

**PROCEEDINGS OF
THE ROYAL SOCIETY B**

BIOLOGICAL SCIENCES

**The evolution of the knee sesamoids in Primates: A
systematic review and phylogenetic meta-analysis**

Journal:	<i>Proceedings B</i>
Manuscript ID	RSPB-2024-0774.R2
Article Type:	Research
Subject:	Evolution < BIOLOGY
Keywords:	Sesamoid, fabella, cyamella, primate, evolution
Proceedings B category:	Evolution

SCHOLARONE™
Manuscripts

Author-supplied statements

Relevant information will appear here if provided.

Ethics

Does your article include research that required ethical approval or permits?:

Statement (if applicable):

CUST_IF_YES_ETHICS :No data available.

Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:

Statement (if applicable):

data is in the ESM

If yes, please tell us how your data or code can be accessed and provide a link to your data if it is in a repository for the editors and reviewers to use.

CUST_DATA_INITIAL_ACCESS :No data available.

If your data is in a repository, please provide any temporary (private) link/s for reviewers/editors to access here.

CUST_REPOSITORY_LINKS :No data available.

Conflict of interest

I/we declare we have no competing interests.

Statement (if applicable):

CUST_STATE_CONFLICT :No data available.

Use of AI

Please provide a statement of any use of AI technology in the preparation of the paper.

No, we have not used AI-assisted technologies in creating this article

CUST_IF_YES_DECLARATION_OF_AI_USE :No data available.

1 Title: Easy to gain but hard to lose. The evolution of the knee sesamoid bones in Primates: A
2 systematic review and phylogenetic meta-analysis

3
4
5 Nelly A. Fragoso Vargas¹, Michael A. Berthaume*²

6
7 ¹Division of Mechanical Engineering and Design, London South Bank University

8 ²Department of Engineering, King's College London

9
10 *corresponding author

11 Email: michael.berthaume@kcl.ac.uk

12 Address: Strand Building, Strand Campus, Strand, London, WC2R 2LS, United Kingdom

13
14
15 ORCID

16 MAB: <https://orcid.org/000-0003-1298-242X>

17 NAFV: <https://orcid.org/0000-0002-8987-1595>

18
19 Keywords

20 Sesamoid, fabella, cyamella, primate, evolution

21

22 1 ABSTRACT

23 Sesamoids are variably present skeletal elements found in tendons and ligaments near joints.
24 Variability in sesamoid size, location, and presence/absence is hypothesized to enable skeletal
25 innovation, yet sesamoids are often ignored. Three knee sesamoids – the cyamella, medial
26 fabella, and lateral fabella – are present in Primates, but we know little about how they evolved,
27 if they are skeletal innovations, or why they are largely missing from Hominoidea. Our
28 phylogenetic comparative analyses suggest sesamoid presence/absence is highly
29 phylogenetically structured and contains phylogenetic signal. Models suggest it is easy to gain
30 but difficult/impossible to lose knee sesamoids, and that the fabellae may have similar
31 developmental/evolutionary pathways that are distinct from the cyamella. Sesamoid
32 presence/absence is uncorrelated to mode of locomotion, suggesting sesamoid biomechanical
33 function may require information beyond sesamoid presence, such as size and location.
34 Ancestral state reconstructions were largely uninformative but highlight how reconstructions
35 using parsimony can differ from those that are phylogenetically informed. Interestingly, there
36 may be two ways to evolve fabellae, with humans evolving fabellae differently from most other
37 primates. We hypothesize the “re-emergence” of the lateral fabella in humans may be
38 correlated with the evolution of a unique developmental pathway, potentially correlated with
39 the evolution of straight-legged, bipedal locomotion.

40

41 2 INTRODUCTION

42 The skeleton has been used to address a myriad of questions in anatomy, biology, and origin.
43 Skeletons are so popular that entire buildings and institutions have been erected with a primary
44 goal being their collection and preservation. Yet, despite centuries of research [1–5], sesamoid
45 bones – small skeletal elements located within tendons and/or ligaments, often near joints [6]
46 – remain poorly understood. This has yielded an incomplete understanding of the skeleton, how
47 it came to be, and how it functions today.

48 Sesamoids are ubiquitous in mammals. Examples include the patella ulnaris in the elbow [5,7–
49 9], prepollex [10–17] and palmar sesamoids [18] in the hand, metacarpal and phalangeal
50 sesamoids in the hands and feet [7,18–27], and patella, cyamella and medial and lateral medial
51 fabellae in the knee [4,5,7,8,18,19,22,28–41]. Unlike other skeletal elements, sesamoids can
52 vary greatly in size, shape, location, histological composition, and presence/absence.
53 Consequently, they have been hypothesized to be an important source of skeletal innovation in
54 a relatively conservative tetrapod bauplan but, oddly, they are often not counted as bones of
55 the skeleton [42].

56 Skeletal innovations enable the skeleton to work in new, novel manners, and sesamoids have
57 done this by redirecting muscle forces [4–6,22,43–51], decreasing tendon-bone friction [52],
58 increasing tendon strength and tendonous connections [53], and sometimes even acting as extra
59 digits [13]. The hypothesized ability for sesamoids, epiphyses, and apophyses to transform into
60 each other throughout evolution [6] give sesamoids further functional flexibility. Given their
61 numerous function and flexibility, sesamoids have been hypothesized to be a source of skeletal
62 innovation in the relatively conservative tetrapod bauplan [6,54].

63 Primates are a diverse clade occupying habitats ranging from savannas, woodlands, and rain
64 forests (e.g., *Pan troglodytes*) to temperate forests (e.g., *Macaca fuscata*) and high-altitude
65 mountains (e.g., *Rhinopithecus bieti*, China [55]). Consequently, primates evolved a wide
66 range of locomotor repertoires which place variable biomechanical demands on their hindlimbs

67 [56–62]. Primates may have developed skeletal innovations in their hindlimbs in response to
68 these demands.

69 The primate knee is a relatively simple joint that experiences high biomechanical loads from
70 large muscles crossing it. There are four sesamoids in the primate knee – the patella, cyamella,
71 and medial and lateral fabellae – that could contribute to skeletal innovation [5,22,29]. The
72 patella, located in the quadriceps tendon, is ubiquitous in primates [5]. It increases the
73 mechanical advantage of the quadriceps by increasing the distance between the muscle's line
74 of action and the center of rotation of the knee, decreasing locomotor energetics and potentially
75 protecting the tendon [63–65]. The cyamella, located in the popliteus tendon, and the medial
76 and lateral fabellae, located in the medial and lateral gastrocnemius tendons, respectively are
77 variably present in primates. Unlike the patella, there has been little experimental or
78 computational work to understand their function.

79 Based on the cyamella's location in lemurs, the cyamella was hypothesized to aid in lower leg
80 rotation [66]. The large cyamella in *Pongo*, which rotates its lower leg to an exceptional degree
81 during quadrumanus locomotion, supports this hypothesis [67]. Le Minor hypothesized the
82 cyamella may reduce the pressure between the popliteus muscle and popliteal tendon [29]. This
83 is consistent with Berthaume and Bull, who hypothesized Class I cyamellae in humans may
84 reduce the pressure/stress where the popliteal tendon wraps around the lateral femoral condyle.
85 They additionally hypothesized Class II/III cyamellae may strengthen the connection between
86 the popliteofibular ligament and popliteus muscle/popliteal tendon, respectively [53].

87 No hypotheses have been generated concerning medial fabella function [5,68]. Medial fabellae
88 are extremely rare in humans [1,69,70]. Based on patellar function, Sarin et al. hypothesized
89 the lateral fabella may increase the mechanical advantage of the gastrocnemius [22]. For
90 humans, this would only be true during the straight-legged portion of gait, as the fabella only
91 contacts the femoral condyle when the leg is straight. The fabellae are reportedly more
92 superiorly located in primates, potentially enabling them to articulate with the femoral condyle,
93 increasing the mechanical advantage of the gastrocnemius, when the knee is bent. The lateral
94 fabella is also hypothesized to stabilize and reinforce the posterolateral corner of the knee,
95 reducing knee rotation [71–73].

96 Here, we reconstruct the evolutionary history of knee sesamoids in primates to address the
97 following questions:

- 98 • How did the cyamella, medial fabella, and lateral fabella evolve in Primates?
- 99 • Are these sesamoids skeletal innovations?
- 100 • Why are they largely missing from Hominoidea?

101 We further investigate the relationship between knee sesamoids and mode of locomotion to see
102 if novelties are related to environment and how the primates move.

103 **3 METHODS**

104 To collect data on knee sesamoids, we conducted a systematic review on knee sesamoid
105 presence/absence in primates. We only considered sesamoid presence/absence as other
106 information on the sesamoids (e.g., size, location) was rarely given. Phylogenetic analyses were
107 carried out to reconstruct the evolutionary history of the knee sesamoids and investigate
108 correlations between sesamoid presence/absence and mode of locomotion.

109 **3.1 SYSTEMATIC REVIEW**

110 Using PRISMA guidelines [74], the following search strategies were employed: (1) computer
111 search of databases, (2) bibliographic review of retrieved articles, and (3) targeted digital
112 review of older, subject-specific journal databases. Textbooks were utilized only if they came
113 up in computer searches or bibliographies.

114 **3.1.1 Computer search**

115 We searched scholar.google.co.uk using the search terms in Table 1. Whenever a search term
116 was used, it was omitted from subsequent searches to prevent result duplication. As “fabella”
117 is a surname, we used additional terms to focus our search. Several additional search terms
118 were used for the cyamella as this sesamoid was only named in 1921 [4,5]. Searches were
119 completed in March (cyamella) and May (fabellae) 2021. Google Scholar alerts were set up to
120 stay apprised of the literature.

121 Titles and abstracts were reviewed by the first author and selected for further review if: (1)
122 sources were on non-human primates, (2) sources were anatomical or veterinary in nature, and
123 (3) a link was provided through which the article could be accessed. Data on humans came
124 from recent systematic reviews and meta-analyses [41,75]. Full texts were reviewed by the first
125 author and excluded if (1) genus-level taxonomic data were missing, (2) articles did not contain
126 primary data on sesamoid presence/absence, or (3) taxa were extinct and sesamoid
127 presence/absence was not observed, but inferred. Sources not in English were translated by
128 people fluent in that language or using Google Translate. While imperfect, Google Translate
129 worked well enough to determine sesamoid presence/absence.

130 **3.1.2 Review of bibliographies**

131 Bibliographic reviews were conducted, and full texts were obtained through
132 scholar.google.co.uk or interlibrary loan. If sources could not be obtained through these routes,
133 they were excluded.

134 **3.1.3 Review of targeted journal databases**

135 During bibliographic reviews, we discovered some early sources (before ~1900) did not appear
136 in the Google search. In December 2020, we searched the digital databases of the following
137 journals, which had previously published papers on primate knee sesamoids, for the term
138 “sesamoid”: Journal of Anatomy and Physiology, Proceedings of the Royal Irish Academy,
139 Proceedings of the Royal Society of London, Proceedings of the Zoological Society of London,
140 Annals and Magazine of Natural History, and The Royal Society of London. We limited our
141 search to papers published before 1920, using the same inclusion/exclusion criteria as above.

142 **3.2 DATA COLLECTION**

143 **3.2.1 Presence/absence data**

144 The first author extracted data on ossified cyamella, medial fabella, and lateral fabella
145 presence/absence. Method of data collection (e.g., dissection, survey of museum skeletons)
146 was used to resolve disagreements between sources, with dissection being the gold standard.
147 Sesamoids were marked as absent if 1) it was explicitly stated in the publication, or 2) other
148 non-patellar sesamoids were mentioned, but the cyamella/fabellae were not. It is therefore
149 possible some taxa were incorrectly marked as “absent”. It is, unfortunately, not possible for
150 us to quantify the Type II error without further, unobtainable knowledge about the primary

151 studies. Random entries were checked by the last author. Any disagreements were discussed,
152 and a consensus solution was reached.

153 Taxonomic classifications were updated using Mammal Species of the World [76],
154 AnimalBase (<http://www.animalbase.org/>), BioLib, Handbook to the Primates (Wikisource,
155 2013), and IUCN Red List (iucnredlist.org). *Semnopithecus orientalis* and *Jacchus sp.* from
156 [5] could not be confidently updated so were excluded, although the former may be *Nasalis*
157 *larvatus orientalis* [77].

158 When present, sample size (number of knees or individuals) was recorded. When absent,
159 sample size was assumed to be “one”. The presence/absence of knee sesamoids was coded as
160 a binary trait with two coding strategies. As sesamoid presence is controlled by both genetics
161 and environment [34,35], the “presence” dataset assumed that if a single specimen had an
162 ossified sesamoid, the taxon had the genetic potential to grow the sesamoid and it was coded
163 as present. The “majority” dataset assumed a prevalence of 50+% was needed for the bone to
164 be coded as present. The creation of the two datasets allowed us to overcome potential bias
165 linked to isolated cases of false positives or negatives in individuals or studies, increasing the
166 robusticity of the study.

167 **3.2.2 Mode of locomotion**

168 Primates were classified as knuckle walker, arboreal quadrupedal, terrestrial quadrupedal,
169 vertical clinger, or suspensory based on published literature [78–88]. Here, “suspensory” is a
170 catch-all term for arm swingers, brachiators, and quadrumanus primates as these primates
171 likely have higher forelimb loads during locomotion than other primates.

172 **3.3 PHYLOGENETIC COMPARATIVE ANALYSES**

173 Four time-calibrated molecular phylogenies of primates were taken from [89] which differ in
174 divergence times, but not tree topology. Genus-level data were excluded except for *Pithecia*
175 *sp.*, *Pygathrix sp.*, and *Tarsius sp.* for which no species-level data was available. *Chiropotes*
176 *satanas* was missing but was the only *Chiropotes* in our dataset; we assigned its data to
177 *Chiropotes utahickae* [90–92]. *Cebus flavius* was not in [89] and was excluded from analysis,
178 as its closest living relatives are some populations of *C. apella* (*Sapajus apella*) [93], which
179 was already in our analysis. It is possible that *C. flavius* is a subspecies of *S. apella*, or that *S.*
180 *apella* is represented by many species. We ran all analyses using all four time-trees. Results
181 were similar across all trees. We therefore only present results from the tree with autocorrelated
182 rates and hard-bounded constraints [89].

183 **3.3.1 Trait evolution and phylogenetic signal**

184 We modelled sesamoids as binary characters and fit eight evolutionary models to the data.
185 Three were continuous-time Markov chain model (simple Mk models [94,95]) which assume
186 there is only one way to transition between having and not having a sesamoid [94,96]. Five
187 were hidden rates models (HR; [97]) which allow for heterogeneity in character evolution
188 across the phylogeny [98]. Biologically, this implies there could be more than one way to gain
189 or lose a sesamoid. For example, sesamoids could form randomly within a tendon or as an
190 ossification centre that is removed from another bone [34,35] Similarly, sesamoids could be
191 lost because they were absorbed into another bone or the genes controlling sesamoid
192 development were silenced [34,35].

193 The three simple Mk models were: 1) equal rates (ER), 2) all rates different (ARD), and 3)
194 irreversible loss model (ILM). The ER model is symmetrical and assumes taxa are as likely to
195 gain as lose a sesamoid. The ARD and ILM models are asymmetrical, with the former assuming

196 unequal transition rates between gaining/losing sesamoids and latter assuming sesamoids can
197 be lost but not gained. The five HR models were: 1) one hidden rate in the absence state (1HRA,
198 there was one way to gain but two ways to lose a sesamoid), 2) one hidden rate in the presence
199 state (1HRP), 3) one hidden rate in the covarion model (1HRCO, transitions between hidden
200 states are set to zero), 4) one full hidden rate (1HR), and 5) two full hidden rates (2HR). The
201 fitMk and fitHRM functions (niter = 5, pi = fitzjohn) from Phytools 2.0-3 were used to fit
202 models in R [98,99]. The default upper bound of the hidden rates model is 100*tree height. As
203 the hidden rate models regularly hit that limit, max.q was used to increase the upper bound to
204 1e9. These transition rates are unusually large, and likely result from a lack of power for fitting
205 this class of model to this data.

206 Akaike information criterion (AICc) was used to compare models [100,101]. Given the issues
207 with the hidden rate models, the best Mk and hidden rate models were chosen separately (Table
208 2), and compared using a likelihood ratio test (Chi-square distribution, Table 3) to determine
209 if there were significant differences in performance. If models performed equally well, the
210 simpler, Mk model was used. The best-fitting model from the likelihood ratio test was used for
211 ancestral state reconstruction (ASR). Marginal likelihoods of internal nodes were plotted using
212 the maximum likelihood (ML) approach with the ancr function in Phytools 2.0-3 [98]. When
213 HR models were used for ASR, the marginal scaled likelihoods probabilities were summed
214 across all applicable hidden states so only presence/absence was reported.

215 **3.3.2 Phylogenetic signal**

216 We tested for phylogenetic signal – the tendency for closely related species to resemble one
217 another more than distantly related species – using Pagel’s λ [102] and the D-statistic [103].
218 FitDiscrete (Geiger 2.0.11) and the best-fit simple Mk model were used to estimate Pagel’s λ
219 [96,102]. Likelihood ratio tests were used to compare the estimates of λ to one where the tree
220 was transformed to a star phylogeny ($\lambda = 0$) to determine statistical significance. We also
221 estimated phylogenetic signal using the D-statistic [103] (phylo.d function, Caper 1.0.3 [104]),
222 which was designed to test for phylogenetic signal in discrete binary traits. $D \cong 0$ indicates
223 trait evolution is consistent with Brownian motion, $D \cong 1$ indicates a random distribution of
224 traits in the phylogeny, and $D < 0$ indicates a character is more conserved than expected under
225 Brownian motion.

226 **3.3.3 Coincidental development and trait correlations**

227 To investigate if the knee sesamoids had shared or distinct evolutionary histories, coincident
228 development among knee sesamoids was quantified using pairwise phylogenetic logistic
229 regressions [105] (phyloglm function, phylolm [106]). The strength of the relationships was
230 measured using R^2_{lik} (R2 function, rr2 package; [107,108]). Phylogenetic logistic regression
231 with a Firth correction [105] were used to examine the relationship between sesamoid
232 presence/absence and mode of locomotion (phyloglm function, phylolm [106]). This method
233 is a modified generalized lineal model that estimates the relationship between one or more
234 discrete independent variable(s) and a discrete binary variable. All analyses were performed
235 on the “presence” and “majority” datasets, separately, and carried out in R 4.2.3 using RStudio
236 [109,110].

237 **4 RESULTS**

238 We identified 2,625 sources through our search and 13 through Google Scholar alerts (see
239 PRISMA chart in the Electronic supplementary information, ESM). Twenty-seven sources
240 were reviewed, and an additional 32 were identified through bibliographic review. 15/59

241 sources excluded: 2 could not be obtained [111,112], 3 were on extinct taxa where sesamoid
242 presence/absence was inferred [113–115], 8 did not include primary data or specify taxa
243 [22,116–122], 1 species was not specified [123] and 1 did not mention sesamoids [124]. The
244 remaining sources, combined with [41,75], yielded data on cyamella, medial fabella, and lateral
245 fabella presence/absence for 73, 85, and 88 taxa, respectively (93 taxa total, see ESM). All
246 sesamoids are present in most primate families but most commonly absent from the apes
247 (Figures 1-2; ESM). There are no reported cyamellae in Atelidae or Hylobatidae, medial
248 fabellae in Aotidae, Hominidae, or Lepilemuridae, or lateral fabellae in Aotidae, although the
249 potential presence of ossified medial fabellae in humans remains contentious.

250 The best simple Mk evolutionary model was ARD for all sesamoids and datasets (Table 2),
251 and the ER model for the cyamella datasets had support. The 1HRA model was the best HR
252 evolutionary model for the cyamella, and the 1HRP model was the best HR evolutionary model
253 for the fabellae (Table 2). Hidden rate models performed better than Mk models for the
254 cyamella majority, medial fabella presence and both lateral fabella datasets (Table 3).

255 Instantaneous rates of change for the ARD models (Table 4) indicate it is always easier to gain
256 than lose sesamoids ($q_{01} > q_{10}$), and fabellae are almost impossible to lose. Similarly, the
257 instantaneous rates of change for the 1HRA model indicate it is easier to gain than lose
258 cyamellae. Transitions between hidden rates were relatively low ($<e^{-4}$) and transitions between
259 other states were exceedingly high (Table 5). Stochastic character mapping was conducted for
260 all Mk models and the HRP fabella models (simmap, Phytools; 100 simulations). Time
261 constraints with HR models mean only results from the presence dataset models are presented
262 here. Results for the ARD models reflect a high level of uncertainty for ancestral states for the
263 cyamella, but a high level of certainty for the fabellae (Table 6, Figure 3). The high number of
264 transitions from absent to present but low number from present to absent (Table 6) reflects the
265 instantaneous rates change results (Table 4).

266 The HRP models for the fabellae show the same pattern of results, with an average of 200+
267 transitions in the tree mostly between present and absent, with few transitions in the hidden
268 rate (Table 7). Simulations consistently demonstrated two evolutionary pathways to having
269 fabellae, one hidden pathway followed by most primates and another pathway for Hominoidea
270 and *Nycticebus* where there is high turnover between fabellae being present and absent (Figure
271 4). It is unlikely fabellae were gained/lost 200+ times in these two clades. Despite the lower
272 AICc values, this calls into question the results from the hidden rate models.

273 The statistical power of the methods were tested on our dataset using the Monte Carlo
274 simulation method from [125], where the ARD models were set to M0 and hidden rate models
275 to M1. Using q-matrices from the M0 models and the sim.char function from Geiger [96], we
276 simulated 1000 datasets and calculated δ , which is twice the difference in log likelihoods
277 between M1 the simulated data ($\delta = -2(\log(L(M1)) - \log(L(M0_{sim})))$). The proportion of
278 δ 's above δ^* , which here is $-2(\log(L(M1)) - \log(L(M0)))$, is the probability that the ARD
279 model can explain the variation in the data. Results consistently demonstrated that, despite the
280 hidden rate models often fitting our data better (Table 3), the ARD models could often still
281 explain the variation observed in our data (Table 8).

282 There was strong phylogenetic signal in our data (Table 9). Pagel's λ was high (0.656 - 0.916)
283 and significant ($p < 0.001$). The D-statistic for one dataset was ~ 0 , suggesting results are
284 consistent with Brownian motion, and other D-statistics were < 0 , suggesting phylogenetic
285 conservatism of knee sesamoids.

286 With the exception of the cyamella presence and medial fabella majority datasets, ASRs tended
287 to disagree with each other. It is likely that the last common ancestor (LCA) of cercopithecines

288 had a cyamella, medial fabella, and lateral fabella. It is also likely that the LCA of strepsirrhines
289 had a cyamella, platyrrhines had medial and lateral fabellae, and hominoids did not have medial
290 or lateral fabellae. There is a large degree of uncertainty, or disagreement between models, for
291 all other ASRs (ESM Table 1, Figures 3; ESM).

292 Coincident development was found for medial and lateral fabellae in both datasets, indicating
293 species with medial fabellae were likely to have lateral fabellae, and vice versa ($R^2_{\text{lik}} = 0.69 -$
294 0.80 , $p < 0.001$). The presence dataset indicated species with lateral fabellae were likely to have
295 cyamellae ($R^2_{\text{lik}} = 0.46$, $p < 0.05$, Table 10). No relationship was found between sesamoid
296 presence/absence and mode of locomotion ($p = 0.957-0.999$; ESM Table 2).

297 **5 DISCUSSION**

298 Knee sesamoid evolution in primates is complex. Looking at the pattern of sesamoids across
299 the primate phylogeny, there is clear clustering within clades that appears to be independent of
300 parameters like body size, diet, environment, and geographic distribution. In terms of the
301 evolutionary history of these bones, Le Minor [29] hypothesized the cyamella was
302 plesiomorphic in primates. Our ASR results for the cyamella are ambiguous and cannot
303 confirm or negate this hypothesis. Sarin et al. [22] used parsimony to hypothesize the lateral
304 fabella was present in the LCA of catarrhines. However, our phylogenetically informed ASRs
305 are generally confident the lateral fabella was absent from the LCA of catarrhines. Lacking
306 congruent information from the ASRs, it is further difficult to make hypotheses about how
307 evolution may have acted on the sesamoids in the past. But given the presence of these
308 sesamoids in other mammalian clades, it would be surprising if the LCA of all primates was
309 lacking these bones.

310 Sesamoids can be *de novo* elements that serve as morphological innovations but contain
311 phylogenetic legacy [126,127]. Given the cyamella, medial fabella, and lateral fabella are
312 highly uncorrelated to mode of locomotion ($p = 0.957-0.999$; ESM Table 2), it is possible these
313 sesamoids serve multiple biomechanical functions, performing different primary functions in
314 different phylogenetic clades [128]. For example, the cyamella may increase the mechanical
315 advantage of the popliteus in *Pongo* but strengthen ligamentous connections in humans.
316 Sesamoids may also act as osteoclast mediated calcium reservoirs [129]. Fabellae can ossify
317 early in *Macaca mulatta* and *M. fascicularis* (1 – 3.25 years) but timing of ossification in other
318 non-human primates is unknown [130–132], making it difficult to identify at what point in a
319 species' life history these bones would become important. The exact location is also unknown
320 in non-human primates but can be highly variable in humans, which can affect the bone's
321 biomechanical function [133]. The potentially multifunctional nature of these sesamoids needs
322 to be investigated further.

323 It is possible there is more than one way to evolve a fabella, as there are multiple ways to grow
324 sesamoids [34], but it is currently difficult to have confidence in the HR models (Table 5, Table
325 7, Figure 4). More data from outgroups may improve character states of internal nodes in our
326 models, which may improve HR model fitting. Excitingly, the idea that *Homo sapiens*, and
327 potentially hominoids, have evolved a way of growing and developing fabellae unique to other
328 primates is consistent with hypotheses on lateral fabella, cyamella, and parafibula evolution in
329 mammals.

330 **5.1 EVOLUTION OF THE LATERAL FABELLA IN HUMANS**

331 Is it possible that there is more than one way to grow, and therefore evolve, a lateral fabella in
332 primates? The high level of correlation between the medial and lateral fabellae suggests these

333 bones may share genetic, growth and development, and/or evolutionary pathways (Table 10).
334 However, within *Homo sapiens*, the lateral fabella is common while the medial fabella is
335 rare/absent, suggesting, in this species, the bones are decoupled [41]. This decoupling is rare
336 in our dataset. As the HRP model suggests it is possible for humans to evolve a lateral fabella
337 that is unique from most other primates, is it possible most primates have evolved to grow
338 medial and lateral fabellae in pairs, whereas Hominoidea has evolved to grow them in a
339 decoupled manner?

340 Based on dissections of human fetuses, Fürst [134] hypothesized the lateral fabella was a pre-
341 cartilage multinucleated blastema fragmented from the fibular head during growth and
342 transported to the posterolateral corner of the femur by the fabellofibular ligament (i.e., the
343 gastrocnemiofibular ligament) during the descent of the primitive femoroperoneal articulation
344 [134–136]. This would make the lateral fabella’s development similar to the patella [137]. This
345 would explain how the fabellae have unique developmental pathways in humans, as there is no
346 equivalent to the fabellofibular ligament on the medial side of the knee. However, in their
347 developmental mouse model, Eyal *et al.* [34] did not observe fabellae developing juxtaposed
348 to the fibula, but rather independently in the gastrocnemius’s lateral tendon. Taken with the
349 HRP models from this study, it is possible Fürst’s hypothesis is true for in Hominoidea and
350 *Nycticebus*, and Eyal *et al.*,’s hypothesis is true for other primates, and that there is more than
351 one way to grow a fabella in primates.

352 **5.2 EVOLUTION OF THE KNEE SESAMOIDS IN PRIMATES**

353 The evolutionary origins of the cyamella and lateral fabella in mammals have often been
354 hypothesized to be linked, and independent of the medial fabella. Pearson and Davin [5]
355 hypothesized the cyamella and lateral fabella evolved from the parafibula, which was itself a
356 fibular crest that previously detached from the fibula (“the detachment model” of sesamoid
357 evolution in Eyal *et al.* [35]). Conversely, Barnett and Lewis [8] hypothesized the cyamella
358 and lateral fabella were pre-existing intratendinous structures (based on “the traction epiphysis
359 theory” from Parsons [3]; now the “intratendinous model” in Eyal *et al.* [35]) which fused
360 together to form the parafibula and attached to the fibula to form the fibular crest¹. Under these
361 hypotheses, the evolution of the cyamella and lateral fabella should be linked, and the evolution
362 of both bones should be independent of the medial fabella. However, our results here do not
363 support this scenario.

364 Not all evolutionary theories link the cyamella and lateral fabella. Fürst [136] proposed an
365 independent evolutionary origin of cyamella and lateral fabella, and that the two bones had
366 different developmental pathways. Based on shifts in the popliteus’s origin from the
367 interosseous space between the tibia and fibula to the lateral femoral condyle, Fürst
368 hypothesized the cyamella was an apophysis detached from the fibular epiphysis. Others have
369 hypothesized the cyamella evolved from the femorofibular disc found in reptiles, where it
370 became enveloped in the popliteal tendon [68,138].

371 Interestingly, the medial fabella is so rare in humans that its development is not known and has
372 largely not been discussed. Jouffroy [139] hypothesized that its absence/reduction in

¹ Under both the detachment and intratendinous models, it would be impossible to have a parafibula, cyamella, and lateral fabella in a single knee. While generally true, three sesamoids were found in a specimen of *Desmodus rotundus*, and it was suggested they were the parafibula, cyamella, and lateral fabella [7]. As it is possible for humans to have two lateral fabellae in the same knee, it is possible this specimen had two lateral fabellae [70,143].

373 prevalence may be correlated with the reduction in medial gastrocnemius size and development
374 of the soleus, but this is untested.

375 **5.3 EVOLUTION OF SESAMOIDS IN TETRAPODS**

376 Not all sesamoids have the same growth and development and thereby evolutionary pathways,
377 but it is possible some are linked. Eyal *et al.* [34] pointed towards potential similarities and
378 differences in growth and development between the patella, fabella, and digit sesamoids in
379 mice, demonstrating the complexities of sesamoid growth and development within a single
380 species. It is therefore possible these bones share similar evolutionary origins. Recently, Abdala
381 and colleagues synthesized many existing models of sesamoid evolution, and proposed the
382 dynamic model, which states:

383 “During evolution, sesamoids can become displaced, attaching to and detaching
384 from the long bone epiphysis and diaphysis. Epiphyses, apophyses and detached
385 sesamoids are able to transform into each other, contributing to the phenotypic
386 variability of the tetrapod skeleton.” (p. 2011) [6]

387 Our results, particularly for the fabellae, suggest some sesamoids can evolve but are then
388 almost impossible to lose. In the context of the dynamic model of sesamoid evolution, this
389 would imply it is easier for an epiphysis or apophysis to become fabellae in primates than for
390 fabellae to become an epiphysis or apophysis. Given the variability in growth and
391 development pathways of sesamoids within organisms [34], our results cannot effectively test
392 the dynamic model, but suggest it may be easier for some epiphyses, apophyses, and detached
393 sesamoids to transform into each other than others. Given the complexities of sesamoid growth
394 and development, and the results of this study, it seems not all sesamoids follow the same
395 evolutionary pathways.

396 **5.4 LIMITATIONS OF THE STUDY**

397 Here, we only considered ossified sesamoids, and ignored information on sesamoid size and
398 location and musculoskeletal architecture, which are biomechanically important. Small
399 samples of non-human primates prohibited the examination of intraspecific variation. More
400 information on sesamoid presence/absence is needed within primates. Additionally, the
401 methods employed for fitting evolutionary models and ASR’s can have low statistical power
402 when taxa sampling is less than 300 taxa, there are character change rates asymmetries, and
403 high tip ratio bias.

404 It is possible some taxa have sesamoids have been incorrectly marked as absent, either because
405 they were not of interest or due to time constraints during dissections means (e.g., Diogo,
406 personal communication). The use of published data also introduces flaws. For example,
407 Pearson and Davin state, “The cyamella as well as both fabellae are present not only in
408 Semnopithecidae, but in macaques... (363) [5]”, but in Le Minor found no cyamellae in 40
409 *Macaca* skeletons or 2 formalin-fixed *Macaca* specimens [29]. Other studies with macaque
410 data also agreed the cyamella was present in *Macaca* [66,130–132,140–142].

411 **6 CONCLUSIONS**

412 Here, we used comparative methods to analyze knee sesamoid evolution in primates. Our
413 results support several conclusions:

- 414 1) The cyamella and fabellae are present in most primate families, but most commonly
415 absent from the apes.

- 416 2) There is high phylogenetic signal in sesamoid presence/absence, with results being
417 most consistent with a Brownian motion and a conserved model of trait evolution.
418 3) It is easier to gain than lose knee sesamoids in primates, suggesting that, once evolved,
419 knee sesamoid presence is highly conserved.
420 4) The medial and lateral fabellae may share similar developmental/genetic pathways, and
421 these pathways may be different in the cyamella. This calls into question the
422 hypothesized evolutionary linked between the cyamella, lateral fabella, and parafibula.
423 5) If knee sesamoids have a biomechanical function, it is independent of mode of
424 locomotion.

425 These results point towards the importance of understanding the evolution of sesamoids in
426 tetrapods, and how sesamoid evolution can be used to test hypotheses about skeletal innovation.
427 A more comprehensive model of sesamoid evolution throughout the entire body may point
428 towards new ways in which the evolution of these bones are linked, and how they have affected
429 the evolution of the tetrapod bauplan.

430 Perhaps most interesting is the possibility that there may be more than one way to evolve
431 fabellae, and that humans may have evolved fabellae differently than most other primates. We
432 hypothesize the “re-emergence” of the lateral fabella in *Homo sapiens* may be correlated with
433 the development of this unique evolutionary pathway, which may potentially correlated with
434 straight-legged, bipedal locomotion. As our models suggest the “decoupling” between the
435 medial and lateral fabella occurred at the root of Hominoidea, it is unlikely it was caused by
436 bipedalism, but it could have served as an exaptation which helped enable the success of
437 bipedalism in hominins. Future work in this area will focus on the biomechanical function of
438 the fabella in humans, and implications for bipedal locomotion.

439 **7 ACKNOWLEDGEMENTS**

440 The authors would like to thank Liam Revell for help with the hidden rate models and
441 interpreting the high transition rates. This manuscript would not be what it is today if it were
442 not for the extraordinary efforts of two anonymous reviewers, the AE, and the editor, John
443 Hutchinson. In partnership with the British Academy, Royal Academy of Engineering, and
444 Royal Society (‘the Academies’) with generous support from the Leverhulme Trust, this
445 research was funded by APEX award APX\R1\211183.
446

8 REFERENCES

- 447
448
449 1. Gruber W. 1875 Monographie über die aus wahren (hyalinischen) Cartilagine
450 praeformirten Ossicula sesamoidea in den Ursprungssehnen der Köpfe des Musculus
451 gastrocnemius bei dem Menschen und bei den Säugetieren. St. Petersburg, VII, serie.
452 2. Parsons FG. 1908 Further Remarks on Traction Epiphyses. *J Anat Physiol* **42**, 388–96.
453 3. Parsons FG. 1904 Observations on Traction Epiphyses. *J Anat Physiol* **38**, 248–58.
454 4. Pearson K, Davin AG. 1921 On the sesamoids of the knee-joint: Part I. Man.
455 *Biometrika* **13**, 133–75.
456 5. Pearson K, Davin AG. 1921 On the sesamoids of the knee-joint: part II. Evolution of
457 the sesamoids. *Biometrika* **13**, 350. (doi:10.2307/2331763)
458 6. Abdala V, Vera MC, Amador LI, Fontanarrosa G, Fratani J, Ponssa ML. 2019
459 Sesamoids in tetrapods: the origin of new skeletal morphologies. *Biological Reviews* ,
460 brv.12546. (doi:10.1111/brv.12546)
461 7. Amador LI, Giannini NP, Simmons NB, Abdala V. 2018 Morphology and Evolution
462 of Sesamoid Elements in Bats (Mammalia: Chiroptera). *Am Mus Novit* **3905**, 1–40.
463 (doi:10.1206/3905.1)
464 8. Barnett CH, Lewis OJ. 1958 The evolution of some traction epiphyses in birds and
465 mammals. *J Anat* **92**, 593–601.
466 9. Koyama E, Yasuda T, Minugh-Purvis N, Kinumatsu T, Yallowitz AR, Wellik DM,
467 Pacifici M. 2010 *Hox11* genes establish synovial joint organization and phylogenetic
468 characteristics in developing mouse zeugopod skeletal elements. *Development* **137**,
469 3795–3800. (doi:10.1242/dev.053447)
470 10. Abella J, Pérez-Ramos A, Valenciano A, Alba DM, Ercoli MD, Hontecillas D,
471 Montoya P, Morales J. 2015 Tracing the origin of the panda’s thumb. *The Science of*
472 *Nature* **102**, 35. (doi:10.1007/s00114-015-1286-3)
473 11. Abella J *et al.* 2016 When Cotton Rats Grasp Like Pandas. *J Mamm Evol* **23**, 309–317.
474 (doi:10.1007/s10914-015-9314-9)
475 12. Endo H, Sasaki N, Yamagiwa D, Uetake Y, Kurohmaru M, Hayashi Y. 1996
476 Functional anatomy of the radial sesamoid bone in the giant panda (*Ailuropoda*
477 *melanoleuca*). *J Anat* **189 (Pt 3)**, 587–92.
478 13. Hutchinson JR, Delmer C, Miller CE, Hildebrandt T, Pitsillides AA, Boyde A. 2011
479 From Flat Foot to Fat Foot: Structure, Ontogeny, Function, and Evolution of Elephant
480 “Sixth Toes”. *Science (1979)* **334**, 1699–1703. (doi:10.1126/science.1211437)
481 14. Mitgutsch C, Richardson MK, Jiménez R, Martin JE, Kondrashov P, de Bakker MAG,
482 Sánchez-Villagra MR. 2012 Circumventing the polydactyly ‘constraint’: the mole’s
483 ‘thumb’. *Biol Lett* **8**, 74–77. (doi:10.1098/rsbl.2011.0494)
484 15. Salesa MJ, Siliceo G, Anton M, Abella J, Montoya P, Morales J. 2006 Anatomy of the
485 ‘false thumb’ of *Tremarctos ornatus* (Carnivora, Ursidae, Tremarctinae):
486 Phylogenetic and functional implications. *Estudios Geológicos* **62**, 389–394.
487 16. Sánchez-Villagra MR, Menke PR. 2005 The mole’s thumb — evolution of the hand
488 skeleton in talpids (Mammalia). *Zoology* **108**, 3–12. (doi:10.1016/j.zool.2004.07.006)
489 17. Wood-Jones F. 1939 The forearm and manus of the giant panda, *Ailuropoda*
490 *melanoleuca* , M.-Edw. with an account of the mechanism of its grasp. *Proceedings of*
491 *the Zoological Society of London* **B109**, 113–129. (doi:10.1111/j.1469-
492 7998.1939.tb00026.x)
493 18. Grassé PP. 1949 *Ed. Traite de zoologie. Anatomie, systématique, biologie. Tome VI.*
494 *onychophores, tardigrades, arthropodes, trilobitomorpes, chélicérates.* Masson et
495 Cie: Paris.

- 496 19. Wirschafter ZT, Tsujimura JK. 1961 The sesamoid bones in long-evans strain rats.
497 *Anat Rec* **141**, 195–204. (doi:10.1002/ar.1091410304)
- 498 20. Vaughan LC, France C. 1986 Abnormalities of the volar and plantar sesamoid bones in
499 Rottweilers. *Journal of Small Animal Practice* **27**, 551–558. (doi:10.1111/j.1748-
500 5827.1986.tb02252.x)
- 501 21. Le Minor JM. 1987 Comparative anatomy and significance of the sesamoid bone of
502 the peroneus longus muscle (os peroneum). *J Anat* **151**, 85–99.
- 503 22. Sarin VK, Erickson GM, Giori NJ, Bergman AG, Carter DR. 1999 Coincident
504 development of sesamoid bones and clues to their evolution. *Anat Rec* **257**, 174–80.
505 (doi:10.1002/(SICI)1097-0185(19991015)257:5<174::AID-AR6>3.0.CO;2-O)
- 506 23. Gingerich PD, Haq M ul, Zalmout IS, Khan IH, Malkani MS. 2001 Origin of Whales
507 from Early Artiodactyls: Hands and Feet of Eocene Protocetidae from Pakistan.
508 *Science (1979)* **293**, 2239–2242. (doi:10.1126/science.1063902)
- 509 24. Vickaryous MK, Olson WM. 2007 Sesamoids and ossicles in the appendicular
510 skeleton. In *Fins into limbs : evolution, development, and transformation* (ed BK
511 Hall), pp. 323–41. University of Chicago Press.
- 512 25. Doherty AH, Lowder EM, Jacquet RD, Landis WJ. 2010 Murine Metapodophalangeal
513 Sesamoid Bones: Morphology and Potential Means of Mineralization Underlying
514 Function. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary
515 Biology* **293**, 775–785. (doi:10.1002/ar.21095)
- 516 26. Seki Y, Hoshino Y, Kuroda H. 2012 Prevalence of sesamoid bones in the
517 interphalangeal joint of the thumb and fingers: A radiographic study. *Clinical Anatomy
518* , n/a-n/a. (doi:10.1002/ca.22201)
- 519 27. Yammine K. 2018 The Relationship Between Digit Independence and Digital
520 Sesamoids in Humans and a Proposal of a New Digital Sesamoid Evolutionary
521 Hypothesis. *Anatomical record* **301**, 1046–60.
- 522 28. McCarthy PH, Wood AKW. 1989 Anatomical and Radiological Observations of the
523 Sesamoid Bone of the Popliteus Muscle in the Adult Dog and Cat. *Anatomia,
524 Histologia, Embryologia: Journal of Veterinary Medicine Series C* **18**, 58–65.
525 (doi:10.1111/j.1439-0264.1989.tb00581.x)
- 526 29. Le Minor JM. 1992 The popliteal sesamoid bone (cyamella) in primates. *Am J Phys
527 Anthropol* **87**, 107–110. (doi:10.1002/ajpa.1330870109)
- 528 30. Kirberger RM, Keet DF, Wagner WM. 2006 Radiologic abnormalities of the
529 appendicular skeleton of the lion (<i>Panthera leo</i>): Incidental findings and
530 Mycobacterium bovis-induced changes. *Veterinary Radiology & Ultrasound* **47**, 145–
531 152. (doi:10.1111/j.1740-8261.2006.00121.x)
- 532 31. Bland YS, Ashhurst DE. 1997 Fetal and postnatal development of the patella, patellar
533 tendon and suprapatella in the rabbit; changes in the distribution of the fibrillar
534 collagens. *J Anat* **190**, 327–342. (doi:10.1046/j.1469-7580.1997.19030327.x)
- 535 32. Carey EJ. 1920 Studies in the dynamics of histogenesis. *Journal of General
536 Physiology* **2**, 357–372. (doi:10.1085/jgp.2.4.357)
- 537 33. Clark J, Stechschulte DJ. 1998 The interface between bone and tendon at an insertion
538 site: a study of the quadriceps tendon insertion. *J Anat* **192**, 605–616.
539 (doi:10.1046/j.1469-7580.1998.19240605.x)
- 540 34. Eyal S, Rubin S, Krief S, Levin L, Zelzer E. 2019 Common cellular origin and
541 diverging developmental programs for different sesamoid bones. *Development* **146**,
542 dev167452. (doi:10.1242/dev.167452)
- 543 35. Eyal S, Blitz E, Shwartz Y, Akiyama H, Schweitzer R, Zelzer E, Dierich A, Dolle P,
544 Chambon P. 2015 On the development of the patella. *Development* **142**, 1831–9.
545 (doi:10.1242/dev.121970)

- 546 36. Holladay SD, Smith BJ, Smallwood JE, Hudson LC. 1990 Absence of an osseous
547 patella and other observations in Macropodidae stifle. *Anat Rec* **226**, 112–114.
548 (doi:10.1002/ar.1092260113)
- 549 37. Inamassu LR, Mamprim MJ, Dadalto CR, Cavaletti FC, Mello MC, Schimming BC.
550 2017 Absence of bony patella in the white-eared opossum (*Didelphis albiventris*):
551 Morphology and diagnostic imaging. *Anat Histol Embryol* **46**, 611–614.
552 (doi:10.1111/ahe.12316)
- 553 38. Reese S, Pfuderer UR, Bragulla H, Loeffler K, Budras K-D. 2001 Topography,
554 Structure and Function of the Patella and the Patelloid in Marsupials. *Anatomia,*
555 *Histologia, Embryologia: Journal of Veterinary Medicine Series C* **30**, 289–294.
556 (doi:10.1046/j.1439-0264.2001.00334.x)
- 557 39. Smith BJ, Holladay SD, Smith SA. 1995 Patella of selected bats: Patterns of
558 occurrence or absence and associated modifications of the quadriceps femoris tendon.
559 *Anat Rec* **242**, 575–580. (doi:10.1002/ar.1092420414)
- 560 40. Dalip D, Iwanaga J, Oskouian RJ, Tubbs RS. 2018 A Comprehensive Review of the
561 Fabella Bone. *Cureus* **10**, e2736. (doi:10.7759/cureus.2736)
- 562 41. Berthaume MA, Di Federico E, Bull AMJ. 2019 Fabella prevalence rate increases over
563 150 years, rates of other sesamoid bones remain constant: a systematic review. *J Anat*
564 **235**, 67–79. (doi:10.1111/joa.12994)
- 565 42. Neumann PE, Gest TR. 2019 How many bones? Every bone in my body. *Clinical*
566 *Anatomy* (doi:10.1002/ca.23425)
- 567 43. Carlsöö S. 1982 The effect of vibration on the skeleton, joints and muscles. *Appl*
568 *Ergon* **13**, 251–258. (doi:10.1016/0003-6870(82)90064-3)
- 569 44. Nussbaum RA. 1982 Heterotopic Bones in the Hindlimbs of Frogs of the Families
570 Pipidae, Ranidae and Sooglossidae. *Herpetologica* **38**, 312–320.
- 571 45. Jerez A, Mangione S, Abdala V. 2009 Occurrence and distribution of sesamoid bones
572 in squamates: a comparative approach. *Acta Zoologica* (doi:10.1111/j.1463-
573 6395.2009.00408.x)
- 574 46. Tsai HP, Holliday CM. 2011 Ontogeny of the Alligator Cartilago Transiliens and Its
575 Significance for Sauropsid Jaw Muscle Evolution. *PLoS One* **6**, e24935.
576 (doi:10.1371/journal.pone.0024935)
- 577 47. Evans HE, de Lahunta A. 2012 *Miller's Anatomy of the Dog*. ebook: Elsevier Health
578 Sciences.
- 579 48. Otero T, Hoyos JM. 2013 Sesamoid elements in lizards. *Herpetol J* **23**, 105–114.
- 580 49. Regnault S, Jones MEH, Pitsillides AA, Hutchinson JR. 2016 Anatomy, morphology
581 and evolution of the patella in squamate lizards and tuatara (*Sphenodon punctatus*). *J*
582 *Anat* **228**, 864–876. (doi:10.1111/joa.12435)
- 583 50. Abdala V, Vera MC, Ponssa ML. 2017 On the Presence of the Patella in Frogs. *Anat*
584 *Rec* **300**, 1747–1755. (doi:10.1002/ar.23629)
- 585 51. Zhang R, Han D, Luo G, Ling L, Li G, Ji Q, Li J. 2018 Macroscopic and microscopic
586 analyses in flexor tendons of the tarsometatarso-phalangeal joint of ostrich (*Struthio*
587 *camelus*) foot with energy storage and shock absorption. *J Morphol* **279**, 302–311.
588 (doi:10.1002/jmor.20772)
- 589 52. Shaw HM, Vázquez OT, Mcgonagle D, Bydder G, Santer RM, Benjamin M. 2008
590 Development of the human Achilles tendon enthesis organ. *J Anat* **213**, 718–724.
591 (doi:10.1111/j.1469-7580.2008.00997.x)
- 592 53. Berthaume MA, Bull AMJ. In press. The cyamella, a popliteal sesamoid bone, in
593 humans: prevalence in a Korean population, systematic review, and meta-analysis.
594 *Clinical Anatomy*

- 595 54. Amador LI. 2022 Sesamoids and Morphological Variation: a Hypothesis on the Origin
596 of Rod-like Skeletal Elements in Aerial Mammals. *J Mamm Evol* **29**, 77–91.
597 (doi:10.1007/s10914-021-09571-8)
- 598 55. Long Y, Kirkpatrick CR, Zhongtai, Xiaolin. 1994 Report on the distribution,
599 population, and ecology of the yunnan snub-nosed monkey (<i>Rhinopithecus
600 bieti</i>). *Primates* 1994 35:2 **35**, 241–250. (doi:10.1007/BF02382060)
- 601 56. Kimura T, Okada M, Ishida H. 1979 Kinesiological characteristics of primate walking:
602 its significance in human walking. In *Environment, Behaviour and Morphology:
603 Dynamic Interactions in Primates* (eds M Morbeck, H Preuschoft, N Gomberg), pp.
604 297–311. New York, NY: Gustav Fischer.
- 605 57. Vilensky JA. 1989 Primate locomotion: utilization and control of symmetrical gaits.
606 *Annu Rev Anthropol* **18**, 17–35.
- 607 58. Demes B, Larson SG, Stern JT, Jungers WL, Biknevicius AR, Schmitt D. 1994 The
608 kinetics of primate quadrupedalism: ‘hindlimb drive’ reconsidered. *J Hum Evol* **26**,
609 353–374. (doi:10.1006/jhev.1994.1023)
- 610 59. Young JW, Patel BA, Stevens NJ. 2007 Body mass distribution and gait mechanics in
611 fat-tailed dwarf lemurs (<i>Cheirogaleus medius</i>) and patas monkeys
612 (<i>Erythrocebus patas</i>). *J Hum Evol* **53**, 26–40.
613 (doi:10.1016/j.jhevol.2007.01.005)
- 614 60. Young JW. 2012 Ontogeny of limb force distribution in squirrel monkeys (<i>Saimiri
615 boliviensis</i>): Insights into the mechanical bases of primate hind limb dominance. *J
616 Hum Evol* **62**, 473–485. (doi:10.1016/j.jhevol.2012.01.003)
- 617 61. Larson SG, Demes B. 2011 Weight support distribution during quadrupedal walking in
618 <i>Ateles</i> and <i>Cebus</i>. *Am J Phys Anthropol* **144**, 633–642.
619 (doi:10.1002/ajpa.21460)
- 620 62. Gebo DL. 2014 *Primate Comparative Anatomy*. Baltimore, Maryland: Johns Hopkins
621 University Press.
- 622 63. Alexander RMcN, Dimery NJ. 1985 The significance of sesamoids and retro-articular
623 processes for the mechanics of joints. *J Zool* **205**, 357–371. (doi:10.1111/j.1469-
624 7998.1985.tb05622.x)
- 625 64. Allen VR, Kambic RE, Gatesy SM, Hutchinson JR. 2017 Gearing effects of the patella
626 (knee extensor muscle sesamoid) of the helmeted guineafowl during terrestrial
627 locomotion. *J Zool* **303**, 178–187. (doi:10.1111/jzo.12485)
- 628 65. Regnault S, Allen VR, Chadwick KP, Hutchinson JR. 2017 Analysis of the moment
629 arms and kinematics of ostrich (*Struthio camelus*) double patellar sesamoids. *J Exp
630 Zool A Ecol Integr Physiol* **327**, 163–171. (doi:10.1002/jez.2082)
- 631 66. Taylor G, Bonney V. 1905 On the homology and morphology of the popliteus muscle:
632 a contribution to comparative myology. *J Anat* **40**, 34–50.
- 633 67. Diogo R *et al.* 2013 *Photographic and Descriptive Musculoskeletal Atlas of
634 Orangutans: with notes on the attachments, variations, innervations, function and
635 synonymy and weight of the muscles*. CRC Press.
- 636 68. Haines RW. 1942 The tetrapod knee joint. *J Anat* **76**, 270–301.
- 637 69. Corvalan C, Tang C, Robinson M. 2018 Fabella and cyamella of the human knee joint
638 discovery by dissection and ultrasound examination. *European Journal of anatomy* **22**,
639 103–109.
- 640 70. Zhang L, Wen Y, He C, Zeng Y, Wang J, Wang G. 2022 Relationship between
641 Classification of Fabellae and the Severity of Knee Osteoarthritis: A Relevant Study in
642 the Chinese Population. *Orthop Surg* **14**, 274–279. (doi:10.1111/os.13006)
- 643 71. Seebacher JR, Inglis AE, Marshall JL, Warren RF. 1982 The structure of the
644 posterolateral aspect of the knee. *J Bone Joint Surg* **64**, 536–541.

- 645 72. Pritchett JW. 1984 The incidence of fabellae in osteoarthritis of the knee. *J Bone Joint*
646 *Surg Am* **66**, 1379–80.
- 647 73. Minowa T, Murakami G, Kura H, Suzuki D, Han S-H, Yamashita T. 2004 Does the
648 fabella contribute to the reinforcement of the posterolateral corner of the knee by
649 inducing the development of associated ligaments? *Journal of Orthopaedic Science* **9**,
650 59–65. (doi:10.1007/S00776-003-0739-2)
- 651 74. O’Dea RE *et al.* 2021 Preferred reporting items for systematic reviews and
652 meta-analyses in ecology and evolutionary biology: a <sc>PRISMA</sc> extension.
653 *Biological Reviews* **96**, 1695–1722. (doi:10.1111/brv.12721)
- 654 75. Berthaume MA, Bull AM. 2020 Human biological variation in sesamoid bone
655 prevalence: the curious case of the fabella. *J Anat* **236**, 228–42.
656 (doi:10.1111/joa.13091)
- 657 76. Reeder DM, Wilson DE. 2005 *Mammal Species of the World A Taxonomic and*
658 *Geographic Reference, Volume 1*. 3rd edn. Johns Hopkins University Press.
- 659 77. Harding LE. 2015 *Nasalis larvatus* (Primates: Colobini). *Mammalian Species* **47**, 84–
660 99. (doi:10.1093/mspecies/sev009)
- 661 78. Fleagle JG, Mittermeier RA. 1980 Locomotor behavior, body size, and comparative
662 ecology of seven Surinam monkeys. *Am J Phys Anthropol* **52**, 301–314.
663 (doi:10.1002/ajpa.1330520302)
- 664 79. Garber PA. 1980 Locomotor behavior and feeding ecology of the panamanian tamarin
665 (<i>Saguinus oedipus geoffroyi</i>, callitrichidae, primates). *Int J Primatol* **1**, 185–
666 201. (doi:10.1007/BF02735597)
- 667 80. Fleagle JG. 2013 *Primate adaptation and evolution*. 3rd edn. San Diego, California:
668 Elsevier Science.
- 669 81. Nekaris KAI. 2001 Activity Budget and Positional Behavior of the Mysore Slender
670 Loris (<i>Loris tardigradus lydekkerianus</i>): Implications for Slow Climbing
671 Locomotion. *Folia Primatologica* **72**, 228–241. (doi:10.1159/000049942)
- 672 82. Ankel-Simons F. 2010 *Primate Anatomy, an Introduction*. 3rd edn. San Diego,
673 California: Elsevier.
- 674 83. Johnson MTJ, Stinchcombe JR. 2007 An emerging synthesis between community
675 ecology and evolutionary biology. *Trends Ecol Evol* **22**, 250–7.
676 (doi:10.1016/j.tree.2007.01.014)
- 677 84. Rawson B. 2009 The socio-ecology of the black-shanked douc in Mondulkiri
678 Province, Cambodia. The Australian National University.
- 679 85. Schmitt D. 2010 Primate Locomotor Evolution: Biomechanical Studies of Primate
680 Locomotion and Their Implications for Understanding Primate Neuroethology. In
681 *Primate Neuroethology* (eds ML Platt, AA Ghazanfar), New York, NY: Oxford
682 University Press.
- 683 86. Fooden J. 1982 *Taxonomy and evolution of the Sinica group of macaques. 3, species*
684 *and subspecies accounts of Macaca assamensis / Jack Fooden*. Chicago, Ill. : Field
685 Museum of Natural History,. (doi:10.5962/bhl.title.3082)
- 686 87. Schubert RL. 2011 The Conservative Nature of Primate Positional Behaviour: Testing
687 for Locomotor and Postural Variation in <i>Colobus vellerosus</i> and
688 <i>Cercopithecus campbelli loweii</i> at Boabeng-Fiema Monkey Sanctuary, Ghana
689 (PhD Thesis). Doctor of Philosophy.
- 690 88. Wright KA, Biondi L, Visalberghi E, Ma Z, Izar P, Frigaszy D. 2019 Positional
691 behavior and substrate use in wild adult bearded capuchin monkeys (*Sapajus*
692 *libidinosus*). *Am J Primatol* **81**. (doi:10.1002/ajp.23067)

- 693 89. Springer MS *et al.* 2012 Macroevolutionary dynamics and historical biogeography of
694 primate diversification inferred from a species supermatrix. *PLoS One* **7**, e49521.
695 (doi:10.1371/journal.pone.0049521)
- 696 90. Barnett AA *et al.* 2012 A proposal for the common names for species of
697 *Chiropotes* (Pitheciinae: Primates). *Zootaxa* **3507**.
698 (doi:10.11646/zootaxa.3507.1.4)
- 699 91. Rylands AB, Mittermeier RA, Silva JS. 2012 Neotropical primates: taxonomy and
700 recently described species and subspecies. *International Zoo Yearbook* **46**, 11–24.
701 (doi:10.1111/j.1748-1090.2011.00152.x)
- 702 92. de Sousa e Silva Júnior J, Figueiredo-Ready WMB, Ferrari SF. 2013 Taxonomy and
703 geographic distribution of the Pitheciidae. In *Evolutionary Biology and Conservation*
704 *of Titis, Sakis and Uacaris*, pp. 31–42. Cambridge University Press.
705 (doi:10.1017/CBO9781139034210.008)
- 706 93. Lima MGM *et al.* 2018 A phylogenomic perspective on the robust capuchin monkey
707 (*Sapajus*) radiation: First evidence for extensive population admixture across
708 South America. *Mol Phylogenet Evol* **124**, 137–150.
709 (doi:10.1016/j.ympev.2018.02.023)
- 710 94. Lewis PO. 2001 A Likelihood Approach to Estimating Phylogeny from Discrete
711 Morphological Character Data. *Syst Biol* **50**, 913–925.
712 (doi:10.1080/106351501753462876)
- 713 95. Harmon LJ. 2019 *Phylogenetic Comparative Methods*.
- 714 96. Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. 2008 GEIGER: investigating
715 evolutionary radiations. *Bioinformatics* **24**, 129–31.
716 (doi:10.1093/bioinformatics/btm538)
- 717 97. Beaulieu JM, Donoghue MJ. 2013 Fruit evolution and diversification in campanulid
718 angiosperms. *Evolution (N Y)* **67**, 3132–3144. (doi:10.1111/evo.12180)
- 719 98. Revell LJ. 2012 phytools: an R package for phylogenetic comparative biology (and
720 other things). *Methods Ecol Evol* **3**, 217–223. (doi:10.1111/J.2041-
721 210X.2011.00169.X)
- 722 99. Boyko JD, Beaulieu JM. 2021 Generalized hidden Markov models for phylogenetic
723 comparative datasets. *Methods Ecol Evol* **12**, 468–478. (doi:10.1111/2041-
724 210X.13534)
- 725 100. Burnham KP, Anderson DR. 2004 Multimodel Inference: Understanding AIC and BIC
726 in Model Selection Multimodel Inference Understanding AIC and BIC in Model
727 Selection. **33**. (doi:10.1177/0049124104268644)
- 728 101. Posada D, Buckley TR. 2004 Model Selection and Model Averaging in Phylogenetics:
729 Advantages of Akaike Information Criterion and Bayesian Approaches Over
730 Likelihood Ratio Tests. *Syst Biol* **53**, 793–808. (doi:10.1080/10635150490522304)
- 731 102. Pagel M. 1999 Inferring the historical patterns of biological evolution. *Nature* **1999**
732 *401:6756* **401**, 877–884. (doi:10.1038/44766)
- 733 103. FRITZ SA, PURVIS A. 2010 Selectivity in Mammalian Extinction Risk and Threat
734 Types: a New Measure of Phylogenetic Signal Strength in Binary Traits. *Conservation*
735 *Biology* **24**, 1042–1051. (doi:10.1111/j.1523-1739.2010.01455.x)
- 736 104. Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2023 caper:
737 Comparative Analyses of Phylogenetics and Evolution in R.
- 738 105. Ives AR, Garland T. 2010 Phylogenetic Logistic Regression for Binary Dependent
739 Variables. *Syst Biol* **59**, 9–26. (doi:10.1093/sysbio/syp074)
- 740 106. Tung Ho L si, Ané C. 2014 A Linear-Time Algorithm for Gaussian and Non-Gaussian
741 Trait Evolution Models. *Syst Biol* **63**, 397–408. (doi:10.1093/sysbio/syu005)

- 742 107. Ives A, Li D. 2018 rr2: An R package to calculate R^2 s for regression models. *J*
743 *Open Source Softw* **3**, 1028. (doi:10.21105/joss.01028)
- 744 108. Ives AR. 2019 R^2 s for Correlated Data: Phylogenetic Models, LMMs, and
745 GLMMs. *Syst Biol* **68**, 234–251. (doi:10.1093/sysbio/syy060)
- 746 109. RStudio Team. 2020 RStudio: Integrated Development Environment for R.
- 747 110. R Core Team. 2021 R: A language and environment for statistical computing.
- 748 111. van Westrienen A. 1907 Das Kniegelenk der Primaten, mit besonderer
749 Berücksichtigung der Anthropoiden. *Petrus Camper* **4**, 1–60.
- 750 112. Vallois H. 1914 Etude anatomique de l'articulation du genou chez les primates.
751 L'Abeille, Montpellier, France.
- 752 113. Rose KD, Walker A. 1985 The skeleton of early Eocene *Cantius*, oldest
753 lemuriform primate. *Am J Phys Anthropol* **66**, 73–89.
754 (doi:10.1002/AJPA.1330660107)
- 755 114. Godfrey LR, Jungers WL, Wunderlich RE, Richmond BG. 1997 Reappraisal of the
756 Postcranium of *Hadropithecus* (Primates, Indroidea). *J Phys Anthropol* **103**,
757 529–556. (doi:10.1002/(SICI)1096-8644(199708)103:4)
- 758 115. MacPhee RDE, Meldrum DJ 1958-. 2006 Postcranial remains of the extinct monkeys
759 of the Greater Antilles, with evidence for semiterrestriality in *Paralouatta*;
760 American Museum novitates : no. 3516.
- 761 116. Aisling WC, Parrott MW. 1955 Retardation of skeletal development in monkeys
762 treated with . *Medical and health physics quaterly report* , 11–16.
- 763 117. Bourne GH. 1975 Collected Anatomical and Physiological Data from the Rhesus
764 Monkey. *Anatomy and Physiology* , 1–63.
- 765 118. Jouffroy FK. 1975 Osteology and Myology of the Lemuriform Postcranial Skeleton. In
766 *Lemur Biology*, pp. 149–192. Boston, MA: Springer US. (doi:10.1007/978-1-4684-
767 2121-7_9)
- 768 119. Gibbs S. 1999 Comparative soft tissue morphology of the extant hominoidea,
769 including man. University of Liverpool, Liverpool.
- 770 120. Makungu M. 2015 Aspects of the Morphological, Radiographic and Ultrasonographic
771 Anatomy of the Red Panda (*Ailurus Fulgens*) and Ring-Tailed Lemur
772 (*Lemur Catta*). University of Pretoria, Pretoria.
- 773 121. Casteleyn C, Bakker J. 2019 The Anatomy of the Common Marmoset. In *The Common*
774 *Marmoset in Captivity and Biomedical Research*, pp. 17–41. Elsevier.
775 (doi:10.1016/B978-0-12-811829-0.00002-9)
- 776 122. Hepburn D. 1892 Comparative Anatomy of the Muscles and Nerves of the Superior
777 and Inferior Extremities of the Anthropoid Apes: Part II. *J Anat Physiol* **26**, 324–56.
- 778 123. Pfitzner W. 1892 Beiträge zur Kenntniss des menschlichen Extremitätenskelets:
779 Zweite Abtheilung. *Morphologische Arbeiten* **1**, 517–762.
- 780 124. Beddard FE. 1893 VII. Contributions to the Anatomy of the Anthropoid Apes. *The*
781 *Transactions of the Zoological Society of London* **13**, 177–218. (doi:10.1111/j.1096-
782 3642.1893.tb00049.x)
- 783 125. Boettiger C, Coop G, Ralph P. 2012 Is your phylogeny informative? Measuring the
784 power of comparative methods. *Evolution (N Y)* **66**, 2240–2251. (doi:10.1111/j.1558-
785 5646.2011.01574.x)
- 786 126. Amador LI. 2021 Sesamoids and Morphological Variation: a Hypothesis on the Origin
787 of Rod-like Skeletal Elements in Aerial Mammals. *J Mamm Evol*
788 (doi:10.1007/s10914-021-09571-8)
- 789 127. Carter DR, Mikić B, Padian K. 1998 Epigenetic mechanical factors in the evolution of
790 long bone epiphyses. *Zool J Linn Soc* **123**, 163–178. (doi:10.1111/j.1096-
791 3642.1998.tb01298.x)

- 792 128. Mottershead S. 1988 Sesamoid bones and cartilages: An enquiry into their function.
793 *Clinical Anatomy* **1**, 59–62. (doi:10.1002/ca.980010110)
- 794 129. Bouillon R, Suda T. 2014 Vitamin D: calcium and bone homeostasis during evolution.
795 *Bonekey Rep* **3**. (doi:10.1038/bonekey.2013.214)
- 796 130. Silverman S, Morgan JP, Ferron R, McNulty W, Merten D. 1983 Radiographic
797 evaluation of appendicular skeletal maturation in the rhesus monkey. *Veterinary*
798 *Radiology* **24**, 25–34. (doi:10.1111/j.1740-8261.1983.tb01711.x)
- 799 131. van Wagenen G, Asling CW. 1958 Roentgenographic estimation of bone age in the
800 rhesus monkey (*Macaca mulatta*). *American Journal of Anatomy* **103**, 163–185.
801 (doi:10.1002/aja.1001030202)
- 802 132. Clifton DK, Bremner WJ, Steiner RA. 1982 An Automated Technique for the
803 Radiographic Determination of Bone Age. *J Med Primatol* **11**, 147–154.
804 (doi:10.1111/j.1600-0684.1982.tb00004.x)
- 805 133. Kawashima T, Takeishi H, Yoshitomi S, Ito M, Sasaki H. 2007 Anatomical study of
806 the fabella, fabellar complex and its clinical implications. *Surgical and Radiologic*
807 *Anatomy* **29**, 611–6. (doi:10.1007/s00276-007-0259-4)
- 808 134. Fürst CM. 1903 *Der musculus popliteus und seine sehne*. London: Williams and
809 Norgate.
- 810 135. Fabbriani C, Oransky M. 1992 The Popliteus Muscle. In *The Knee and the Cruciate*
811 *Ligaments*, pp. 48–61. Berlin, Heidelberg: Springer Berlin Heidelberg.
812 (doi:10.1007/978-3-642-84463-8_4)
- 813 136. Fürst CM. 1914 Über die Entwicklung und Reduktion der Fibula beim Rinde. *Z*
814 *Morphol Anthropol* **18**, 93–110.
- 815 137. Eyal S, Blitz E, Shwartz Y, Akiyama H, Schweitzer R, Zelzer E. 2015 On the
816 development of the patella. *Development (Cambridge)* **142**, 1831–1839.
817 (doi:10.1242/dev.121970)
- 818 138. Barnett CH, Napier JR. 1953 The form and mobility of the fibula in metatherian
819 mammals. *J Anat* **87**, 207–13.
- 820 139. Jouffroy F-K. 1962 La musculature des membres chez les lémuriens de Madagascar :
821 etude descriptive et comparative. *Mammalia* **26**, 1–326.
- 822 140. Keith A. 1894 The Ligaments of the Catarrhine Monkeys, with References to
823 corresponding Structures in Man. *J Anat Physiol* **28**, 149–68.
- 824 141. Frey H. 1913 Der Musculus triceps surae in der Primatenreihe. *Morphologische*
825 *Jahrbuch* **47**.
- 826 142. Owen R. 1853 *Descriptive Catalogue of the Osteological Series Contained in the*
827 *Museum*.
- 828 143. Başaran S, Coşkun Benlidayı İ. 2023 Coexistence of symptomatic cyamella and
829 multiple fabellae: A case report. *Arch Rheumatol* **38**, 156–158.
830 (doi:10.46497/ArchRheumatol.2022.9521)
- 831

832 **9 TABLES**833 *Table 1. Systematic review search terms.*

	Search terms
Cyamella	cyamella, cyamellae, cyamelle, cyamelli, cyamellus, "fabella distalis", "fabella of the popliteus", "fibular patella", "os sesamoideu muscoli poplitei", "os sesamoideum m. Poplitei", "popliteal fabella", "popliteus sesamoid", "sesamoid poplitella", "sesamoideum genu inferius laterale"
Fabellae	fabella knee OR sesamoid, "sesamoid bone of the gastrocnemius", "sesamoid bone of Vesalli"
Early journals	sesamoid

834

835

Table 2. Simple Mk and HR evolutionary models. Observed states were absent (0) or present (1), and hidden states as A or B. Best-fitting Mk and HR models are bold. lnL = Log-likelihood.

Bone	Model	States	Transition matrix		Presence				Majority			
			Structure	Rates	lnL	AICc	Δ AICc	Weight	lnL	AICc	Δ AICc	Weight
Cyamella	ER	0,1	All	Equal	-34.452	70.904	3.075	0.173	-33.161	68.323	1.134	0.358
	ILM	0,1	0->1 not allowed	---	-36.578	75.157	7.328	0.021	-36.578	75.157	7.968	0.012
	ARD	0,1	All	Different	-31.914	67.829	0	0.806	-31.594	67.189	0	0.631
	1HRA	0, 0A, 1	0A-1 not allowed	Different	-30.072	68.143	0	0.635	-27.596	63.192	0	0.796
	1HRP	0, 1, 1A	1A-0 not allowed	Different	-31.351	70.703	2.56	0.177	-30.588	69.177	5.984	0.04

	1HRCO	0, 0A, 1, 1A	0A-1A not allowed	Different	-29.43	70.859	2.716	0.163	-27.267	66.535	3.342	0.15
	1HR	0, 0A, 1, 1A	All	Different	-29.303	74.606	6.463	0.025	-27.592	71.184	7.991	0.015
	2HR	0, 0A, 0B, 1, 1A, 1B	All	Different	-27.596	83.192	15.049	0.000	-26.885	81.77	18.578	0
	ER	0,1	All	Equal	-27.566	57.132	8.555	0.014	-22.021	46.043	5.306	0.066
	ILM	0,1	0->1 not allowed	---	-32.871	67.741	19.164	0.000	-40.709	83.418	42.681	0.000
	ARD	0,1	All	Different	-22.289	48.577	0	0.986	-18.368	40.737	0	0.934
Medial fabella	1HRA	0, 0A, 1	0A-1 not allowed	Different	-19.486	46.972	3.108	0.149	-18.268	44.535	2.461	0.204
	1HRP	0, 1, 1A	1A-0 not allowed	Different	-17.932	43.864	0	0.705	-17.037	42.074	0	0.698
	1HRCO	0, 0A, 1, 1A	0A-1A not allowed	Different	-17.638	47.277	3.413	0.128	-17.037	46.074	4	0.094
	1HR	0, 0A, 1, 1A	All	Different	-17.638	51.277	7.413	0.017	-18.268	52.535	10.461	0.004
	2HR	0, 0A, 0B, 1, 1A, 1B	All	Different	-17.416	62.833	18.969	0	-18.239	64.477	22.403	0
	ER	0,1	All	Equal	-27.970	57.939	10.561	0.005	-27.134	56.269	8.675	0.013
	ILM	0,1	0->1 not allowed	---	-32.871	67.741	20.363	0.000	-35.565	73.131	25.537	0.000
	ARD	0,1	All	Different	-21.689	47.378	0	0.995	-21.797	47.594	0	0.987
Lateral fabella	1HRA	0, 0A, 1	0A-1 not allowed	Different	-21.689	51.378	6.962	0.026	-21.663	51.326	6.744	0.029
	1HRP	0, 1, 1A	1A-0 not allowed	Different	-18.208	44.416	0	0.844	-18.291	44.582	0	0.855
	1HRCO	0, 0A, 1, 1A	0A-1A not allowed	Different	-18.208	48.416	4	0.114	-18.291	48.582	4	0.116
	1HR	0, 0A, 1, 1A	All	Different	-18.185	52.369	7.953	0.016	-21.663	59.326	14.744	0.001
	2HR	0, 0A, 0B, 1, 1A, 1B	All	Different	-17.943	63.885	19.469	0	-21.663	71.326	26.744	0

837 *Table 3. Comparison of best-fitting simple Mk model and HR models. Best-fitting Mk and HR models are bold. * indicates p-*
 838 *values < 0.05.*

Bone	Dataset	Model	lnL	AICc	Params	Δ AICc	χ^2 test(lnL)	p-value
Cyamella	Presence	ARD	-31.914	67.829	2	0.584	3.686	0.158
		1HRA	-30.072	68.143	4			
	Majority	ARD	-31.594	67.189	2	7.996	3.046	0.018*
		1HRA	-30.072	63.192	4			
Medial fabella	Presence	ARD	-22.289	48.577	2	4.713	9.356	0.009*
		1HRP	-17.611	43.864	4			
	Majority	ARD	-18.368	40.737	2	1.337	2.663	0.264
		1HRP	-17.037	42.074	4			
Lateral fabella	Presence	ARD	-21.689	47.378	2	2.962	8.028	0.018*
		1HRP	-17.675	43.350	4			
	Majority	ARD	-21.797	47.594	2	3.012	7.012	0.030*
		1HRP	-18.291	44.582	4			

839

840 *Table 4. Instantaneous rate of change (q) using best fitting simple Mk models, q01 - absence to presence, q10 - presence to*
 841 *absence. The ratio q01/q10 indicates it is easier to gain than lose a sesamoid.*

Bone	Dataset	q01	q10	q01/q10
Cyamella	Presence	7.174	1.662	4.315
	Majority	4.035	0.978	4.126
Medial fabella	Presence	4.379	0.083	52.863
	Majority	2.357	0	inf
Lateral fabella	Presence	4.423	0.079	55.951
	Majority	2.674	0	inf

842

843 *Table 5. Instantaneous rate of change (q) using best fitting HR models, q00A - absence to hidden absence, q0A0 - hidden*
 844 *absence to absence, q11A - presence to hidden presence, q1A1 - hidden presence to presence.*

Bone	Dataset	q01	q10	q00A	q0A0	q11A	q1A1
Cyamella	Presence	991402.914	9576974.286	3.184	0	---	---
	Majority	938262.37	78195.143	0	3.178	---	---
Medial fabella	Presence	117.069	308.341	---	---	0	0.253
	Majority	57.161	417.782	---	---	0	0.277
Lateral fabella	Presence	119.221	314.056	---	---	0	0.245
	Majority	5053715.793	27020340.846	---	---	11.207	0

845

846 Table 6: Average number of state transitions in stochastic character mapping (ARD models).

Bone	Dataset	Transitions		Avg. number of state changes	Mean proportion of time spent in each state	
		0 to 1	1 to 0		0	1
Cyamella	Presence	16.76	14.2	30.96	0.214	0.786
	Majority	10.71	7.94	18.65	0.251	0.749
Medial fabella	Presence	10.84	0.73	11.57	0.229	0.771
	Majority	8.2	0	8.2	0.310	0.690
Lateral fabella	Presence	11.31	0.82	12.13	0.221	0.779
	Majority	8.93	0	8.93	0.297	0.703

847 Table 7: Stochastic character mapping HRP models.
848

Bone	Dataset	Transitions						Avg. number of state changes
		0 to 1	0 to 1*	1 to 0	1 to 1*	1* to 0	1* to 1	
Medial fabella	Presence	109.16	0	110.88	0	0	2.47	222.51
Lateral fabella	Presence	112.06	0	113.91	0	0	2.45	228.42

849 Table 8: Power of the data, following [125].
850
851

	Cyamella		Medial fabella		Lateral fabella	
	Presence	Majority	Presence	Majority	Presence	Majority
δ^*	-3.686	-7.996	-9.356	-2.663	-8.028	-7.012
$((\delta - \delta^*) / 1000 \text{ sim}) * 100\%$	73.1%	76.1%	88.9%	45.9%	91.2%	73.1%

852 Table 9: Measures of phylogenetic signal using Pagel's λ and D-statistic. * indicates λ is significantly different from 0 based on a likelihood ratio test, p -value < 0.05.
853
854

Bone	Dataset	λ	D	Probability D consistent with	
				Brownian motion	Random association
Cyamella	Presence	0.656*	0.040	0.445	0.001
	Majority	0.795*	-0.101	0.614	0
Medial fabella	Presence	0.853*	-0.360	0.842	0
	Majority	0.916*	-0.489	0.946	0
Lateral fabella	Presence	0.868*	-0.326	0.824	0
	Majority	0.867*	-0.449	0.906	0

855

856 *Table 10. Phylogenetic logistic regression model's R-squared (R²lik) values for coincidental development. Sesamoid*
 857 *presence columns are predicting sesamoids presence rows. * indicates p<0.05.*

Bone	Bone Dataset	Cyamella	Medial fabella	Lateral fabella
	Cyamella	Presence	---	0.45
Majority		---	0.61	0.62
Medial fabella	Presence	0.43	---	0.72***
	Majority	0.55	---	0.80***
Lateral fabella	Presence	0.46*	0.69***	---
	Majority	0.55	0.79***	---

858

859

860 10 FIGURE CAPTIONS

861 *Figure 1: Marginal ASRs of the cyamella in primates using ARD (left) and IHRA (right) evolutionary models. Pie charts*
 862 *indicate proportional likelihoods of presence (black) and absence (white) of cyamella at each node. (right) absence values*
 863 *for hidden and observed rates are summed. Scale bar = 10 million years.*

864 *Figure 2: Marginal ASRs of the lateral fabella in primates using ARD (left) and IHRP (right) evolutionary models. Pie*
 865 *charts indicate proportional likelihoods of presence (black) and absence (white) of cyamella at each node. (right) presence*
 866 *values for hidden and observed rates are summed. Results for medial fabella are similar and in the ESM. Scale bar = 10*
 867 *million years.*

868 *Figure 3: Results from stochastic mapping for ARD models (left - presence, right - majority). Black indicates the sesamoid is*
 869 *present, green absent. Scale bar = 10 million years.*

870 *Figure 4: Results from a simulation, stochastic mapping for HRP model, presence dataset, lateral fabella. Black indicates*
 871 *the sesamoid is present, grey is hidden rate present (1*), and green absent. Scale bar = 10 million years.*

872

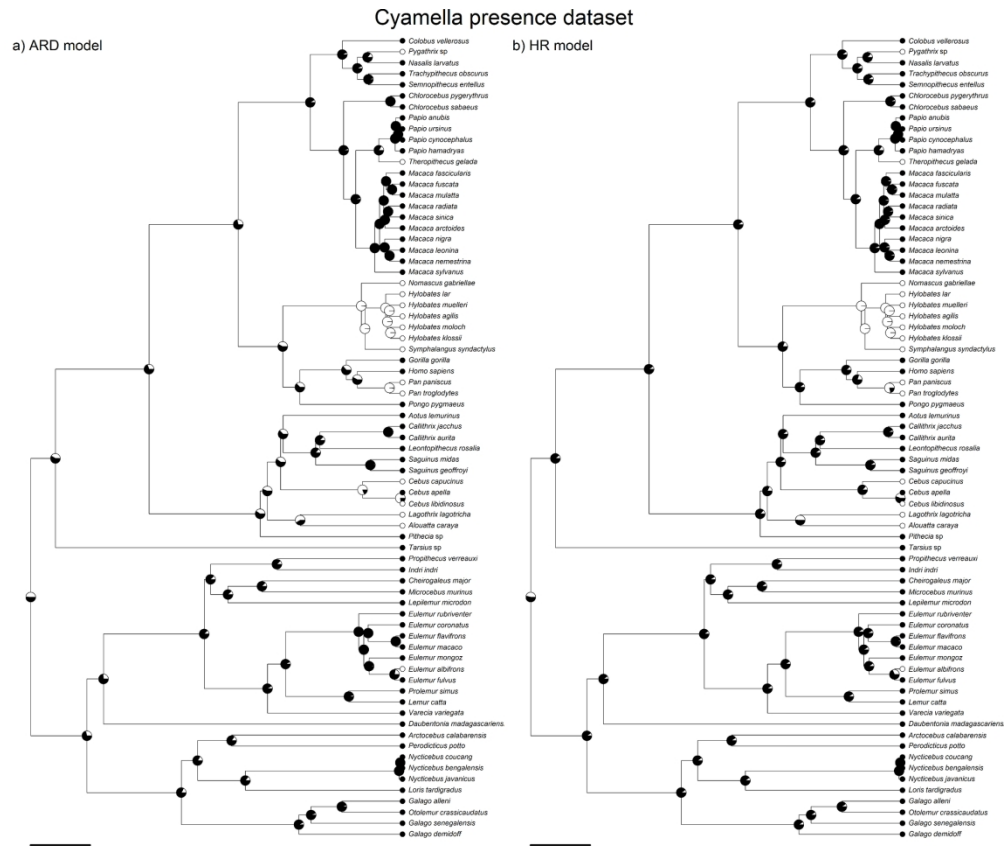


Figure 1

222x190mm (300 x 300 DPI)

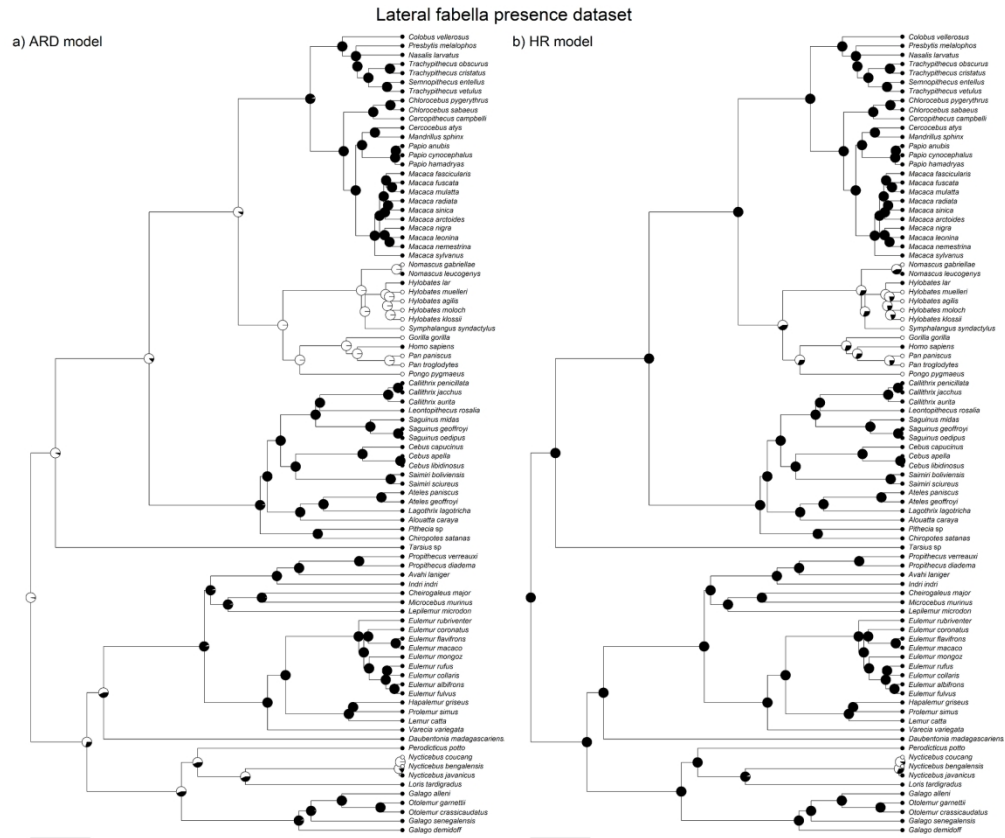


Figure 2

222x190mm (300 x 300 DPI)

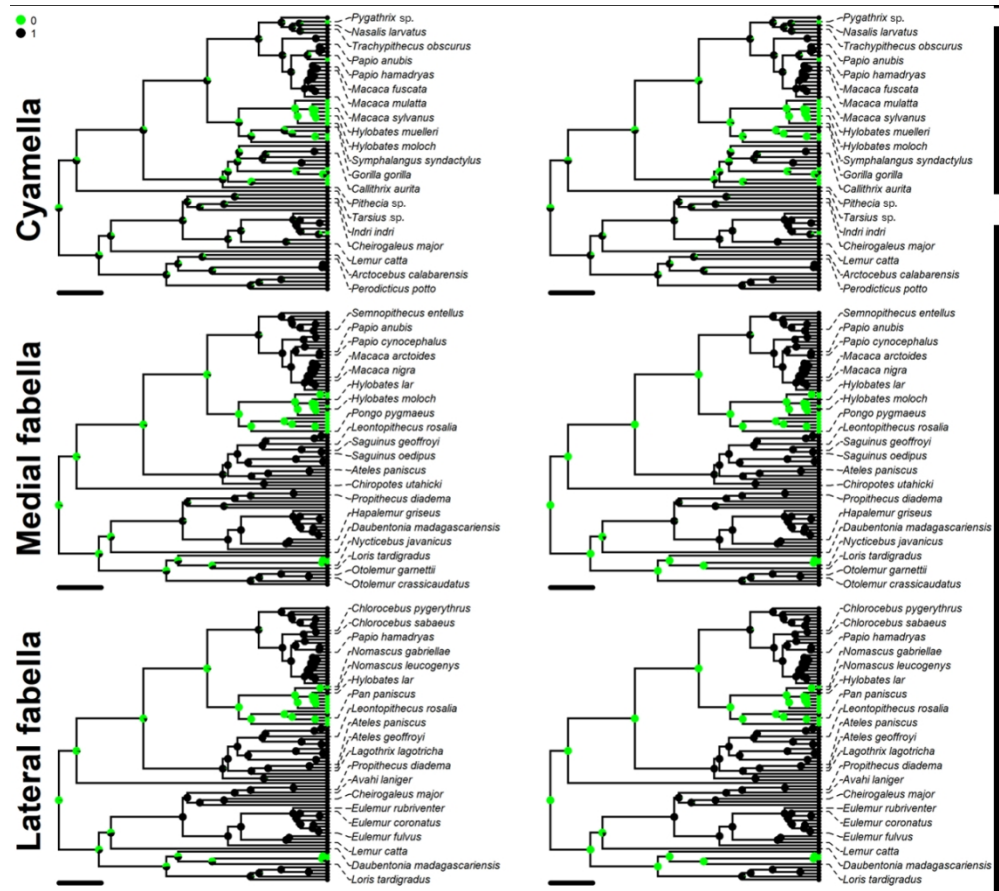


Figure 3

214x190mm (150 x 150 DPI)

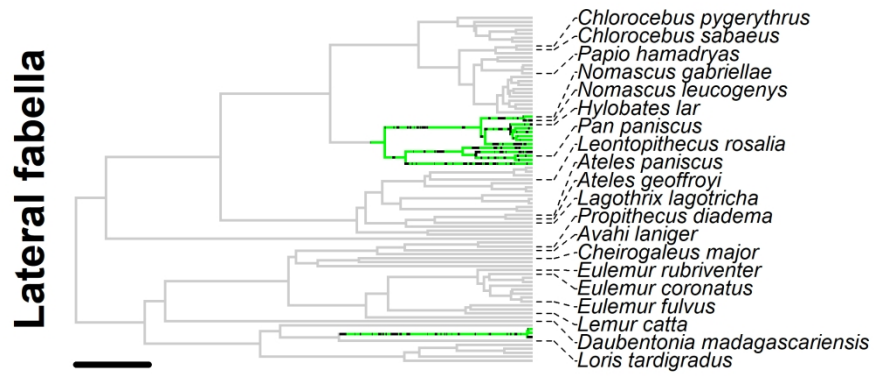


Figure 4

203x76mm (300 x 300 DPI)