* by Zapfe and Hürzeler (1957), being  
116 subsequently considered a junior subjective synonym of the latter (e.g., Andrews et al.,  
117 1996; Harrison and Gu, 1999; Moyà-Solà et al., 2001; Harrison, 2005, 2013; Alba et al.,  
118 2010) or a distinct genus (e.g., Begun, 2002; Alba and Moyà-Solà, 2012; Arias-Martorell et  
119 al., 2015; Alba et al., 2015; this study). From a locomotor viewpoint, *E. vindobonensis* has  
120 been variously depicted as an arboreal or semiterrestrial generalized quadruped with  
121 varying degrees of climbing and suspensory abilities (see discussion in Arias-Martorell et  
122 al., 2015). From a phylogenetic perspective, its purported stem catarrhine status has been  
123 supported by features such as the short and only partially enclosed ectotympanic, the  
124 presence of entepicondylar foramen in the distal humerus, and single hinge-like  
125 carpometacarpal joint in the thumb (Zapfe, 1961; Szalay and Delson, 1979; Harrison,  
126 1987, 2005; Andrews et al., 1996; Begun, 2002, 2017).

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<sup>1</sup> Age uncertainly based on the boundaries recognized for MN6 (van der Meulen et al., 2011).

127           The external morphology of the petrosal bone of *E. vindobonensis* (Zapfe, 1961;  
128 Szalay, 1975; Fricano, 2018) has been of utmost significance in the discussion of its  
129 phylogenetic affinities, given that the presence of a tubular ectotympanic is considered  
130 synapomorphic of crown catarrhines (e.g., Szalay, 1975; Szalay and Delson, 1979;  
131 Harrison, 1987, 2005; Andrews et al., 1996; Begun, 2002; Zalmout et al., 2010; Alba et al.,  
132 2015; Nengo et al., 2017). The possibility remains that such ossification took place to  
133 some extent independently in cercopithecoids, hominoids and/or other anthropoids such  
134 as pliopithecoids (Begun, 2002, 2017; Alba et al., 2015). However, other features of  
135 *Epipliopithecus* also appear plesiomorphic as compared to crown catarrhines and show no  
136 particular similarities with hominoids, namely: the large postglenoid process separated  
137 from the acoustic meatus, as in platyrrhines (Zapfe, 1961); the lack of ossification in the  
138 tentorium cerebelli (unlike in most platyrrhines and stem anthropoids, but similar to  
139 *Aegyptopithecus* and crown catarrhines; Kay et al., 2009a); and the deep subarcuate  
140 fossa (Zapfe, 1961), as in platyrrhines and most anthropoids except hominids (Gannon et  
141 al., 1988; Kunitatsu et al., 2019). In contrast, the inner ear morphology of *Epipliopithecus*  
142 has not been described and therefore its potential phylogenetic implications remain  
143 unexplored.

144

### 145 1.3. *The bony labyrinth of the inner ear*

146           Among the inner cavities of the petrosal, the bony labyrinth of the inner ear is  
147 constituted by the semicircular canals (SCs) and the vestibule (which together host the  
148 soft-tissue structures linked with the sense of balance) plus the cochlea. Semicircular  
149 canal size (e.g., Spoor et al., 2007; Silcox et al., 2009; Ryan et al., 2012; Grohé et al.,  
150 2018) and orientation (David et al., 2010; Malinzak et al., 2012; Berlin et al., 2013; Perier  
151 et al., 2016; Gonzales et al., 2019) have been frequently used for inferring agility, while the  
152 shape of the canals as a whole has tentatively been linked to positional behavior (Le

153 Maître et al., 2017). At the same time, recent studies have demonstrated that the SCs bear  
154 strong phylogenetic signal among anthropoids (Lebrun, 2010, 2012; Urciuoli et al., 2019,  
155 2020; del Rio et al., 2020; Morimoto et al., 2020) and other mammals (e.g., Grohé et al.,  
156 2015; Mennecart et al., 2016, 2017; Costeur et al., 2018).

157 Although adaptively relevant characters may constitute synapomorphies of  
158 particular clades, arguably their relationship with function makes them potentially more  
159 prone to homoplasy. However, the correlation between SC morphology and positional  
160 behavior has recently been questioned by some studies (i.e., Rae et al., 2016; del Río et  
161 al., 2020; Morimoto, et al., 2020), and SC shape variation has been shown to largely follow  
162 the expectations of a Brownian motion mode of evolution in both platyrrhines (del Río et  
163 al., 2020) and catarrhines (Urciuoli et al., 2020). These results are in accordance with  
164 those obtained for the bony labyrinth as a whole, showing that its morphology reflects  
165 phylogenetic relatedness as inferred from molecular data (Lebrun et al., 2010; Ekdale,  
166 2013; Macrini, et al., 2013; Billet et al., 2015). Cumulatively, this evidence suggests that  
167 bony labyrinth morphology is phylogenetically informative among mammals (Mennecart et  
168 al., 2017) and may thus potentially illuminate the phylogenetic relationships of extinct  
169 primates. Following Mennecart and Costeur (2016), who suggested that inner ear  
170 structures might be highly informative for large cladistics analyses, Urciuoli et al. (2020)  
171 explored catarrhine SC shape variation among catarrhines and proposed several potential  
172 synapomorphies for crown hominoids.

173 Here we test between two different phylogenetic hypotheses for *Epipliopithecus*,  
174 one hypothesis being that *Epipliopithecus* is a stem catarrhine, the other hypothesis that  
175 *Epipliopithecus* is a hominoid, based on the information provided by the shape of the SCs  
176 and vestibule. This morphology is described here for the first time using a three-  
177 dimensional geometric morphometric (3DGM) approach applied to a broad sample of  
178 extant and fossil anthropoids (Urciuoli et al., 2020). We refrained from analyzing the entire



179 bony labyrinth (i.e., including also the cochlea) because its potential for phylogenetic  
180 reconstruction among primates is currently unclear. A recent analysis in platyrrhines  
181 suggested that cochlear shape departs from a Brownian motion mode of evolution  
182 (Blomberg's  $K < 1$ ; del Río et al., 2020), thus potentially reflecting a greater influence of  
183 function (and likely homoplasy due to similar selection pressures) than is the case for the  
184 SCs and vestibule. This is in agreement with previous studies linking several macroscopic  
185 cochlear features to hearing capabilities (e.g., Manoussaki et al., 2006; Kirk and Gosselin-  
186 Ildari, 2009; Coleman and Colbert, 2010). More detailed morphometric analyses of this  
187 structure among anthropoids is thus required to determine whether cochlear morphology  
188 can be meaningfully used to decipher the phylogenetic relationships of extinct catarrhines  
189 such as *Epipliopithecus*.

190

## 191 **2. Materials and methods**

### 192 *2.1. Described material*

193 We inspected three petrosals of *E. vindobonensis* belonging to two individuals from  
194 Devínska Nová Ves, Slovakia (Zapfe, 1960, 1961): NMB OE 303a, b (individual III), left (a)  
195 and right (b), housed in the Naturhistorisches Museum of Basel, Switzerland<sup>2</sup>; and NHMW  
196 1970/1397/0003 (individual II), right, housed in the Naturhistorisches Museum of Wien,  
197 Austria.

198

### 199 *2.2. Comparative sample*

200 The comparative sample includes  $\mu$ CT scans of 162 dried crania and temporal  
201 bones belonging to 31 extant anthropoid species (see Supplementary Online Material  
202 [SOM] Table S1 for the sample size of the extant species), plus five fossil anthropoids

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<sup>2</sup> Morimoto et al. (2020) included the bony labyrinth of NMB OE 303a in their comparative study but did not depict or specifically describe its morphology.

203 (SOM Table S2): the stem anthropoid *Parapithecus* (Bush et al., 2004), the stem  
204 catarrhine *Aegyptopithecus* (Simons et al., 2007), the stem platyrrhines *Dolichocebus* (Kay  
205 et al., 2009b) and *Homunculus* (Fulwood et al., 2016), and the hominoid *Oreopithecus*  
206 (Rook et al., 2004).

207

### 208 2.3. *Sample preparation*

209 NMB OE 303 was scanned with a Phoenix Nanotom®, GE at the Biomaterials  
210 Science Centre of the University of Basel (Switzerland) obtaining a voxel size of 25 µm.  
211 NHMW 1970/1397/0003 was scanned at the Vienna µCT-Lab using a Viscom X8060  
212 (Viscom XT9190-THP X-ray tube) obtaining a voxel size of 22 µm. The canals and  
213 vestibule of NMB OE 303a, b were filled with air, while in NHMW 1970/1397/0003 they  
214 were partially filled with sediment. In both cases we segmented the SCs and vestibule  
215 cavities using the ‘watershed’ tool of Avizo v. 9.0.1 (FEI Visualization Sciences Group,  
216 Houston), with additional manual corrections for NHMW 1970/1397/0003. The 3D surfaces  
217 of NMB OE 303b and NHMW 1970/1397/0003 were mirrored for comparison. The 3D  
218 meshes of the two individuals are available from MorphoSource (see Table 1).

219 The µCT scans of most extant comparative species and of fossil anthropoids were  
220 accessed from MorphoSource.org digital repository (<https://www.morphosource.org>) with  
221 the exception of *Oreopithecus bambolii* petrosal, which was kindly provided by Lorenzo  
222 Rook (see SOM Table S2 for voxel sizes). Further details about the µCT scans of the  
223 extant comparative sample (voxel sizes, exact source, DOI, etc.) can be found in Urciuoli  
224 et al. (2020: Supplementary File 1). The slice stacks of these crania were processed using  
225 Avizo v. 9.0.1. and the left bony labyrinth was segmented using the semiautomatic  
226 ‘watershed’ tool of Avizo (with additional manual corrections in the case of partially filled  
227 canals found in the fossil specimens) and digitally extracted; when the left bony labyrinth  
228 was unavailable, the right one was mirrored. As in Urciuoli et al. (2020), the SCs and the

229 vestibule were separated from the cochlea by cutting the generated 3D meshes  
230 immediately inferior to the saccule and the oval window, using landmarks placed along the  
231 maximum curvature of the junction between the vestibule and the cochlea as reference for  
232 the cutting plane (Fig. 1). The resulting holes were filled with a flat surface using Geomagic  
233 Studio v. 2014.3.0 (3D Systems, Rock Hill, USA). Prior to the 3DGM analysis, the surfaces  
234 were first roughly prealigned by manually superimposing the meshes to ensure biological  
235 correspondence. Subsequently, the alignment was automatically refined using the Avizo  
236 module 'Align Surface' with the 'rigid + uniform' option. Similar to Procrustes  
237 superimposition, this module minimizes the distances between the faces of each surface  
238 by scaling, translating and rotating the analyzed meshes. The phylogenetic relationships of  
239 the extinct taxa included in the analyses, relative to extant anthropoids, are summarized in  
240 Figure 2.

241

#### 242 2.4. *Shape analysis*

243 Differences in vestibule and SC shape were evaluated using a landmark-free 3DGM  
244 technique based on deformation, which relies on the geometrical correspondence of  
245 continuous surfaces and computes the magnitude and direction of deformation of the  
246 analyzed meshes from a group-average template (Glaunès and Joshi, 2006; Durrleman et  
247 al., 2012a, b; Dumoncel et al., 2014; Beaudet et al., 2016; Urciuoli et al., 2020). The  
248 deformations are mathematically modeled to obtain a one-to-one correspondence of the  
249 3D space using the open-source software Deformetrica 4 (Bône et al., 2018). This  
250 technique yields results similar to landmark-based 3DGM methods while more easily  
251 tracking changes in volume (Urciuoli et al., 2020), and is less prone to biases introduced  
252 by the design of landmarking protocols, caused by the inherent difficulty to adequately  
253 capture complex 3D shapes based on a reduced number of homologous landmarks.

254 Due to the high computational power required, the sets of vectors, representing the  
255 flow of deformations from the initial position of the control points on the template to the  
256 target shape, were computed in the Barcelona Supercomputing Center (BSC) using the  
257 MinoTauro cluster (<https://www.bsc.es/marenostrum/minotauro>). To identify major patterns  
258 of shape variation across the sample, the resulting sets of vectors were inspected using  
259 between-group principal component analysis (bgPCA; Mitteroecker and Bookstein, 2011),  
260 using major clades (platyrrhines, cercopithecoids, hylobatids, and hominids) as the  
261 grouping factor (Urciuoli et al., 2020). To address recent concerns about the use of bgPCA  
262 based on highly multivariate data sets, such as those generated by 3DGM, and to rule out  
263 the presence of spurious groupings in our results (Bookstein, 2019; Cardini, et al., 2019),  
264 we computed cross-validated bgPCA scores. These were obtained by iteratively repeating  
265 the bgPCA on a subset of the sample. The cross-validated bgPCA scores were then  
266 compared to those obtained with standard bgPCA (Cardini and Polly, 2020). The affinities  
267 of fossil specimens with the groups defined a priori in the bgPCA were evaluated using the  
268 ‘typprobClass’ function of the Morpho package v. 2.7 (Schlager, 2017) in R v. 3.6.1 (R  
269 Core Team, 2019). This function computes posterior probabilities of group membership  
270 based on the Mahalanobis distances between the bgPC scores of fossil specimens and  
271 group centroids. Null hypotheses of group membership were rejected at  $p < 0.05$ .  
272 Similarities among anthropoid species were also evaluated by running a cluster analysis  
273 (Ward’s method) on the Mahalanobis distances between pairs of bgPCA species centroid  
274 scores using the ‘ward.D2’ method of the ‘hclust’ function of the ‘stats’ package in R. The  
275 cophenetic correlation coefficient, which allows one to evaluate how faithfully the obtained  
276 dendrogram preserves the pairwise distances between the original unmodeled datapoints,  
277 was calculated using the same package.

278 In addition, we inspected the volumetric proportions of *Epipliopithecus* and the  
279 remaining fossil taxa included in the analysis, and determined the correlation between log-

280 transformed cube root canal volume (ln VolSC, mm) and log-transformed canal length (ln  
281 L, mm) by means of ordinary least-squares regression. Given that previous analyses  
282 identified an allometric grade shift between hominids and nonhominid anthropoids (Urciuoli  
283 et al., 2020), separate regression lines were computed for hominids and nonhominid  
284 anthropoid taxa using the 'stats' package in R.

285

## 286 2.5. *Phylomorphospace, ancestral state estimation, and phylogenetic signal*

287 To intuitively visualize the direction and magnitude of evolutionary change we relied  
288 on a phylomorphospace approach (Sidlauskas, 2008), by which a phylogenetic tree is  
289 projected onto the tangent space defined by the bgPCA of our shape data. Ancestral  
290 states for the internal nodes are estimated using a maximum likelihood method for  
291 continuous characters via the 'fastAnc' function of the 'phytools' version 0.6-60 package  
292 for R (Revell, 2012), while the tips of the tree branches correspond to the centroid scores  
293 for the included taxa. We repeated the analyses using two composite phylogenetic trees,  
294 one with *Epipliopithecus* as a stem catarrhine and the other with this taxon as a stem  
295 hominoid (Figs. 2 and 3). For extant taxa we relied on a Bayesian phylogenetic analysis of  
296 eleven mitochondrial and six autosomal genes downloaded from the 10kTrees Website v.  
297 3 (Arnold et al., 2010). Extinct species were added based on their phylogenetic position,  
298 their divergence being arbitrarily placed 1 Myr before the estimated divergence age of the  
299 next derived node, and tip ages based on their chronostratigraphic age. We used the  
300 following tip age estimates: *Epipliopithecus* 14.15 Ma (mean of 14.85 and 13.45 Ma, the  
301 maximum-minimum age range for MN6 in central Europe according to van der Meulen et  
302 al., 2011); *Aegyptopithecus* and *Parapithecus*, 29.85 Ma (mean of 30.2 and 29.5 Ma,  
303 based on the revised age range of the fauna of quarries I and M of the Jebel Qatrani  
304 Formation of the Fayum depression by Seiffert, 2006); *Dolichocebus*, 20.5 Ma (mean of  
305 21.0 and 20.0 Ma age provided by Kay, 2015); *Homunculus*, 17.2 Ma (mean of 17.9 and

306 16.5 Ma age provided by Kay, 2015); and *Oreopithecus* 6.75 Ma (mean of 7.0 and 6.5 Ma  
307 for the last occurrence according to Rook et al., 2000).

308 The phylogenetic signal embedded in the shape data was measured using Pagel's  
309  $\lambda$  (Pagel, 1999) and Blomberg's K (Blomberg et al., 2003), together with the multivariate  
310 version of Blomberg's K ( $K_{\text{mult}}$ ; Adams, 2014). Pagel's  $\lambda$  and Blomberg's K were computed  
311 using the 'phylosig' function of the 'phytools' package in R, while  $K_{\text{mult}}$  was computed with  
312 the 'physignal' function of the 'geomorph' package v. 3.1.0 in R (Adams et al., 2019).  
313 These metrics were computed based on extant taxa only (Arnold et al., 2010).

314 Ancestral node morphologies were computed from the bgPC scores for the last  
315 common ancestors (LCAs) estimated by means of maximum likelihood, which were  
316 rotated and translated from the morphospace back into the deformation field space,  
317 generating a set of momentum vectors that were used in Deformetrica 4 to warp the  
318 template surface into the target LCA morphology. Volumetric proportions for the LCAs  
319 were computed based on the rescaled 3D models obtained from the phylomorphospace  
320 approach; the scaling factor for each LCA was estimated using the 'anc.ML' function of the  
321 R package 'phytools'. Morphological similarities between *Epipliopithecus* and the LCA  
322 centroids were assessed by means Euclidean distances between the *Epipliopithecus*  
323 centroid and the LCA bgPC scores, weighted on the basis of the percentage of variance  
324 explained by each bgPC and computed using the 'distances' function of the 'distances'  
325 package version 0.1.8 in R (Savje, 2019).

326 The two phylogenetic hypotheses for *Epipliopithecus* depicted in Figure 3 were  
327 assessed further based on the coding of seven discrete characters that were deemed of  
328 phylogenetic significance based on shape comparisons and analyses. The resulting  
329 character-taxon matrix was analyzed for character congruence against a fixed topology  
330 consistent with the phylogenetic hypotheses depicted in Figure 3. For both cladograms,  
331 three indices customarily employed in cladistics (Farris, 1989) were computed in PAUP\* v.

332 4.0a168 for Mac (Swofford, 2003) to assess the most parsimonious hypothesis: the  
333 consistency index (CI), the retention index (RI), and the rescaled consistency index (RC).

334

### 335 **3. Results**

#### 336 *3.1. Description and comparisons*

337 The three bony labyrinths of *E. vindobonensis* are well preserved—except for the  
338 lateral canal of NMB OE 303b, which shows a small fracture in the bony encasing—and  
339 are not affected by diagenetic deformation, thereby permitting a straightforward extraction  
340 of the 3D surfaces of the vestibular apparatus bony labyrinth (Fig. 4a–c). Overall, the  
341 canals are fairly slender, as in platyrrhines and cercopithecins, falling within their variability  
342 as shown by a bivariate plot of SC volume vs. length (Fig. 5; Table 2; SOM Table S3). The  
343 bony vestibule is large, albeit less so than in hominids. The anterior and posterior canals  
344 are larger than the lateral canal, as in platyrrhines (Fig. 4e–i) and modern humans (Fig.  
345 4u).

346 The *E. vindobonensis* common crus (CC) is long, as in extant platyrrhines (Fig. 4g–  
347 i) and in *Dolichocebus* (Fig. 4e), but unlike in most catarrhines. The trajectories of the  
348 anterior and posterior canal form a right angle when merging at the CC apex. Despite  
349 some similarities, the morphology of *Epipliopithecus* is clearly distinguishable from that of  
350 *Dolichocebus* and *Parapithecus* (Fig. 4d), as the CC is not posteromedially inclined and  
351 the anterior canal connection is placed more laterally.

352 The anterior canal of *E. vindobonensis* is slightly wider than tall (as in *Hoolock*; Fig.  
353 4q), yet clearly rounded and lacking the vertical compression characteristic of extant  
354 hominoids (Fig. 4o–u), the anterosuperior elongation typical of hylobatids and *Pongo* (Fig.  
355 4o–r; Urciuoli et al., 2020), and the extreme superior projection found in *Ateles* (Fig. 4g).  
356 The anterior canal of *Epipliopithecus* further differs from that of the stem anthropoid  
357 *Parapithecus* (Fig. 4d), the stem platyrrhine *Dolichocebus* (Fig. 4e), and the stem

358 catarrhine *Aegyptopithecus* (Fig. 4j), characterized by an almost triangular morphology  
359 (albeit less so in the last genus). The superiormost portion of the anterior canal bends  
360 medially, causing a moderate torsion of the canal trajectory. This morphology is also found  
361 in the stem platyrrhine *Homunculus* (Fig. 4f) and, to a lesser extent, *Chlorocebus* (Fig. 4l)  
362 and *Dolichocebus* (Fig. 4e), while in most cercopithecoids it is much more bent (e.g.,  
363 *Macaca*; Fig. 4m). A sinuous trajectory of the anterior canal, although with a different  
364 morphology, is also displayed by other taxa (e.g., *Cebus*; Fig. 4i) and thus is not very  
365 informative from a phylogenetic viewpoint. Despite the aforementioned similarities,  
366 *Epipliopithecus* differs from the stem platyrrhines *Homunculus* (Fig. 4f) and *Dolichocebus*  
367 (Fig. 4e), from most extant platyrrhines (particularly *Ateles*; Fig. 4g), and from the stem  
368 catarrhine *Aegyptopithecus* (Fig. 4j), in displaying a much less mediolaterally compressed  
369 anterior canal.

370 The posterior canal of *Epipliopithecus* is slightly taller than wide, similar to that of  
371 *Alouatta* (Fig. 4h) and *Symphalangus* (Fig. 4p), but differs from the latter by displaying a  
372 less arched connection with the CC. The orientation of the posterior canal relative to the  
373 plane defined by the anterior canal is different in the two individuals of *Epipliopithecus*: it  
374 forms an obtuse angle in NHMW 1970/1397/0003 (resembling the hylobatid condition), but  
375 forms a right angle in NMB OE 303 (as in other anthropoids; SOM Fig. S2).

376 The lateral canal is rounded and smaller than the other canals (more so in NMB OE  
377 303), as in stem platyrrhines (Fig. 4e, f) and the stem catarrhine *Aegyptopithecus* (Fig. 4j),  
378 although in *Epipliopithecus* this canal is not strongly compressed mediolaterally as in the  
379 latter taxon (Fig. 4j). The trajectory of the ampullary portion of the lateral canal slightly  
380 bends superiorly (more so in NMB OE 303; Fig. 4b, c), while the insertion of its slender  
381 part is located anteriorly to the base of the CC (particularly in NHMW 1970/1397/0003; Fig.  
382 4a), so that—as in extant hominoids but unlike cercopithecoids—the lateral canal does not  
383 intersect the plane defined by the posterior canal. The lateral canal also shows a wave-like



384 shape, with its lateral-most tip pointing downwards, superficially resembling some  
385 individuals of *Pongo* (Fig. 4r), while differing from the morphology of *Trachypithecus* (Fig.  
386 4k) and *Macaca* (Fig. 4m), where the canal bends inferiorly right before the ampullary  
387 portion.

388

### 389 3.2. Shape analysis

390 The bgPCA discriminates major anthropoid clades with just minimal overlap when  
391 the three axes are considered simultaneously (Fig. 6), thus closely resembling the  
392 previous results by Urciuoli et al. (2020) despite the increased number of platyrrhine taxa  
393 included here. The bgPCA results reported in Figure 6 closely resemble those derived  
394 using a cross-validated bgPCA (SOM Fig. S1), indicating that group separation is not  
395 spurious (Cardini and Polly, 2020).

396 The first principal component (bgPC1, which explains 59% of the variance) mainly  
397 reflects differences in volumetric proportions among the SCs and the volume they occupy  
398 relative to that of the bony vestibule, separating hominids (stout canals; quite negative  
399 scores) from both cercopithecoids and hylobatids (slender canals; positive to slightly  
400 negative scores), while platyrrhines (including stem taxa), the stem anthropoid  
401 *Parapithecus*, the stem catarrhine *Aegyptopithecus*, the stem hominoid *Oreopithecus*, and  
402 *Epipliopithecus* occupy an intermediate position in the morphospace. In particular, the two  
403 *Epipliopithecus* individuals, due to their fairly slender canals (Fig.4a–c), display similar  
404 intermediate scores along this axis, overlapping extensively with both extant and extinct  
405 platyrrhines in the overlap zone of cercopithecoids and hominoids (Fig. 6a, c).

406 In turn, bgPC2 (which explains 30% of the variance) accounts for differences in the  
407 size and shape of the anterior and posterior canals (Fig. 6a, d), in the position of the lateral  
408 canal ampullary insertion on the vestibule, and in CC length, separating most platyrrhines  
409 (positive scores) from catarrhines (moderately positive to negative scores). In particular,

410 platyrrhines possess large and very superiorly elongated canals in the portion close to the  
411 CC apex, as well as a flat lateral canal, which also connects more inferiorly on the  
412 vestibule with its ampullary portion. Catarrhines are more variable in these features,  
413 showing rounded to vertically compressed anterior and posterior canals, a shorter CC, and  
414 a variably sinuous lateral canal with its ampullary portion connecting more superiorly.  
415 *Epipliopithecus* displays moderately positive scores, falling within the range of several  
416 extant platyrrhines (*Aotus*, *Alouatta*, *Callithrix* and *Callicebus*), due to their large anterior  
417 and posterior canals, coupled with a long CC and a small lateral canal. Both the stem  
418 platyrrhines and *Oreopithecus* show similar moderately positive scores, while  
419 *Aegyptopithecus* and *Parapithecus* show markedly positive values due to their superiorly  
420 elongated vertical canals (Fig. 6a).

421 Finally, bgPC3 (which explains 11% of the variance) is driven by the position of the  
422 lateral canal relative to the posterior one, by the size and orientation of the posterior canal,  
423 as well as the shape of the anterior canal and CC thickness (Fig. 6b, e), separating  
424 hylobatids (most positive values) from most extant and fossil anthropoids (intermediate to  
425 negative scores). Hylobatids have a much larger gap between the lateral and posterior  
426 canals than other anthropoids except some modern humans, and their posterior canal is  
427 also smaller than, and forms an obtuse angle with, the large and anteriorly-protruding  
428 anterior canal. In contrast, in most cercopithecoids, *Aotus*, and *Callithrix*, the lateral canal  
429 broadly intersects with the posterior canal, while in the African great apes, *Theropithecus*,  
430 and *Cebus* the canals are only minimally separated. In addition, in all extant anthropoids  
431 except hylobatids, the plane of the posterior canal forms a right angle with the anterior  
432 canal, which does not project anteriorly. Both *Epipliopithecus* individuals display positive  
433 scores (NMB OE 303 with lower values), overlapping with some hylobatids (mainly  
434 *Hoolock*) and other extant anthropoids (particularly the hominids *Homo* and *Pongo*, the  
435 platyrrhines *Ateles* and *Alouatta*, and the cercopithecoids *Theropithecus* and *Piliocolobus*).

436 The slightly dissimilar bgPC3 scores for the two *Epipliopithecus* individuals result from  
437 differences in orientation between the posterior and anterior canals (obtuse angle in  
438 NHMW 1970/1397/0003 vs. right angle in NMB OE 303; SOM Fig. S2), causing a wider  
439 separation between the lateral and posterior canals (Fig. 4a–c).

440 When the three bgPCs are considered together, the two *Epipliopithecus* individuals  
441 show the greatest morphological similarities with platyrrhines (less so in NHMW  
442 1970/1397/0003), as demonstrated by Mahalanobis distances from group centroids and by  
443 their posterior probabilities of group membership (Table 3), leading us to reject close  
444 similarities to the remaining groups for NMB OE 303, and to all anthropoid groups for  
445 NHMW 1970/1397/0003 ( $p < 0.05$ ). *Aegyptopithecus*, *Parapithecus*, *Oreopithecus*, and  
446 stem platyrrhines also closely resemble extant New World monkeys, with *Oreopithecus*  
447 also showing marginal affinities with cercopithecoids (Table 3). We obtain very similar  
448 results when considering all catarrhines as a single group, with all fossils being classified  
449 as platyrrhines (Table 4). For *Oreopithecus* and NHMW 1970/1397/0003, group  
450 membership for catarrhines cannot be rejected. However, both specimens show much  
451 lower Mahalanobis distances to the platyrrhine centroid (almost three times) than to that of  
452 catarrhines. The two *Epipliopithecus* individuals are closer to one another than they are to  
453 other fossil taxa (except for one individual of *Homunculus*, MPM-PV 3501), in turn showing  
454 similarities with stem platyrrhines, *Aegyptopithecus* and *Oreopithecus* (Table 5). A cluster  
455 analysis based on the momenta of the deformation fields confirms these results (Fig. 7).  
456 *Epipliopithecus* clusters with *Alouatta* and *Ateles* (large and rounded vertical canals and a  
457 large gap between the lateral and posterior canals), as well as *Pithecia* (obtuse angle  
458 formed by the anterior and posterior canals), within a larger cluster that includes the  
459 remaining extant platyrrhines and the other fossil taxa included in the analysis. In  
460 particular, *Aegyptopithecus* and *Homunculus* cluster with *Saimiri* and *Cebus* (flat lateral  
461 canal and similarities in the anterior canal morphology), while *Oreopithecus* clusters with

462 *Callicebus* (orientation of the anterior and posterior canals). Hylobatids cluster within a  
463 larger group that also includes most cercopithecoids, and extant great apes cluster  
464 together due to their distinctive stout volumetric proportions (Urciuoli et al., 2020).

465

### 466 3.3. *Phylogenetic signal and phylomorphospace*

467 Like previous analyses (Urciuoli et al., 2020; del Rio et al., 2020; Morimoto, et al.,  
468 2020, our results indicate that the vestibule and SCs embed significant phylogenetic signal  
469 ( $K_{\text{mult}} = 1.134$ ,  $p < 0.001$ ), suggesting these traits conform to a Brownian motion model of  
470 evolution, with closely related taxa resembling one another slightly more than expected  
471 ( $K_{\text{mult}} > 1$ ). The phylogenetic signal computed for each bgPC separately is significant in all  
472 instances (Table 6), with bgPC1 and bgPC2 suggesting the same evolutionary mode as  
473  $K_{\text{mult}}$  ( $K > 1$ ). Conversely, we observe that the variance accumulates within clades for  
474 bgPC3 ( $K < 1$ ), thus suggesting that changes along this axis might be more strongly  
475 affected by homoplasy.

476 The phylogenetic signal detected justifies the application of the phylomorphospace  
477 approach (Fig. 8). The results indicate that the reconstructed LCAs of crown anthropoids  
478 (Fig. 9a) and crown catarrhines (Fig. 9c) fall within the variability of extant New World  
479 monkeys, being very close to the platyrrhine LCA (Fig. 9b)—irrespective of the  
480 phylogenetic hypothesis used in the analysis for *Epipliopithecus* (i.e., stem catarrhine vs.  
481 stem hominoid, Figs. 3 and 8; SOM Fig. S3). Cercopithecoids and hominoids appear much  
482 more derived in SC morphology than platyrrhines, but in different directions. The crown  
483 anthropoid, crown platyrrhine and crown catarrhine LCAs are reconstructed as possessing  
484 large and slightly vertically-elongated canals (more so in the crown anthropoid and crown  
485 platyrrhine LCAs; Fig. 9a, b) coupled with a long CC (shorter in the crown catarrhine LCA;  
486 Fig. 9c), intermediate volumetric proportions (similar to those found in New World monkeys  
487 and cercopithecins; Fig. 10), and a coplanar lateral canal that does not intersect the plane

488 of the posterior one (Fig. 9a–c). The LCA of crown catarrhines also shows a slightly more  
489 superiorly bent ampullary portion, more so than in *Epipliopithecus* (Fig. 9c). In contrast, the  
490 reconstructed crown hominoid LCA (Fig. 9d) is found in an area of the morphospace  
491 devoid of extant taxa and, according to our estimation, it already displayed some derived  
492 characters that are not found in *Epipliopithecus* (i.e., moderately vertically-compressed  
493 anterior canal, stouter canal proportions, lateral ampulla connecting more superiorly with  
494 the vestibule).

495 From a phenetic viewpoint, based on weighted Euclidean distances between  
496 *Epipliopithecus* and the bgPC scores for the reconstructed LCAs (Table 7), the former  
497 taxon is most similar to the crown catarrhine ancestral condition, and also closer to the  
498 crown anthropoid and platyrrhine LCAs, than to the ancestral conditions reconstructed for  
499 either hominoids or cercopithecoids.

500 We further synthesized the information provided by the phylomorphospace  
501 approach by defining seven discrete characters coded in a cladistic fashion (Table 8; Fig.  
502 11). Their coding for the reconstructed LCAs as well as both extant and extinct  
503 anthropoids included in the analyses is reported in Table 9 and SOM Table S4. When the  
504 character states for extinct and extant taxa are analyzed against the two phylogenetic  
505 hypotheses by considering parsimony as a criterion (Table 10), *Epipliopithecus* is more  
506 parsimoniously interpreted as a stem catarrhine (Fig. 3a) than as a stem hominoid (Fig.  
507 3b). The phylogenetic implications of the seven coded characters (Fig. 11; Tables 8 and 9;  
508 SOM Table S4) are discussed below and illustrated in Figure 12.

509 Size of the vestibule relative to the semicircular canals Extant hominids differ from all the  
510 remaining extant taxa in possessing a relatively larger vestibule, which may be thus  
511 interpreted as a synapomorphy of at least crown hominids. Among the extinct taxa, only  
512 the purported stem hominoid *Oreopithecus* displays the derived hominid condition,  
513 indicating either an independent acquisition of this feature in this taxon (as supported by

514 our LCA reconstructions) or a secondary reversal in hylobatids. *Epipliopithecus*, in any  
515 case, retains the plesiomorphic condition of nonhominoid anthropoids.

516 Robusticity of the semicircular canals This character has the same distribution as the size  
517 of the vestibule relative to the SCs. Extant hominids and *Oreopithecus* differ from the  
518 remaining taxa by displaying stouter proportions. Accordingly, such proportions might be  
519 interpreted either as convergent between *Oreopithecus* and hominids, or as a hominoid  
520 synapomorphy with subsequent reversal in hylobatids. Our LCA reconstructions do not  
521 provide clear support for either possibility, as they suggest an intermediate ancestral  
522 condition in the overlap zone between hominoids and nonhominoid catarrhines. In either  
523 case, for this character *Epipliopithecus* displays the more plesiomorphic condition of  
524 nonhominoid anthropoids.

525 Shape of the anterior semicircular canal This character is more variable than the  
526 preceding ones, both within anthropoid subclades, and sometimes even within the same  
527 species. However, extant catarrhines generally differ from platyrrhines by possessing an  
528 anterior canal that is not superiorly elongated, being instead either rounded (as in humans  
529 and most cercopithecoids) or vertically compressed (as in great apes and generally  
530 hylobatids, although in the latter it varies intraspecifically between rounded and vertically  
531 compressed). Our LCA reconstructions suggest that the ancestral anthropoid condition—a  
532 superiorly elongated anterior canal—is symplesiomorphic not only for platyrrhines but also  
533 for the stem catarrhine *Aegyptopithecus*. They further support the view that a rounded  
534 anterior SC is synapomorphic of crown catarrhines, while a vertically compressed anterior  
535 SC would be synapomorphic for crown hominoids + *Oreopithecus*. In this regard,  
536 *Epipliopithecus* is more derived than *Aegyptopithecus* but less so than *Oreopithecus*. This  
537 character, therefore, unambiguously supports for *Epipliopithecus* a catarrhine status more  
538 derived than in *Aegyptopithecus*, although it would be consistent with either a stem  
539 catarrhine or a stem hominoid status.

540 Shape of the anterior portion of the semicircular canal Hylobatids and orangutans differ  
541 from the rest of the sample by displaying an anterosuperiorly-projecting anterior portion of  
542 the anterior canal. This condition may be interpreted as a crown hominoid synapomorphy  
543 subsequently reversed in hominines, as further supported by the fact that *Oreopithecus*  
544 displays the derived condition for hominoids. Alternatively, this feature might have been  
545 independently acquired in *Oreopithecus*, as suggested by our LCA reconstructions, which  
546 only recover it as a hylobatid synapomorphy. Given the possession of other SC hominoid  
547 synapomorphies in *Oreopithecus*, we tend to favor the former interpretation, even if both  
548 are equally parsimonious. In any case, *Epipliopithecus* retains the more plesiomorphic  
549 condition of non-hominoid anthropoids.

550 Shape of the posterior semicircular canal Although this character is somewhat variable  
551 within anthropoid subclades and sometimes even within species, some generalities can be  
552 drawn. In platyrrhines, the posterior canal is generally elongated superiorly to some extent,  
553 whereas most cercopithecoids have a rounded posterior canal, and hominoids generally  
554 vary between a rounded and a vertically compressed morphology (only sometimes  
555 superiorly elongated in *Pan*). Our LCA reconstructions indicate that platyrrhines and  
556 *Aegyptopithecus* retain the ancestral anthropoid condition (superiorly elongated posterior  
557 canal), whereas the rounded morphology would be synapomorphic for crown hominoids.  
558 *Epipliopithecus* displays the plesiomorphic anthropoid condition and thus differs from  
559 *Oreopithecus*, which displays the derived catarrhine morphology.

560 Shape of the lateral semicircular canal ampullary portion Extant hominoids differ from the  
561 remaining extant taxa and all the analyzed extinct genera by displaying a markedly  
562 superiorly-bent ampullary portion of the lateral canal. Both *Epipliopithecus* and  
563 *Oreopithecus* thus display a more plesiomorphic condition than crown hominoids, as  
564 further confirmed by our LCA reconstructions.

565 Length of the common crus This character is also variable to some extent, but platyrrhines  
566 generally display a longer CC than extant catarrhines, with hominoids having an even  
567 shorter CC than most cercopithecoids. Our LCA reconstructions support an intermediate  
568 length of the CC as synapomorphic of crown catarrhines, with a short CC being  
569 synapomorphic for hominoids. *Epipliopithecus* resembles *Aegyptopithecus* and  
570 platyrrhines by retaining the ancestral anthropoid condition, whereas *Oreopithecus*  
571 displays the derived hominoid morphology.

572

#### 573 **4. Discussion**

574 Our analysis of the SC and vestibule morphology of *Epipliopithecus* allows us to  
575 refine our understanding of the evolution of this anatomical region in anthropoid primates  
576 and to refine previous hypotheses proposed by Urciuoli et al. (2020). The results of our  
577 deformation-based 3DGM analysis and the reconstruction of ancestral morphotypes for  
578 main anthropoid clades indicate that, like the stem catarrhine *Aegyptopithecus*,  
579 *Epipliopithecus* displays a platyrrhine-like morphology most similar to that reconstructed  
580 for the crown catarrhine LCA. This might be compatible with *Epipliopithecus* being either a  
581 stem catarrhine, or a crown catarrhine only slightly postdating the cercopithecoid-hominoid  
582 split. However, the fact that *Epipliopithecus* most closely resembles the crown anthropoid  
583 (and platyrrhine) LCAs (Table 7) suggests that the semicircular morphology of this taxon is  
584 most consistent with its status as a stem catarrhine. This conclusion is further supported  
585 by the analysis of seven discrete characters coded for this anatomical area—which  
586 indicate that this is the most parsimonious hypothesis, for reasons discussed in greater  
587 detail below.

588

##### 589 *4.1. Epipliopithecus as a hominoid*



590           Based on the morphology of the SCs and vestibule, *Epipliopithecus* lacks multiple  
591 hominoid synapomorphies, including a large vestibule relative to the canals, stout SCs,  
592 vertically-compressed anterior canal, anterosuperiorly- projecting anterior portion of the  
593 anterior canal, markedly superiorly-bent ampullary portion of the lateral canal, and short  
594 CC. Urciuoli et al.(2020) already interpreted some of these features (vertically-compressed  
595 anterior canal and markedly superiorly-bent ampullary portion of the lateral canal) as  
596 potential crown hominoid synapomorphies, whereas they interpreted others (large  
597 vestibule and stout canals) as hominid synapomorphies. Urciuoli et al. (2020) interpreted a  
598 superiorly-bent ampullary portion of the lateral canal as a hominoid synapomorphy.  
599 However, hominoids are, in fact, characterized by the possession of a markedly bent  
600 trajectory, whereas other catarrhines display a flat to slightly superiorly-bent ampullary  
601 portion of the lateral canal. This is the case for *Epipliopithecus*, which displays much less  
602 bending of the lateral canal than in *Oreopithecus* or any extant hominoid.

603           The possession of a large vestibule and stout canals was previously interpreted as  
604 being synapomorphic for hominids (Urciuoli et al., 2020) because hylobatids display a  
605 different ('monkey-like') condition. The differences in volumetric proportions between  
606 *Epipliopithecus* and hominids are particularly clear (Fig. 10), with the former closely  
607 resembling platyrrhines, *Aegyptopithecus*, and the inferred ancestral catarrhine condition.  
608 Given that both features are present in *Oreopithecus*, they may be interpreted as hominoid  
609 synapomorphies subsequently reversed in hylobatids—thereby supporting a more basal  
610 branching for *Epipliopithecus*. However, their interpretation as hominid synapomorphies is  
611 equally parsimonious, as it would only imply their independent acquisition in *Oreopithecus*.  
612 Therefore, neither a large vestibule nor stout canals can be used to unambiguously  
613 discount a hominoid status for *Epipliopithecus*. A similar caveat applies to the lack of an  
614 anterosuperiorly-projecting anterior canal in *Epipliopithecus*. This condition was previously  
615 interpreted as an autapomorphy of *Hylobates* (Le Maître, et al., 2017) or as a hylobatid

616 synapomorphy (Spoor and Zonneveld, 1998; Urciuoli, et al. 2020). However, given its  
617 presence in orangutans and *Oreopithecus*, it is more readily interpreted as a hominoid  
618 synapomorphy subsequently reversed in hominines. The interpretation of some of the  
619 potential hominoid synapomorphies lacking in *Epipliopithecus* is ambiguous due to  
620 homoplasy (convergence and/or reversal). However, it is worth noting that, except for the  
621 markedly superiorly bent ampullary portion of the lateral canal, *Oreopithecus* further  
622 displays two more unambiguous hominoid synapomorphies (vertically compressed anterior  
623 canal and short CC). The absence of these features in *Epipliopithecus* thus conclusively  
624 excludes a more derived hominoid status for the latter as compared with *Oreopithecus*.

625 *Epipliopithecus* also displays some hylobatid-like features in the spatial  
626 configuration between the lateral and posterior canals, as well as in the orientation  
627 between the anterior and posterior canals. According to Urciuoli et al. (2020), the lack of  
628 intersection between the lateral and posterior canals and the presence of an obtuse angle  
629 between the anterior and posterior canals would be synapomorphic for hominoids and  
630 hylobatids, respectively. However, only *Hylobates* consistently displays both features,  
631 while most anthropoid taxa, as well as the two *Epipliopithecus* individuals, show a  
632 considerable amount of intraspecific variation. Hence, we refrained from coding these  
633 features in a cladistic manner, especially in view of the low phylogenetic signal ( $K < 1$ )  
634 recovered for bgPC3 (accounting for the variation in the configuration of these features),  
635 which suggests a substantial degree of homoplasy. Indeed, previous analyses  
636 hypothesized that suspensory species possess more obtuse angles between the vertical  
637 canals (Gonzales et al., 2019), as this configuration provides an increased sensitivity for  
638 pitch (at the expense of roll) head movements (Muller and Verhagen, 2002a,b,c). The  
639 similarities between NHMW 1970/1397/0003, hylobatids, and some atelids (Spoor and  
640 Zonneveld, 1998; Gonzales et al., 2019) would thus agree with previous inferences about  
641 the locomotor repertoire of this taxon including some degree of suspensory behaviors

642 (Zapfe, 1958; Fleagle, 1983; Langdon, 1986; Rose, 1994; Arias Martorell et al., 2015). In  
643 contrast, the more plesiomorphic condition of NBM OE 303III (characterized by tangent  
644 lateral and posterior canals, and vertical canals approximating a right angle), also found in  
645 *Aegyptopithecus* and some nonsuspensory platyrrhine species, suggests caution when  
646 using SC orientation alone for inferring positional behaviors (Perier et al., 2016; contra  
647 Malinzak et al., 2012; Berlin et al., 2013).

648

#### 649 4.2. *Epipliopithecus* as a stem catarrhine

650 *Epipliopithecus* resembles both stem platyrrhines and the stem catarrhine  
651 *Aegyptopithecus* in lacking all of the aforementioned hominoid synapomorphies, thereby  
652 retaining the plesiomorphic anthropoid condition—a relatively small vestibule, slender SCs,  
653 anterosuperiorly nonprojecting anterior portion of the anterior canal, superiorly elongated  
654 posterior canal, ampullary portion of the lateral canal not markedly bent superiorly, and  
655 long CC. The fact that *Epipliopithecus* lacks hominoid synapomorphies displayed by  
656 *Oreopithecus* could still be consistent with a more basal stem hominoid status. However,  
657 such an interpretation is contradicted by the retention in *Epipliopithecus* of a superiorly  
658 elongated posterior canal and a long CC—contrasting with the rounded posterior canal  
659 and moderately short CC that are synapomorphic of crown catarrhines. The catarrhine  
660 status of *Epipliopithecus* and other pliopithecoids is well established based on multiple  
661 features, such as the loss of the second premolars and the presence of a C<sup>1</sup>/P<sub>3</sub> honing  
662 complex (e.g., Harrison, 2013). The catarrhine status of *Epipliopithecus* is further  
663 supported by the possession of a rounded anterior canal, which is intermediate between  
664 the primitive morphology (superiorly elongated anterior canal) retained by platyrrhines and  
665 *Aegyptopithecus*, and the more derived (vertically compressed) morphology  
666 synapomorphic of hominoids. In this regard, *Epipliopithecus* is more derived toward crown  
667 catarrhines than the propiopithecoid *Aegyptopithecus*, in agreement with other cranial

668 features such as the possession of a partially enclosed tubular ectotympanic in  
669 *Epipliopithecus* (e.g., Harrison, 2013).

670 In summary, based on the morphology of the SCs and vestibule, *Epipliopithecus* is  
671 most parsimoniously interpreted as a stem catarrhine more derived than *Aegyptopithecus*,  
672 due to its possession of a crown catarrhine synapomorphy—rounded anterior canal—  
673 coupled with the lack of two additional crown catarrhine synapomorphies (superiorly  
674 elongated posterior canal and long CC) and multiple hominoid and/or hominid  
675 synapomorphies as described above. The shapes of the anterior and posterior canals and  
676 CC should be considered with caution in light of the intraspecific variability displayed by  
677 these characters in some taxa (SOM Table S4). Previous analyses noted a structural  
678 relationship between the morphology of these canals and the extension of the subarcuate  
679 fossa (Jeffery and Spoor, 2006; Jeffery et al., 2008), and this relationship has been  
680 uncritically assumed in some studies (Spoor et al., 2007; Silcox et al., 2009; Gonzales et  
681 al., 2019). However, in most cases the fossa simply expands within the space left available  
682 from the ossification of the canals, with little or no influence on their shape (Jeffery et al.,  
683 2008; see also Urciuoli et al., 2020). In support of the latter hypothesis, we observe  
684 meager dissimilarities in the anterior canal morphology of NHMW 1970/1397/0003 and  
685 NBM OE 303III—except for the angle, as discussed above—irrespective of the marked  
686 differences in the morphology of the fossa between the two individuals (Zapfe, 1960).  
687 While a large amount of morphological variation has been documented within ruminant  
688 genera (Mennecart and Costeur, 2016), variation in CC length and shape has not been  
689 exhaustively analyzed in primates (Spoor and Zonneveld, 1998; Ekdale 2013; Lee et al.,  
690 2013). In the present study, we found considerable intraspecific variation in CC length for  
691 some species of monkeys and apes. Nevertheless, our results support a clear morphocline  
692 from the ancestral condition (long CC) retained by platyrrhines, *Aegyptopithecus*, and  
693 *Epipliopithecus*, to the most derived condition (short CC) characteristic of hominoids, with

694 cercopithecoids displaying an intermediate condition that is likely synapomorphic for crown  
695 catarrhines as a whole. Therefore, *Epipliopithecus* SC morphology supports its  
696 interpretation as more derived than *Aegyptopithecus* toward crown catarrhines, but  
697 excludes a crown catarrhine status and, in particular, a closer relationship with hominoids  
698 (unlike in the case of *Oreopithecus*).

699

## 700 **5. Conclusions**

701 Our results are in broad agreement with previous analyses suggesting that  
702 *Epipliopithecus* displays a ‘typical monkey’ inner ear morphology (Morimoto et al., 2020),  
703 while *Oreopithecus* possesses SC and vestibule features derived toward the crown  
704 hominoid condition (Urciuoli et al., 2020). At the same time, our study further refines  
705 previous comparisons of SC and vestibule morphology between *Epipliopithecus* and other  
706 anthropoids, enabling us to test competing hypotheses about the phylogenetic position of  
707 this taxon (i.e., stem catarrhine vs. stem hominoid).

708 From a phenetic viewpoint, for this anatomical area *Epipliopithecus* more closely  
709 resembles platyrrhines and the stem catarrhine *Aegyptopithecus*, as well as the  
710 reconstructed ancestral catarrhine morphotype. The fact that *Epipliopithecus* shows  
711 greater similarities with the platyrrhine and anthropoid ancestral morphotypes, rather than  
712 with those of cercopithecoids or hominoids, supports the view that *Epipliopithecus* is a  
713 stem catarrhine instead of a stem hominoid. From a cladistic perspective, this  
714 interpretation is confirmed based on a series of crown catarrhine and crown hominoid  
715 synapomorphies. *Epipliopithecus* is more parsimoniously interpreted as a stem catarrhine  
716 than as a stem hominoid based on the vestibular morphology analyzed here because it  
717 lacks several catarrhine and all hominoid synapomorphies. Specifically, the possession of  
718 a rounded posterior canal reinforces the view that *Epipliopithecus* is more derived than  
719 *Aegyptopithecus* among stem catarrhines.

720 The information provided by the SCs and vestibule is thus congruent with the  
721 ectotympanic morphology of *Epipliopithecus* (see review in Fricano, 2018), which is more  
722 plesiomorphic than in crown catarrhines but more derived than in propliopithecoids. Some  
723 similarities between *Epipliopithecus* and hylobatids are based on characters that are too  
724 variable within species to be of use for phylogenetic assessment. Such features might  
725 have evolved independently between some atelids and hylobatids, due to similar  
726 locomotor-related selection pressures, and do not support the close phylogenetic link  
727 classically hypothesized between pliopithecoids and hylobatids (Hürzeler, 1954; Zapfe,  
728 1960, 1961; Simons and Fleagle, 1973), particularly given that *Epipliopithecus* displays no  
729 crown hominoid synapomorphies. We therefore conclude that the SC and vestibular  
730 morphology reinforces the most commonly held view that, in accordance with most  
731 (Zalmout et al., 2010; Stevens et al., 2013; Nengo et al., 2017) but not all (Alba et al.,  
732 2015) recent cladistic analyses, *Epipliopithecus* is best interpreted as a stem catarrhine  
733 rather than a stem hominoid.

734

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756

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1065 Table 1. Digital object identifiers (DOIs) of the 3D virtual models of the vestibule and  
1066 semicircular canals of *Epipliopithecus vindobonensis* available from  
1067 MorphoSource.org (<https://www.morphosource.org>).  
1068

Catalog No.	Museum	DOI
NMBOE 303a (individual III)	NMBOE	<a href="https://doi.org/10.17602/M2/M113935">https://doi.org/10.17602/M2/M113935</a>
NMBOE 303b (individual III)	NMBOE	<a href="https://doi.org/10.17602/M2/M113933">https://doi.org/10.17602/M2/M113933</a>
NHMW 1970/1397/0003 (individual II)	NHMW	<a href="https://doi.org/10.17602/M2/M113932">https://doi.org/10.17602/M2/M113932</a>

1069 Abbreviations: NMB OE = Naturhistorisches Museum Basel, Switzerland; NHMW =  
1070 Naturhistorisches Museum Wien, Austria.

1071 Table 2. Log-transformed cube root of canal volume (ln VoISC, mm<sup>3</sup>) and log-  
 1072 transformed canal length (ln L, mm) measured for the fossil taxa included in the  
 1073 analysis.<sup>a</sup>

Catalog No.	Taxon	ln VoISC	ln L
NMBOE 303a	<i>Epipliopithecus vindobonensis</i>	3.640	0.993
NMBOE 303b	<i>Epipliopithecus vindobonensis</i>	3.602	0.910
NHMW 1970/1397/0003	<i>Epipliopithecus vindobonensis</i>	3.593	0.916
CGM 85785	<i>Aegyptopithecus zeuxis</i>	3.365	0.847
MPM-PV 30501	<i>Homunculus patagonicus</i>	3.391	0.780
MPM-PV 30502	<i>Homunculus patagonicus</i>	3.359	0.720
MPM-PV 30503	<i>Homunculus patagonicus</i>	3.359	0.784
MACN 14128	<i>Dolichocebus gaimanensis</i>	3.802	0.803
BAC 208	<i>Oreopithecus bambolii</i>	3.295	0.803
DPC 18651	<i>Parapithecus grangeri</i>	3.640	0.993

1074 Abbreviations: BAC = Baccinello (field acronym; housed at Naturhistorisches Museum  
 1075 Basel, Switzerland); CGM = Egyptian Geological Museum, Cairo, Egypt; MPM-  
 1076 PV = Museo Regional Provincial Padre M.J. Molina, Río Gallegos, Argentina;  
 1077 MACN = Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; DPC = Duke  
 1078 Lemur Center, Durham, NC, USA.

1079 a

1080 See [SOM Table S1](#) for the specimens included in the extant comparative sample.

1081 Table 3. Mahalanobis distances ( $D^2$ ) and posterior probabilities of group membership  
 1082 ( $p$ ) based on the scores for fossil specimens in the between-group principal  
 1083 component analysis for the entire anthropoid sample. [a](#), [b](#)

	$D^2$	Cercopithecoidea	Hominidae	Hylobatidae	Platyrrhini
<i>Epipliopithecus vindobonensis</i> (NHMW 1970/1397/0003)	17.179	10.539	6.485	<b>3.437</b>	
<i>Epipliopithecus vindobonensis</i> (NMB OE 303a)	12.190	14.262	6.588	<b>0.779</b>	
<i>Epipliopithecus vindobonensis</i> (NMB OE 303b)	13.307	15.085	6.682	<b>1.056</b>	
<i>Oreopithecus bambolii</i> (BAC 208)	8.083	5.450	11.574	<b>1.579</b>	
<i>Aegyptopithecus zeuxis</i> (CGM 85785)	12.430	9.133	15.513	<b>0.990</b>	
<i>Homunculus patagonicus</i> (MPM-PV 3501)	11.817	13.356	11.017	<b>0.073</b>	
<i>Homunculus patagonicus</i> (MPM-PV 3502)	10.336	12.736	12.056	<b>0.165</b>	
<i>Homunculus patagonicus</i> (MPM-PV 3503)	10.083	7.449	11.284	<b>0.590</b>	
<i>Dolichocebus gaimanensis</i> (MACN 14128)	5.204	13.516	12.687	<b>1.935</b>	
<i>Parapithecus grangeri</i> (DPC 18651)	6.533	17.859	13.047	<b>2.110</b>	
$P$		Cercopithecoidea	Hominidae	Hylobatidae	Platyrrhini
<i>Epipliopithecus vindobonensis</i> (NHMW 1970/1397/0003)	0.006	0.007	0.018	<b>0.029</b>	
<i>Epipliopithecus vindobonensis</i> (NMB OE 303a)	0.018	<0.001	<0.001	<b>0.678</b>	
<i>Epipliopithecus vindobonensis</i> (NMB OE 303b)	0.013	<0.001	<0.001	<b>0.608</b>	
<i>Oreopithecus bambolii</i> (BAC 208)	0.052	0.005	<0.001	<b>0.530</b>	
<i>Aegyptopithecus zeuxis</i> (CGM 85785)	0.001	<0.001	<0.001	<b>0.688</b>	
<i>Homunculus patagonicus</i> (MPM-PV 3501)	0.003	<0.001	<0.001	<b>0.980</b>	
<i>Homunculus patagonicus</i> (MPM-PV 3502)	0.003	<0.001	<0.001	<b>0.919</b>	
<i>Homunculus patagonicus</i> (MPM-PV 3503)	0.019	0.001	<0.001	<b>0.848</b>	

	<b>D<sup>2</sup></b>	<b>Cercopithecoidea</b>	<b>Hominidae</b>	<b>Hylobatidae</b>	<b>Platyrrhini</b>
	<i>Dolichocebus gaimanensis</i> (MACN 14128)	0.013	<0.001	<0.001	<b>0.612</b>
	<i>Parapithecus grangeri</i> (DPC 18651)	0.002	<0.001	<0.001	<b>0.411</b>

1084 Abbreviations: NHMW = Naturhistorisches Museum of Wien, Austria;  
1085 NMB = Naturhistorisches Museum of Basel, Switzerland; BAC = NMB accession number  
1086 for *Oreopithecus bambolii* specimens; CGM = Egyptian Geological Museum, Cairo, Egypt;  
1087 MPM-PV = Museo Regional Provincial Padre M.J. Molina, Río Gallegos, Argentina;  
1088 MACN = Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; DPC = Duke  
1089 Lemur Center, Durham, NC, USA.

1090 a

1091 Note that these are probability estimates of having a particular score given membership in a  
1092 particular group, not the likelihood of group membership in each of the a priori defined groups  
1093 given a particular score (the greater the number, the higher the probability).

1094 b

1095 The lowest distance (D<sup>2</sup>) and highest posterior probability of group membership (*p*) for each  
1096 specimen are bolded.

1097 Table 4. Mahalanobis distances ( $D^2$ ) and posterior probabilities of group membership  
 1098 ( $p$ ) based on the scores for fossil specimens in the between-group principal  
 1099 component analysis for the entire anthropoid sample and considering all catarrhines  
 1100 as a single group.<sup>a,b</sup>

	$D^2$	Catarrhini	Platyrrhini
<i>Epipliopithecus vindobonensis</i> (NHMW 1970/1397/0003)	13.016		<b>5.341</b>
<i>Epipliopithecus vindobonensis</i> (NMB OE 303a)	11.837		<b>1.654</b>
<i>Epipliopithecus vindobonensis</i> (NMB OE 303b)	13.040		<b>2.098</b>
<i>Oreopithecus bambolii</i> (BAC 208)	9.085		<b>3.890</b>
<i>Aegyptopithecus zeuxis</i> (CGM 85785)	16.900		<b>3.204</b>
<i>Homunculus patagonicus</i> (MPM-PV 3501)	13.814		<b>0.135</b>
<i>Homunculus patagonicus</i> (MPM-PV 3502)	13.057		<b>0.284</b>
<i>Homunculus patagonicus</i> (MPM-PV 3503)	10.989		<b>1.806</b>
<i>Dolichocebus gaimanensis</i> (MACN 14128)	8.645		<b>2.417</b>
<i>Parapithecus grangeri</i> (DPC 18651)	12.592		<b>3.670</b>
<i>P</i>		Catarrhini	Platyrrhini
<i>Epipliopithecus vindobonensis</i> (NHMW 1970/1397/0003)	0.109		<b>0.241</b>
<i>Epipliopithecus vindobonensis</i> (NMB OE 303a)	0.022		<b>0.876</b>
<i>Epipliopithecus vindobonensis</i> (NMB OE 303b)	0.017		<b>0.847</b>
<i>Oreopithecus bambolii</i> (BAC 208)	0.124		<b>0.673</b>
<i>Aegyptopithecus zeuxis</i> (CGM 85785)	0.002		<b>0.886</b>
<i>Homunculus patagonicus</i> (MPM-PV 3501)	0.002		<b>0.985</b>
<i>Homunculus patagonicus</i> (MPM-PV 3502)	0.002		<b>0.968</b>
<i>Homunculus patagonicus</i> (MPM-PV 3503)	0.034		<b>0.935</b>
<i>Dolichocebus gaimanensis</i> (MACN 14128)	0.013		<b>0.841</b>
<i>Parapithecus grangeri</i> (DPC 18651)	0.002		<b>0.795</b>



1101 Abbreviations: NHMW = Naturhistorisches Museum of Wien, Austria;  
1102 NMB = Naturhistorisches Museum of Basel, Switzerland; BAC = NMB accession number  
1103 for *Oreopithecus bambolii* specimens; CGM = Egyptian Geological Museum, Cairo, Egypt;  
1104 MPM-PV = Museo Regional Provincial Padre M.J. Molina, Río Gallegos, Argentina;  
1105 MACN = Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; DPC = Duke  
1106 Lemur Center, Durham, NC, USA.

1107 a

1108 Note that these are probability estimates of having a particular score given membership in a  
1109 particular group, not the likelihood of group membership in each of the a priori defined groups  
1110 given a particular score (the greater the number, the higher the probability).

1111 b

1112 The lowest distance and highest probability for each specimen are bolded.

1113 Table 5. Mahalanobis distances ( $D^2$ ) between specimens of *Epipliopithecus* and  
 1114 other fossils based on between group principal component analysis scores.

$D^2$	NHMW 1970/1397/0003	NMB OE 303a	NMB OE 303b
<i>Epipliopithecus vindobonensis</i> (NHMW 1970/1397/0003)	–	1.332	1.285
<i>Epipliopithecus vindobonensis</i> (NMB OE 303a)	1.332	–	0.176
<i>Epipliopithecus vindobonensis</i> (NMB OE 303b)	1.285	0.176	–
<i>Oreopithecus bambolii</i> (BAC 208)	2.244	1.901	2.055
<i>Aegyptopithecus zeuxis</i> (CGM 85785)	2.360	1.804	1.927
<i>Homunculus patagonicus</i> (MPM-PV 3501)	1.943	0.919	1.033
<i>Homunculus patagonicus</i> (MPM-PV 3502)	2.246	1.251	1.388
<i>Homunculus patagonicus</i> (MPM-PV 3503)	1.914	1.450	1.592
<i>Dolichocebus gaimanensis</i> (MACN 14128)	3.081	2.077	2.243
<i>Parapithecus grangeri</i> (DPC18651)	3.201	2.017	2.161

1115 Abbreviations: NHMW = Naturhistorisches Museum Wien, Austria; NMB  
 1116 OE = Naturhistorisches Museum Basel, Switzerland; BAC = Baccinello (housed at NMB);  
 1117 CGM = Egyptian Geological Museum, Cairo, Egypt; MPM-PV = Museo Regional Provincial  
 1118 Padre M.J. Molina, Río Gallegos, Argentina; MACN = Museo Argentino de Ciencias  
 1119 Naturales, Buenos Aires, Argentina; DPC = Duke Lemur Center, Durham, NC, USA.

1120 Table 6. Phylogenetic signal computed for the between-group principal analysis  
 1121 applied to the deformation fields of the extant anthropoid comparative sample. The  
 1122 variance explained by each principal component (bgPC) and the  $p$ -value for the  
 1123 statistics are given within parentheses.

	<b>bgPC1 (59%)</b>	<b>bgPC2 (30%)</b>	<b>bgPC3 (11%)</b>
<b>Pagel's <math>\lambda</math></b>	1.000 ( $p < 0.0001$ )	0.843 ( $p < 0.0001$ )	0.925 ( $p < 0.0001$ )
<b>Blomberg's K</b>	1.148 ( $p < 0.0001$ )	1.446 ( $p < 0.001$ )	0.732 ( $p < 0.001$ )

1124 Table 7. Weighted Euclidean distances computed between the between-group  
1125 principal component scores of the reconstructed last common ancestors (LCAs)  
1126 and the *Epipliopithecus* centroid.

	<b>LCA</b>	<b>Distance</b>
Crown anthropoids		1.304
Crown platyrrhines		1.141
Crown catarrhines		0.989
Crown cercopithecoids		1.646
Crown hominoids		1.256

1127 Table 8. Definition of the discrete characters of semicircular canal (SC) and vestibule  
 1128 morphology used in this paper.

Character No.	Character statements (characters + character states) <sup>a</sup>
#1	Size of the vestibule relative to the SCs: 0 = small; 1 = large.
#2	Robusticity of the SCs: 0 = slender; 1 = stout.
#3	Shape of the anterior SC: 0 = vertically compressed; 1 = rounded; 2 = elongated superiorly.
#4	Shape of the anterior portion of the anterior SC: 0 = non-projecting anterosuperiorly; 1 = anterosuperiorly projecting.
#5	Shape of the posterior SC: 0 = vertically compressed; 1 = rounded; 2 = elongated superiorly.
#6	Shape of the lateral SC ampullary portion: 0 = flat or only slightly bent superiorly; 1 = markedly bent superiorly.
#7	Length of the CC: 0 = long; 1 = intermediate; 2 = short.

1129 a

1130 See [Figure 11](#) for an illustration of the character states.

1131 Table 9. Character states coded for the estimated last common ancestors (LCAs)  
 1132 and for the fossil taxa included in the analysis.<sup>a</sup>

Species/LCAs	#1	#2	#3	#4	#5	#6	#7
<i>Epipliopithecus vindobonensis</i>	0	0	1	0	2	0	0
<i>Aegyptopithecus zeuxis</i>	0	0	2	0	2	0	0
<i>Dolichocebus gaimanensis</i>	0	0	2	0	2	0	0
<i>Homunculus patagonicus</i>	0	0	2	0	0, 2	0	0
<i>Oreopithecus bambolii</i>	1	1	0	1	1	0	2
<i>Parapithecus grangeri</i>	0	0	2	0	2	0	0
Crown anthropoid LCA	0	0	2	0	2	0	0
Crown platyrrhine LCA	0	0	2	0	2	0	0
Crown catarrhine LCA	0	0	1	0	1	0	1
Crown cercopithecoïd LCA	0	0	1	0	1	0	1
Crown hominoid LCA	0	0	0	0	1	1	2
Crown hylobatid LCA	0	0	0	1	1	1	2
Crown hominid LCA	1	1	0	0	1	1	2

1133 a

1134 See character definitions in [Table 7](#) and [SOM Table S2](#) for the coding of extant species.

1135 Table 10. Measures of character congruence for the two main phylogenetic  
 1136 hypotheses (i.e., stem catarrhine vs. stem hominoid) discussed in this paper  
 1137 for *Epipliopithecus*. The higher the index, the more parsimonious the hypothesis.<sup>a</sup>

Metrics	Stem catarrhine ( <a href="#">Fig. 3a</a> )	Stem hominoid ( <a href="#">Fig. 3b</a> )
Tree length	22	24
CI	0.455	0.417
RI	0.826	0.797
RC	0.376	0.332

1138 Abbreviations: CI = consistency index; RI = retention index; RC = rescaled consistency  
 1139 index.

1140 a

1141 See also [Figure 3](#) and [SOM Table 2](#) for character descriptions.

1142 **Figure captions**

1143

1144 **Figure 1.** Illustration of the protocol used for digitally separating the cochlea (green) from  
1145 the semicircular canals and the vestibule (blue). a) In anterior view, the first landmark  
1146 (yellow filled circle) is placed anteriorly to the oval window, on the point of maximum  
1147 surface curvature of the ridge-like morphology formed by the narrowing of the vestibule. b)  
1148 In posterior view, three landmarks are placed along the junction between the bony  
1149 vestibule and the cochlea, defined by the line of maximum surface curvature found  
1150 immediately below the bulge formed by the saccular recess. A cutting plane (here  
1151 perpendicular to the view and depicted by a black line) is best fitted to the identified  
1152 landmarks using the 'Points To Fit' option of the 'Clipping Plane' module of Avizo version  
1153 9.0.1 (FEI Visualization Sciences Group, Houston) via a customized script (available upon  
1154 request to A.U.), and used as a reference for a straight cut. Abbreviations: asc = anterior  
1155 semicircular canal; psc = posterior semicircular canal; lsc = lateral semicircular canal; CC  
1156 = common crus.

1157

1158 **Figure 2.** Cladogram of extant and fossil anthropoids showing the two phylogenetic  
1159 hypotheses for *Epipliopithecus*. The solid line (A) denotes the most widely accepted  
1160 phylogenetic position of *Epipliopithecus* as a stem catarrhine, whereas the dashed line (B)  
1161 denotes the alternative hypothesis that *Epipliopithecus* would be more closely related to  
1162 hominoids. Key nodes are highlighted as follows: gray circle = crown anthropoids; green  
1163 circle = crown platyrrhines; blue circle = crown catarrhines; orange circle = crown  
1164 hominoids. Skulls and crania (not to scale) were taken from the following sources for  
1165 illustrative purposes only: extant skulls and *Aegyptopithecus*, Wikimedia Commons;  
1166 *Dolichocebus*, Kay et al. (2009b: Fig. 1); *Homunculus*, Tejedor and Rosenberger (2008:  
1167 Fig. 2); *Oreopithecus* (reconstruction), Moyà-Solà and Köhler (2000: Fig. 5);



1168 *Epipliopithecus*, photograph of a cast; *Parapithecus*, digital reconstruction with  
1169 photographic texture made by Steven Heritage.

1170

1171 **Figure 3.** Phylogenetic trees used for the phylomorphospace approach. They differ in  
1172 considering *Epipliopithecus* as a stem catarrhine (a) or a stem hominoid (b).

1173

1174 **Figure 4.** Rendered 3D models of the semicircular canals and vestibule of *Epipliopithecus*  
1175 *vindobonensis* (all specimens depicted as from the left side) and selected extant  
1176 anthropoids, in lateral (left), superior (middle), and posterior (right) views: a) *E.*  
1177 *vindobonensis* (individual II, NHMW 1970/1397/0003, mirrored); b) *E. vindobonensis*  
1178 (individual III, NMB OE 303a); c) *E. vindobonensis* (individual III, NMB OE 303b, mirrored);  
1179 d) *Parapithecus grangeri* (DPC 18651); e) *Dolichocebus gaimanensis* (MACN 14128); f)  
1180 *Homunculus patagonicus* (MPM-PV 3501); g) *Ateles geoffroyi* (MCZ 29628); h) *Alouatta*  
1181 *palliata* (DU EA LP12); i) *Cebus apella* (MCZ27891); j) *Aegyptopithecus zeuxis* (CGM  
1182 85785); k) *Trachypithecus cristatus* (MCZ35603); l) *Chlorocebus pygerythrus* (SIU 4796);  
1183 m) *Macaca fascicularis* (MCZ 35765); n) *Oreopithecus bambolii* (BAC 208); o) *Hylobates*  
1184 *lar* (MCZ 41424); p) *Symphalangus syndactylus* (AMNH.M 106583); q) *Hoolock hoolock*  
1185 (AMNH.M 83425); r) *Pongo pygmaeus* (IPS10647); s) *Gorilla gorilla* (AMNH.M 167338); t)  
1186 *Pan paniscus* (MCZ 38019); u) *Homo sapiens* (EMBR 179). Scale bars equal 5 mm.

1187

1188 **Figure 5.** Bivariate plot of canal log-transformed cube root canal volume (mm; Ln VolSC)  
1189 vs. log-transformed canal length (mm; Ln L). Separate regression lines are depicted for  
1190 hominids (red line) and for nonhominid anthropoids (blue line). *Epipliopithecus* (NHMW  
1191 1970/1397/0003 and NMB OE 303a, b) falls within the variability of nonhominid  
1192 anthropoids, similar to all extinct taxa except *Oreopithecus*. Measurements for the included  
1193 fossil taxa given in Table 6.

1194

1195 **Figure 6.** Patterns of vestibule and semicircular canal shape variation among major  
1196 anthropoid clades based on the results of a between-group principal component analysis,  
1197 as depicted by bivariate plots between principal components (bgPCs): a) bgPC2 vs.  
1198 bgPC1; b) bgPC3 vs. bgPC1. Variance explained by each component is given along each  
1199 axis. c–e) Extreme conformations of maximum (above) and minimum (below) bgPC  
1200 scores: c) bgPC1; d) bgPC2; e) bgPC3. Four groups (platyrrhines, cercopithecoids,  
1201 hylobatids, and hominids) were defined a priori, whereas specimens of *Epipliopithecus*  
1202 *vindobonensis* were plotted post hoc onto the morphospace. Renderings in lateral (left),  
1203 superior (middle), and posterior (right) views of warped 3D models representing the  
1204 extreme conformations for each bgPC are placed close to the corresponding axis. Convex  
1205 hulls depict the range of variation for a priori defined groups using the following color code:  
1206 green = platyrrhines; blue = cercopithecoids; red = hylobatids; orange = hominids.

1207

1208 **Figure 7.** Dendrogram resulting from a cluster analysis (Ward's method) based on  
1209 Mahalanobis distances computed between the species centroids of the between-group  
1210 principal component analysis (bgPCA) of shape data. The cophenetic correlation  
1211 coefficient is 0.703.

1212

1213 **Figure 8.** Phylomorphospace of the anthropoid semicircular canal. The phylogenetic tree  
1214 (with *Epipliopithecus* included as a stem catarrhine; Fig. 3a) is projected onto the tangent  
1215 space defined by the between-group principal components (bgPCs) as depicted in Figure  
1216 6. The internal nodes (i.e., the ancestral states) were estimated using maximum likelihood:  
1217 a) bgPC2 vs. bgPC1; b) bgPC3 vs. bgPC1. Variance explained by each component is  
1218 given along each axis. Convex hulls depict the range of variation for a priori defined  
1219 groups using the following color code: green = platyrrhines; blue = cercopithecoids; red =

1220 hylobatids; orange = hominids. The ancestral nodes discussed for assessing  
1221 *Epipliopithecus* phylogenetic affinities do not change consistently in their position in the  
1222 morphospace irrespective of the phylogenetic hypothesis used for their estimation (see  
1223 SOM Fig. S3 for the alternative phylogenetic tree including *Epipliopithecus* as a stem  
1224 hominoid). Key nodes are highlighted as follows: gray circle = crown anthropoids; green  
1225 circle = crown platyrrhines; blue circle = crown catarrhines; orange circle = crown  
1226 hominoids.

1227

1228 **Figure 9.** Reconstruction of the semicircular canals and vestibule for the last common  
1229 ancestors (LCAs) of the following clades: a) crown anthropoids; b) crown platyrrhines; c)  
1230 crown catarrhines; d) crown hominoids. The renderings of each 3D model are depicted in  
1231 lateral (left), superior (middle), and posterior (right) views.

1232

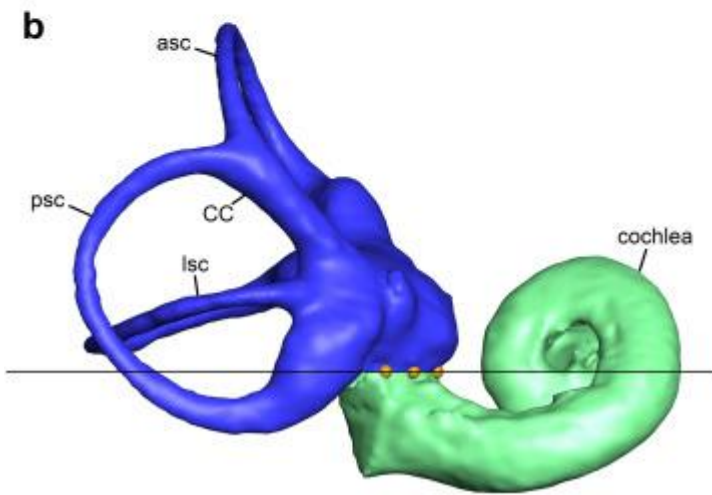
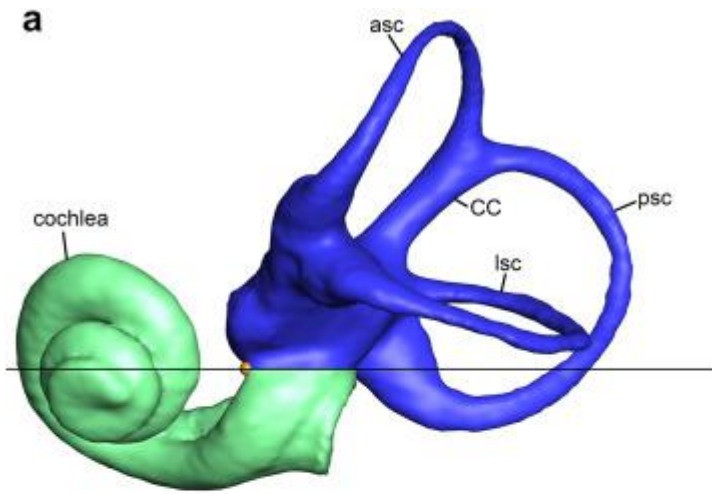
1233 **Figure 10.** Box-and-whisker plot of allometric residuals based on best-fit line of the  
1234 nonhominid anthropoid regression of log-transformed cube root of canal volume and log-  
1235 transformed canal length (as depicted in Fig. 5). Vertical lines correspond to the median,  
1236 boxes depict interquartile range, whiskers represent maximum and minimum values within  
1237 1.5 times the interquartile range, and black dots are outliers. Sample sizes for extant  
1238 groups are the following: Platyrrhini ( $n = 40$ ), Cercopithecoidea ( $n = 75$ ), Hylobatidae ( $n =$   
1239  $17$ ), Hominidae ( $n = 30$ ).

1240

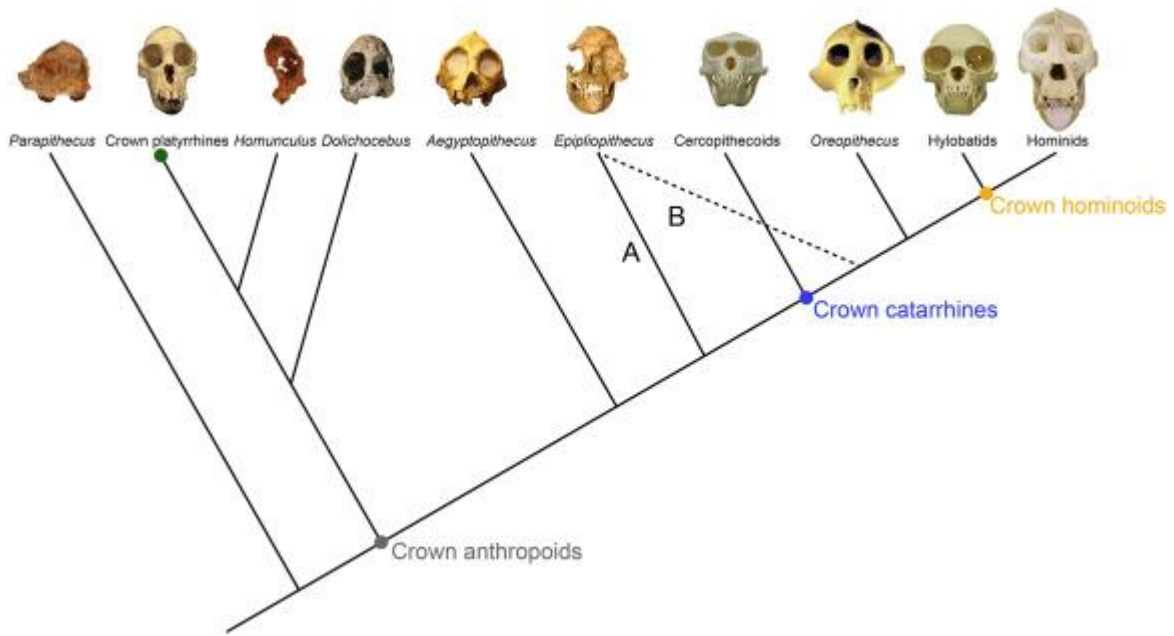
1241 **Figure 11.** Illustration of the discrete characters of semicircular canal (SC) and vestibule  
1242 morphology used in this paper. Numbers preceding each state (0, 1, 2) correspond to  
1243 character states numbered in Tables 8 and 9, and SOM Table S4.

1244

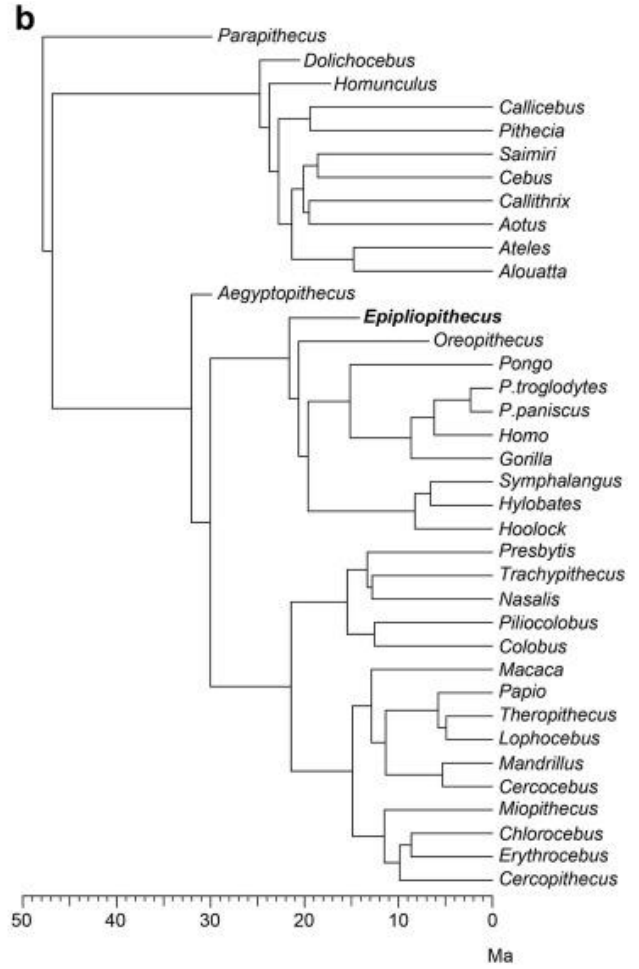
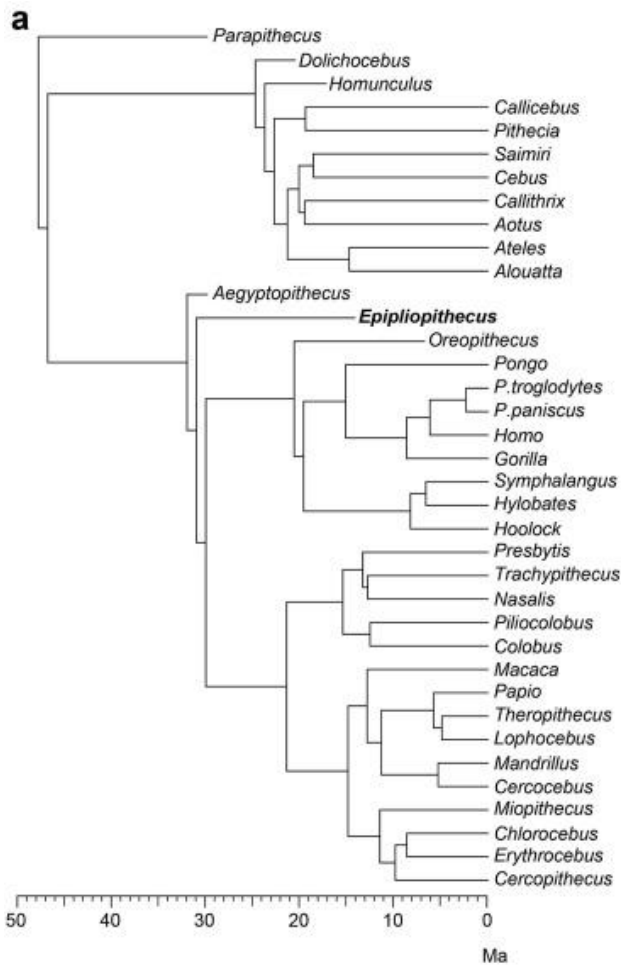
1245 **Figure 12.** Simplified cladogram of crown anthropoids and selected extinct catarrhines  
1246 (*Epipliopithecus* and *Oreopithecus*) summarizing the main synapomorphies inferred for the  
1247 various clades in semicircular canal and vestibule morphology. The four extant anthropoid  
1248 clades distinguished (platyrrhines, cercopithecoids, hylobatids and hominids) are depicted  
1249 as terminal nodes. The synapomorphies inferred for each node are summarized below;  
1250 character number (preceded by a hash) and character state (within parentheses) are  
1251 provided after each synapomorphy within brackets. a) *Epipliopithecus* + crown catarrhines:  
1252 rounded anterior canal [#3(1)]; b) Crown catarrhines: rounded posterior canal [#5(1)],  
1253 moderately short CC [#7(1)]; c) *Oreopithecus* + crown hominoids: vertically compressed  
1254 anterior canal [#3(0)], anterosuperiorly-projecting anterior portion of the anterior canal  
1255 [#4(1)], short CC [#7(2)]; d) Crown hominoids: markedly superiorly bent ampullary portion  
1256 of the lateral canal [#6(1)]; e) Crown hominids (unless *Oreopithecus* + crown hominoid  
1257 synapomorphies [node c] with reversal in hylobatids): large vestibule relative to the SCs  
1258 [#1(1)], stout SCs [#2(1)]. Abbreviations: CC = common crus; SC = semicircular canals.  
1259 See Figure 11 for an illustration of the various character states and Table 9 and SOM  
1260 Table S4 for the scoring of reconstructed last common ancestors and individual taxa,  
1261 respectively.



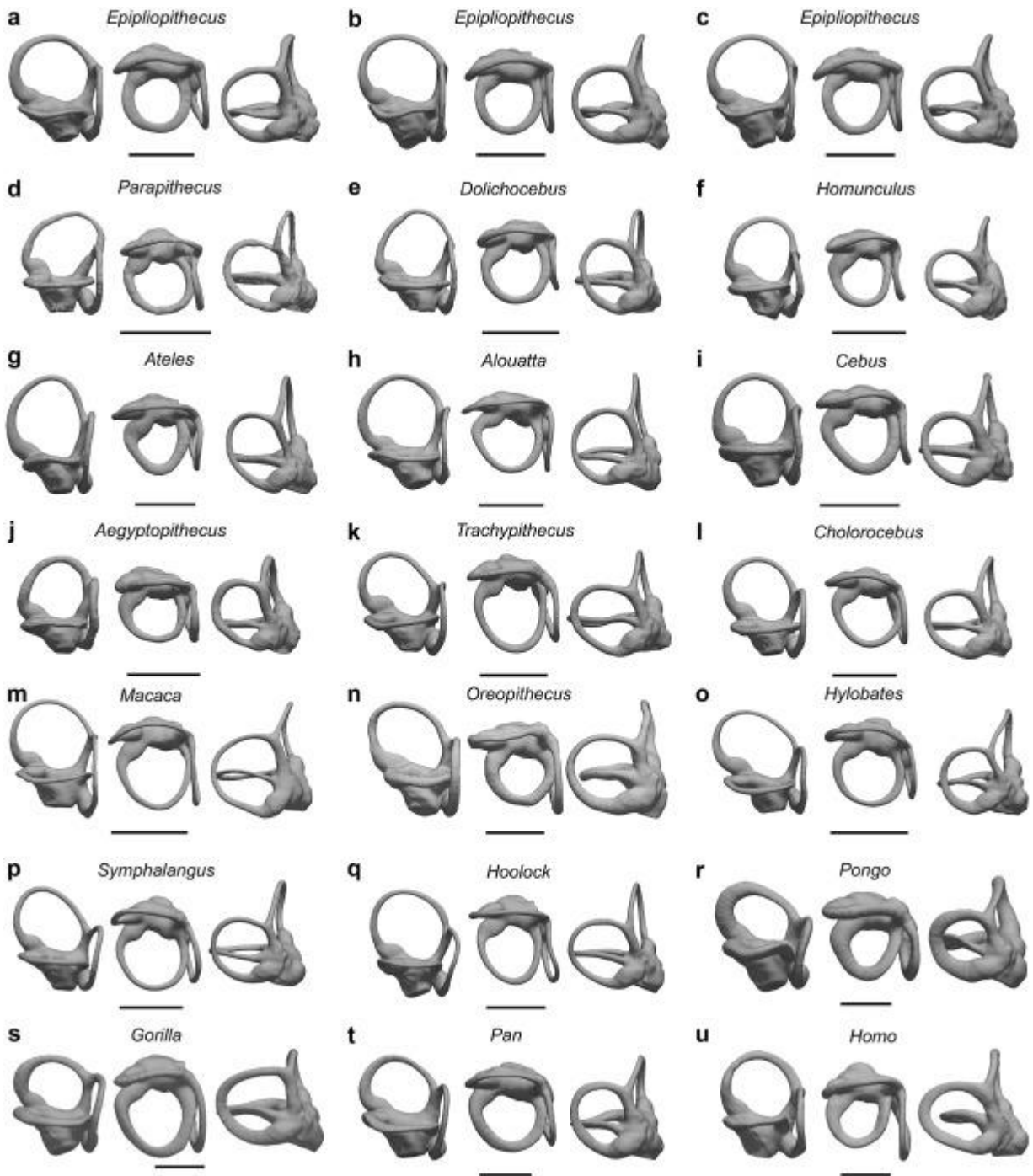
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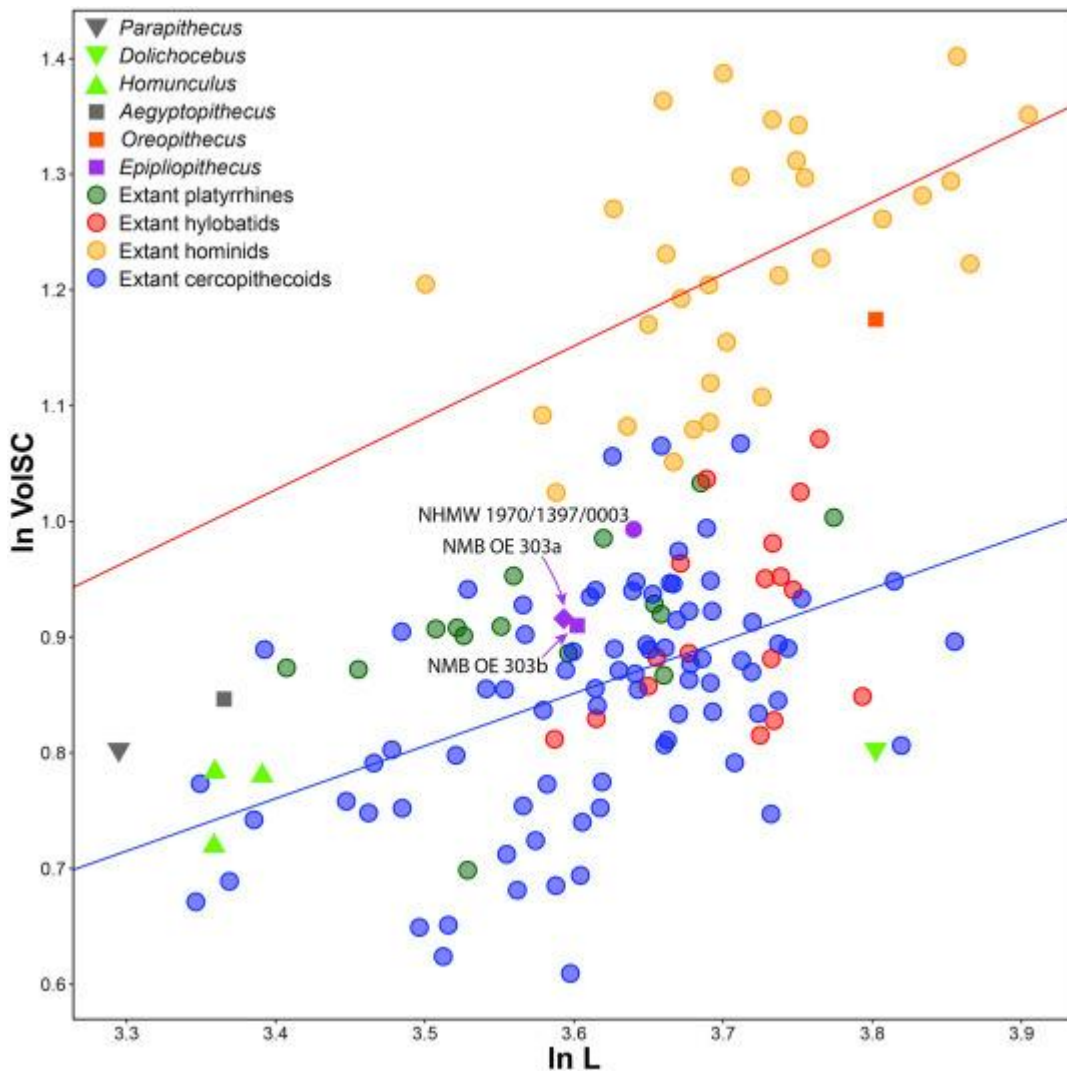
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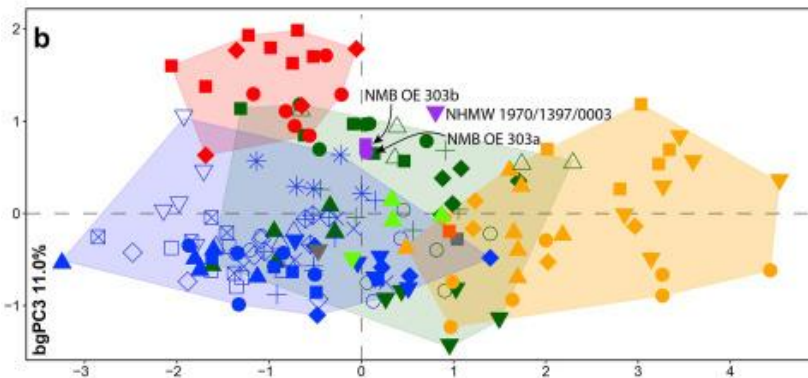
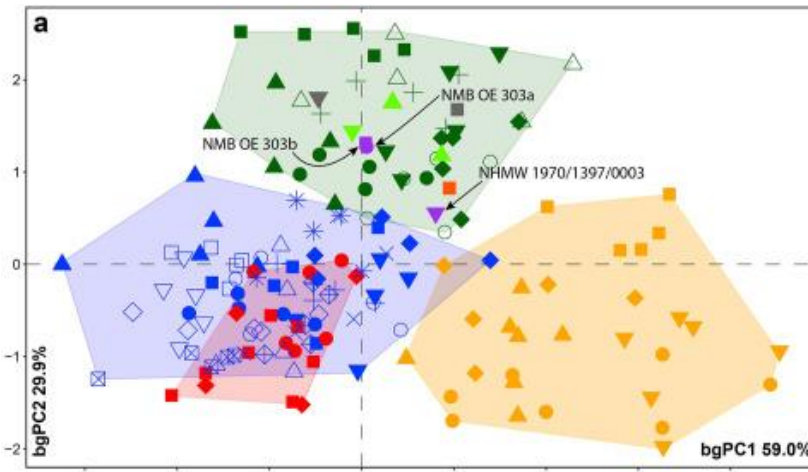
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1266



- |                     |                         |                        |                          |                          |
|---------------------|-------------------------|------------------------|--------------------------|--------------------------|
| ■ <i>Ateles</i>     | + <i>Miopithecus</i>    | ⊠ <i>Presbytis</i>     | ■ <i>Hylobates</i>       | ▼ <i>Parapithecus</i>    |
| ● <i>Alouatta</i>   | ◆ <i>Chlorocebus</i>    | ● <i>Cercocebus</i>    | ◆ <i>Symphalangus</i>    | ■ <i>Aegyptopithecus</i> |
| ◆ <i>Cebus</i>      | ▼ <i>Erythrocebus</i>   | ○ <i>Papio</i>         | ● <i>Hoolock</i>         | ▲ <i>Homunculus</i>      |
| + <i>Saimiri</i>    | ■ <i>Cercopithecus</i>  | ○ <i>Macaca</i>        | ● <i>Gonilla</i>         | ▼ <i>Dolichocebus</i>    |
| ▲ <i>Aotus</i>      | ▲ <i>Colobus</i>        | □ <i>Lophocebus</i>    | ▼ <i>Pongo</i>           | ■ <i>Oreopithecus</i>    |
| ▼ <i>Callithrix</i> | ▽ <i>Ptilocolobus</i>   | △ <i>Mandillus</i>     | ◆ <i>Pan paniscus</i>    | ▼ <i>Epipliopthecus</i>  |
| ○ <i>Callicebus</i> | × <i>Nasalis</i>        | * <i>Theropithecus</i> | ▲ <i>Pan troglodytes</i> |                          |
| △ <i>Pithecia</i>   | ⊠ <i>Trachypithecus</i> |                        | ■ <i>Homo</i>            |                          |



+  
-  
bgPC1

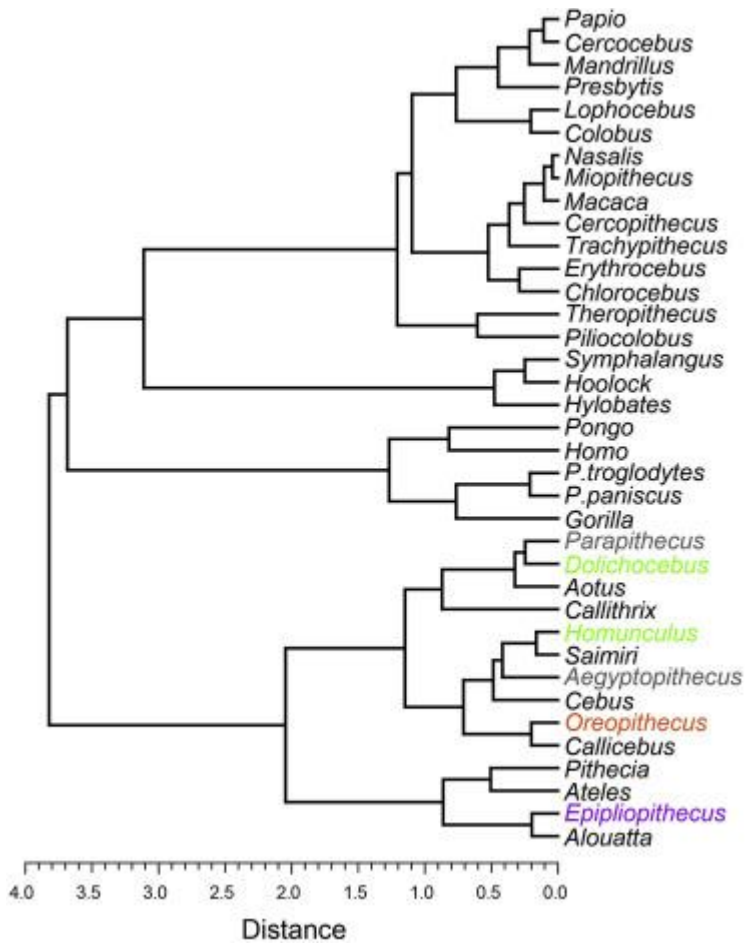


+  
-  
bgPC2

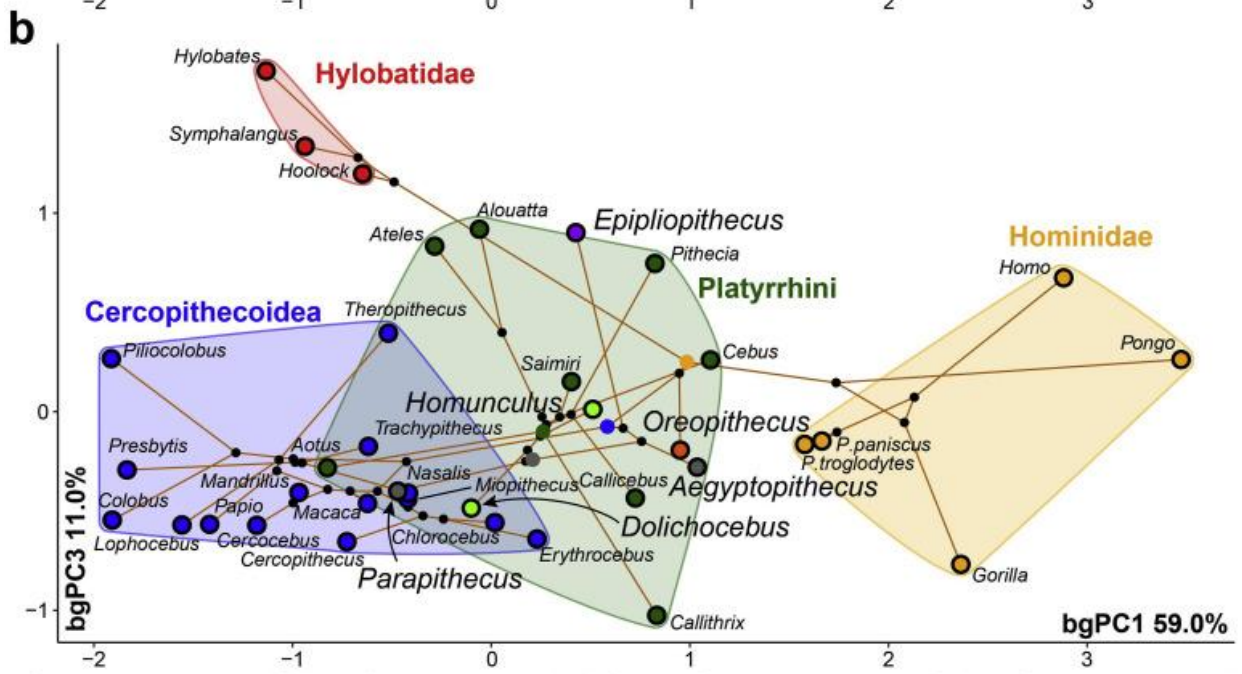
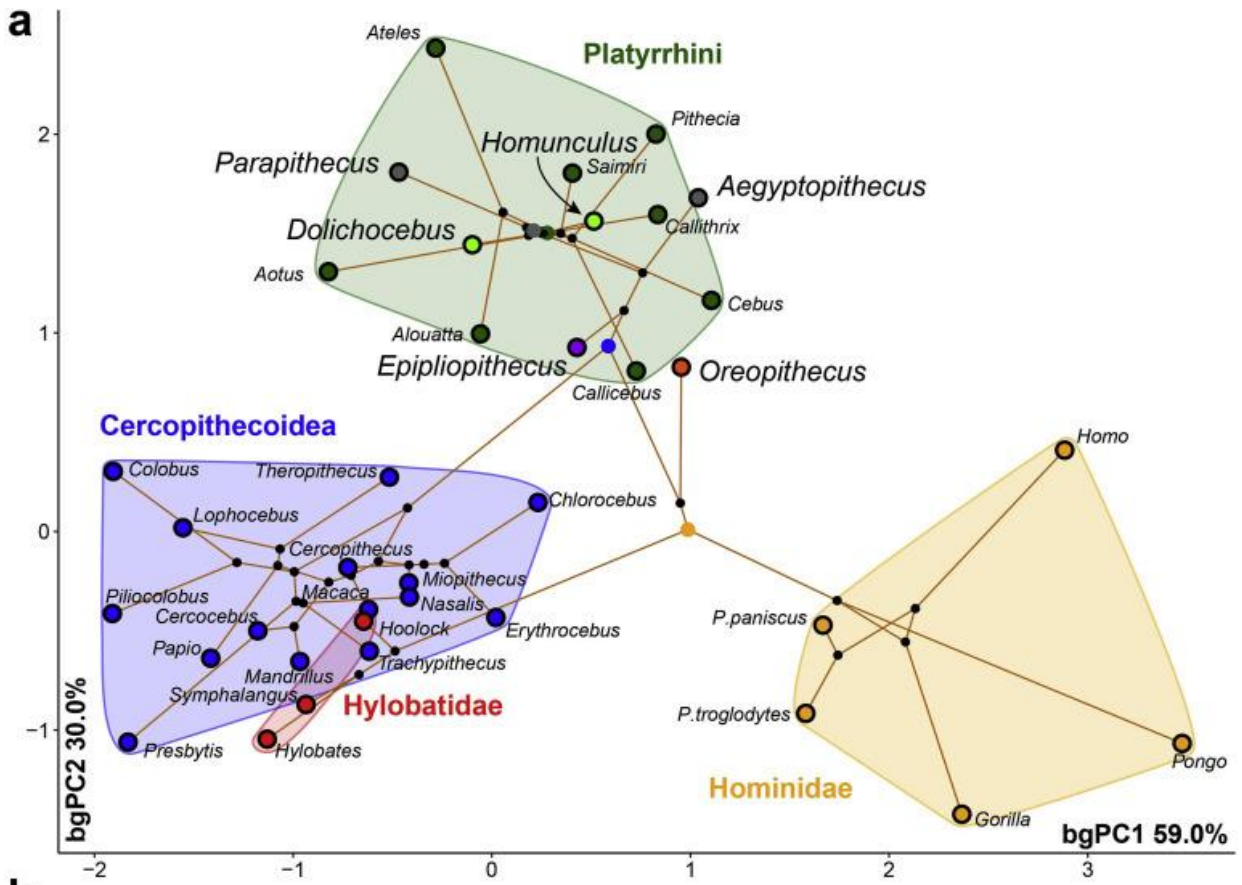


+  
-  
bgPC3



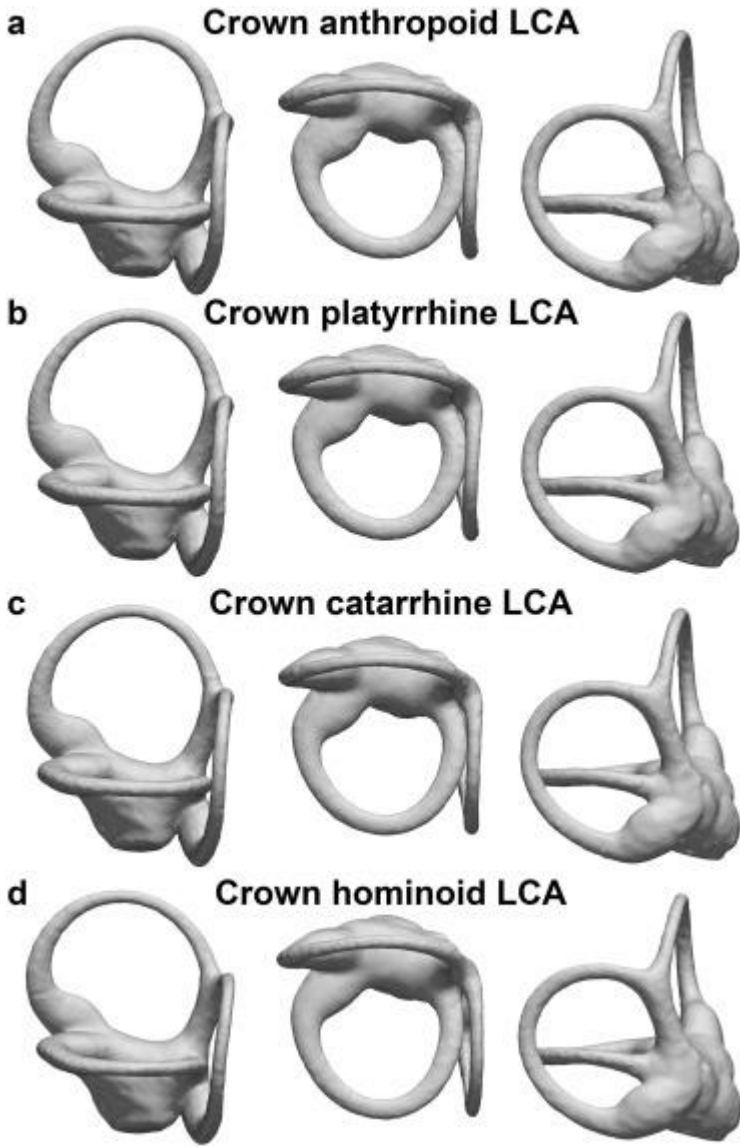


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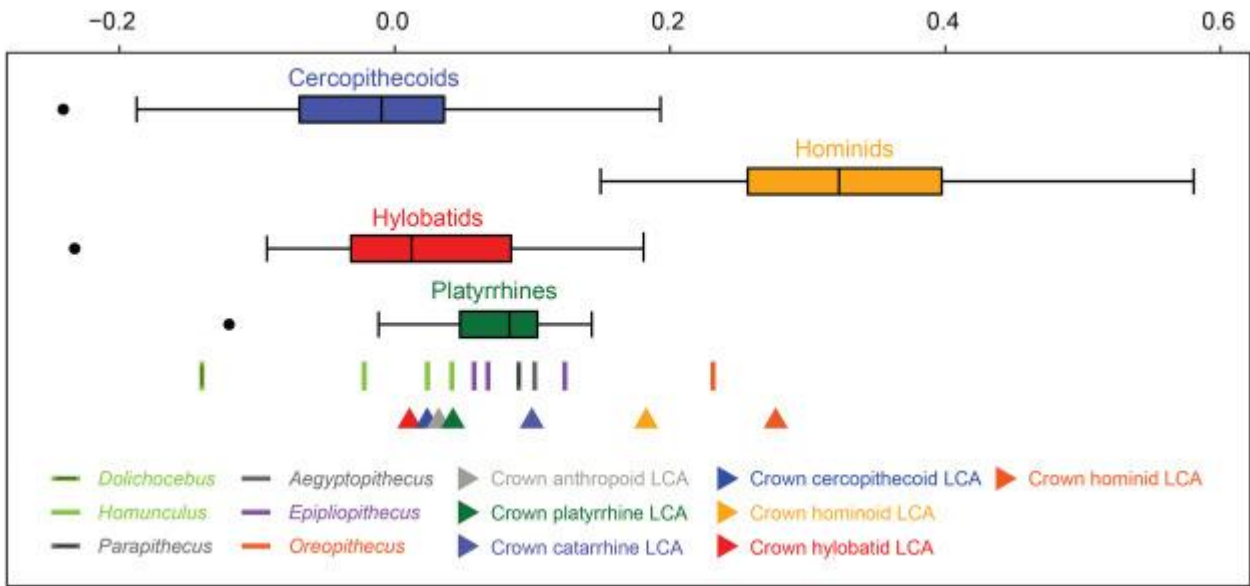


1269

● Crown anthropoid LCA ● Crown platyrrhine LCA ● Crown catarrhine LCA ● Crown hominoid LCA



1270



1271



**Character #1: Size of the vestibule relative to the SCs**

(0) small

(1) large



**Character #2: Robusticity of the SCs**

(0) slender

(1) stout



**Character #3: Shape of the anterior SC**

(0) vertically compressed

(1) rounded

(2) elongated superiorly



**Character #4: Shape of the anterior portion of the anterior SC**

(0) non-anterosuperiorly projecting

(1) anterosuperiorly projecting



**Character #5: Shape of the posterior SC**

(0) vertically compressed

(1) rounded

(2) elongated superiorly



**Character #6: Shape of the lateral SC ampullary portion**

(0) flat or only slightly bent superiorly

(1) markedly bent superiorly

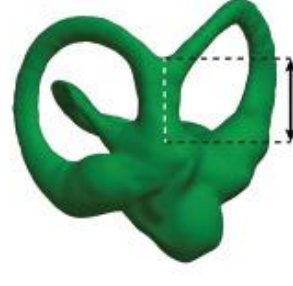
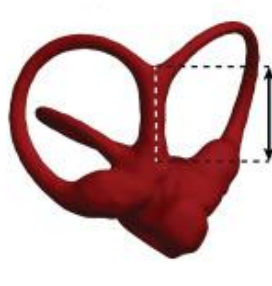


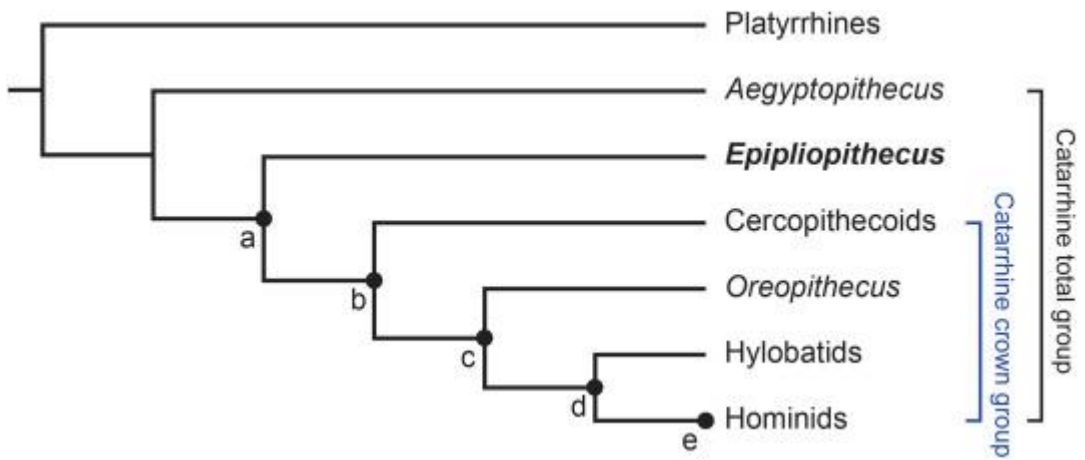
**Character #7: Length of the CC**

(0) long

(1) intermediate

(2) short





1273