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1 **Pattern and process in hominin brain size evolution are scale-dependent**

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21
22 **Abstract:** A large brain is a defining feature of modern humans, yet there is no consensus
23 regarding the patterns, rates, and processes involved in hominin brain size evolution. We use a
24 reliable proxy for brain size in fossils, endocranial volume (ECV), to better understand how brain
25 size evolved at both clade- and lineage-level scales. For the hominin clade overall, the dominant
26 signal is consistent with a gradual increase in brain size. This gradual trend appears to have been
27 generated primarily by processes operating within hypothesized lineages – 64% or 88%
28 depending on whether one uses a more or less speciose taxonomy, respectively. These processes
29 were supplemented by the appearance in the fossil record of larger-brained *Homo* species and the
30 subsequent disappearance of smaller-brained *Australopithecus* and *Paranthropus* taxa. When the
31 estimated rate of within-lineage ECV increase is compared to an exponential model that
32 operationalizes generation-scale evolutionary processes, it suggests that the observed data were

33 the result of episodes of directional selection interspersed with periods of stasis and/or drift; all
34 of this occurs on too fine a time scale to be resolved by the current human fossil record, thus
35 producing apparent gradual trends within lineages. Our findings provide a quantitative basis for
36 developing and testing scale-explicit hypotheses about the factors that led brain size to increase
37 during hominin evolution.

38 **Keywords:** hominin evolution, endocranial volume, phenotypic evolution, evolutionary mode,
39 microevolution, macroevolution

40

41 1. Introduction

42 The large brain of *Homo sapiens* is a defining hallmark of humankind. The brains of
43 ancient hominins do not fossilize, but the estimated volume of a fossil cranium (i.e., endocranial
44 volume or ECV) is a reliable proxy for brain size [1–3]. From studying fossil ECV trends
45 through time, we know that brain size in the hominin clade increased more than threefold from
46 *Australopithecus* – the earliest unambiguous hominin taxon – to our own species. Nevertheless,
47 researchers currently disagree about the manner by which hominin brain size increased. They
48 either claim ECV increased gradually through time [4–7] or via brief episodes of rapid increase
49 separated by extended periods of stasis (i.e., the punctuated equilibrium model) [8–11]. Based on
50 these inferred patterns, researchers then attempt to draw conclusions about what drove hominin
51 ECV increase (e.g., episodes of climate change drove the rapid ECV increase in the punctuated
52 equilibrium model [12,13]).

53 Caution must be exercised, however, when developing and evaluating these cause-and-
54 effect hypotheses. For one, such hypotheses need to specify the taxonomic level at which the
55 effect is observed because evolutionary patterns are scale-dependent. Evolution is hierarchical,

56 and trends at lower taxonomic levels can look very different when combined at higher taxonomic
57 levels (i.e., Simpson's paradox; figure 1a) [14–17]. Furthermore, different taxonomic levels
58 imply different evolutionary mechanisms [14,16,17]. Patterns within lineages (i.e., hypothesized
59 ancestor-descendant sequences) are determined by microevolutionary, population-level processes
60 (i.e., anagenesis). The most popular hypotheses related to hominin ECV increase – which include
61 links to the appearance and development of uniquely human traits such as socio-cultural
62 complexity, symbolic behavior, and language [2,12,13,18] – are in this category. Patterns
63 observed at the clade-level, on the other hand, are the result of processes operating across
64 multiple lineages and therefore can also be shaped by macroevolutionary processes (i.e.,
65 origination by lineage-splitting and extinction) in addition to microevolutionary ones. For
66 example, from one time period to the next, the mean ECV of a clade can increase because (1)
67 existing lineages evolve larger brains anagenetically, (2) a new lineage originates with a brain
68 size greater than the pre-existing clade mean, or (3) a lineage with a brain size smaller than the
69 clade mean goes extinct (figure 1b). We must first understand how hominin brain size has
70 increased across taxonomic scales in order to properly infer the evolutionary processes and
71 potential drivers involved.

72 Existing research seldom specifies taxonomic scale when examining whether hominin
73 ECV data more closely match a pattern of gradualism or one of punctuated equilibrium. Some
74 studies have analyzed changes in hominin brain size within a lineage [5,7,9–11], while others
75 have done so at the level of the entire hominin clade [4,6,18–20]. It is perhaps not surprising then
76 that both models (i.e., gradualism and punctuated equilibrium) have found support from various
77 analyses with no consensus being reached. Other researchers have argued that the data better
78 support a model that combines elements of both gradualism and punctuated equilibrium

79 [18,21,22], or they claim that the two models cannot be distinguished [23,24]. The thesis of our
80 investigation is that taxonomic scale must be made explicit when describing patterns of hominin
81 ECV evolution and attempting to infer the processes that generated them.

82 Here, we address the issue of taxonomic scale dependence by examining patterns of
83 hominin ECV change at each of three successively lower taxonomic levels. We first estimate the
84 evolutionary mode of hominin ECV change at the clade level. We then partition clade-level ECV
85 change into anagenetic (microevolution) and origination and extinction (macroevolution)
86 components. Finally, because hypotheses for hominin ECV increase are presently dominated by
87 microevolutionary explanations, we compare the rate of within-lineage ECV change to that
88 expected from an extrapolated microevolutionary model to assess whether observed increases
89 can be solely accounted for by population-level, directional selection. By understanding how
90 hominin ECV patterns change across different taxonomic levels, we can gain a more nuanced
91 understanding of hominin brain size evolution. This work specifically addresses when and at
92 what scale ECV change most likely occurred, and lays a foundation for future research to orient
93 hypothesized evolutionary mechanisms with scale-specific phenotypic patterns.

94

95 **2. Materials and Methods**

96 Our dataset is composed of published absolute ECVs for specimens whose geological age
97 ranges encompass dates anywhere between 3.2 and 0.5 Ma (i.e., beginning with the earliest
98 uncontroversial hominin taxon, *Australopithecus*, and ending when the ECVs of fossil crania
99 begin to overlap with the range of modern humans) (figure 2 & table S1). ECV measurements
100 were \log_{10} -transformed prior to all analyses because our methods assume linear changes in ECV,
101 and we were interested in proportional differences (e.g., a doubling from 400 to 800 cm³ was

102 considered more biologically meaningful than an equivalent 400 cm^3 increase from 1000 to 1400
103 cm^3) [25]. We analyzed absolute and not relative brain size because the use of relative brain size,
104 which requires estimation of fossil hominin body masses, introduces additional error into
105 analyses [18].

106 Clade-level ECV increase was analyzed using the “paleoTS” R package [26] to fit six
107 statistical models of evolutionary modes to the observed ECV data (i.e., random walk,
108 gradualism, stasis, stasis-stasis [i.e., clade-level “punctuated equilibrium”], stasis-random walk,
109 and stasis-gradualism) (figure S1) [27–30]. Random walk and gradualism were modeled as
110 having bin-to-bin ECV transitions drawn from a normal distribution, where the mean equals zero
111 in the random walk model (i.e., increases and decreases are equiprobable) and a non-zero value
112 in the gradualism model (i.e., biased towards increases or decreases) [27,29]. Stasis was modeled
113 as normally distributed variation around an optimal ECV mean, both of which stay constant
114 through time [27,29,31]. The remaining complex models were modeled as permutations of the
115 three simpler models separated by an estimated age point where the transition occurs [30]. To
116 operationalize these models, we grouped all ECV data into 0.2 Ma bins (to maximize the number
117 of binned samples within the time series), fit the models to the data by maximizing likelihood,
118 and assessed relative model fit using the bias-corrected Akaike information criterion (AICc)
119 transformed into weights (which sum to one across all models, with higher weights representing
120 more model support) [32]. We resampled age estimates to examine the possible influences of
121 dating error on our model selection results (figures S2 & S3), and we also explicitly incorporated
122 inter-observer error in estimating ECV for individual fossils into our model (figures S2 & S3 &
123 table S2). We conducted sensitivity analyses to evaluate potential effects of bin location and/or
124 bin size on the apparent clade-level pattern (see Appendix S1).

125 To investigate how clade-level ECV patterns were driven by mechanisms operating at
126 lower taxonomic levels, we divided the ECV data into 0.3 Ma time bins – the smallest bin size
127 that yielded no temporal gaps within lineages – and then additively partitioned between-bin,
128 clade-level ECV changes into their anagenetic, origination, and extinction components [33; see
129 Appendix S1]. If lineages survive from one time bin to the next, clade-level change attributed to
130 anagenesis is defined as the difference in mean ECV of surviving lineages between adjacent time
131 bins. Clade-level change due to origination is calculated as the mean of all ECVs (including non-
132 surviving lineages) in the later time bin minus the mean of ECVs from surviving lineages in the
133 same bin, and extinction is the mean ECV of surviving lineages in the earlier time bin minus all
134 ECVs in the same bin. Clade-level changes between time bins with no surviving lineages cannot
135 be partitioned into separate origination/extinction components. Instead of determining which
136 evolutionary mode best characterizes each lineage, this method quantifies the relative importance
137 of microevolution (anagenesis) and macroevolution (origination and extinction) in driving the
138 broader clade-level pattern during a specific time period. We should emphasize that origination
139 and extinction in this case refer, respectively, to observed first and last appearances of species’
140 *cranial* specimens (from which ECV could be estimated) and not the observed appearances of
141 the species as a whole nor their true, unknown ages of origination and extinction [34]. We refer
142 to ‘first appearances’ and ‘last appearances’ when describing these phenomena. Because our
143 partitioning method required assigning specimens to anagenetic lineages, we conducted these
144 analyses using taxonomies that recognized smaller and larger numbers of lineages (‘less’ and
145 ‘more’ speciose, respectively) to determine if taxonomic philosophy had any influence on our
146 results (figure S4). Similar to our clade-level analyses, we also resampled age and ECV estimates
147 to examine the effect of dating and inter-observer measurement error on our results (figure S3),

148 and conducted sensitivity analyses to evaluate the effects of bin location and size (see Appendix
149 S1).

150 Finally, we examined the rate of ECV change within lineages. Increases in ECV are
151 usually hypothesized as being caused only by natural selection at the population level. However,
152 these hypotheses are difficult to test given the large time scale discrepancy between
153 microevolutionary processes (i.e., generational time scales of 10^1 years in extant great apes [35])
154 and the time scales of hominin fossil assemblages (i.e., typical temporal resolution of 10^5 years).
155 Furthermore, as mentioned previously, macroevolutionary processes (i.e., origination and
156 extinction) can independently influence ECV, which confounds attempts to estimate how ECV
157 changes at the population level. To address this issue, we used the results from our partitioning
158 analyses to isolate the component of ECV evolution attributable only to within-lineage change
159 (i.e., anagenesis). We then used a simple exponential growth model to investigate whether
160 published estimates of the magnitude and rate of natural selection on generational time scales can
161 be extrapolated to predict observed within-lineage ECV change on geological time scales.
162 Proportional change over multiple generations in some trait for a given population can be
163 calculated with the equation: $(1 + e_{\mu}\beta_{\mu})^t$, where β_{μ} is selection strength (mean-standardized
164 selection gradient [36]), e_{μ} is a measure of evolutionary potential quantifying the expected trait
165 response to selection (mean-standardized evolvability) [37], and t is the number of generations
166 [37]. Using a database of morphological traits, Hereford and colleagues found median β_{μ} is 0.28
167 for multi-trait studies that take into account trait covariance [36]. This is an appropriate
168 assumption here since hominin brain and body size are known to be highly correlated [38], so
169 selection strength acting on brain size will likely be diminished due to selection on other
170 correlated traits (including, but not limited to, body size) acting in different directions. As a

171 result, univariate selection gradients are spuriously too high and are not appropriate for
172 predicting actual evolutionary change for traits that are correlated with others [36]. Hominin
173 brain size has an e_{μ} of 0.006%, as estimated from modern human phenotypic data [38; M.
174 Grabowski, pers. comm.]. The bin size in our additive partitioning analyses is 0.3 Ma, which
175 translates to 11,110 generations, assuming a hominin generation time of 27 years [35]. If ECV
176 change from the extrapolated exponential model matches observed anagenetic change in the
177 fossil record, this would parsimoniously suggest that hypothesized drivers of natural selection
178 (e.g., socio-cultural complexity, symbolic behavior, and complex language) were operating
179 consistently, rather than episodically, to increase ECV within hominin populations.

180 Some fossil cranial specimens are particularly incomplete, distorted, or crushed. The
181 inclusion of such specimens (i.e., *Australopithecus garhi* [BOU-VP-12/130], *Paranthropus*
182 *aethiopicus* [Omo L.338y-6], *Paranthropus boisei* [Omo 323-1976-896], and *Homo erectus s.l.*
183 [KNM-OL 45500, Lantian, OH 12, Sangiran 3, Sangiran 31, Yunxian, and Zhoukoudian VI])
184 could potentially bias ECV estimates and thus affect our results and inferences. To address this
185 potential shortcoming and further evaluate the robustness of our results, we repeated our clade-
186 level model selection and lower-level additive partitioning analyses with these ten specimens
187 removed from the dataset.

188 All analyses were done in R 3.0.3 [39]. See the electronic supplementary material for
189 more details on how we collected and analyzed the data, as well as the R script for executing
190 analyses.

191

192 **3. Results**

193 Results from fitting evolutionary models at the clade level show gradualism is by far the
194 best fit for describing hominin ECV change over time (figure 3a & table S3). All mean ECV
195 estimates of the observed time series fall within the 95% probability envelope predicted by the
196 gradualism model (figures 3b & S1), and model R^2 is 0.676 (table S4). Multiple sensitivity
197 analyses demonstrate that support for the gradualism model is robust to bin size or location
198 (figure S5).

199 The second set of analyses shows that clade-level changes between bins – which are the
200 sum of their anagenetic and first and last appearances components – are always positive (figure
201 4), thus corroborating the gradualism result described above. When we decompose clade-level
202 changes using the less speciose taxonomy, the gradualism pattern is mainly driven by brain size
203 increase within lineages, accounting for 88% of total clade-level change (figures 4 & S6). Before
204 2.6 Ma, however, the extent to which anagenetic change outpaces macroevolutionary change is
205 obscured by dating uncertainty in both the less and more speciose taxonomies (figure 4). Despite
206 the dominance of anagenetic (microevolutionary) processes in the less speciose taxonomy, there
207 are still times when macroevolutionary processes are important. The nontrivial influence of first
208 appearances between 2.3 and 2 Ma and last appearances between 2 and 1.7 Ma (figures 4 & S6)
209 is driven by the appearance of *Homo* and disappearance of southern African *Australopithecus*-
210 *Paranthropus*, respectively, at *c.*2 Ma (figure S7). The disappearance of eastern African
211 *Paranthropus* at *c.*1.4 Ma (figure S7) appears to drive the clade-level pattern between 1.4 and 1.1
212 Ma (figures 4 & S6).

213 Using the more speciose taxonomy, anagenesis is still the principal driver of clade-level
214 ECV increase (64% of clade-level change). However, because more lineages are included,
215 macroevolutionary processes inevitably take on a greater role relative to that observed in the less

216 speciose taxonomy (figures 4 & S6). Examples include the first appearances of *Paranthropus*
217 *robustus*, early *Homo*, and *Homo ergaster* c.2 Ma for the time period between 2.3 and 2 Ma; the
218 disappearances of *Australopithecus africanus* and *P. robustus* c.2 Ma and the first appearance of
219 *Homo erectus sensu stricto* c.1.7 Ma for the time period between 2 and 1.7 Ma; the
220 disappearances of eastern African *Paranthropus* and early *Homo* c.1.4 Ma for the time period
221 between 1.4 and 1.1 Ma; and the disappearance of *H. ergaster* c.0.8 Ma for the time period
222 between 0.8 and 0.5 Ma (figures 4, S6, & S7).

223 To summarize the results from both hypothesized taxonomies, within-lineage ECV
224 increase is the primary driver of clade-level change at 1.7-1.4, 1.1-0.8, and 0.5-0.2 Ma.
225 Macroevolutionary processes are important at 2-1.7 Ma (though anagenesis also contributes here
226 in the less speciose taxonomy) and at 1.4-1.1 Ma (qualitatively similar to the results of ref. [18]).
227 These patterns are robust to taxonomic philosophy, dating error, inter-observer ECV
228 measurement error, bin location, and bin size (figures 4, S6, S8, & S9).

229 For the final set of analyses, we find hominin ECV within lineages is expected to increase
230 via directional selection by $0.08 \log_{10} \text{cm}^3$, or a factor of 1.2, over the course of 0.3 Ma (the bin
231 size of our additive partitioning analyses). When comparing this expectation (black, horizontal
232 line in figure 4) to observed within-lineage increases in fossil hominin ECV, we see the observed
233 increases are always below the expected increase derived from the exponential model (except for
234 the 1.7-1.4 Ma time period; figures 4 & S6). These findings are consistent with previous research
235 showing that evolutionary rates in fossil lineages are slower than those in modern
236 microevolutionary studies, even when fossil lineages show evidence of directional trends [40].

237 Our results are unaffected by the removal of especially incomplete or damaged specimens
238 (figure S10 & table S5).

239

240 **4. Discussion**

241 Our results show that fossil hominin ECV data at the clade level are most consistent with
242 a gradual pattern of ECV increase through time. Understanding how this pattern emerged from
243 processes that operate at lower taxonomic levels is more complicated. Our analyses are
244 consistent with microevolutionary mechanisms as the dominant driver of clade-level change (64
245 or 88% of change using a more or less speciose taxonomy, respectively), alternating with
246 secondary macroevolutionary mechanisms. This implies changing selective pressures and shifts
247 in the relative importance of different evolutionary processes through time.

248 To date, most explanations for hominin brain size increase have focused on
249 microevolutionary mechanisms. These hypotheses can explain anagenetic patterns but may not
250 be relevant for patterns caused by origination and extinction [14,41]. For example, some
251 researchers argue extinction is an emergent phenomenon because species do not go extinct for
252 the same reasons individual organisms die [41]. ECV increase via anagenesis and lineage
253 splitting are likely different enough processes that it makes sense to understand how each
254 independently influenced ECV increase. Our results emphasize that origination and extinction
255 were also important in shaping ECV patterns at the clade level, and both micro- and
256 macroevolutionary change influenced hominin brain size to different extents at different times
257 (figures 4 & S6). Therefore, we must construct new, comprehensive theories to explain potential
258 influences on hominin brain size evolution.

259 Periods when macroevolutionary processes drove clade-level ECV increase were, by
260 definition, characterized by a combination of factors promoting origination and extinction. These
261 factors may have included large-scale climate and environmental change [12,42], habitat

262 fragmentation and vicariance [43], interspecific interactions [44], etc. It is worth repeating here
263 that inferred periods of macroevolutionary importance were estimated using observed first and
264 last appearance dates of lineages' cranial specimens, and these dates are very likely to shift as
265 new fossil specimens are discovered (specifically, first appearances would become older, and last
266 appearances would become younger) [34].

267 It is noteworthy that almost all the first and last appearances are associated with an
268 increase in average clade-level brain size, and the importance of each is staggered in time (i.e.,
269 appearance of large-brained species mostly from *c.*2.3 to 1.7 Ma and disappearance of smaller-
270 brained species from *c.*1.7 to 0.5 Ma) (figures 4 & S6). The connection between first
271 appearances and larger brain size is an example of directional speciation [14], where there is a
272 consistent, biased shift in the phenotypes of daughter lineages relative to that of their ancestral
273 lineages. Directional speciation may be caused by developmental or evolutionary constraints that
274 bias phenotypic change towards larger ECV, or selection for larger brains in peripatric
275 populations [14,16,17]. The association between last appearances and smaller-brained species
276 may signal some kind of extinction selectivity, either directly or indirectly related to ECV (e.g.,
277 extinction rates may be correlated with geographic range size which in turn is correlated with
278 body and brain size). This result is corroborated by smaller-brained species having shorter
279 lineage durations (mean species' ECV vs. mean species' duration: Spearman's $\rho = 0.41$), and
280 therefore higher mean extinction rates [25] (this also suggests greater persistence of larger-
281 brained species).

282 If species with larger ECVs are found to have higher diversification rates (origination
283 minus extinction rates), this may suggest that species sorting also caused clade-level ECV to
284 increase [45,46]. Just as natural selection operates via differential birth/death of individuals

285 associated with a given trait, species sorting operates via differential origination/extinction of
286 species, in this case, associated (directly or indirectly) with brain size. Species sorting is implied
287 by the increased variation in brain size between 2.0-1.5 Ma (figure 2), generated by the addition
288 of larger-brained lineages via directional speciation; this increased variation was later culled by
289 selective extinction of smaller-brained lineages (figures 4 & S6). If species sorting is borne out,
290 it would suggest that all three mechanisms known to influence phenotypic evolution within a
291 clade (i.e., anagenesis, directional speciation, and species sorting) were acting in concert at
292 multiple taxonomic scales to produce the directional ECV trend observed at the hominin clade
293 level (as proposed elsewhere for hominin body mass and stature [47]). Moreover, the potential
294 influence of species sorting requires a reorientation of how we think about hominin brain size
295 evolution, since oft-proposed microevolutionary mechanisms are not necessary and may not be
296 sufficient to generate higher-level sorting.

297 Inferring the potential drivers for periods of anagenetic change is more difficult. Within-
298 lineage trends are typically explained as being caused by *only* directional selection. However, the
299 observed rate of within-lineage ECV increase is too slow to be consistent with uniform
300 directional selection, given our knowledge from empirical microevolutionary studies [48] and
301 theoretical models (like the exponential model above) about the rate at which natural selection
302 operates. In fact, to ‘force’ the model prediction downwards to match the observed data (i.e.,
303 mean anagenetic increase in the less speciose taxonomy; figure 4), one would need to decrease
304 the mean-standardized selection gradient by 50% from 0.28 to 0.14 (if evolvability is held
305 constant). In their compilation of mean-standardized selection gradients, Hereford and colleagues
306 found that such low estimates are so small as to not be significantly different from zero (see
307 figure 3 in ref. [36]). Our finding is consistent with those from other researchers who have shown

308 that rates of hominin phenotypic evolution are consistent with, or even slower than, random
309 genetic drift alone [49–51]. The potential prevalence of genetic drift should perhaps not be
310 surprising given the rarity of hominins in the fossil record [52], which implies small population
311 sizes, but drift is difficult to reconcile with the strongly directional ECV pattern we find within
312 hominin lineages.

313 We hypothesize that the seemingly too slow within-lineage evolutionary rate is caused by
314 the dynamics of the selective pressures themselves (i.e., the adaptive landscape) over
315 evolutionary time [40,53,54]. Microevolutionary studies have shown that populations can
316 respond rapidly to selection pressures on generational time scales (i.e., populations rapidly climb
317 the adaptive peak and stay at the summit). Such high rates, however, need not characterize the
318 tempo at which the adaptive peak *itself* moves over geological time [40]. Therefore, selection
319 was for larger ECV on average but must have fluctuated and included episodes of stasis and/or
320 drift. All of this occurs on too fine a time scale to be resolved by the current hominin ECV fossil
321 record, resulting in emergent directional trends within lineages. If this is the case, the
322 microevolutionary question of interest shifts to what caused ECV selection pressures to fluctuate
323 but still ultimately select for larger ECVs on average at a geologically gradual pace [40]?

324

325 **5. Conclusion**

326 Traditionally, a gradual trend has been interpreted as the result of consistent directional
327 selection at the population level for larger brains. However, when taxonomic scale is accounted
328 for, we find the gradual, clade-level trend was generated primarily by within-lineage mechanisms
329 that likely involved both directional selection *and* stasis and/or drift. In addition to these within-
330 lineage processes, directional speciation producing larger-brained lineages, higher extinction

331 rates of smaller-brained lineages, and potentially higher-level species sorting all worked together
332 to generate the strongly trended, emergent clade-level pattern. Our findings illustrate the
333 complicated, multi-causal nature of hominin ECV evolution and the need for future hypotheses
334 and models to recognize and incorporate this hierarchical complexity. There is no one canonical
335 scale at which to conduct evolutionary research, and different questions can and should be asked
336 when studying ECV increase at different scales. The analytical framework we suggest can be
337 used to generate more precise hypotheses pinpointing when and at what taxonomic level ECV
338 increase occurred, thus enabling stronger tests of proposed explanations. For example,
339 predictions of the rate and magnitude of ECV increase from models invoking microevolutionary
340 processes (e.g., stone tool innovation, major dietary shifts) can be benchmarked against the
341 anagenetic partitions in figures 4 & S6.

342 Within just the past few years, it has been made clear through fossil discoveries, or
343 through comprehensive analyses permitted by those discoveries, that many of the so-called
344 ‘defining’ characteristics of modern humans emerged through evolutionary processes that were
345 significantly more complicated than had previously been appreciated. For example, we now have
346 direct fossil evidence of a widely diverse set of adaptations for bipedalism in Pliocene hominins
347 [55] and direct archaeological evidence that stone tool technologies were potentially
348 manufactured and used by hominins well before the emergence of the ‘handy man,’ *Homo*
349 *habilis* [56,57]. This trend of falsifying and then refining hypotheses after the emergence of new
350 fossil data is inevitable in palaeobiology. However, it has proved easier to accumulate, but more
351 difficult to reject, hypotheses for why ECV increased in the hominin clade. Certain hypotheses
352 may actually prove unfalsifiable if they explain evolutionary patterns in ways that are too
353 imprecise and overly general [58]. Palaeoanthropologists, as with other practitioners of historical

354 science, cannot conduct experiments with their data, so they must rely on theory to develop
355 precise, falsifiable predictions to elucidate the mechanisms underlying observed patterns [58–
356 60]. Informed by micro- and macroevolutionary theory, our taxonomically scale-explicit
357 analyses provide a revised, quantitatively rigorous framework for both developing and testing
358 hypotheses and models related to the evolution of hominin brain size. This moves us closer to
359 identifying and understanding what ultimately drove the evolution of large brains in the human
360 clade.

361

362 **Data accessibility.** The datasets supporting this article have been uploaded as part of the
363 electronic supplementary material and are also available via the Dryad Digital Repository at
364 <http://dx.doi.org/10.5061/dryad.c30g9>.

365 **Competing interests.** We have no competing interests.

366 **Author contributions.** All authors contributed to the formulation of the project. A.M.Z.,
367 K.G.H., E.R., and A.D. collected data. A.D. formulated the research design and performed
368 analyses. A.D. wrote the paper with contributions from B.A.W. and K.G.H.

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374

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494

495 **Figure captions**

496 **Figure 1.** Theoretical plots demonstrating (A) how patterns within lineages may not necessarily
497 hold when combined and examined at the level of the entire clade and (B) how clade-level brain
498 size can increase via anagenesis, origination, or extinction. (A) On the left, lineages exhibit
499 gradual trends, but the clade-level pattern shows a punctuated equilibrium pattern. This is
500 because the direction and magnitude of change within each group of co-occurring lineages
501 cancel each other out so that, on average, an emergent stasis pattern is generated. On the right,
502 each lineage experiences stasis, but because origination events produce more and larger ECV
503 increases than decreases on average, a gradual clade-level trend is produced. (B) The vertical
504 dashed line represents a bin edge separating two bins. In all three cases, clade-level brain size is
505 increasing, and the increase is attributed solely to the process being illustrated. In “Anagenesis,”

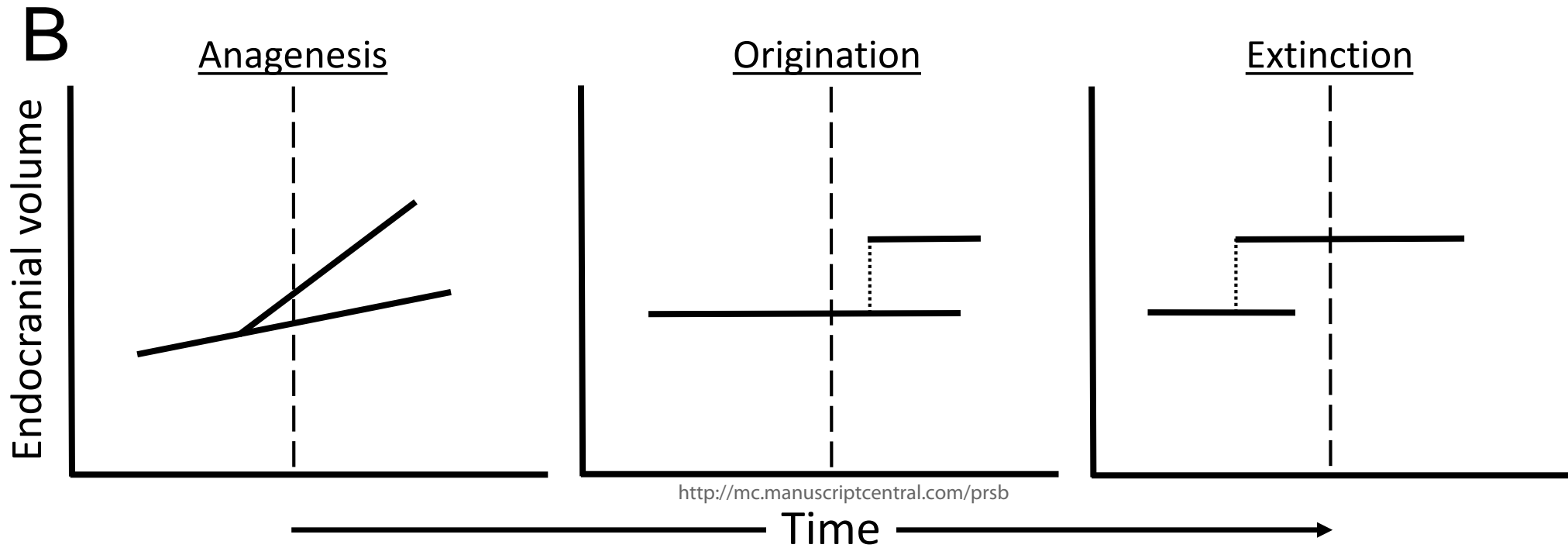
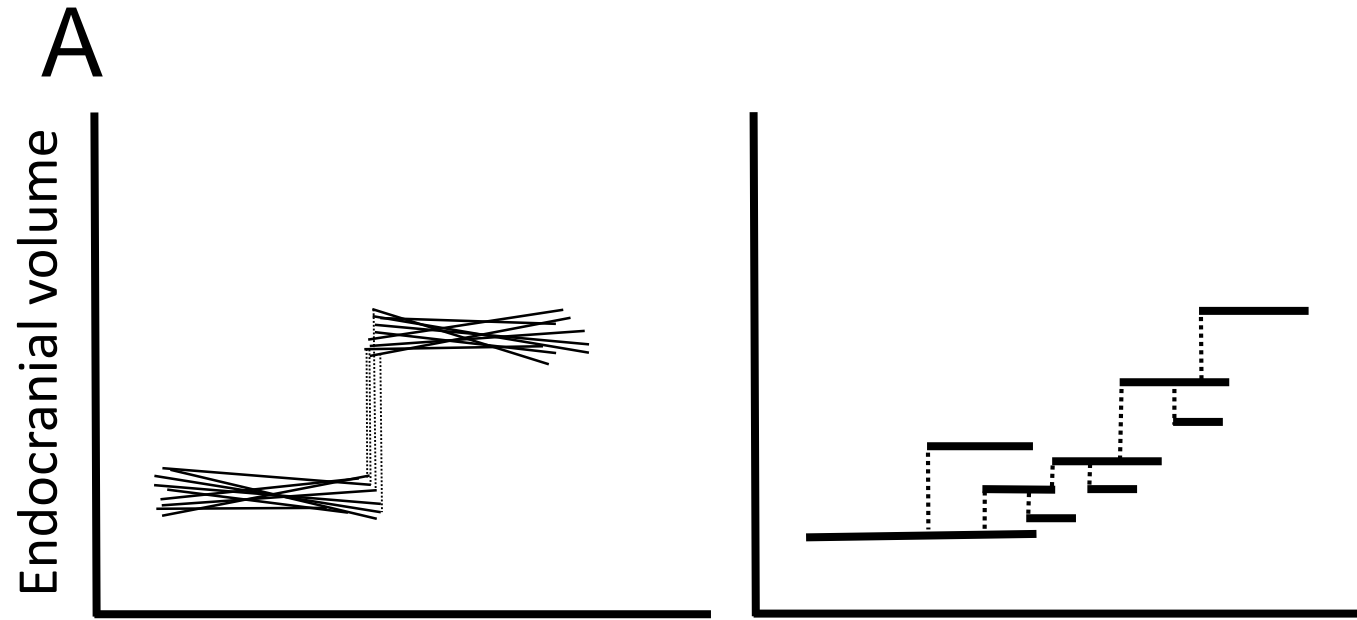
506 we see two lineages survive from the earlier time bin into the later time bin, and both lineages
507 exhibit an increase in ECV over time. In “Origination,” a lineage-splitting event creates a
508 daughter species with a larger ECV in the later time bin, leading to an increase in overall clade-
509 level ECV. In “Extinction,” the smaller-brained lineage goes extinct in the earlier time bin,
510 causing clade-level ECV to increase in the subsequent time bin.

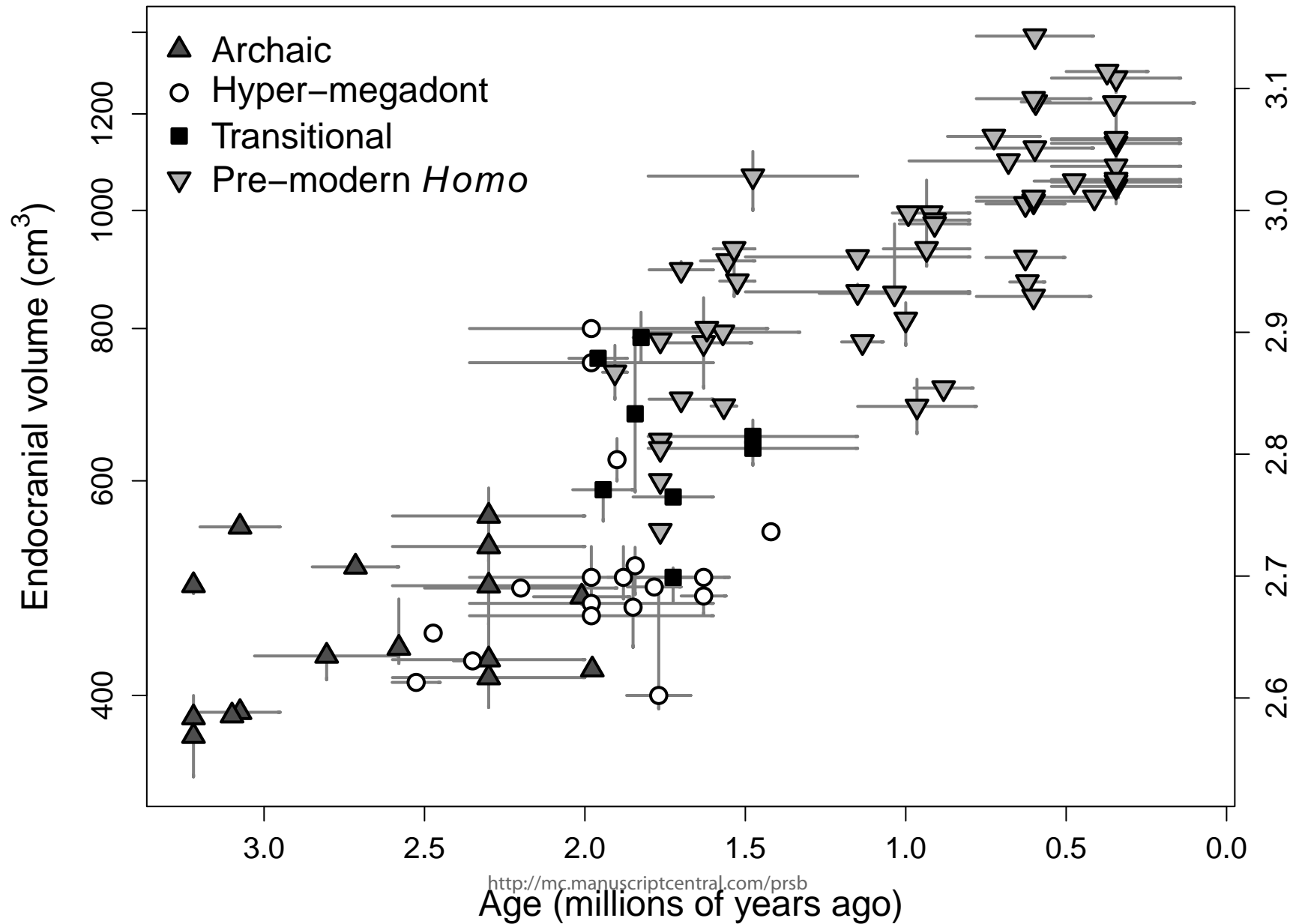
511 **Figure 2.** Time series of hominin ECV included in our analyses. Points represent ECV and age
512 midpoints, and bars represent ranges of error on the estimate (or mean \pm 3 SD for dates with
513 normally distributed error [see Appendix S1]). Points are coded by hominin grade [58].
514 Specifically, archaic species include *Australopithecus afarensis*, *Australopithecus africanus*, and
515 *Australopithecus sediba*; hyper-megadont and megadont species include *Australopithecus garhi*,
516 *Paranthropus aethiopicus*, *Paranthropus boisei*, and *Paranthropus robustus*; transitional species
517 include *Homo habilis sensu stricto* and *Homo rudolfensis*; and pre-modern *Homo* species include
518 *Homo erectus sensu stricto*, *Homo ergaster*, *Homo georgicus*, and *Homo heidelbergensis*. The
519 left y-axis is on a logarithmic scale, while the right y-axis’ tick labels are \log_{10} -transformed
520 values.

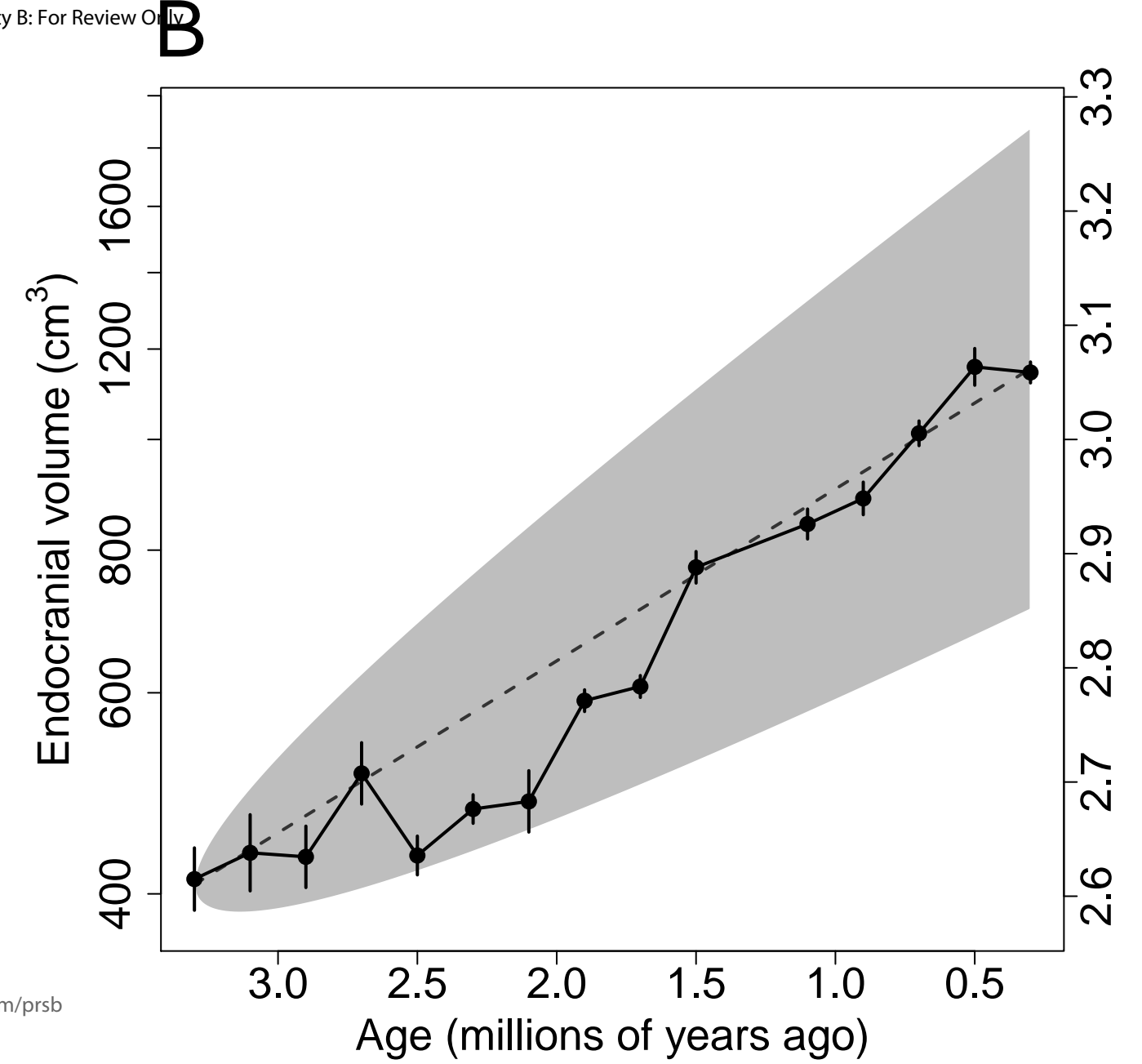
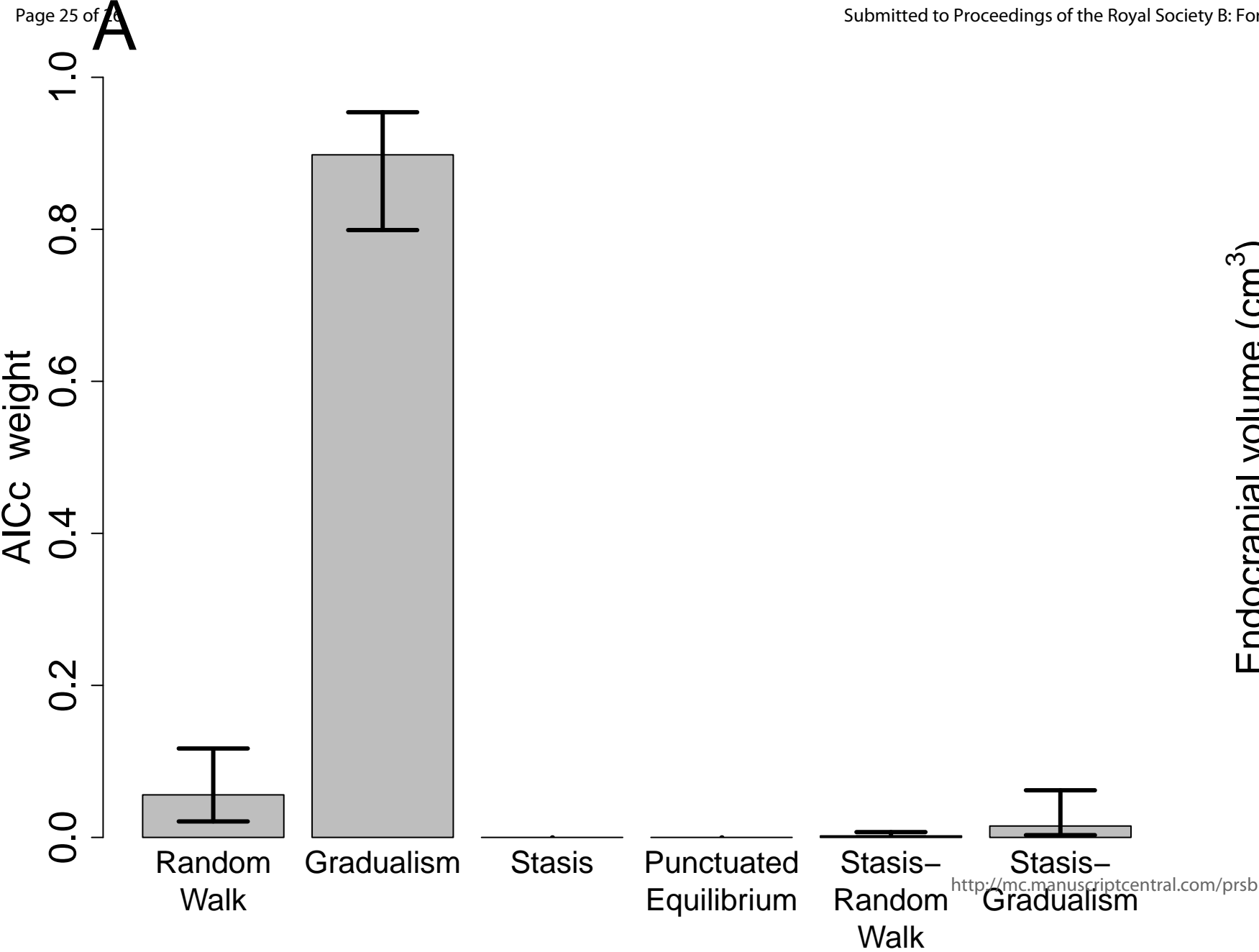
521 **Figure 3.** (A) Model selection results of the clade-level analysis testing six evolutionary modes.
522 Bias-corrected Akaike information criterion (AICc) weights sum to one across all models, with
523 higher weights representing more model support. Bars represent AICc weight medians, and error
524 bars represent 1st and 3rd quartiles from resampling age estimates (see Appendix S1). (B)
525 Gradualism model fit for the clade-level ECV time series using 0.2 Ma bins. Binning here was
526 done using observed (not resampled) age midpoints for plotting purposes only (see Appendix
527 S1). Points are mean ECV estimates, and error bars are \pm 1 SE. Dotted line represents the

528 expected evolutionary trajectory of the fitted gradualism model surrounded by the 95%
529 probability envelope in gray. Y-axes as in figure 2.

530 **Figure 4.** Additive partitioning of clade-level ECV transitions into their anagenetic and observed
531 first and last appearances components. Ages separated by hyphens indicate over which two age
532 bins (represented by their midpoints) the ECV transition is measured. “First/last appearances”
533 represents macroevolutionary change that cannot be partitioned into separate first or last
534 appearances components (see “Methods”). The sum of all partition means within a given time
535 period equals the mean clade-level change, which in this case are all positive. Error bars are ± 1
536 SE calculated by randomly resampling age estimates (see Appendix S1). The horizontal black
537 line represents the expected amount of within-lineage ECV increase over 0.3 Ma given our
538 knowledge of how quickly natural selection operates from microevolutionary studies. Insets
539 depict the cumulative effect of each component’s mean (excluding “First/last appearances”) on
540 the net clade-level trend (black line). Vertical dotted lines in the inset correspond to the vertical
541 dotted lines in the main figure. The top graph uses a taxonomy that recognizes fewer taxa, while
542 the bottom graph uses a taxonomy that recognizes a larger number of taxa.







Change in endocranial volume ($\log_{10}\text{cm}^3$)