

1 **Title: Phylogeny, ancestors and anagenesis in the hominin fossil record**

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15

16 **Author contributions:** CPF designed and implemented the ML stratocladistic procedure,
17 performed analyses, interpreted results, and drafted the manuscript. DCF made conceptual
18 contributions to the stratocladistic approach developed here, contributed to the manuscript, and
19 helped interpret results. EG gathered temporal occurrence ranges, helped interpret results, and
20 edited the manuscript. LMM helped focus the scope of the hominin analysis, helped interpret
21 results, and contributed to the manuscript.

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23 **Supplementary data:** Software used in this study is implemented in the *mandos* package and is
24 available on GitHub (github.com/carolinetomo/mandos). All trees tested using the stratocladistic
25 likelihood procedure and their associated AIC scores are available on GitHub (WEB
26 ADDRESS—will upload prior to submission). This repository also contains the morphological

27 matrix and stratigraphic range files and all scripts needed to reproduce results. Stratigraphic
28 occurrences and their associated citations are provided as supplementary information. The
29 supplement also includes an online appendix that describes and tests the morphological
30 likelihood calculation on trees containing anagenetic relationships.

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49 **Abstract:** Probabilistic approaches to phylogenetic inference have recently gained traction in
50 paleontological studies. Because they directly model processes of evolutionary change,
51 probabilistic methods facilitate a deeper assessment of variability in evolutionary pattern by
52 weighing evidence for competing models. Although phylogenetic methods used in
53 paleontological studies have generally assumed that evolution proceeds by splitting cladogenesis,
54 extensions to previous models help explore the potential for morphological and temporal data to
55 provide differential support for contrasting modes of evolutionary divergence. Recent
56 methodological developments have integrated ancestral relationships into probabilistic
57 phylogenetic methods. These new approaches rely on parameter-rich models and sophisticated
58 inferential methods, potentially obscuring the respective contributions of data and models. In this
59 study, we describe a simple likelihoodist approach that combines probabilistic models of
60 morphological evolution and fossil preservation to reconstruct both cladogenetic and anagenetic
61 relationships. By applying this approach to a dataset of fossil hominins, we demonstrate the
62 capability of existing models to unveil evidence for anagenesis presented by morphological and
63 temporal data. This evidence was previously recognized by qualitative assessments, but largely
64 ignored by quantitative phylogenetic analyses. For example, we find support for directly
65 ancestral relationships in multiple lineages: *Sahelanthropus* is ancestral to later hominins;
66 *Australopithecus anamensis* is ancestral to *Au. afarensis*; *Au. garhi* is ancestral to *Homo*; *H.*
67 *antecessor* is ancestral to *H. heidelbergensis*, which in turn is ancestral to both *H. sapiens* and *H.*
68 *neanderthalensis*. These results show a benefit of accommodating direct ancestry in
69 phylogenetics. By so doing, quantitative results align more closely with previous qualitative
70 expectations.

71 **Keywords:** anagenesis, phylogenetics, morphology, paleontology, hominin

72 **Introduction:** Phylogenetic methods that rely upon probabilistic evolutionary models have
73 recently begun to emerge as important tools for addressing paleobiological issues at
74 macroevolutionary timescales (Wright and Hillis 2014; Puttick et al. 2017). Probabilistic
75 approaches appear promising in their performance relative to earlier cladistic methods and offer
76 several important advantages. These include their tendency to increase the clarity with which
77 models are specified and their ability to weigh evidence under competing evolutionary models
78 using modern inferential machinery. While probabilistic approaches have long been dominant in
79 molecular phylogenetics, their application to paleontological datasets is largely untapped. Yet
80 the extension of approaches developed for extant taxa to fossil taxa will allow for the testing of a
81 broader range of evolutionary hypotheses that are designed to reflect differences in the
82 morphological patterns underlying divergence between fossil taxa.

83 Most previous approaches to phylogenetic reconstruction depict evolutionary relatedness
84 using patterns of ‘hypothetical’ ancestry in which more closely related taxa are represented as
85 possessing more recent common (hypothetical) ancestors. However, when fossil taxa are
86 included in phylogenetic analyses, we might reasonably consider whether direct ancestry
87 between temporally disjunct taxa or samples can be detected (Foote 1996). Although there is a
88 spectrum of possible patterns of temporal distribution reflecting directly ancestral relationships,
89 these may be dichotomized into cladogenesis and anagenesis.

90 Characterization of the relative prevalence of cladogenesis and anagenesis in the fossil
91 record and their bearing on the study of evolutionary mode has long been a fundamental question
92 in paleobiology (Simpson 1944; Stanley 1998; Levinton 2001). Although the significance of
93 these contrasting models of evolutionary change in interpreting patterns in the fossil record has
94 been fiercely debated (Gould and Eldredge 1977; Gould 1980; Levinton and Chris 1980;

95 Gingerich 1985; Futuyma 1987), anagenetic change has been widely observed in the fossil
96 record and can impact inferences of evolutionary processes (MacLeod 1991). This may be
97 particularly important when constructing and testing hypotheses of phylogenetic relationships,
98 where accommodation of anagenetic change may improve accuracy and yield insights otherwise
99 unattainable (Gingerich 1979; Fox et al. 1999; Aze et al. 2011; Strotz and Allen 2013; Aze et al.
100 2013).

101 Quantitative phylogenetic approaches have usually assumed the universality of
102 cladogenesis. Until recently, this fundamental limitation has remained largely intact, despite the
103 development of increasingly sophisticated probabilistic approaches to phylogenetic inference.
104 Since most of the major developments in probabilistic approaches to phylogenetics were
105 developed for molecular data (but see Lewis 2001), their use has been largely restricted to
106 neontological applications. As a result, there has been relatively little impetus in the areas most
107 engaged in phylogenetic research to consider phyletic evolution, leaving the role of anagenesis in
108 phylogenetic reconstruction under-explored.

109 The conceptual issues discussed above are particularly relevant in taxa such as the
110 hominin clade (humans and all other taxa more closely related to humans than to genus *Pan*),
111 where hypotheses of direct ancestry are often proposed. Discerning human evolutionary patterns
112 is a focus traceable to Darwin (1871), and ancestry is almost certainly more frequently proposed
113 (even if informally) for clusters hominin fossils than for those from other taxonomic groups.
114 Nonetheless, there are few formal routes for recognizing this status based on quantitative
115 evaluations of traits.

116 Although quantitative approaches to phylogenetics have typically ignored anagenesis,
117 stratocladistic methods were developed to leverage temporal occurrence data to help reconstruct

118 phylogenetic trees that have the potential to express direct ancestor-descendant relationships
119 (Fisher 2008). Stratocladistics uses the criterion of maximum parsimony (MP) to minimize both
120 the number of homoplasious character changes and unsampled stratigraphic intervals implied by
121 topologies that include both bifurcating and serially linked segments of phyletic lineages. Several
122 authors have expressed objections both to the use of temporal data in phylogenetic inference and
123 the capability of available data to adequately test ancestral and collateral relationships between
124 species (Smith 2000). Nevertheless, direct ancestors are expected to occur in the fossil record
125 (Foote 1996), and the integration of temporal data has been shown to improve reconstruction
126 accuracy over morphological analyses alone (Fox et al. 1999). In addition, those earlier
127 criticisms, which have been frequently raised by proponents of cladistic methodologies, are also
128 less relevant when placed in the context of the modern probabilistic approaches. While cladistics
129 operates at the level of cladograms, both stratocladistics and recent probabilistic approaches
130 reconstruct phylogenetic trees. This renders earlier criticism of temporal data largely irrelevant
131 given the current landscape of phylogenetic methodology. As such, it stands to reason that
132 probabilistic approaches are remiss when they fail to accommodate the possibility of ancestor-
133 descendant relationships between temporally heterogeneous taxa.

134 There have been several attempts to explicitly extend the intent and logic of
135 stratocladistics into probabilistic approaches using maximum-likelihood (ML) (Huelsenbeck and
136 Rannala 1997; Wagner 1998). However, these have not found widespread use. Aspects of these
137 have been appropriated more recently by methods that use some combination of morphological,
138 fossil preservation, and lineage diversification models to infer relationships and lineage
139 divergence times in a Bayesian context (Pyron 2011). This framework has been extended to
140 explicitly accommodate ancestor-descendant relationships by modelling lineage diversification

141 and fossil preservation processes (Stadler 2010; Bapst and Hopkins 2016; Stadler et al. 2017), in
142 particular through the use of the ‘Fossilized Birth-Death’ (FBD) prior (Heath et al. 2014; Zhang
143 et al. 2016). However, the assumptions and ramifications of doing so have not been well
144 explored.

145 One outstanding question regarding these approaches is the extent to which
146 morphological data themselves are able to illuminate questions of direct ancestor-descendant
147 relationships without explicitly modelling the process of lineage diversification. This may be
148 especially important in clades with gappy fossil records, such as many lineages of terrestrial
149 vertebrates. In these cases, there may be less information available to reconstruct speciation and
150 extinction parameters, and so a characterization of the identifiability of hypotheses of direct
151 ancestry from morphology alone can benefit future studies in these taxa. In addition,
152 methodological extensions of Bayesian tip-dating methods that accommodate serial sampling of
153 lineages have been largely developed for use in epidemiological systems, where they are used to
154 model molecular sequence evolution along single lineages. Although these systems are useful
155 models of patterns in the fossil record, their sampling is often incomplete, and so they may
156 sometimes call for different approaches in practice. Non-Bayesian *a posteriori* time-scaling
157 (APT) approaches, such as *cal3*, that accommodate ancestor-descendant relationships also exist
158 (Bapst 2013). These apply divergence times to unscaled cladograms that have been inferred from
159 character data alone. Although both Bayesian and APT approaches have been shown effective
160 when applied to fossil taxa (Bapst 2013; Bapst and Hopkins 2016; Gavryushkina et al. 2017;
161 Stadler et al. 2017), there has been limited discussion of the statistical properties, limitations, and
162 implications of using existing paleontological data and probabilistic models to identify
163 anagenesis. Nevertheless, anagenesis is an evolutionary question of critical importance, and so

164 the development of a probabilistic approach using likelihoodist criteria may be broadly beneficial
165 by clearly quantifying the evidence for anagenesis present in paleontological data.

166 Although cladistic methods have been applied to improve understanding of certain
167 aspects of hominin evolution (Delson et al. 1977; Chamberlain and Wood 1987; Strait et al.
168 1997; Irish et al. 2013), their exclusive focus on bifurcating relationships has precluded the study
169 of direct ancestry except in cases where character polarity and specimen sampling have been
170 carefully considered (Kimbel et al. 2006). More recently, Bayesian approaches have been
171 suggested to provide a clearer view of hominin evolutionary relationships (Dembo et al. 2015;
172 2016), but their results still contain ambiguities. For example, like earlier cladistic approaches
173 (Strait et al. 1997; Strait 1999), results from Bayesian analyses conflict with qualitative
174 interpretations of hominin relationships in several key instances. This divide is exemplified by
175 considering the taxa *Homo heidelbergensis* and *Homo antecessor*, for whom hypotheses of
176 anagenesis are often considered. For example, previous studies have alternatively suggested that
177 either *Homo heidelbergensis* or *Homo antecessor* may be directly ancestral to *Homo sapiens* and
178 *Homo neanderthalensis* (Mounier et al. 2009), while some have debated the suggestion that
179 *Homo antecessor* is ancestral to *Homo heidelbergensis* (Stringer 2012). Others have suggested
180 alternately that *Homo heidelbergensis* is either a chronospecies directly ancestral to *H.*
181 *neanderthalensis*, or directly ancestral to both *H. sapiens* and *H. neanderthalensis* (Rightmire
182 1998; Rosas and Bermúdez De Castro 1998; Stringer 2012). This uncertainty is underscored by
183 the suggestion that cladistic methods and data are unreliable in their ability to describe hominin
184 evolutionary patterns and history (Collard and Wood 2000).

185 In this study, we describe an approach to phylogenetic inference that combines models of
186 stratigraphic preservation and morphological evolution to reconstruct time-scaled phylogenies

187 and distinguish between anagenesis and cladogenesis using ML and the Akaike Information
188 criterion (AIC). This approach seeks to simplify existing methods, such as the APT and FBD
189 approaches described above, to clearly identify the signal for directly ancestral relationships
190 presented by morphological data alone. Unlike more complex approaches, ours seeks only to
191 identify information in morphological and temporal data that establishes differential support for
192 ancestor-descendant and bifurcating relationships. As a result, our approach explicitly relies on
193 models of morphological evolution and stratigraphic preservation rather than on models of
194 lineage diversification.

195 We apply our new approach in hominins using a morphological supermatrix borrowed
196 from the literature (Dembo et al. 2015; 2016). Hominins are a particularly compelling case study
197 for our questions surrounding the identifiability of phylogenetic models that incorporate
198 anagenesis. Although cladistic and phylogenetic methods have been applied to hominins
199 (Chamberlain and Wood 1987; Strait et al. 1997; Strait 1999; Irish et al. 2013; Dembo et al.
200 2015; 2016), previous methods' exclusive focus on bifurcating relationships has led to their
201 inability to fully address outstanding hypotheses of hominin evolution, which are often
202 predicated upon the occurrence of anagenesis. Our analysis identified several areas of anagenetic
203 change in hominins, demonstrating cases where temporal data both corroborate and refute results
204 achieved using morphology alone. We recognize that increasingly thorough compilation of
205 morphological data and new fossil discoveries is likely to continue to revise and refine current
206 understanding of hominin evolution. Nevertheless, our approach sheds light on the capabilities of
207 existing models and data to accommodate anagenetic change without becoming entangled in a
208 complex web of Bayesian assumptions. Moving forward, application of our method in hominins
209 provides general demonstration of the importance of accommodating anagenetic change in

210 phylogenetic methods to generate deeper understanding of evolutionary patterns in the fossil
211 record.

212

213 **Materials and methods:**

214 *Inference of ML topology.* Our approach evaluates the likelihood of candidate topologies using
215 probabilistic models of fossil preservation and morphological evolution (Huelsenbeck and
216 Rannala 1997; Lewis 2001). We perform a semi-automated tree search by calculating the
217 likelihoods of these models on a set of candidate topologies. This approach tests hypotheses of
218 direct ancestorship by combining branches with non-overlapping ranges and comparing
219 cladogenetic and anagenetic models using the AIC. All code developed for these analyses is
220 publicly available and implemented in the *mandos* package
221 (www.github.com/carolinetomo/mandos).

222 *Identification of a fully-bifurcating ML tree.* Our approach has yet to be implemented with a fully
223 automated tree searching algorithm, so we combine semi-automated rearrangements with manual
224 perturbations to search for the ML topology. This is done by exploring tree-space surrounding a
225 starting tree estimated from morphological characters alone. In this study, we obtained a ML
226 starting tree using RAxML, version 8.2.11, using the Mk model of morphological evolution
227 (Lewis 2001). The morphological data were separated into partitions according to the number of
228 possible states (i.e., binary, trinary, etc.) and analyzed under separate models. This partitioning
229 scheme was maintained for all subsequent morphological likelihood calculations, including those
230 used below in the AIC comparisons. We then performed a series of nearest neighbor interchange
231 (NNI) and subtree pruning and regrafting (SPR) operations. These yielded a set of 1700
232 candidate topologies from which we identified the fully-bifurcating topology best supported by

233 both morphologic and stratigraphic data. This tree provided a starting point drawn from both
234 morphologic and stratigraphic lines of evidence. From here, we explored ancestor-descendant
235 relationships using the model-testing approach described below.

236 *Modelling stratigraphic preservation.* Stratigraphic likelihoods were calculated under a
237 homogeneous Poisson process of geologic preservation. When applied to phylogenetics,
238 inference under this model has been shown to accurately recover simulated phylogenetic
239 relationships (Huelsenbeck and Rannala 1997). The likelihood function is derived from a
240 Poisson process as the probability of observing the first occurrence (o_f), last occurrence (o_l) and
241 number (n_o) of occurrences in the stratigraphic record given some origination and extinction time
242 (t_f and t_l , respectively) and preservation rate (λ). These likelihoods are calculated independently
243 for each (i) of b total lineages and multiplied to yield the overall tree likelihood (see
244 (Huelsenbeck and Rannala 1997) for full derivation):

$$245 \quad \hat{L} = \prod_{i=1}^b \frac{(o_f^i - o_l^i)^{n_o^i - 2} \lambda^{n_o^i} e^{-\lambda(t_f^i - t_l^i)}}{(n_o^i - 2)!}$$

(Eq. 1)

246 This equation reaches its maximum as branching and extinction times approach the first and last
247 occurrences in the fossil record, and so the likelihood is maximized across the tree when the total
248 amount of unsampled time implied by the topology is minimized. Although this approach differs
249 from stratocladistic parsimony in its treatment of occurrence data as continuous rather than
250 discrete, this property causes the preservation model to behave as a statistical formalization of
251 the stratigraphic parsimony debt calculations undertaken in parsimony-based stratocladistic
252 analyses. We estimate lineage origination and termination times along with preservation rate
253 using multivariate numerical optimization routines implemented in SciPy (Jones et al. n.d.).

254 When combined with morphological data and models of character evolution, this approach
255 represents a comprehensive extension of traditional stratocladistics based entirely upon
256 probabilistic models.

257 *Identification of anagenesis.* Using the bifurcating topology with the highest likelihood under
258 both stratigraphic and morphologic models, we manually identified a set of potential ancestor-
259 descendant relationships. To explore a more comprehensive range of both anagenetic and
260 cladogenetic arrangements, we also extensively perturbed results manually and compared
261 likelihoods. Although a fully-automated tree searching approach will ultimately be desirable in
262 future versions of our method, our approach to tree-searching is similar to those used in previous
263 stratocladistic studies. Starting with the fully bifurcating tree, we identified putative ancestor-
264 descendant arrangements by collapsing each branch with a temporal range beginning earlier than
265 the range represented by its sister lineage. We isolated each putative episode of anagenesis and
266 compared the morphologic and stratigraphic likelihoods of anagenetic and cladogenetic
267 arrangements using AIC scores. This was required because cladogenetic nodes assume one more
268 parameter than anagenetic nodes (i.e., the branch length of the new lineage), and so bifurcating
269 trees contain more parameters than anagenetic trees. Comparison of AIC scores enables a
270 comparison of the relative quality of models with different numbers of parameters. AIC score is
271 calculated from the number of model parameters (k), and the log-likelihood (L):

$$272 \quad AIC = 2k - 2 \ln L$$

(Eq. 2)

273 Since models with larger numbers of parameters are more prone to overfitting, they are biased
274 toward possessing higher likelihoods than less complex models. As a result, likelihood scores of

275 models that differ in dimension are not directly comparable. AIC scores represent the amount of
276 information lost by a model when representing data, with lower scores indicative of models that
277 preserve a greater amount of information. AIC accommodates for differences in parameter count
278 between models by penalizing the addition of additional parameters, seeking to optimize the
279 trade-off between improvements in model fit associated with added parameters and the loss of
280 statistical power that results from overparameterization. In our use, AIC facilitates comparison of
281 phylogenetic models of differing dimensions by penalizing the addition of branches that are
282 better explained through an anagenetic pattern. The parameter count, k , for each phylogeny is
283 calculated by summing the number of estimated branch lengths for each tree with the number of
284 parameters used in the partitioned Mk substitution model.

285 Under the Poisson preservation model, stratigraphic likelihood predictably improves
286 when unsampled time implied by the phylogeny is reduced, and so the acceptance of anagenetic
287 arrangements also requires the support of morphology. This requires a novel calculation of
288 morphological likelihood where the probability of transitioning from an observed, rather than an
289 uncertain, parental character state to a single or multiple descendant character states is calculated
290 under the Mk model (Fig. 1). This calculation differs from that used on multi-furcating nodes.
291 Since the sequences at internal nodes representing unobserved taxa are unknown, the likelihood
292 of character data at the tips is typically calculated by summing over all possible states at each
293 unobserved internal node (Felsenstein 1981). However, when dealing with anagenesis, the sets of
294 character states at some internal nodes are known. In these cases, the likelihood is calculated as
295 the conditional probability of observing the set of traits at the tips given the set of traits
296 possessed by the putative ancestor. Anagenetic arrangements are only accepted when there has
297 been a sufficiently small amount of character change. This procedure resembles model testing

298 procedures used to reconstruct ancestral DNA sequences, which compare conditional likelihoods
299 of different permutations of character states at ancestral nodes (Yang et al. 1995). Like
300 stratocladistics, this use of probabilistic models of character change enables morphology to
301 occupy a central role in identifying anagenesis. As a result, this approach can in principle be used
302 to test anagenesis even in the absence of a temporal model. A demonstration and test of this
303 method using simulated data is provided in the supplement.

304 *Morphological matrix.* We performed our analysis on a supermatrix of 391 discrete craniodental
305 characters compiled by Dembo and colleagues (Dembo et al. 2015; 2016). We removed all
306 ambiguous character states, as researchers did not identify whether these were truly ambiguous
307 or polymorphic. While ambiguous character codings are unlikely to provide significant
308 phylogenetic information, existing Markov models of discrete character evolution do not
309 accommodate polymorphism. We excluded the taxa *Kenyanthropus platyops* and *Homo naledi*
310 from the present analysis. The features that are diagnostic of *K. platyops* have been suggested to
311 result from taphonomic distortion resulting from matrix expansion, rather than from true
312 biological differences (White 2003). Thus, we omitted this taxon in hopes of shedding greater
313 light on the remaining, more widely accepted hominin taxa. *Homo naledi* was omitted because
314 the data provided in the original study yielded an ML topology placing *H. naledi* as sister to *H.*
315 *sapiens*. Although the phylogenetic affinity of *H. naledi* is a major outstanding question in
316 paleoanthropology, the confusing signal presented by the *H. naledi* data, which are relatively
317 recently acquired and therefore represent less well-studied fossils overall, reduced our
318 confidence in the ability of this dataset to resolve its placement. Therefore, to avoid any
319 confounding effects from the potential unreliability of the *H. naledi* data, we performed our

320 analyses on the remaining subset of the data after *H. naledi* was removed. This enabled us to
321 explore the phylogenetic relationships between better-known hominins.

322 *Geologic occurrence times.* We surveyed the literature to obtain the observed temporal range of
323 each taxon in continuous time. Reported radiometric dates for the oldest and youngest fossils
324 were taken as the first and last observations. Some specimens are ambiguous in their taxonomic
325 assignment; these were excluded from the analysis. We also gathered the number of total
326 occurrences as the number of localities where each taxon has been identified as listed in
327 MacLachy et al. (2010), and supplemented these with additional localities identified in the
328 literature. Cases where multiple specimens belonging to the same taxon have been identified at a
329 single locality were treated as single occurrences. Although we recognize the potential ambiguity
330 in delineating between sites, localities, and occurrences, we attempted to coarsely characterize
331 the total number of occurrences using the number of sites at which each taxon occurs. This
332 approach is more likely to underestimate the number of occurrences than overestimate them,
333 which we expect to yield more conservative statistical support for competing topologies under
334 the preservation model. A comprehensive list of the sites used to define temporal ranges for all
335 taxa is provided in the supplement.

336

337 **Results and Discussion:**

338 *Anagenesis in the hominin fossil record:* Our analysis yielded evidence for several instances of
339 anagenesis in the hominin fossil record (Fig. 2). Our analysis reconstructed *Australopithecus*
340 *anamensis* as directly ancestral to *Au. afarensis*. This result agrees with broad acceptance of *Au.*
341 *anamensis* and *Au. afarensis* as phyletically linked chronospecies (Leakey et al. 1995; Ward et
342 al. 2001; Kimbel et al. 2006). Although our analysis recovered *Ar. ramidus* as sister to the

343 anagenetic *Au. anamesis*-*Au. afarensis* branch, the morphological data did not support the
344 collapse of *Ar. ramidus*. Nevertheless, *Ar. ramidus* possessed poor character sampling in the
345 matrix, and so its placement should be regarded as tentative. *Sahelanthropus tchadensis* is
346 recovered as a direct ancestor to the rest of the hominin clade. This result should also be treated
347 cautiously due to the small number of characters recovered for analysis of this portion of the
348 phylogeny, but it is in line with with *Sahelanthropus*' status as the oldest recognized hominin
349 (Brunet et al. 2002; Guy et al. 2005; Zollikofer et al. 2005).

350 Consistent with an early appraisal (Asfaw et al. 1999), our final analysis inferred *Au.*
351 *garhi* to be directly ancestral to the *Homo* clade (Fig.2a). This conflicts with cladistic analyses
352 that placed *Au. garhi* as outgroup to *Au. africanus*, *Paranthropus*, and *Homo* (Strait 1999).
353 However, when anagenesis is not considered and phylogeny is inferred from morphology alone,
354 we recover the same placement for *Au. garhi* as the cladistic result (Fig. 2b). Like the example
355 above, this may reflect the constraint that strictly bifurcating methods impose on phylogenetic
356 reconstructions among fossil taxa. However, preference for *Au. garhi* as ancestral to *Homo* is
357 weak, with an only slightly improved AIC score over the *Au. garhi* outgroup hypothesis (Table
358 1).

359 Our results also better reconcile quantitative and qualitative interpretations of the
360 evolutionary mode and relationships among the *Homo* species leading to modern humans and
361 Neanderthals. Paleoanthropologists have variously interpreted *Homo heidelbergensis* as either:
362 1) a direct ancestor to both Neanderthals and modern humans (Rightmire 1998; Mounier et al.
363 2009; Stringer 2012; Buck and Stringer 2014), or 2) a chronospecies leading to Neanderthals
364 (Rosas and Bermúdez De Castro 1998). However, quantitative phylogenetic analysis has placed
365 *H. heidelbergensis* as sister to Neanderthals (Dembo et al. 2015). Our ML result based on

366 morphological characters alone places *H. heidelbergensis* as sister to *H. sapiens*. However, when
367 temporal data are incorporated and anagenesis is accommodated, AIC support improves
368 substantially, and *H. heidelbergensis* is collapsed to represent a direct ancestor of modern
369 humans and Neanderthals (Fig. 3). We also uncover one other instance of anagenesis in this
370 clade. Opinions are divided as to whether *H. antecessor* represents a direct ancestor of later
371 hominin species or is an evolutionary dead end (Bermúdez de Castro et al. 1997; Stringer 2012;
372 Dembo et al. 2015), but our results provide support for combining *H. antecessor* and *H.*
373 *heidelbergensis* into a single lineage. This suggests a long episode of anagenetic evolution
374 immediately prior to the divergence between modern humans and Neanderthals.

375 Overall, our reconstruction of relationships among later species of *Homo* immediately
376 preceding and encompassing modern humans and Neanderthals supports the hypothesis that *H.*
377 *heidelbergensis* is directly ancestral to both modern humans and Neanderthals. This result
378 differs from the hypothesis supported by the analysis performed by Dembo and colleagues
379 (Dembo et al. 2015), and is instead more consistent with an earlier exploratory statistical analysis
380 (Mounier et al. 2009), and with the position frequently suggested by paleoanthropologists
381 (Rightmire 1998; Stringer 2012; Buck and Stringer 2014). While previous phylogenetic analyses
382 have yielded results that equivocate or disagree with the common interpretation of *H.*
383 *heidelbergensis* as the last common ancestor of modern humans and Neanderthals, our analysis
384 shows that the consideration of direct ancestry can generate statistical support for phylogenetic
385 results that conform more closely to positions generated through researchers' subjective
386 interpretations and exploratory data analyses. This finding supports a general argument against
387 the use of cladistic and phylogenetic methods that are restricted to bifurcating relationships in
388 fossil taxa, where the possibility of variability in evolutionary mode (i.e., occurrence of both

389 anagenesis and cladogenesis) is at odds with an assumption that evolution proceeds by
390 cladogenesis alone (Fig. 2).

391 Our results differ markedly from previous phylogenetic studies seeking to reconstruct
392 hominin phylogeny using probabilistic and cladistic methods. In key regions of the tree, results
393 achieved under our method reveal support for hypotheses more consistent with many qualitative
394 interpretations of hominin relationships, demonstrating the importance of explicitly
395 accommodating anagenesis in the phylogenetic reconstruction of fossil taxa. This may explain
396 some of the historical difficulty in reconciling paleontological interpretations of hominin
397 relationships with cladistic results. For instance, Dembo and colleagues' results are inconsistent
398 with earlier suggestions that *Au. anamensis* and *Au. afarensis* are chronospecies differentiated
399 through anagenesis. However, by considering ancestor-descendant relationships and
400 incorporating temporal data, our analysis reveals that a linked *Au. anamensis*-*Au. afarensis*
401 lineage is the arrangement most strongly supported by the data. Generally, this suggests that
402 cladograms and strictly bifurcating phylogenies may be inadequate when describing evolutionary
403 relationships between fossil taxa, and so ancestor-descendant relationships should be considered
404 during topological inference. Further, we argue that explicit testing of ancestor-descendant
405 relationships is important even in cases where bifurcating trees are not wholly misleading, as
406 their omission precludes us from considering the full range of possible evolutionary scenarios.
407 Although previous studies addressing hominin phylogeny using probabilistic methods represent a
408 significant step forward in weighing alternative evolutionary hypotheses, we suggest that their
409 phylogenetic reconstructions have suffered from methodological limitations that were not
410 generally perceived. We suggest that overcoming these limitations can provide a substantial step
411 forward in closing the gap between the paleobiologists' interpretations and previous cladistic and

412 phylogenetic results. In particular, we show through our analyses that the apparent discordance
413 between quantitative and qualitative assessments of evolutionary relationships can be reconciled
414 by extending phylogenetic models to explicitly accommodate anagenesis.

415

416 *Ancestors, anagenesis, and evolutionary processes.* Our method does not seek to distinguish
417 between speciation modes at a mechanistic level. As noted by Fisher (2008), overlap between the
418 extinction and origination times of taxon pairs does not necessarily preclude an ancestor-
419 descendant relationship. Instead, it is possible for ancestral and descendant lineages to coexist.
420 This reality may complicate the identification and evolutionary interpretation of ancestor-
421 descendant relationships from temporal data alone. Doing so requires diversification and
422 preservation models that contain additional parameters that quantify completeness of the fossil
423 record. Such models are currently implemented in the *cal3* time-scaling method, which seeks to
424 distinguish between splitting, budding, and anagenesis from a cladogram with a fixed topology
425 (Bapst and Hopkins 2016). Our approach is distinct both theoretically and operationally from
426 *cal3*, instead relying most heavily on morphological evidence to weigh the likelihood of
427 ancestor-descendant relationships without considering the completeness of fossil sampling. At
428 the population level, one might expect some temporal overlap between ancestral and descendant
429 taxa undergoing anagenetic change, especially if the participants are widely distributed
430 geographically. As a result, even if the temporal ranges corresponding to taxa identified as
431 ancestor-descendant pairs are discovered to slightly underestimate the time of coexistence, the
432 inference may simply highlight the fuzziness in the taxonomic placement of fossils belonging to
433 lineages undergoing continuous transformation and in discerning between anagenesis and
434 evolutionary budding given incomplete sampling (Fig. 4). This interpretation is consistent with

435 previous authors' treatment of temporal ranges when identifying anagenesis between taxa, which
436 have allowed a period of overlap between putative ancestor-descendant pairs (Aze et al. 2011;
437 Strotz and Allen 2013).

438 We use the term 'ancestor' modelled loosely after Gingerich (1979). Ancestors identified
439 through our method represent collections of samples possessing a suite of morphological
440 character states that is not sufficiently differentiated from a single or a set of subsequently
441 occurring samples to warrant assignment to distinct lineages. In our usage, we consider
442 anagenesis as any evolutionary change occurring along these serially linked phyletic lineage
443 segments. Thus, the taxonomic and phylogenetic units of analysis are fundamentally important to
444 the formulation and interpretation of our results. Hominin taxa are often represented by only one
445 or a small number of samples, and the number of species may be overestimated (White 2003).
446 This may complicate the ability to meaningfully characterize phylogenetic relationships from a
447 precise mechanistic view. Nevertheless, morphological and temporal data can be combined to
448 summarize the relative support for anagenetic and cladogenetic patterns in the inheritance of
449 observed character states (i.e. even in cases where distinctiveness may not be at the species
450 level).

451 Under our method, ancestor-descendant relationships might be interpreted either as true
452 anagenesis (i.e., a single population undergoing gradual transformation), or as some form of
453 budding cladogenesis. Previous researchers have argued that true anagenesis is rare compared to
454 budding when analyzing the fossil records of densely-sampled marine invertebrate lineages using
455 more complex preservation models (Bapst and Hopkins 2016). Nevertheless, we suggest that
456 distinction between these two modes may often be impossible in terrestrial vertebrate lineages
457 with large sampling gaps. For example, our results among early hominin species include multiple

458 inferred direct ancestors, but the large gaps in stratigraphic sampling throughout this region of
459 the tree hamper the ability to determine whether these relationships represent true anagenesis or
460 budding that has been obfuscated by poor sampling.

461 Instead of relying upon hope that more complex preservation models are robust to wide
462 sampling gaps, our method disregards the completeness of sampling to evaluate the support for
463 ancestor-descendant pairs using morphology. Although temporal data occupy an important place
464 in our approach, they are largely used as a guide to constrain the set of possible ancestors and
465 descendants and to provide additional insight when morphological data are equivocal. Coarsely
466 speaking, our approach focuses on patterns in morphological differentiation and lineage
467 *disparification*, while approaches such as *cal3* model lineage *diversification*. Further empirical
468 and simulation-based work is needed to determine the relative merits of methods of testing
469 ancestor-descendant relationships, such as *cal3*, that explicitly focus on diversification patterns,
470 and ours, which weighs morphological patterns more heavily. We speculate that their relative
471 accuracy may depend largely on the completeness of sampling in the rock record and the
472 correlation strength between morphological change and lineage diversification, although other
473 factors may also be important.

474 The scales at which phylogenetic data are sampled may further complicate mechanistic
475 evolutionary interpretations. Morphological character matrices often lack samples across the
476 entire stratigraphic range of each taxon, and so generally assume morphological stasis within
477 lineages. It is therefore often impossible to observe gradual morphological change within and
478 between taxa. These considerations might cause anagenetic relationships identified here to
479 represent either true anagenesis or some form of ‘pseudo-anagenesis’, where stratigraphic and
480 morphological data appear consistent with anagenesis but the persistence of the ancestor has not

481 been sampled. The ancestor-descendant relationships identified by our method may be
482 interpreted in several ways. As sampled, these results may be roughly conceived as anagenesis in
483 the sense that the mode of evolutionary change between taxa is indistinguishable from evolution
484 occurring along a single lineage, depending upon the completeness of sampling and the degree to
485 which morphological disparity correlates with true biological species diversity. This
486 interpretation is consistent with historical usage by paleobiologists (Gingerich 1979; Smith 1994;
487 Levinton 2001). Thus, our approach seeks to reveal the extent to which existing cladistic and
488 temporal data can provide evidence for non-branching evolutionary modes and does not seek to
489 resolve conceptual issues that may stem from incomplete sampling, lineage diversification, or
490 population-level evolutionary change. Regardless of the fine-scale evolutionary interpretation,
491 failure to accommodate phyletic change and ancestor-descendant relationships when inferring
492 phylogenetic relationships can generate views of evolutionary history that are positively
493 misleading in the sense that incorrect results cannot improve with the addition of new data.

494 *Some practical methodological considerations.* Concerns regarding the accuracy of probabilistic
495 approaches have been raised, stemming from the reliance of these methods on the overly
496 simplistic Lewis Mk model of morphological evolution (Goloboff et al. 2017). These critics
497 advocate the use of cladistic methods, arguing that Markov models inadequately capture the
498 complexities of morphological evolution. Although we agree that existing substitution models
499 oversimplify these processes, our results suggest that the accommodation of ancestor-descendant
500 hypotheses in probabilistic methods can improve the fidelity of phylogenetic reconstructions,
501 even when Lewis Mk is used as the underlying model of morphological change. As a result,
502 concerns regarding the adequacy of existing morphological substitution models may be partially
503 alleviated by considering hypotheses of direct ancestorship. This is supported by simulation

504 work showing that stratocladistics outperforms cladistics in topology reconstruction (Fox et al.
505 1999). Further exploration is needed to demonstrate more thoroughly the limitations of our new
506 approach, which builds upon stratocladistics by incorporating the benefits of probabilistic
507 analyses, including 1) more explicit statements of the assumptions involved, and 2) the ability to
508 weigh competing models using modern inferential criteria.

509 The method we describe seeks to enhance understanding of the fossil record by explicitly
510 testing support for existing hypotheses of direct ancestorship while attempting to make more
511 explicit assumptions than stratocladistics or recently developed Bayesian methods. Although it
512 shares features with recent methods that use mechanistic evolutionary models in a Bayesian
513 context to infer ancestral relationships (Zhang et al. 2016), our approach is intended as a
514 foundational, minimally complex framework for exploring the behavior of probabilistic models
515 to evaluate support for anagenesis in temporal and morphological data. As such, our method
516 should be viewed as a complement to, rather than a simplification of, existing Bayesian
517 approaches. That is, our method encourages examination of the informativeness of the data
518 without the increased complexity of assessing prior probabilities. Our method further differs
519 from both existing Bayesian and parametric APT approaches by explicitly omitting
520 diversification parameters and instead placing morphological data in a central role when
521 evaluating hypotheses of direct ancestry. In doing so, temporal data help to delineate the set of
522 possible ancestors and play an important role in measuring the fit of candidate trees to the
523 observed stratigraphic record. Our method does not seek to reconstruct diversification processes,
524 and instead focuses on identifying hypotheses that best describe only the information contained
525 within morphological and temporal datasets. Assessment of information contained within
526 datasets and tests of hypotheses can also be achieved using Bayesian approaches (Lewis et al.

527 2016), but likelihoodist approaches such as ours streamline these procedures by reducing
528 complications presented by prior probabilities and Bayesian Markov-chain Monte Carlo
529 sampling.

530 Although Bayesian methods can be beneficial in certain circumstances, our method
531 simplifies identification of anagenetic hypotheses using evolutionary and stratigraphic models.
532 We observe that the likelihood surface surrounding certain nodes may possess low peaks (Table
533 1), which likely results from sparse sampling and relatively low information in the
534 morphological characters. Since Bayesian approaches often average results across this surface, it
535 is possible that they may fail to capture those relationships best supported by the data by
536 including information from weakly supported hypotheses. This is of greater concern in
537 paleontological than neontological data because the increased abundance of molecular data is
538 often likely to result in more clearly defined peaks in the likelihood surface. In cases where
539 information is sparse, likelihoodist approaches such as ours offer the benefit of filtering through
540 noisy and equivocal signal to reveal the hypothesis best supported by the data. Although these
541 benefits are also achievable through Bayesian approaches, additional caution must be taken to
542 select priors that do not dominate weakly informative data. In addition, careful thought should be
543 given when summarizing the posterior/likelihood surface. Averaging across a relatively flat
544 surface might yield poor results (Yang and Zhu 2018), while the comparison of individual point
545 estimates, as is done here, may more clearly shed light on models best supported by the data
546 while clearly capturing their relative support.

547 *How can we proceed?* Anagenesis and splitting cladogenesis were most pertinent to our analysis
548 of hominin evolution, and the straightforward dichotomy between these simplified the
549 assumptions and interpretation of our tests. Our approach may need to explicitly accommodate

550 budding before being applied to groups with very dense fossil records. However, the assumptions
551 required, which may often include morphological stasis within lineages, may make application to
552 some phylogenetic datasets impractical. This is especially true in cases such as hominins, for
553 which the fossil record implies large sampling gaps, and characters representative across
554 stratigraphic ranges are often sampled from only a single individual. Expansions of our approach
555 through implementation of new models will further test the implications of existing
556 paleontological datasets for reconstructing complex evolutionary and geologic processes over
557 deep timescales. We hope that the example provided here will encourage integration of more
558 diverse evolutionary modes into phylogenetic methods yielding better explanations of temporal
559 patterns in critical parts of life's history.

560 As we emphasize above, the approach described here should be viewed as an attempt to
561 explore the capability of phylogenetic methods to identify the signal of anagenesis using existing
562 models to interrogate morphological and stratigraphic data. In doing so, we acknowledge that
563 there are many complicated biological and geological factors that could be incorporated into this
564 framework. For instance, previous researchers have accommodated heterogeneity in fossil
565 preservation rates across time and among lineages (Foote 1997; 2001; Gavryushkina et al. 2014).
566 There have also been several concerns raised in the literature regarding the adequacy of existing
567 models of discrete trait evolution to inform complex evolutionary scenarios (Goloboff et al.
568 2017; Brown et al. 2017). Alternative models that use continuous characters may help to improve
569 some of these issues (Felsenstein 1988; Goloboff et al. 2006; Parins-Fukuchi 2017). Moving
570 forward, elaborations making use of new data sources and models will only continue to improve
571 resolution of evolutionary patterns in the fossil record.

572 Finally, we acknowledge that our empirical results beg qualification. In particular, we
573 expect that future studies will generate a more comprehensive and authoritative view of hominin
574 evolution as improved data continue to become available. For instance, although we are currently
575 cautious about making strong statements concerning the ancestral position of *Sahelanthropus*
576 using this dataset, additional information may resolve this issue. This may be the case for several
577 other areas of the hominin tree, which may be better resolved as temporal and taxonomic gaps in
578 sampling are better filled by new discoveries. In addition, we concede the possibility that more
579 comprehensive automated tree searching routines may reveal support for hypotheses that we
580 failed to consider under our semi-automated approach. Therefore, instead of providing an
581 authoritative view of hominin evolution, our study provides a springboard for future studies by
582 showing that the accommodation of anagenesis can improve our view of the processes and
583 relationships underpinning the evolution of fossil taxa. Nevertheless, due to the improved
584 support and congruence of hypotheses that explicitly consider ancestor-descendant relationships,
585 we recommend that future phylogenetic studies in hominins avoid methods that only consider
586 bifurcating relationships. Future studies that build upon existing work in other taxa will also be
587 important to better characterize the extent to which this suggestion can be generalized across the
588 tree of life. Although the accommodation of directly ancestral relationships is especially relevant
589 in hominin taxa, for which hypotheses of anagenesis have been long entertained through
590 qualitative anatomical assessment, these results may also be important in other taxa. Further
591 empirical work will be needed to develop a better understanding of the extent to which the
592 consideration of direct ancestors can improve resolution of evolutionary patterns throughout the
593 fossil record.

594

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758 **Tables:**

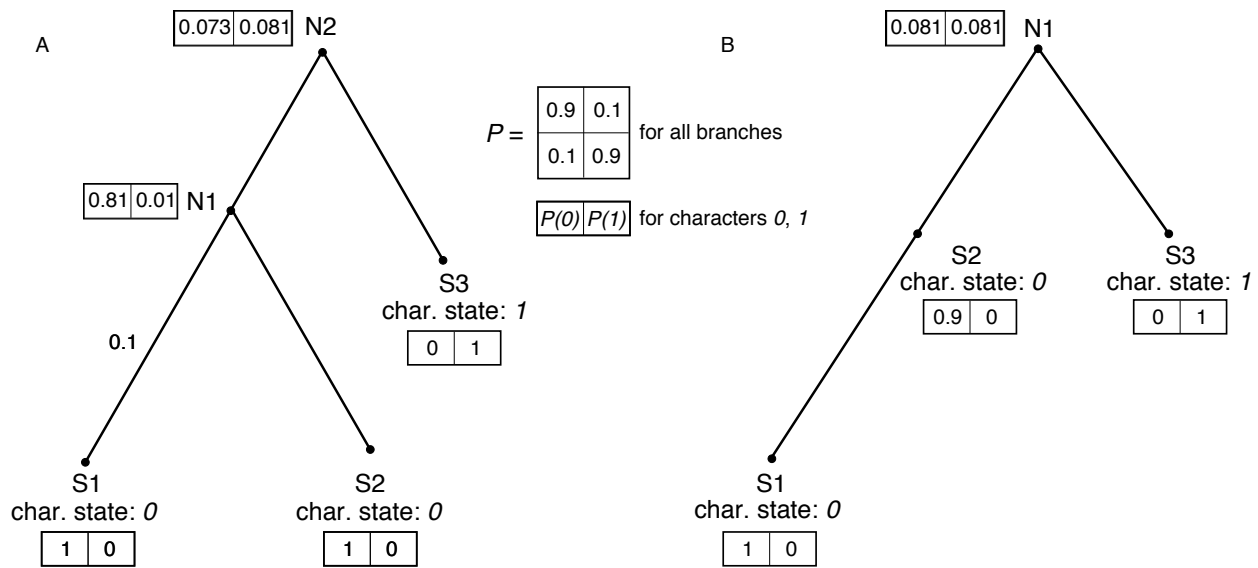
Hypothesis	AIC score
<i>Au. garhi</i> outgroup to <i>Paranthropus</i> and <i>Homo</i>	9271.11
<i>Au. garhi</i> directly ancestral to <i>Homo</i>	9264.30

759 **Table 1.** Support for alternative hypotheses regarding the placement of *Au. garhi*.

760

761 **Figures:**

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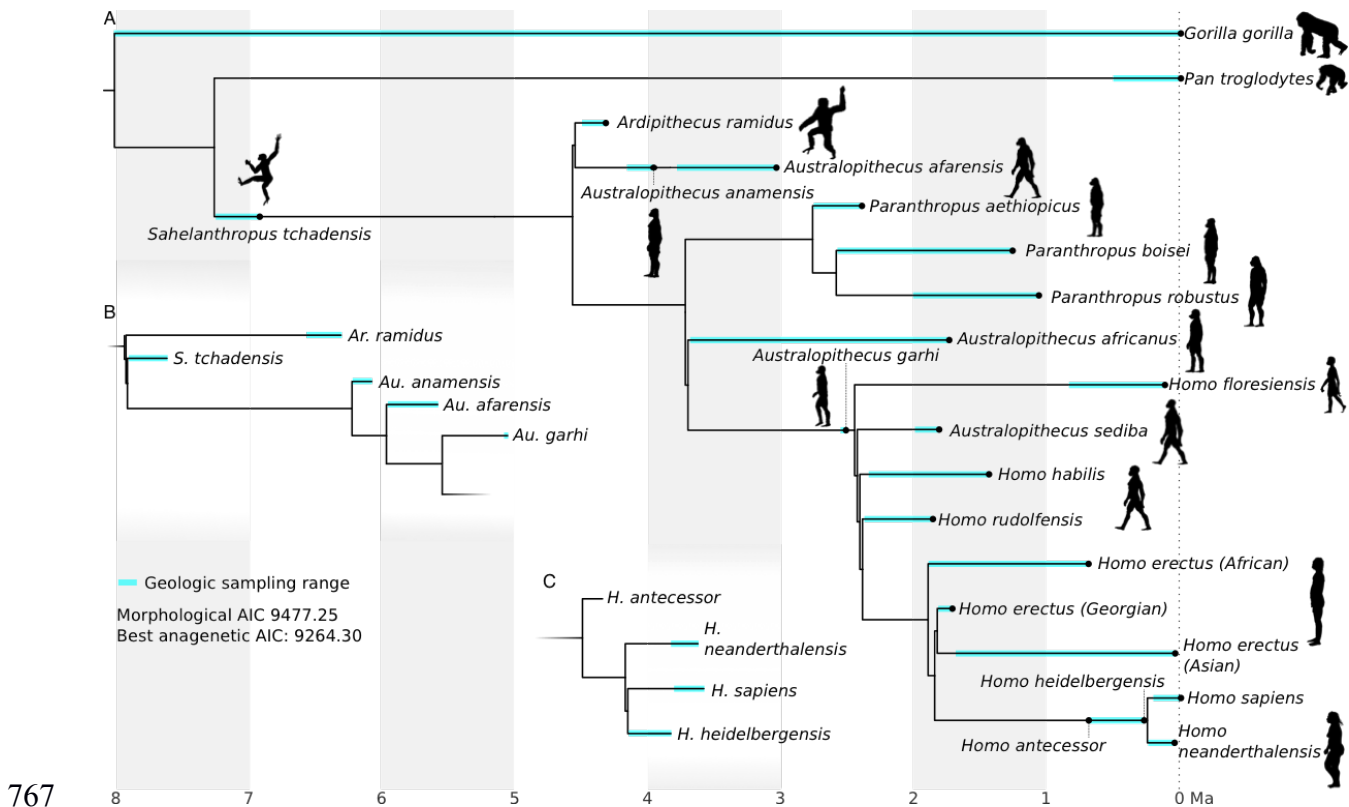


763

764 **Fig. 1.** Comparison between anagenetic and cladogenetic trees. A) Likelihoods are calculated on

765 bifurcating arrangements using the standard ‘pruning algorithm’. B) Anagenetic likelihoods are

766 calculated using a novel approach, where ancestral states may be known.



767

768 **Fig. 2.** Phylogenetic relationships between hominin species. A) Reconstruction with the best AIC

769 score when temporal data are considered alongside morphological data and anagenesis is

770 accommodated. B, C) Areas of the tree inferred from morphology alone that differ from

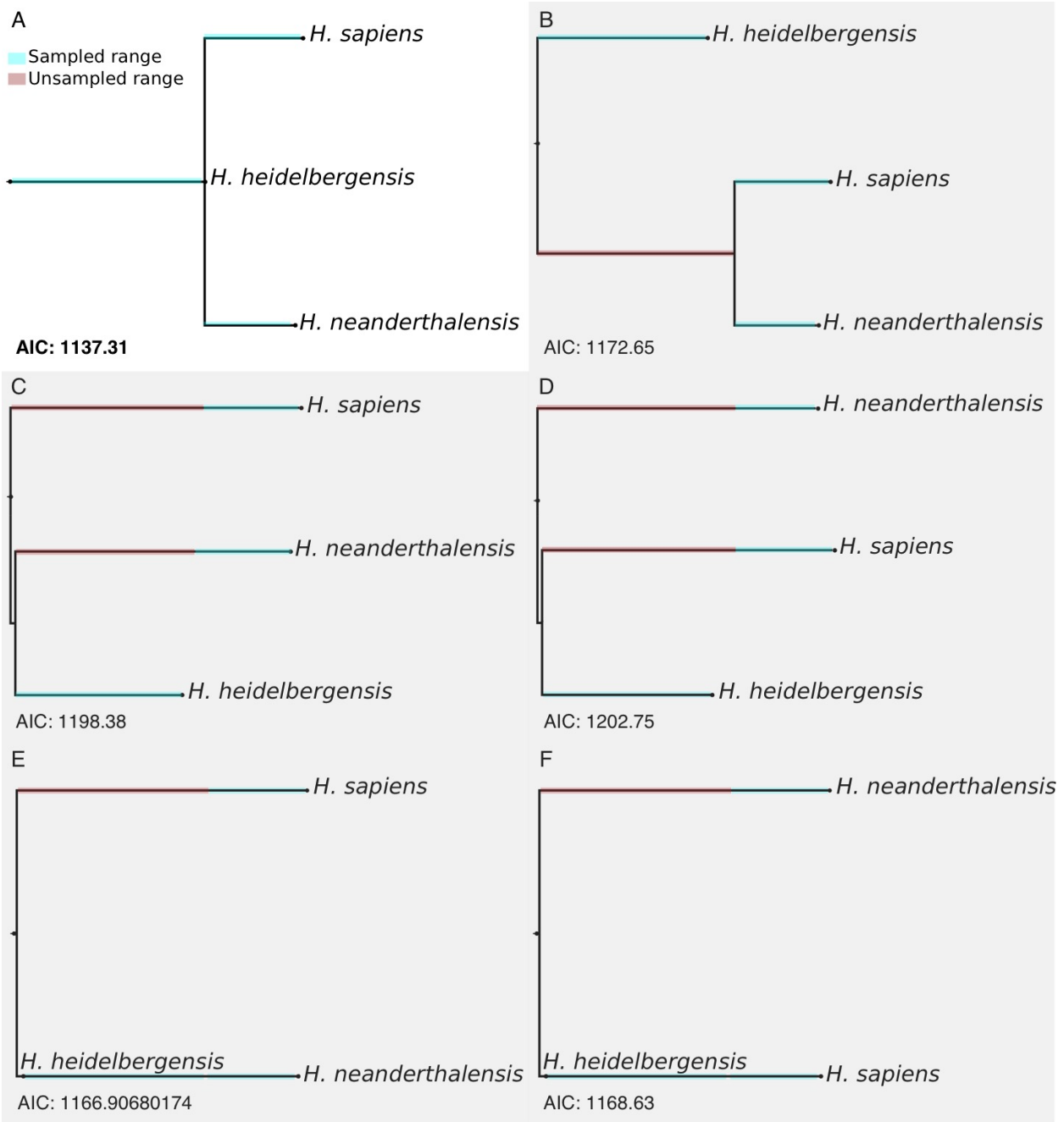
771 panel A. Both regions display misleading results when anagenesis is not considered. This

772 is reflected in the improvement in AIC observed in the preferred anagenetic topology.

773 Silhouettes obtained from phylopic.org.

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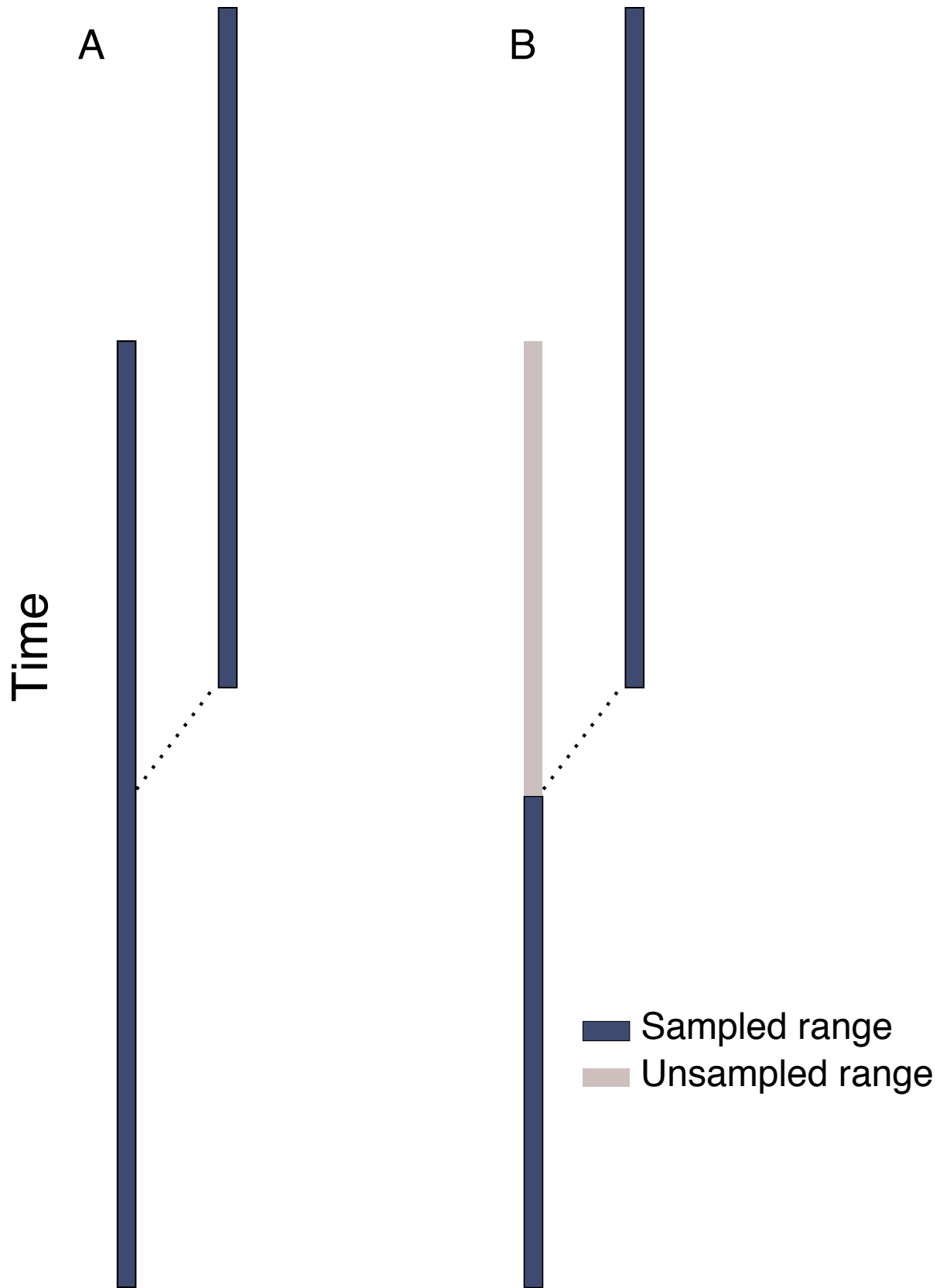
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Fig. 3. AIC scores calculated for each possible arrangement between *H. sapiens*, *H.*

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neanderthalensis, and *H. heidelbergensis*.



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Figure 4. A) Speciation mode interpreted as budding when sampling is complete. B) Incomplete

781 stratigraphic sampling may create an inability to distinguish between anagenesis and
782 budding when sampling is sparse.