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1 *Sequential trait evolution did not drive deep-time diversification in sharks*

2

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11

12 **Author contributions**

13 GG et FC designed the project. AM collected and analyzed the data with advice from GG and
14 FC. AM wrote the draft, with input from GG and FC throughout.

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36 ***Declaration of Competing Interest***

37 The authors declare that they have no known competing financial or personal interests that
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39

40 ***Data availability statement***

41 *Raw data:* <https://doi.org/10.6084/m9.figshare.24581718.v1>

42 *Code:* <https://github.com/Alexis-Marion/Sequential-trait-evolution-sharks>

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48

49 **Abstract**

50 Estimating how traits evolved and impacted diversification across the tree of life
51 represents a critical topic in ecology and evolution. Although there has been considerable
52 research in comparative biology, large parts of the tree of life remain underexplored. Sharks are
53 an iconic clade of marine vertebrates, and key components of marine ecosystems since the early
54 Mesozoic. However, few studies have addressed how traits evolved or whether they impacted
55 their extant diversity patterns. Our study aimed to fill this gap by reconstructing the largest
56 time-calibrated species-level phylogeny of sharks and compiling an exhaustive database for
57 ecological (diet, habitat) and biological (reproduction, maximum body length) traits. Using
58 state-of-the-art models of evolution and diversification, we outlined the major character shifts
59 and modes of trait evolution across shark species. We found support for sequential models of
60 trait evolution and estimated a small to medium-sized lecithotrophic and coastal-dwelling most
61 recent common ancestor for extant sharks. However, our exhaustive hidden traits analyses do
62 not support trait-dependent diversification for any examined traits, challenging previous works.
63 This suggests that the role of traits in shaping sharks' diversification dynamics might have been
64 previously overestimated and should motivate future macroevolutionary studies to investigate
65 other drivers of diversification in this clade.

66

67 **Keywords:** Concealed trait, elasmobranchs, hidden states, molecular dating, phylogenetic
68 comparative methods, trait-dependent diversification

69 **Introduction**

70 The heterogeneity in species richness and phenotypic disparity across the tree of life is a
71 striking feature. While some clades underwent long periods of phenotypic and ecological stasis
72 (Cabral et al., 2021; Davis et al., 2014; Maho et al., 2019), others experienced rapid
73 diversification (Turner, 2007; Grant & Grant 2002; Pinto et al., 2008). Evolutionary biologists
74 have long sought to explain how richness and disparity patterns vary over time. On the one
75 hand, the extreme species richness of some clades may be attributed to numerous and rapid
76 events of phenotypic diversification following the colonization of new habitats and through the
77 acquisition of key innovations (Simpson, 1953; Schluter, 2000; Alfaro et al., 2009). On the
78 other hand, mass extinction selectivity may explain why some clades are more depauperate and
79 functionally homogeneous than others (Monarrez et al., 2023). Ultimately, the heterogeneity in
80 diversification rates (speciation minus extinction) has shaped extant diversity patterns and
81 numerous studies have attempted to decipher the underlying factors of such heterogeneity.
82 Several studies have suggested that both abiotic forcing and biotic interactions (e.g. Benton,
83 2009; Ezard et al., 2011; Drury et al., 2016; Condamine et al., 2019) may be responsible for
84 extant diversity patterns with biological and ecological traits being key features to
85 understanding the diversification history of clades (e.g. Rabosky et al., 2013, Helmstetter et al.,
86 2023; Wiens, 2023). Over the last two decades, as phylogenetic data and comparative methods
87 became increasingly available, trait evolution models and trait-dependent diversification have
88 become major topics in macroevolution and macroecology (Maddison et al., 2007; Ng & Smith,
89 2014; Beaulieu & O'Meara, 2016; Helmstetter et al., 2023; Wiens, 2023). Yet,
90 macroevolutionary dynamics remain to be explored across a substantial portion of the tree of
91 life.

92 This statement applies to sharks, clade Selachimorpha, that form an iconic and speciose
93 group (~545 extant species; Ebert et al., 2021) of cartilaginous fishes (Chondrichthyes).

94 Roaming the oceans at least since the Triassic (201.4-251.9 million years ago [Myr], Cappetta,
95 2012), sharks have experienced numerous events of rapid diversification (Guinot et al., 2012;
96 Guinot & Cavin, 2016, 2020; Brée et al., 2022), but also clade-specific diversity decline
97 (Condamine et al., 2019), and large extinction events (Guinot & Cavin, 2016; Guinot &
98 Condamine, 2023). Sharks are highly morphologically diverse and display strong phenotypic
99 disparity as well as a wide range of ecotypes, from small deepwater ectoparasites (*Isitius*
100 *brasilliensis*) and giant filter-feeders (*Rhincodon typus*) to large pelagic macropredators
101 (*Carcharodon carcharias*) (Compagno, 1990; Weigmann, 2016) (Figure 1). Strikingly, some
102 phenotypic profiles appear to be strongly correlated with species richness. For instance, two of
103 the most speciose shark families, Pentanchidae and Etmopteridae, include species with highly
104 similar size range, maternal investment, habitat type, and diet (Ebert et al., 2021). Likewise,
105 Lamniformes, Hexanchidae, Ginglymostomatidae and Echinorhiniformes are among the most
106 depauperate extant clades, mostly represented by macropredators to top predators (Ebert et al.,
107 2021). As these particular phenotypes appear to have evolved independently in various shark
108 clades, while resulting in comparable species richness, trait evolution might, at least in part,
109 explain the current pattern of diversity across shark species. Furthermore, some traits like diet,
110 habitat, reproductive strategy, and size have been previously proposed as possible drivers of
111 diversification dynamics in other groups (e.g. Thomas et al., 2009; Price et al. 2012; Pyron &
112 Burbrink, 2014; Helmstetter et al., 2016; Recknagel et al., 2021; Liedtke et al., 2022; but see
113 Fitzjohn, 2010; Pyron & Burbrink, 2012; Román-Palacios et al., 2019). However, the role of
114 trait evolution on shark diversification remains poorly understood.

115 Few studies have attempted to decipher patterns of trait evolution and their putative link
116 with diversification dynamics in sharks, which might be explained by two main factors. First,
117 most knowledge on deep-time shark evolution comes from their dense fossil record, which is
118 mainly composed of isolated teeth (Cappetta, 2012). While dental characters serve as reliable

119 proxies for extrapolating the ecology of extinct clades (Guinot & Condamine, 2023; Cooper et
120 al. 2023), traits available for extinct species are limited in comparison with those observable
121 from extant species (parity modes, behavior, longevity). Namely, we lack direct fossil evidence
122 of phenotypic evolution for most traits. Second, as fossil trait data are rare, neontological data
123 and comparative methods might be the only available resources for studying the role of trait
124 over the diversification pattern of sharks. Still, such methods require calibrated phylogenies
125 and to date, only two extant timetrees for sharks have been reconstructed (Sorenson et al., 2014;
126 Stein et al., 2018).

127 Previous studies that attempted to decipher patterns of deep-time trait evolution and
128 diversification among sharks identified two pathways (filter-feeding and mesothermy) toward
129 gigantism (Pimiento et al., 2019), estimated that ancestral sharks were most likely oviparous
130 (Katona et al., 2023; Blackburn & Hughes, 2024), and that coral-reef habitats likely increased
131 speciation rates among Carcharhinidae (Sorenson et al., 2014). However, such studies relied on
132 frameworks neglecting rate heterogeneity throughout the phylogeny, which may impact model
133 selection (Herrera-Alsina et al., 2019; Boyko & Beaulieu, 2021). Furthermore, these analyses
134 used relatively small-sized (<55% of extant diversity) species-level phylogenies (Sorenson et
135 al., 2014; Stein et al., 2018), which is thought to have a critical effect on trait-dependent
136 diversification analyses (Davis et al., 2013; Helmstetter et al., 2023; Mynard et al., 2023).
137 Therefore, considerable progress remains to be achieved regarding the understanding of trait
138 evolution in sharks and their potential role in the diversification history of this clade.

139 Here, we study how some selected ecological (diet, habitat) and biological (body size,
140 reproduction) traits evolved across shark clades and whether they are linked with the observed
141 shark diversity pattern through a potential effect on diversification rates. We first reconstructed
142 the most exhaustive species-level shark phylogeny (~69% of species sampled), time-calibrated
143 with 16 vetted fossil calibrations. Second, we jointly estimated the tempo and mode of trait

144 evolution using cutting-edge comparative methods of trait evolution. Last, we tested whether
145 traits and their evolution across the shark phylogeny could represent one of the driving factors
146 for their observed extant diversity pattern.

147

148 **Materials and methods**

149 *Taxon sampling and molecular dataset*

150 We compiled a list of 545 valid shark species based on both the literature (e.g. Weigman,
151 2016; Ebert et al., 2021) and an exhaustive review of recently described species (e.g. Cordova
152 & Ebert, 2021 ; Ebert et al. 2021 ; Long et al., 2021 ; White et al., 2021 ; Ito et al., 2022 ; Ebert
153 & Jang 2022 ; Fricke et al., 2023 Weigmann et al., 2023 ; White et al., 2023a, White et al.,
154 2023b). The molecular dataset is composed of 16 genes, including 13 mitochondrial coding
155 genes: Cytochrome B, Cytochrome oxidase 1, 2, and 3, Nicotinamide adenine dinucleotide 1,
156 2, 3, 4, 4L, 5 and 6, ATP synthase subunit 6 and 8, two mitochondrial ribosomal genes: 12S
157 and 16S, and one nuclear coding gene: recombination activating gene 1.

158 Sequences from online databases are often prone to misidentification, and sharks are no
159 exception (Naylor et al., 2012). Such ambiguities regarding a sequence's origin may lead to
160 dramatic consequences in phylogenetic reconstructions. Consequently, we adopted a cautious
161 approach to thoroughly select molecular sequences, following a scoring method highlighted in
162 Supplementary Material S1. Selected sequences with corresponding scores and associated
163 accession numbers are presented in Supplementary Data S1. Following this method, we
164 collected molecular data for 374 shark species (68.6% of the extant diversity), along with four
165 ray species as outgroups. We performed gene alignments using MUSCLE 3.8.1551 (Edgar,
166 2004), examined each alignment visually, and concatenated sequences by species.

167

168 *Phylogenetic inferences and molecular dating*

169 We inferred phylogenetic relationships through a maximum-likelihood approach as
170 implemented in IQ-TREE 2.2.7 (Minh et al., 2020). We selected the best model of sequence
171 evolution using ModelFinder (Kalyaanamoorthy et al., 2017) in conjunction with partition
172 clustering setting codon positions for each protein-coding gene (*-MFP+MERGE* option). The
173 rearrangement of the trees is done by exchanging all nearest neighbours (*-allnni* option). Clade
174 support was assessed with 1,000 ultrafast bootstrap replicates (UFBS; Hoang et al., 2018), with
175 resampling of the alignment sites in the partitions. We considered strong branch support when
176 $UFBS \geq 95$ (Hoang et al., 2018). Preliminary tests showed outlier topologies and non-robust
177 clade support ($UFBS < 95$) in Squaliformes. We guided the topology search by forcing inter-
178 family relationships within the order (*-g* option) using the topology obtained from 172 ortholog
179 exon sequences by Straube et al. (2015).

180 We jointly estimated phylogenetic relationships and divergence times using a Bayesian
181 relaxed molecular clock calibrated with fossils through a node-dating approach. The shark fossil
182 record provides direct temporal evidence to inform the minimum age of several clades
183 (Sorenson et al., 2014; Stein et al., 2018). Still, fossils must be rigorously selected since the
184 fossil age and its taxonomic affiliation can severely affect the divergence time estimates (Ho &
185 Phillips, 2009; Sauquet et al., 2012). We mitigated this challenge by choosing fossil calibrations
186 following the recommendations described by Parham et al. (2012). We selected 16 calibration
187 points that met at least 4 out of 5 established criteria (**Table 1**, Supplementary Material S2,
188 Supplementary Data S2).

189 Using the same rationale as in the IQ-TREE analysis, we partially constrained
190 phylogenetic relationships by enforcing family relationships for Squaliformes, and by
191 informing BEAST with the output of IQ-TREE, enforcing the monophyly of calibrated nodes,
192 and constraining the monophyly of Galeomorphii and Galeoidea. We performed divergence
193 time estimations of the shark phylogeny under the Bayesian framework of BEAST 1.10.4

194 (Suchard et al., 2018). Using BEAUti, we filled in the data, parameters, and prior distributions
195 to generate input files for BEAST. Molecular partitions were determined and grouped according
196 to ModelFinder from the IQ-TREE analysis. We used an uncorrelated relaxed molecular clock
197 model with a lognormal distribution (UCLD), which assumes that evolutionary rates can vary
198 for each branch independently of neighboring branches (Drummond et al., 2006). The
199 branching tree prior was set to a constant birth-death model with incomplete taxonomic
200 sampling (Stadler, 2009), informed with a sampling fraction of 0.686. The choice of this model
201 rather than a pure-birth model without extinction was motivated by results showing that such
202 priors can considerably affect age estimates in ancient clades (Condamine et al., 2015). The
203 birth-death process was informed with the following priors: a uniform prior between 0 and 2
204 with a starting value of 0.1 for the mean growth rate, and a uniform prior between 0 and 2 with
205 a starting value of 0.5 for the relative death rate. We also used an exponential prior with a mean
206 of one-third for the standard deviation of the UCLD model, a uniform prior between 0 and 0.5,
207 and an initial value of 0.1 for the mean of the UCLD model. Here, we used a uniform
208 distribution as a prior for the fossil calibrations. The rationale for using uniform priors over
209 other prior distributions is motivated by two reasons. First, estimating divergence times from
210 non-uniform prior is highly sensitive to parameter choice, as divergence estimates may vary by
211 hundreds of millions of years (Warnock et al., 2012; 2015). Subtle changes in the parameters
212 describing the priors have a detrimental effect on the posterior divergence time estimates. Since
213 there is often no material basis for choosing among the parameters or the distributions they
214 control, the time priors in most studies are unwarranted. Such parameters are often set
215 arbitrarily, with few justifications provided (Sauquet, 2013; Warnock et al., 2012; Nguyen &
216 Ho, 2020). Second, the placement of a fossil calibration is critical when dating a tree, and
217 ideally, evolutionary biologists should aim to use well-preserved and complete fossils when
218 performing a molecular dating analysis, as it can dramatically impact its phylogenetic

219 placement and further dating (Ho & Philipps 2009). Unfortunately for shark species, although
220 the fossil record is dense, it is mostly composed of tooth remains and complete fossils are scarce
221 (Cappetta, 2012), which makes the placement of a fossil to a particular clade for calibration
222 difficult. As most probability densities (lognormal or exponential) put strong weight on the age
223 of a fossil (Ho & Phillips, 2009), misplaced calibrations may have an impact on dating at large
224 scales. Conversely, as the uniform density is conservative, it is more forgiving regarding the
225 placement of the calibration. Accordingly, we have not used non-uniform priors in this study
226 group.

227 We performed eight independent BEAST runs of three Monte Carlo Markov chains
228 (MCMC) for 100 million generations. We sampled parameters and trees every 10,000
229 generations. The convergence and the burn-in period were determined with effective sample
230 size (ESS) and graphically for each run using Tracer 1.7.1 (Rambaut et al., 2018). We
231 considered that each run converged when the ESS of the posterior likelihood and 95% of
232 parameters were above 200. The amount of burn-in for each run was assessed visually for each
233 BEAST run (varying between 5 and 60%). We combined all the runs with LogCombiner 1.10.4
234 (Suchard et al., 2018). Finally, a maximum clade credibility tree was computed with
235 TreeAnnotator 1.10.4 (Suchard et al., 2018) to estimate median ages and 95% height posterior
236 density (HPD) for all nodes.

237

238 ***Trait data collection***

239 We compiled ecological and biological trait data for every shark species based on a
240 detailed review of the literature (Supplementary Data S3). Following Violle et al. (2007), we
241 defined a trait as a feature only measurable at the individual level and which does not require
242 additional information from other organizational levels or environments. Therefore, this
243 definition encompasses maximum body length, reproductive mode, trophic level, diet, and the

244 maximum number of offspring per female. We also considered habitat, which is not a trait *per*
245 *se*, but a proxy for multiple unmeasured traits (behavior, physiology). We retained maximum
246 body length, reproductive mode, habitat, and diet as they could be obtained for most species at
247 global scale. Other traits were investigated, such as trophic level and maximum number of
248 offspring per female per litter but were neither sufficiently represented nor reliable (Martin &
249 Malleffet 2022, Ebert et al., 2021).

250 We discretized body length data using model-based clustering relying on a Gaussian
251 mixture model with the *Mclust* function of the R package “mclust” 6.0.0 (Fraley et al., 2012).
252 We inferred the optimal number of categories using the Bayesian information criterion. The
253 best-fitting model was a three-class model with categories herein defined as ‘small’, ‘medium’,
254 and ‘large’ (Supplementary Figure S1). Dividing a continuous trait into discrete categories may
255 result in separating taxa with highly similar ecologies. However, we argue that for our dataset
256 such a categorization does not represent an issue because closely-related species are almost
257 always clustered in the same size class (*e.g.* genera *Apristurus*, *Etmopterus*, *Mustelus*,
258 *Centrophorus*). Furthermore, while some trait-dependent models can incorporate continuous
259 data (*e.g.* QuaSSE; FitzJohn 2010), they do not account for hidden traits yet. These models are
260 therefore more sensitive to false positives or model misspecifications (Herrera-Alsina et al.,
261 2019).

262 Sharks possess a wide variety of reproductive modes with at least six identified types,
263 ranging from oviparity to placental viviparity (Wourms, 1977; Wourms & Lombardi, 1992;
264 Compagno, 1990; Parsons et al., 2008; Ebert et al., 2021). To avoid overparameterization in
265 subsequent analyses, we retained four modes of reproduction: oviparity (egg-laying in the
266 external environment), lecithotrophic viviparity (retention and hatching of eggs in the maternal
267 uteri, without further nutrient supply), placental viviparity (development of embryos in the
268 maternal uteri where the placenta creates a trophic link between the mother and the embryos),

269 and oophagy *sensu lato* (retention and hatching of eggs in the maternal uteri, consumption of
270 unfertilized eggs and embryos) (Supplementary Figure S2). Still, we purposefully did not
271 consider histotrophy as a reproductive strategy (limited maternal input, usually through uterine
272 secretion; Hamlett et al., 2005), but instead considered histotrophic species as yolk-sac
273 viviparous. The limit between yolk-sac viviparity and histotrophy is tenuous (Compagno, 1988;
274 Musick et al., 2005), and therefore we preferred to avoid identification issues by considering
275 these two states as one.

276 We then defined the following five habitat categories: deep water (-200 m and below),
277 outer continental shelf, shallow-water reefs, coastal settings, and open ocean (Supplementary
278 Data S3). Finally, we extracted diet data using the trait database from Pimiento et al. (2023),
279 who considered six diet categories (Supplementary Data S3). However, these categories
280 presented highly contrasted tip ratios (one character state over- or underrepresented, e.g.,
281 plankton and invertebrates/fishes *sensu* Pimiento et al. 2023), which is known to affect the
282 accuracy and precision of parameter estimates (Davis et al., 2013). We therefore categorized
283 the diet data of Pimiento et al. (2023) into three groups: ‘Invertebrate-feeders’ (Microphagous
284 and Invertebrates), ‘Mesopredators’ (fishes-invertebrates), and ‘Macropredators’ (fishes,
285 sharks, and tetrapods) (Supplementary Data S3). We coded unavailable data as ‘NA’ for species
286 that could not be assessed for specific traits.

287

288 ***Modeling trait evolution***

289 We tested scenarios of trait evolution with the *corHMM* function in the R package
290 “corHMM” 2.8 (Boyko & Beaulieu, 2021). CorHMM can model discrete trait evolution and
291 allows distinct transition rate classes on different parts of a phylogeny by treating rate classes
292 as hidden rates. Thus, corHMM offers a powerful framework for testing hypotheses of trait
293 evolution, as it does not detect false signals where there are none. In our case, the introduction

294 of such rate classes would help determine whether we could reliably find support for our
295 sequential models against a set of heterogeneous models. For each trait, we implemented an
296 equal rate (ER) model, a symmetric rate (SYM) model, and an all rates differ (ARD) model. In
297 addition to these models, we implemented an alternative sequential model for each trait
298 (denoted ARD_{seq} , SYM_{seq} , and ER_{seq} ; Supplementary Figure S3). For each model, we
299 performed the analysis with one, two, and three rate categories. We first tested whether the
300 transition between small-sized to large-sized sharks was plausible. We then verified the
301 prediction regarding parity evolution, which stipulates lecithotrophic viviparity is an obligate
302 intermediate state between oviparity and derived forms of viviparity (Wourms & Lombardi,
303 1992). We also tested whether direct transitions from distinct habitats were sequential (direct
304 transition to Deepwater, Reefs, or Oceanic settings). Finally, we tested whether transitions
305 between invertebrate-feeders and macropredators were sequential. We tested the fit of each
306 model with AICc, ΔAIC , and ωAIC , using the *akaike.weights* function of the R package “qpcR”
307 1.4.1 (Ritz & Spiess, 2008).

308

309 ***Linking trait and diversification dynamics***

310 To test whether diversification dynamics were trait-dependent in sharks and to estimate
311 ancestral states, we implemented seven Several Examined and Concealed States-Dependent
312 Speciation and Extinction (SecSSE) models using the *cla_secsse_ml* function in the R package
313 “SecSSE” 3.0.0 (Herrera-Alsina et al., 2019). We choose SecSSE since such models can
314 account for concealed traits in the estimation of diversification processes with a multi-state trait.
315 Furthermore, SecSSE is part of the SSE (States-dependent Speciation and Extinction) model
316 suite, which jointly estimates both the parameters underlying trait evolution and diversification.
317 Such models are robust to the biases highlighted by Maddison (2006), who stated that in the
318 presence of a trait state that confers higher diversification, failure to account for it will lead to

319 an overestimation of transitions rate from and to this character state. MuHiSSE is another
320 implementation of the SSE models accounting for multiple traits with hidden states, but more
321 suited for a four-state case scenario (two binary traits: Nakov et al., 2018).

322 The implementation of concealed traits offers alternative models that reduce the risk of
323 wrongly choosing a state-dependent diversification model over alternative ones (Beaulieu &
324 O'Meara, 2016; Herrera-Alsina et al., 2019; Helmstetter et al., 2023). In this sense, SecSSE
325 models may not detect any signal if the examined trait only weakly explains diversification
326 dynamics (Herrera-Alsina et al., 2019). We defined models that could be either constant rate
327 (CR), examined trait-dependent (ETD) or concealed trait-dependent (CTD). ETD models test
328 for rate heterogeneity that is associated with the focal trait, which is equivalent to the MuSSE
329 model (FitzJohn, 2012). Conversely, CTD models test for rate heterogeneity associated with
330 the concealed trait. Lastly, CR models test for constant rates, which is the true null hypothesis
331 (i.e. diversification dynamics cannot be explained by any traits). For CTD and ETD models, we
332 created three sets of models: one solely estimating speciation rates, one estimating extinction
333 rates, and one estimating net diversification. For a medium-size phylogeny (374 species),
334 estimating more than 15 parameters is not advised (Etienne, 2023, *pers. comm.*). To avoid
335 overparameterization and keep the likelihood parameter space low, we put the same constraints
336 on transition rates as the best-fitting corHMM model for each trait, while still jointly estimating
337 transition and diversification rates. We disallowed double transitions and estimated one shared
338 parameter for simple transitions between hidden states. We defined three concealed states for
339 maximum body-size, four concealed states for reproduction, five for habitats, and three for diet
340 as it is considered best practice to have as many concealed states as there are examined states
341 (Herrera-Alsina et al., 2019). Following Herrera-Alsina et al. (2019), we used three sets of
342 initial parameters to avoid finding a local optimum. One set was estimated using the standard
343 birth-death model (*bd_ML* function in the R package “DDD” 5.2.2; Etienne et al., 2012), one

344 was halved, and the other was doubled. For each trait state, we computed the ratio of sampled
345 diversity in the tree out of the total extant diversity using our trait database (Supplementary
346 Data S3). We assessed the relative fit of each alternative model with AICc, Δ AIC, and ω AIC.
347 Following Helmstetter et al. (2023), all characteristics for each model are available in
348 Supplementary Data S4. Since corHMM and SecSSE have different implementations and
349 assumptions, comparing the results of both models will increase the reliability of our
350 interpretation. We performed ancestral state estimation using the function *secsse_loglik*
351 (“SecSSE” 3.0.0) based on the best-fitting diversification model and by extracting the marginal
352 ancestral state estimate for the best-fitting trait evolution model, for SecSSE and corHMM,
353 respectively.

354

355 *Sensitivity analyses*

356 We performed analyses of trait evolution on a consensus tree. However, comparative
357 analyses are sensitive to topology and dating uncertainties. We re-ran each corHMM and
358 SecSSE analysis on a posterior distribution of 100 trees sampled from the post-burn-in
359 distribution of BEAST to consider these uncertainties. We assessed the significance of each
360 model by performing a non-parametric alternative of the repeated measure ANOVA (Friedman
361 test) comparing the AICc of each model and then performing pairwise comparisons of each
362 model with a paired signed-rank Wilcoxon test using the R package “rstatix” (Kassambara,
363 2023) where we reported the T statistic and *p*-value.

364

365 **Results**

366 *Dated species-level shark phylogeny*

367 The concatenated molecular matrix of 16 markers contains 15,815 nucleotides, of which
368 7,982 are informative sites. ModelFinder estimated 16 independent molecular partitions for the

369 dataset. Generally, nucleotide sequence evolution models correspond to complex GTR-type
370 models with gamma distribution (+ Γ) and proportion of invariant sites (+I). After multiple
371 independent replicates, the most likely topology obtained with IQ-TREE is well resolved and
372 robust (**Figure 2**), with more than 85.3% of the nodes being strongly supported (UFBS \geq 95)
373 and 67.3% of nodes having maximum support (UFBS = 100). Mean and median node supports
374 are 96.53 and 100, respectively (Supplementary Figure S4). This phylogeny represents 374
375 species (68.62 % of all extant diversity) sampled.

376 The phylogeny of sharks is divided into two major clades: Galeomorphii (UFBS = 100)
377 and Squalomorphii (UFBS = 100). All orders are monophyletic with high support for intra and
378 inter-clade relationships (**Figure 2**). Still, the placement of the Echinorhiniformes is poorly
379 supported (UFBS < 95), which is in line with the alternative topological hypotheses in the
380 literature (Naylor et al., 2012; Sorenson et al., 2014; Stein et al., 2018; Supplementary Figure
381 S5). Of the 27 non-monotypic families defined in Ebert et al. (2021) and sampled in this study,
382 three are not monophyletic. The Somniosidae (Squaliformes) are found paraphyletic, with
383 representatives of the family Oxynotidae being nested within. All nodes within the
384 Somniosidae/Oxynotidae clade are strongly supported (UFBS = 99). The family Scyliorhinidae
385 (Carcharhiniformes) is paraphyletic and divided into three strongly supported groups (UFBS =
386 100) found as successive early offshoots within Carcharhiniformes: the first offshoot includes
387 members of the family Scyliorhinidae, the second the family Atelomycteridae and the last,
388 family Pentanchidae *sensu stricto*. The family Proscyliidae (Carcharhiniformes) is not
389 monophyletic as it contains representatives of the family Pseudotriakidae whose placement is
390 strongly supported (UFBS = 100). Weakly supported nodes (UFBS < 95) are mainly found in
391 four families: Squalidae (Squaliformes), Triakidae (Carcharhiniformes), Pentanchidae, and
392 especially Carcharhinidae (Carcharhiniformes), the latter having short internal branches
393 (**Figure 2**).

394 Combined Bayesian inferences with BEAST converged with high ESS (>200) values for
395 95% of the parameters (Supplementary Data S5). Comparisons of prior and posterior ages for
396 the 16 clades constrained by fossil calibration show low sensitivity of the posterior distribution
397 given realized prior distributions (Supplementary Figure S6). After combining the eight
398 inferences, the resulting chronogram places the origin of sharks at 295.08 Ma in the Paleozoic,
399 in the early Permian (95% HPD = 266.19 - 320.71 Ma; **Figure 3**, Supplementary Figure S7,
400 **Table 1**). The two super-orders do not seem to have the same tempo of diversification, as
401 Galeomorphii diversified early in the Permian (median = 292.41 Ma; HPD = 267.86-320.26
402 Ma), while Squalomorphii diversified later in the Triassic (median = 241.93 Ma, HPD = 219.74-
403 267.96 Ma). Likewise, estimates of divergence times further show that all nine orders originated
404 at different times, with the Orectolobiformes and Carcharhiniformes being the first to diversify
405 (respectively: median = 247.55 Ma, HPD = 221.04-273.91 Ma, median = 198.29 Ma, HPD =
406 180.80-219.45 Ma), whereas most of the remaining orders diversified from the Cretaceous
407 onward (**Figure 3**, Supplementary Figure S7). Further implications for the origin, divergence
408 time and phylogenetic relationships of major shark lineages are discussed in Supplementary
409 Material S3.

410

411 *Trait evolution and diversification across the phylogeny*

412 Trait-evolution analyses performed with corHMM yielded support for sequential
413 evolution scenarios for each trait. For maximum body length, reproduction, and diet, top-
414 ranking scenarios were a two-rate category symmetrical sequential model ($AIC_{\omega} = 0.63$; **Table**
415 **2**) a two-rate category equal-rates sequential model ($AIC_{\omega} = 0.95$; **Table 2**) and a two-rate
416 category all-rate-differ sequential model ($AIC_{\omega} = 0.99$; **Table 2**), respectively. However, in
417 terms of AIC_c , the model with the lowest AIC_c for habitat evolution is a two-rates category
418 symmetrical model ($AIC_{\omega} = 0.72$; **Table 2**). Consequently, as there was no substantial

419 difference in AICc between this model and the second best-fitting one ($\Delta\text{AICc} = 2.57$; paired
420 signed-rank Wilcoxon test, statistic = 2582, $P = 0.85$), we choose to retain the latter (one-rate
421 sequential ARD_{seq} model) as it is much less parametrized (14 vs. 22 parameters). Outputs from
422 the sensitivity analyses support our results for body size (Friedman test, $\text{df} = 17$, $n = 100$,
423 statistic = 1674.611, $P < 0.00001$), reproduction (Friedman test, $\text{df} = 17$, $n = 100$, statistic =
424 1609.196, $P < 0.00001$), habitat (Friedman test, $\text{df} = 17$, $n = 100$, statistic = 1657.406, $P <$
425 0.00001) and diet (Friedman test, $\text{df} = 17$, $n = 100$, statistic = 1681.555, $P < 0.00001$).

426 Maximum-likelihood estimations of trait-dependent diversification and evolution with
427 SecSSE showed no symptoms of overparameterization as all models reached similar likelihood
428 optima across all three alternative runs. Across all three traits, we found that CTD models were
429 always chosen over ETD, and CR models ($\text{AIC}_{\omega_{\text{body-size}}} = 0.88$, $\text{AIC}_{\omega_{\text{habitat}}} = 0.98$,
430 $\text{AIC}_{\omega_{\text{reproduction}}} = 0.92$, and $\text{AIC}_{\omega_{\text{diet}}} = 0.71$; **Table 3**), suggesting that concealed traits alone
431 better explain the current pattern of extant shark diversity than focal traits and concealed traits.
432 Rates are reported in Supplementary Table S1. These results are further supported by the
433 sensitivity analyses for body size (Friedman test, $\text{df} = 6$, $n = 100$, statistic = 592.157, $P <$
434 0.00001), reproduction (Friedman test, $\text{df} = 6$, $n = 71$, statistic = 421.871, $P < 0.00001$), habitat
435 (Friedman test, $\text{df} = 6$, $n = 100$, statistic = 560.31, $P < 0.00001$), and diet (Friedman test, $\text{df} =$
436 6, $n = 96$, statistic = 575.75, $P < 0.00001$).

437 Our analysis on maximum body length indicates that transition rates from small to
438 medium-sized sharks are twice as much as frequent as transitions from medium to large sharks
439 (0.006 vs. 0.003 event/lineage/Myr; **Figure 4A**). Ancestral body length estimation indicates a
440 small- to medium-sized most recent common ancestor for all sharks with high support
441 (probability $>96\% \pm 3\%$). We estimated at least four major transitions towards large size
442 occurring in Rhincodontidae/Ginglymostomatidae ($\sim 80\% \pm 1\%$), Lamniformes ($\sim 98\% \pm$
443 0.2%), Hexanchidae ($\sim 84\% \pm 0.4\%$), and some Carcharhinidae ($>99\%$). Conversely, we

444 detected at least three major shifts toward small size in Etmopteridae ($>98\% \pm 0.2\%$),
445 Hemiscylliidae ($>93\% \pm 0.5\%$), and at the root of Carcharhiniformes ($\sim 89\% \pm 1\%$). Transition
446 rates for reproduction are found to be all equal (0.0007 event/lineage/Myr; **Figure 4B**),
447 suggesting a certain degree of lability across reproductive states. The probable ancestral
448 reproductive strategy of sharks is estimated to be lecithotrophic viviparity ($>61\% \pm 0.5\%$),
449 although the possibility for the ancestral condition to be oviparity should not be discarded
450 ($>38\% \pm 0.5\%$; 54% according to corHMM, see Supplementary Table S2). Following the
451 scenario of a lecithotrophic ancestral state, we found at least three main transitions to oviparity
452 in Heterodontiformes ($>99\%$), Hemiscylliidae ($>99\%$), and the most common ancestor of all
453 Carcharhiniformes ($>99\% \pm 0.1\%$). We found two significant appearances of oophagy: one in
454 Lamniformes ($\sim 99\% \pm 0.1\%$) and one in Pseudotriakidae ($>60\% \pm 0.2\%$). Conversely, our
455 results support one appearance of placentotrophy among carcharhinoids ($\sim 99\% \pm 0.1\%$). Last,
456 we found strong rate heterogeneity for habitat with transitions from outer shelves and coastal
457 settings being generally more frequent than transitions to these habitats, with transitions from
458 outer shelves to deepwater being ten times more frequent than the opposite (respectively 0.01
459 and 0.001 event/lineage/Myr, **Figure 5A**). Estimation of the ancestral habitat of sharks supports
460 a coastal setting ($\sim 79\% \pm 25.6\%$). Model estimates indicate at least four independent
461 colonizations of outer shelf settings at the root of Squalomorphii ($\sim 57\% \pm 10\%$) and three
462 associated with the Carcharhiniformes: one at the origin of the extant Scyliorhinidae ($>97\% \pm$
463 0.4%), one at the root of Pentanchidae ($>60\% \pm 10\%$), and one at the root of
464 Proscylliidae/Pseudotriakidae ($>69\% \pm 8\%$). We found at least two independent colonizations
465 of deepwater environments in some Pentanchidae ($>89\% \pm 4\%$) and Squaliformes ($>85\% \pm$
466 4%). We further found two major colonization events of reef environments, one occurring for
467 the recent common ancestor of Heterodontiformes ($>99\%$) and one occurring at the root of non-
468 parascylliid Orectolobiformes ($\sim 99\% \pm 0.5\%$). Although there are several minor independent

469 invasions of the oceanic realm, we found only one major transition at the root of Lamniformes
470 ($\sim 96\% \pm 1\%$). Finally, ancestral state estimations for diet did not yield any meaningful results
471 as most nodes had equal probability for all three trait states (**Figure 5B**) and no significant shifts
472 could be identified across the phylogeny for this trait.

473 Strikingly, SecSSE and corHMM yielded similar transition rate estimates, especially for
474 habitat (Supplementary Figure S8). Likewise, the ancestral states estimated with SecSSE and
475 corHMM are broadly congruent (Supplementary Table S2), as we found shifts occurring at
476 similar locations and with comparable probability. Still, the ancestral state estimation for diet
477 yielded contrasted results between corHMM and SecSSE, as the ancestral state probability
478 estimated by corHMM is less equiprobable than SecSSE but is also non-informative as each
479 state probability seems to be largely proportionate to its relative abundance in the sampled
480 dataset (Supplementary Table S2).

481

482 **Discussion**

483 *Traits may not explain the current pattern of extant shark diversity*

484 Over the past decade, the interest in trait-dependent diversification has surged with the
485 increased availability of well-sampled phylogenies, trait data, and cutting-edge comparative
486 methods. However, a single study addressed the potential link between traits and the extant
487 pattern of diversity among shark species, so far. Sorenson et al. (2014) found that diversification
488 dynamics among sharks were likely correlated with habitat, finding strong evidence of a reef-
489 mediated increase in speciation rates among Carcharhinidae. However, our study challenges
490 these findings by failing to find evidence of habitat-dependent diversification. The
491 inconsistency between these results can be attributed to two reasons. First, the phylogeny from
492 Sorenson et al. (2014) covered less than half of the total shark species richness. Yet, a low
493 sampling fraction has been shown to favor trait-dependent over trait-independent models and

494 to decrease the accuracy of rate estimation (Helmstetter et al., 2023; Mynard et al., 2023).
495 Second, the authors performed their analyses using a MuSSE framework (FitzJohn, 2012).
496 While MuSSE and non-hidden-state SSE-like models in general (Maddison et al., 2007) have
497 been extensively used in the past decade, they have been criticized for their high sensitivity to
498 type I errors (Rabosky & Goldberg, 2015; Beaulieu & O'Meara, 2016; Herrera-Alsina et al.,
499 2019). It is thus likely that the results from Sorenson et al. (2014) showing habitat-dependent
500 diversification are spurious.

501 Although we always found better support for concealed trait-dependent diversification,
502 we still found that the relative fit of trait-dependent over constant-rate models was always
503 better, suggesting that in a simpler framework (i.e. no concealed traits), trait-dependent
504 diversification would have been detected. Here, while ETD models outperformed CR models,
505 this does not necessarily mean that focal traits are good predictors of diversification. This all
506 comes down to adequacy issues: if one model has slightly less fit than the other, it will be
507 selected, but none of them is necessarily 'good'. Hidden trait models aim to avoid this scenario
508 by comparing CR and ETD models with a hypothetical hidden trait model that is likely better
509 to explain diversity patterns. Here, we found support for CTD models, suggesting that an
510 unmeasured feature may better explain extant diversity patterns. Here, most combinations of
511 traits are closely-associated with specific clades (*e.g.* Etmopteridae are small-sized, yolk-sac
512 viviparous, deepwater sharks). Therefore, traits may instead represent weak proxies for
513 unmeasured clade-specific features that affect diversification, explaining why they are detected
514 as affecting diversification when comparing ETD with CR models.

515 The main goal of the hidden trait framework (HiSSE, SecSSE) is to avoid systematic
516 selection of a state-dependent diversification model by comparing it against an alternative
517 hidden trait model. Although this framework is promising, one drawback is that SecSSE models
518 may struggle to detect moderate diversification signals associated with the focal trait. Thus, if

519 the focal trait is not the main driver of diversification, SecSSE or HiSSE might favor a CTD
520 model over the ETD model (Herrera-Alsina et al., 2019). Consequently, it would be unrealistic
521 to explain all diversification signals with one trait at a time. A way to mitigate this challenge
522 would be to implement models where the effects of several traits on diversification are tested
523 all at once. Such a method was implemented by O’Meara et al. (2016) for grouping several
524 combinations of characters in one set and testing its diversification rates against other sets in a
525 MuSSE framework (FitzJohn, 2012). Although this method yielded promising results by adding
526 context-dependency for each trait, it is still parameter-rich (at least 40 states in our case) and
527 may not reflect any biological reality (i.e., grouping sharks with contrasting ecology). Instead,
528 one alternative method may be combining traits to obtain phenotypic profiles outlining most
529 morphological and ecological variation for any group through clustering. Such approaches have
530 been tested in macroecological studies in Northeastern Pacific sharks (Siders et al., 2022).
531 While the authors have drawn critical results describing the major axes of functional diversity
532 of sharks, functional clustering grouped together species with very different traits (e.g., large
533 oceano-pelagic apex predator [tiger shark] with medium-sized benthic and sluggish shark
534 [angel shark], and medium-sized deep-sea predator [frilled shark]), and may not be biologically
535 realistic.

536 Furthermore, trait-dependent diversification may be one of many potential factors shaping
537 current biodiversity patterns. Punctual events, tectonics, eustatism, biogeography, biotic
538 interactions, and climate change are a non-exhaustive list of factors that likely played a role in
539 the diversification history of sharks (Brée et al., 2022; Condamine et al., 2019; Guinot & Cavin,
540 2020) and other clades (Lidgard et al., 2021; Liow et al., 2015; Mittelbach et al., 2007; Welton,
541 2015; Zaffos et al., 2017). Recently, the fossil-based analysis of Guinot & Condamine (2023)
542 highlighted the dramatic impact of the Cretaceous-Paleogene mass extinction around 66 Ma on
543 elasmobranch diversity, as more than 62% of species disappeared during this event. This mass

544 extinction was highly selective, with different patterns of extinction and recovery according to
545 clades and ecological groups (Guinot & Condamine, 2023). Therefore, extinctions of such a
546 magnitude may also have a dramatic impact on extant diversification patterns. This should
547 motivate future studies to explore extant diversity patterns in light of such mass extinctions.
548 More broadly, future research investigating deep-time patterns of diversity should proceed by
549 integrating both the fossil record and extant phylogenies in a common framework to capture
550 the full extent of macroevolutionary processes (Silvestro et al., 2018; Brée et al., 2022).

551

552 *Diet evolution in sharks is highly labile*

553 Diet is a fundamental component of animal biology. While a large body of literature
554 attempted to decipher the tempo and mode of diet evolution over the diversification of
555 numerous metazoan lineages (Price et al., 2012; Wiens et al., 2015, Burin et al., 2016; Poore et
556 al., 2017; Román-Palacios, et al., 2019), how diet evolved in sharks remained unexplored. We
557 attempted to address this using two different methodologies of trait evolution and ancestral state
558 estimation. However, we did not find any meaningful trait shifts, specific estimated ancestral
559 states, nor trait-dependent diversification effects. Most extant sharks have a broad range of prey
560 (Ebert et al., 2021) that can vary seasonally (MacNeil et al., 2005; Dicken et al., 2017), through
561 ontogeny (Lowe et al., 1996; Ebert, 2002), and between sexes (Assemat et al., 2022). Thus, the
562 diet of sharks seems to be highly labile with few taxa possessing a specialized feeding ecology
563 (e.g., Dalatiidae, Megachasmidae, Rhincodontidae). Strikingly, this high degree of diet-
564 preference lability is both present at the intra- and interspecific levels. This is especially true
565 when considering the high rates of transition between states (e.g. transition from Invertebrate-
566 feeder to Mesopredator: 0.046 event/lineage/Myr; **Figure 5B**). This high degree of lability
567 contrasts with previous research suggesting that diet is phylogenetically conserved across the

568 animal tree of life (Román-Palacios et al., 2019), and may explain why diet is not a
569 diversification driver in sharks.

570

571 *Evolutionary trajectories of shark body size*

572 Based on our results, we identified several key events in the evolution of body length
573 among sharks. Interestingly, shifts toward large size occurred mostly in macropredatory clades
574 (Carcharhinidae, Lamnidae, Ginglymostomatidae, Hexanchidae, Stegostomatidae) or filter-
575 feeding clades (Rhincodontidae, Megachasmidae, Cetorhinidae), which is consistent with
576 previous studies (Pimiento et al., 2019). Strikingly, all filter-feeding clades are nested within
577 large macropredatory clades: Megachasmidae and Cetorhinidae within Lamniformes, and
578 Rhincodontidae being sister-clade to Stegostomatidae and Ginglymostomatidae. This may
579 suggest that a large body length might be a prerequisite for transitions to filter-feeding, and
580 gigantic size to occur. Conversely, major shifts towards small size occurred only twice, in
581 highly speciose and deepwater-associated families (Pentanchidae and Etmopteridae). Although
582 we did not include any fossil in our analyses, our estimated shifts are remarkably coherent with
583 data from the fossil record, especially for large-sized Lamniformes, which are recovered as
584 early as the early Cretaceous (Condamine et al., 2019) and large-sized Carcharhiniformes,
585 which are recovered from the Oligocene onward (Condamine et al., 2019; Brée et al., 2022).
586 Thus, this may suggest that comparative phylogenetic methods can prove to be a reliable tool
587 when inferring deep-time events of character evolution.

588

589 *Evolution of reproductive strategies through time*

590 The evolution of reproductive strategy in chondrichthyans is a long-standing topic in
591 evolutionary and developmental biology (Wourms, 1977; Wourms, 1981; Wourms &
592 Lombardi, 1992; Dulvy & Reynolds, 1997; Blackburn, 2015; Buddle et al., 2019; Katona et al.,

593 2023; Blackburn & Hughes, 2024). However, phylogenetic uncertainties have hindered
594 comparative analysis (Blackburn, 2015), and few studies have addressed this topic at global
595 scale. By performing the most exhaustive comparative analysis of reproduction strategies, our
596 results bring new insights into the ancestral shark's reproduction strategies, the sequential
597 evolution of these strategies, and their lability across shark clades.

598 Our analyses challenge the long-lasting consensus regarding oviparity as ancestral among
599 sharks (Wourms, 1977; Dulvy & Reynolds, 1997; Blackburn, 2005; Katona et al., 2023;
600 Blackburn & Hughes, 2024) as we found support for a lecithotrophic viviparous ancestor
601 (~61%). Thus, oviparous clades (*e.g.*, Heterodontiformes, Orectolobiformes,
602 Carcharhiniformes) may have undergone a reversion from their viviparous ancestor. This
603 finding, although contrasting with recent studies (Katona et al., 2023; Blackburn & Hughes,
604 2024), is not unlikely, given plausible cases of reversion towards oviparity documented in
605 squamates (Pyron & Burbrink, 2014) and other elasmobranchs (Dulvy & Reynolds, 1997).
606 Furthermore, two fossilized pregnant females of the lower Carboniferous chondrichthyan
607 *Harpagofututor volsellorhinus* were recovered exhibiting up to five fetuses (Grogan & Lund,
608 2011). As the fetuses were intact, showed no sign of disturbance and displayed no yolk sac, this
609 suggests that viviparity - and possibly matrotrophy - could be recovered in a probable
610 holocephalan lineage as early as 318 Ma (Grogan & Lund, 2011). However, such direct
611 evidence is rare among elasmobranchs and the alternative hypothesis of an oviparous ancestor
612 for extant sharks (38% probability; 54% according to corHMM, see Supplementary Table S2)
613 cannot be ruled out. This is especially true when considering that Hybodontiformes, the extinct
614 sister clade of crown elasmobranchs, were most likely oviparous (Cappetta, 2012). Clearly, the
615 debate for the ancestral reproduction strategy among sharks remains open.

616 We also found support for a sequential scenario in the evolution of reproductive strategies,
617 which is, to our knowledge, the first formal test for this long-lasting hypothesis (Wourms &

618 Lombardi 1992). According to our results, lecithotrophic viviparity might be an obligate
619 intermediate state between oviparity and derived forms of viviparity. Still, while we found no
620 support for direct transition between oviparous and matrotrophic clades, a very limited number
621 of such transitions will still likely favor a sequential model.

622 We further found that sharks display a high degree of lability in their reproductive biology
623 as we found several events of reversal toward ancestral parity modes across the phylogeny, as
624 well as strong heterogeneity of reproductive strategy inside clades. For instance, species of the
625 genus *Mustelus* could be placentotrophic and histotrophic, or a mix of both (e.g. *Mustelus*
626 *higmani*, Macías-Cuyare et al., 2020), while members of the genus *Galeus* could either be yolk-
627 sac viviparous or oviparous, and the species *Nebrius ferrugineus* is either oophagous or yolk-
628 sac viviparous, depending on the geographic area (Ebert et al., 2021). One underlying factor
629 that could explain this striking pattern is that all chondrichthyans have internal fertilization
630 (Blackburn, 2005), which is usually portrayed as a preadaptation towards live-bearing
631 (Blackburn, 1985; Wourms 1992). Moreover, to our knowledge, all sharks display a tertiary
632 egg membrane, or egg capsule (Musick et al., 2005; Oddone & Capapé 2022), a structure
633 encapsulating the embryo at least for the first month of gestation and acting as a first layer of
634 protection (Wourms 1977; Oddone & Capapé 2022). Viviparous species might therefore still
635 retain the potential anatomical structures and genes responsible for egg-laying, which could
636 facilitate transitions between these reproductive strategies.

637

638 ***Patterns of habitat evolution across the shark tree of life***

639 Understanding the habitat where clades originated and diversified is a crucial and
640 complex topic in evolutionary biology (Boucot & Janis, 1983, Chamberlin 1900; Sallan et al.,
641 2018). Using a comprehensive database controlling for environmental sampling bias and
642 Bayesian statistics, Sallan et al. (2018) revealed that coastal environments may have served as

643 a cradle for the diversification of early marine vertebrates. Strikingly, our results point to a
644 similar conclusion as we found strong support for coastal settings, not reefs, acting as ancestral
645 habitats during early shark diversification. Interestingly, although early sharks likely dwelled
646 in nearshore settings (Underwood, 2006), this ecology only accounts for a small percentage of
647 the total extant diversity of this clade and is mostly represented among carcharhinoids and, to
648 a much lesser extent, among early diverging Carcharhiniformes (Atelomycteridae,
649 Scyliorhinidae, and Pentanchidae). This nearshore ecology seems highly conserved in this
650 clade, as shallow marine scyliorhinid-like Carcharhiniformes are recovered as early as the
651 Middle Jurassic and throughout their evolutionary history (Underwood 2006; Underwood &
652 Ward, 2004). This raises the question of why such a pattern of habitat conservatism occurs
653 among some Carcharhiniformes, while nearshore sharks almost totally disappeared in other
654 clades.

655 Such a disappearance is exemplified by Lamniformes, which have largely disappeared
656 from coastal settings. Lamniformes, or mackerel sharks, form an order of medium to large-
657 sized sharks mainly dwelling in oceanic waters. Even though most extant Lamniformes are
658 oceano-pelagic (80%), their early representatives were shallow-water dwellers (Kriwet et al.,
659 2008; Rees, 2005) and were frequent in coastal settings until the Oligocene (Adnet et al. 2020).
660 Analyses of the fossil record have shown that mackerel sharks have experienced a gradual
661 decline throughout the second half of the Cenozoic, likely due to inter-clade interaction with
662 medium and large Carcharhiniformes and climate cooling (Condamine et al., 2019). As both
663 clades used to have overlapping size ranges, tooth morphologies, and most likely overlapping
664 ecology, this decline was likely driven by passive replacement, which led to the extinction of
665 coastal Lamniformes, probably from the Oligocene onward. Although mostly recovered among
666 mackerel sharks, this pattern might also explain the extant diversity of habitat recovered among
667 sharks. Ecological radiation and conservatism should therefore be interpreted in light of

668 extinction events and deep-time ecological interactions. Other evolutionary processes may
669 explain the wide range of habitats represented among sharks. One, if not the most, striking
670 pattern of habitat transition is the convergent colonization of deepwater environments. We
671 estimated two major invasions of deepwater habitats and subsequent radiation during the
672 Cretaceous, occurring in two phylogenetically distant clades: Squaliformes and Pentanchidae
673 (Carcharhiniformes), which are supported by the fossil record. Squaliformes are more abundant
674 in deepwater assemblages from the Late Cretaceous onward (Adnet & Cappetta, 2001; Cappetta
675 et al., 2021; Feichtinger et al., 2023), while deep-sea Carcharhiniformes are scarce during the
676 early part of their evolutionary history, but common in post-Paleocene deepwater assemblages
677 (Marsili, 2007; Pollerspöck and Straube 2017; Brée et al. 2022). Although we did not detect a
678 global effect of habitat on shark diversification, these two deep-sea clades are among the most
679 speciose among sharks. Strikingly, a similar pattern can be found among Batoidea (rays and
680 skates) where Rajiformes, the most speciose batoid order (~300 species), mostly encompasses
681 deep-sea taxa (Last et al. 2016). Furthermore, most deep-sea clades display short internal
682 branches while presenting longer intermediate and terminal branches, which may be explained
683 by an early radiation within these clades. Ecological opportunity through the colonization of
684 new habitats is known to be an underlying factor in adaptive radiation (Yoder et al., 2010).
685 Therefore, colonization of deep-sea habitats may not enhance diversification rates *per se*, but
686 may have represented an ecological opportunity for elasmobranchs in their evolutionary
687 history, and have supported their subsequent diversification.

688

689 ***Limitations of the study***

690 Although our results provide important insights into the patterns of trait evolution in the
691 evolutionary history of sharks, further interpretations should be formulated with care, and three
692 main reservations arise from our analyses. The first is related to our sampling effort. Although

693 we generated the most comprehensive phylogeny of sharks to date, almost one-third of the
694 shark species richness remains to be sequenced. Specifically, some clades (e.g. Dalatiidae,
695 Pentanchidae) or trait categories (oviparous, small-sized) are undersampled, which is known to
696 severely decrease the estimation of diversification rates while increasing the probability of false
697 positives (Mynard et al., 2023). Likewise, almost 28% of sampled species in the phylogeny do
698 not have data for reproductive strategy and almost one-third of extant elasmobranchs lack data
699 on diet. Most knowledge of sharks' diet comes from stomach content, which is notoriously
700 known to be misleading (Smale, 1991). Consequently, much remains to be known regarding
701 the diet of sharks. Recently, Pimiento et al. (2023) attempted to address this issue by imputing
702 missing diet data using other traits, and our analyses on diet rely on their comprehensive dataset.
703 However, while their imputation approach significantly reduced the number of missing data,
704 imputed values, although robust (Pimiento et al., 2023), remain estimations from other proxies
705 and are consequently less reliable than direct observations.

706 The second concern stems from the nature of the data. We focused on neontological
707 data, and while abundant, easily measurable, and thus widely used in macroevolutionary
708 studies, they remain posterior evidence of long-term evolution processes. Conversely, fossil
709 data provide the most direct temporal evidence when inferring character evolution through time.
710 Therefore, macroevolutionary studies should aim to employ cross-disciplinary data (Brée et al.,
711 2022; Finarelli & Flynn, 2006; Liow et al., 2023; Slater et al., 2012; Silvestro et al., 2018 but
712 see Beaulieu & O'Meara, 2023). While this might be an ideal working framework (see Brée et
713 al., 2022), obtaining relevant fossil data may be challenging. The shark fossil record is mostly
714 composed of isolated teeth (Cappetta, 2012), and although dental characters can be informative
715 regarding some phenotypical and ecological traits (Cooper et al., 2023), they may be irrelevant
716 for others (behavior, reproduction). In this case, relying on neontological data might greatly
717 complement the fossil record to infer past macroevolutionary events.

718 Our last concern relates to the range of models we implemented. A common issue with
719 phylogenetic comparative models may be their tendency to be over-parameterized (Boyko &
720 Beaulieu, 2023), as model selection is de facto flawed with a set of over-parameterized models.
721 Furthermore, these models assumed time-constant rates, which may be considered biologically
722 unrealistic, especially given prior knowledge from the fossil record. Although this assumption
723 could be relaxed by incorporating multiple class rates in corHMM (thus treating different parts
724 of the phylogeny as heterogeneous, *e.g.* backbone *vs.* tips) it may not reflect truly a time-
725 variable model. Nevertheless, the inclusion of time-varying parameters also has important
726 limitations in terms of identifiability, as highlighted by Louca & Pennel (2020). Fortunately,
727 such limitations are unlikely to apply to SSE models, which are clade-dependent and time-
728 independent (Helmstetter et al., 2022).

729

730 **Conclusion**

731 In this study, we reconstructed the most comprehensive time-calibrated species-level
732 phylogeny for sharks accounting for ~69% of extant diversity. We compiled an exhaustive
733 database for maximum body length, reproduction modes, and habitat for all shark species. We
734 outlined the major character shifts and modes of trait evolution across the shark tree of life and
735 found support for sequential models of trait evolution. We also estimated a small to medium-
736 sized lecithotrophic coastal-dwelling most recent common ancestor for extant sharks. However,
737 our results did not support trait-dependent diversification, which contrasts with previous
738 findings in the literature. Therefore, this should motivate future studies to investigate other
739 potential factors driving diversity patterns, like extinction events, biotic interactions, and
740 environmental variations. Overall, our study advocates using neontological data to complement
741 the fossil record as they can provide valuable information for inferring past macroevolutionary
742 events.

743

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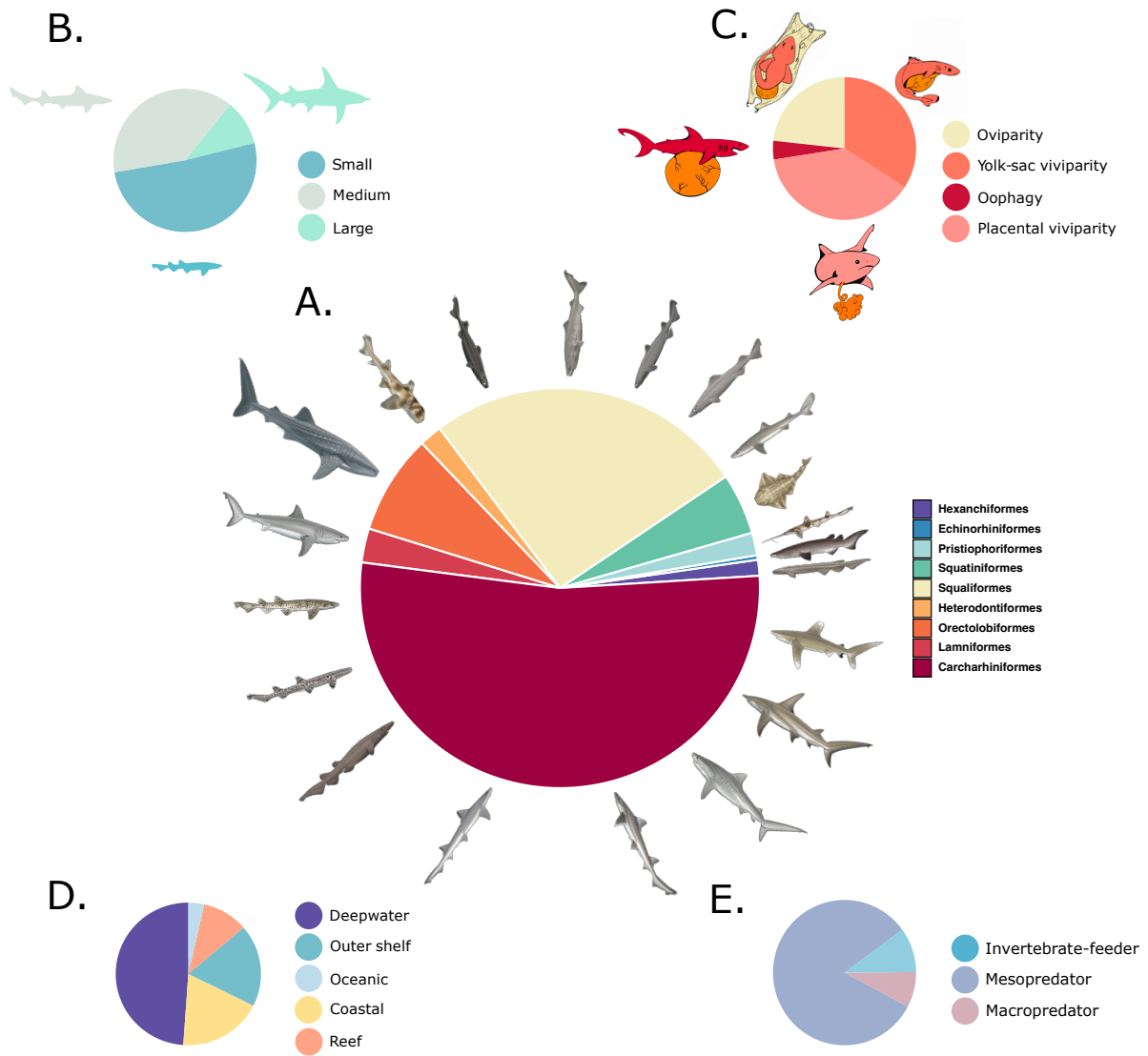
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1120 **Figure 1.** Distribution of species richness within shark orders (A), size category (B),

1121 reproduction mode (C), habitat (D), and diet (E). Each color corresponds to either an order of

1122 sharks or a trait category. Shark images courtesy of M. Dando, artist (sizes not to scale).

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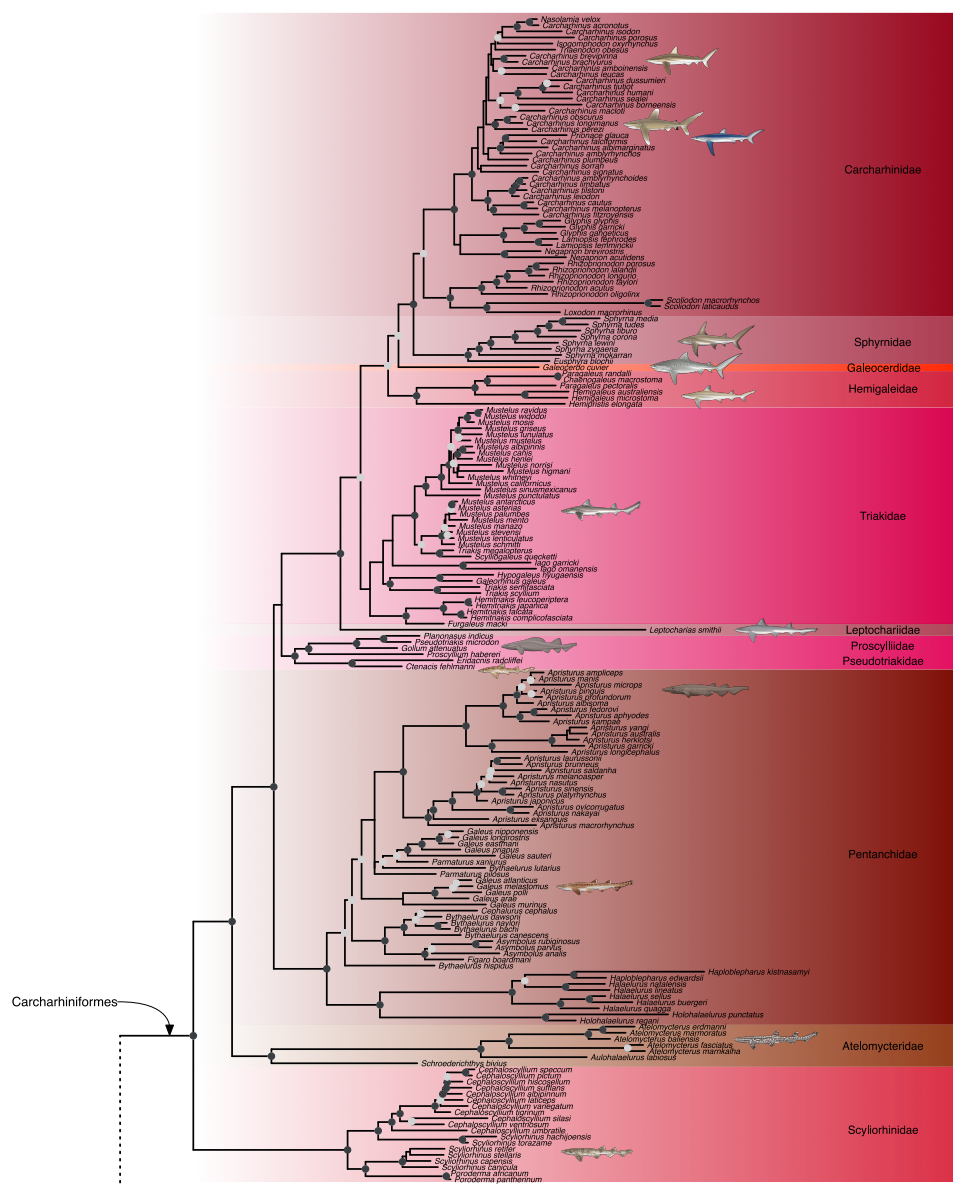


Figure 2A. (caption on the next page)

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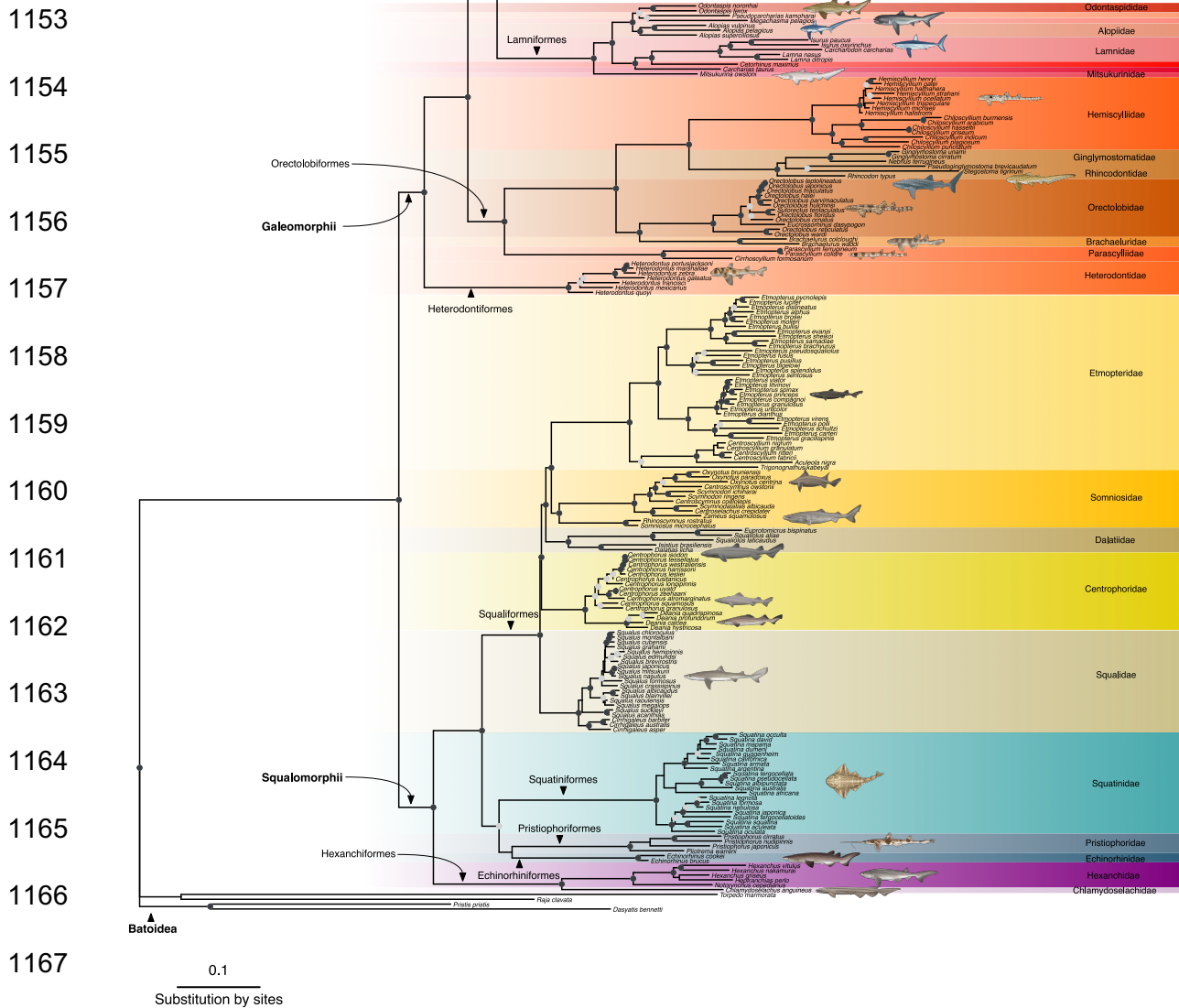
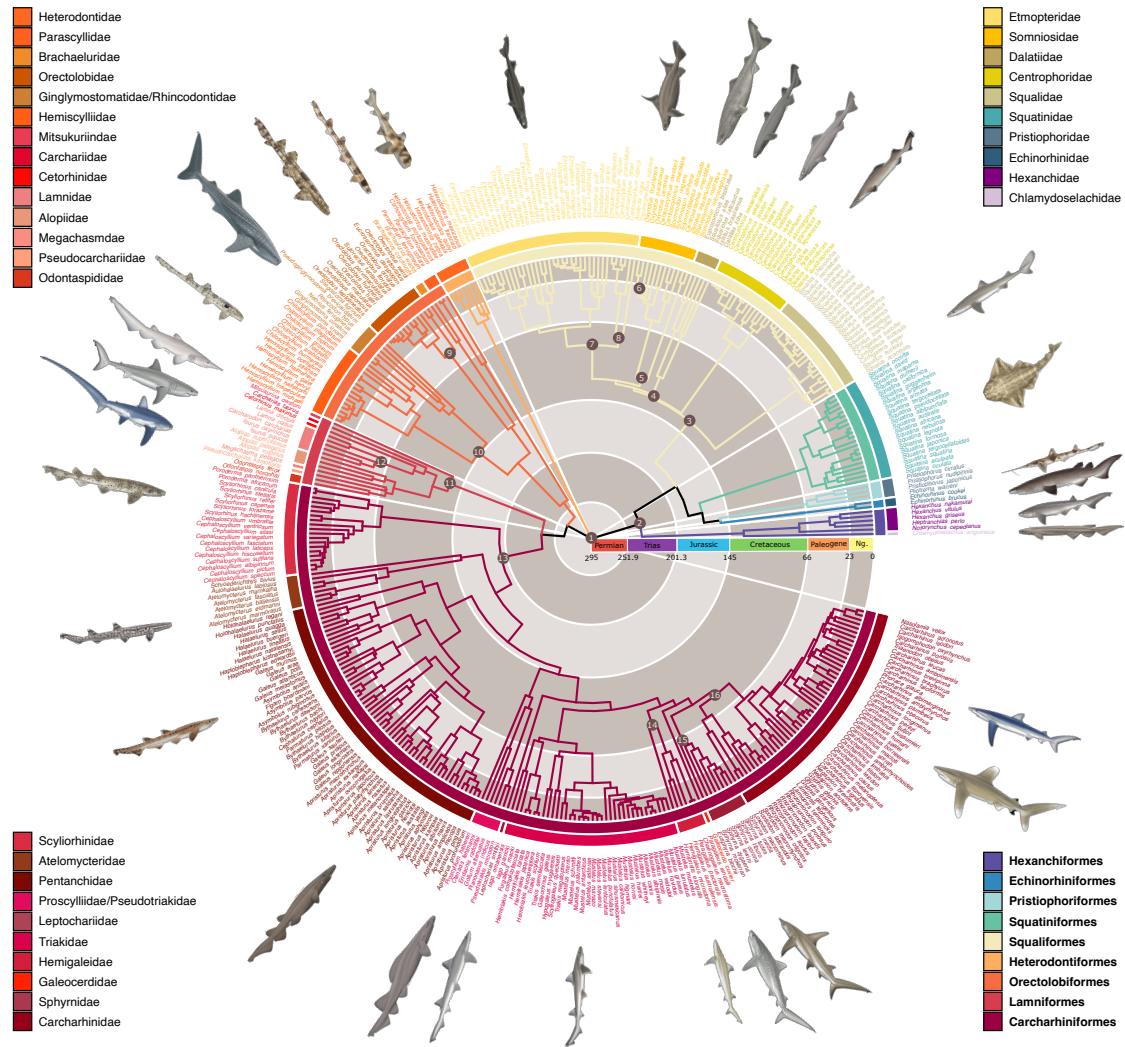


Figure 2. Maximum-likelihood molecular phylogeny of Selachimorpha inferred from 16 genes.

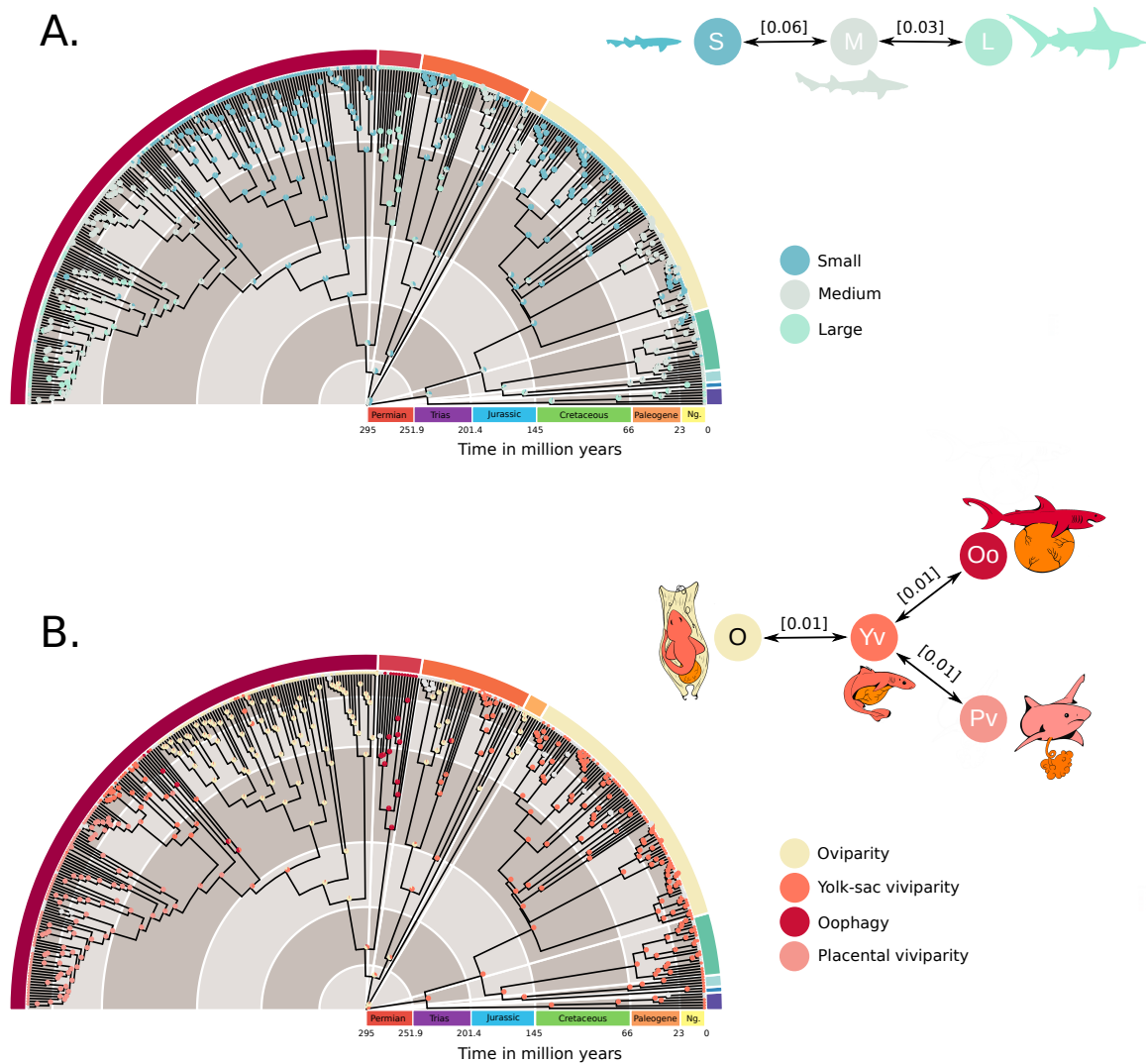
The phylogeny includes 374 shark species and 4 outgroups (skates and rays). Subtree A represents the order Carcharhiniformes, whereas subtree B includes all other orders. The shark phylogeny was reconstructed with 13 mitochondrial protein-coding genes, two mitochondrial RNA genes, and one nuclear protein-coding gene. Black circles indicate maximum support. A gray circle represents supports at nodes ≥ 95 . Superorder names are in bold, and orders are indicated by a black arrow. Families are coloured individually. Branch lengths are expressed in substitutions per site with the scale placed at the bottom of the figure. Shark names with an asterisk correspond to the associated illustration. Shark images courtesy of M. Dando, artist (sizes not to scale).



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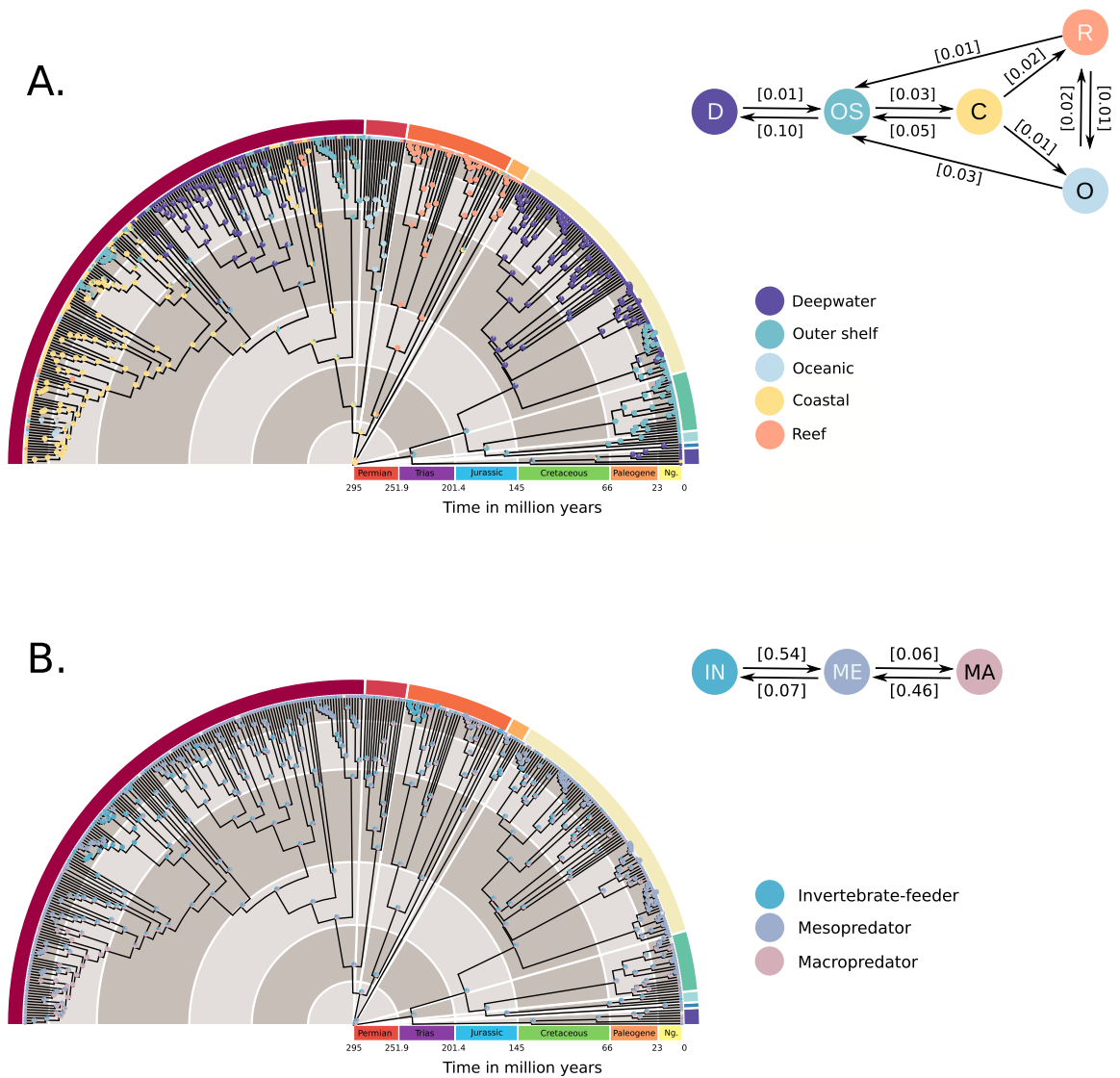
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1180 **Figure 3.** Bayesian time-calibrated phylogeny of sharks and fossil calibration. Concentric
 1181 shaded circles represent divisions into geological periods. The divergence times have been
 1182 estimated using 16 fossil calibrations with uniform priors and 16 molecular clocks. The
 1183 numbers at nodes indicate placements of the fossil calibrations (see **Table 1**, Supplementary
 1184 Data S2, Supplementary Material S2). Branches are coloured according to the order. Species
 1185 names are coloured according to their family-level taxonomy. Shark images courtesy of M.
 1186 Dando, artist (sizes not to scale).



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1188 **Figure 4.** SecSSE ancestral state estimates and transition rates for maximum body-size (A),
 1189 and reproductive strategy (B) in sharks. Concentric shaded circles represent divisions into
 1190 geological periods. Ancestral trait estimates are represented at nodes by pie charts indicating
 1191 the probability of a state. Ball and stick diagrams represent transition rates between trait states
 1192 estimated with SecSSE. Transition rates are multiplied by 10.



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1194 **Figure 5.** SecSSE ancestral state estimates and transition rates for habitat (A), and diet (B) in

1195 sharks. Concentric shaded circles represent divisions into geological periods. Ancestral trait

1196 estimates are represented at nodes by pie charts indicating the probability of a state. Ball and

1197 stick diagrams represent transition rates between trait states estimated with SecSSE. Transition

1198 rates are multiplied by 10.

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| Number | Node calibrated | Fossil taxa | CR1 | CR2 | CR3 | CR4 | CR5 | Prior | Min age | Max age | Median age (Myr) | 95% HPD (Myr) |
|--------|----------------------------|--|-----|-----|-----|-----|-----|-------|---------|---------|------------------|-------------------|
| 1 | Selachimorpha | <i>Reifia minuta</i> Duffin, 1980 | ✓ | ✓ | X | ✓ | ✓ | Unif. | 208.5 | 358.9 | 295.08 | [266.19 : 320.71] |
| 2 | Squalomorphii | <i>Notidanoides arzoensis</i> Beaumont, 1960 | ✓ | ✓ | X | ✓ | ✓ | Unif. | 192.9 | 358.9 | 241.93 | [219.74 : 267.96] |
| 3 | Squaliformes | <i>Protosqualus albertsi</i> Thies, 1981 | ✓ | ✓ | ✓ | ✓ | ✓ | Unif. | 121.4 | 192.9 | 134.65 | [121.61 : 147.10] |
| 4 | Stem Centrophoridae | <i>Protocentrophorus baifcus</i> (Dallinkevicius, 1935) | ✓ | ✓ | ✓ | ✓ | ✓ | Unif. | 93.9 | 192.9 | 133.42 | [121.68 : 146.70] |
| 5 | Somniosidae | <i>Protosynotus misburgiensis</i> Herman, 1975 | ✓ | ✓ | X | ✓ | ✓ | Unif. | 89.8 | 192.9 | 119.01 | [105.11 : 131.86] |
| 6 | Oxyotinae | <i>Oxyotus crochardi</i> (Melton, 1981) | ✓ | ✓ | ✓ | ✓ | ✓ | Unif. | 15.97 | 89.8 | 28.59 | [23.07 : 34.00] |
| 7 | Etmopteridae | <i>Proetmopterus hemmoorensis</i> (Herman, 1982) | ✓ | ✓ | ✓ | ✓ | ✓ | Unif. | 66 | 192.9 | 92.20 | [83.07 : 100.40] |
| 8 | Stem <i>Trigonognathus</i> | <i>Trigonognathus virginiae</i> (Cappetta & Adnet, 2000) | ✓ | ✓ | ✓ | ✓ | ✓ | Unif. | 41.2 | 93.9 | 83.39 | [74.13 : 93.02] |
| 9 | Orectolobidae | <i>Orectolobus ziegenhinei</i> (Cappetta & Case, 2016) | ✓ | ✓ | X | ✓ | ✓ | Unif. | 41.2 | 174.7 | 51.23 | [42.22 : 63.83] |
| 10 | Stem Ginglymostomatidae | <i>Cantioscyllium alhauifi</i> Kiwet, 1999 | ✓ | ✓ | X | ✓ | ✓ | Unif. | 121.4 | 174.7 | 146.52 | [132.43 : 164.34] |
| 11 | Lamniformes | <i>Protolamna</i> sp. (Rees, 2005) | ✓ | ✓ | X | ✓ | ✓ | Unif. | 132.6 | 208.5 | 136.00 | [132.62 : 144.71] |
| 12 | Lamnidae | <i>Isurrolamna infata</i> (Lerliche, 1905) | ✓ | ✓ | X | ✓ | ✓ | Unif. | 56 | 132.6 | 60.72 | [56.02 : 66.31] |
| 13 | Carcharhiniformes | <i>Elysea leesi</i> Underwood & Ward, 2004 | ✓ | ✓ | X | ✓ | ✓ | Unif. | 165.3 | 251.9 | 198.29 | [180.80 : 219.45] |
| 14 | Hemigaleidae | <i>Hemipistis curvatus</i> Dames, 1883 | ✓ | ✓ | X | ✓ | ✓ | Unif. | 33.9 | 165.3 | 88.82 | [78.97 : 98.10] |
| 15 | Sphyrnidae | <i>Sphyrna</i> sp. Cappetta & Case, 2006 | ✓ | ✓ | X | ✓ | ✓ | Unif. | 41.2 | 165.3 | 62.30 | [55.29 : 70.09] |
| 16 | Carcharhinidae | <i>Abdouria africana</i> (Arambourg, 1952) | ✓ | ✓ | X | ✓ | ✓ | Unif. | 61.6 | 165.3 | 80.41 | [77.45 : 94.07] |

1203 **Table 1.** Fossil calibrations used to infer divergence times in sharks. For each calibrated node,
1204 a uniform prior (Unif.) distribution is set based on a fossil taxon conferring a minimum age
1205 (Min. age) and on a conservative maximum age (Max. age) depending on a much deeper
1206 calibration. For each fossil, the five criteria (CR1 to CR5) from Parham et al. (2012) have been
1207 evaluated with checks indicating approval of the criterion, while crosses denote disapproval.
1208 For each node, we also report the estimated median age (Myr) and the 95% height posterior
1209 density (Myr) from the BEAST inferences.

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| (A) Model ranking for Maximum body-size | | | | | | | | | |
|---|-----------------|------------------|------------|----------------|------------|--------|-------|-------|--|
| Model | Rate categories | Transition type | Sequential | Log Likelihood | Parameters | AICc | ΔAICc | ωAICc | |
| bds_2_SYMseq | 2 | Symmetrical | Yes | -240.26 | 6 | 492.74 | 0 | 0.63 | |
| bds_3_SYMseq | 3 | Symmetrical | Yes | -235.03 | 12 | 494.91 | 2.17 | 0.21 | |
| bds_2_SYM | 2 | Symmetrical | No | -240.26 | 8 | 496.91 | 4.17 | 0.08 | |
| bds_2_ARDseq | 2 | All rates differ | Yes | -238.30 | 10 | 497.20 | 4.45 | 0.07 | |
| bds_3_ARDseq | 3 | All rates differ | Yes | -232.28 | 18 | 502.49 | 9.75 | 0 | |
| bds_2_ARD | 2 | All rates differ | No | -239.68 | 14 | 508.52 | 15.78 | 0 | |
| bds_3_SYM | 3 | Symmetrical | No | -239.87 | 15 | 511.08 | 18.34 | 0 | |
| bds_3_ARD | 3 | All rates differ | No | -231.75 | 24 | 514.93 | 22.19 | 0 | |
| bds_2_EQseq | 2 | Equal | Yes | -259.32 | 4 | 526.75 | 34.00 | 0 | |
| bds_1_SYMseq | 1 | Symmetrical | Yes | -262.51 | 2 | 529.05 | 36.30 | 0 | |
| bds_1_ARDseq | 1 | All rates differ | Yes | -261.11 | 4 | 530.32 | 37.58 | 0 | |
| bds_1_SYM | 1 | Symmetrical | No | -262.51 | 3 | 531.08 | 38.33 | 0 | |
| bds_1_EQseq | 1 | Equal | Yes | -264.68 | 1 | 531.37 | 38.63 | 0 | |
| bds_3_EQseq | 3 | Equal | Yes | -256.64 | 9 | 531.77 | 39.03 | 0 | |
| bds_1_ARD | 1 | All rates differ | No | -261.11 | 6 | 534.44 | 41.70 | 0 | |
| bds_2_EQ | 2 | Equal | No | -276.28 | 4 | 560.67 | 67.93 | 0 | |
| bds_3_EQ | 3 | Equal | No | -272.97 | 9 | 564.43 | 71.69 | 0 | |
| bds_1_EQ | 1 | Equal | No | -283.80 | 1 | 569.61 | 76.87 | 0 | |

| (B) Model ranking for Reproduction | | | | | | | | | |
|------------------------------------|-----------------|------------------|------------|----------------|------------|--------|-------|-------|--|
| Model | Rate categories | Transition type | Sequential | Log Likelihood | Parameters | AICc | ΔAICc | ωAICc | |
| rp_2_EQseq | 2 | Equal | Yes | -74.05 | 4 | 156.21 | 0 | 0.95 | |
| rp_2_SYMseq | 2 | Symmetrical | Yes | -71.47 | 10 | 163.54 | 7.34 | 0.02 | |
| rp_3_EQseq | 3 | Equal | Yes | -73.22 | 9 | 164.93 | 8.73 | 0.01 | |
| rp_2_EQ | 2 | Equal | No | -78.73 | 4 | 165.57 | 9.37 | 0.01 | |
| rp_1_SYMseq | 1 | Symmetrical | Yes | -79.95 | 4 | 168.01 | 11.80 | 0 | |
| rp_1_EQseq | 1 | Equal | Yes | -83.09 | 1 | 168.18 | 11.98 | 0 | |
| rp_1_ARD | 1 | All rates differ | No | -71.97 | 12 | 168.80 | 12.59 | 0 | |
| rp_1_ARDseq | 1 | All rates differ | No | -76.61 | 8 | 169.62 | 13.42 | 0 | |
| rp_1_EQ | 1 | Equal | No | -83.99 | 1 | 169.99 | 13.78 | 0 | |
| rp_1_SYM | 1 | Symmetrical | No | -79.35 | 6 | 170.94 | 14.73 | 0 | |
| rp_2_SYM | 2 | Symmetrical | No | -71.47 | 14 | 172.11 | 15.90 | 0 | |
| rp_3_SYMseq | 3 | Symmetrical | Yes | -67.77 | 18 | 173.48 | 17.27 | 0 | |
| rp_3_EQ | 3 | Equal | No | -78.60 | 9 | 175.69 | 19.49 | 0 | |
| rp_2_ARDseq | 2 | All rates differ | Yes | -71.77 | 18 | 181.46 | 25.26 | 0 | |
| rp_3_SYM | 3 | Symmetrical | No | -69.35 | 24 | 190.14 | 33.93 | 0 | |
| rp_2_ARD | 2 | All rates differ | No | -67.54 | 26 | 191.12 | 34.92 | 0 | |
| rp_3_ARDseq | 3 | All rates differ | Yes | -65.75 | 30 | 196.92 | 40.71 | 0 | |
| rp_3_ARD | 3 | All rates differ | No | -63.81 | 42 | 222.54 | 66.34 | 0 | |

| (C) Model ranking for Habitat | | | | | | | | | |
|-------------------------------|-----------------|------------------|------------|----------------|------------|--------|-------|-------|--|
| Model | Rate categories | Transition type | Sequential | Log Likelihood | Parameters | AICc | ΔAICc | ωAICc | |
| ht_2_SYM | 2 | Symmetrical | No | -237.28 | 22 | 521.44 | 0 | 0.72 | |
| ht_1_ARDseq | 1 | All rates differ | Yes | -247.42 | 14 | 524.01 | 2.57 | 0.20 | |
| ht_1_SYMseq | 1 | Symmetrical | Yes | -256.06 | 7 | 526.43 | 4.99 | 0.06 | |
| ht_3_SYM | 3 | Symmetrical | No | -224.77 | 36 | 529.45 | 8.01 | 0.01 | |
| ht_1_SYM | 1 | Symmetrical | No | -256.06 | 10 | 532.73 | 11.29 | 0 | |
| ht_1_ARD | 1 | All rates differ | No | -247.42 | 20 | 537.22 | 15.78 | 0 | |
| ht_1_EQseq | 1 | Equal | Yes | -269.33 | 1 | 540.67 | 19.23 | 0 | |
| ht_2_SYMseq | 2 | Symmetrical | Yes | -256.07 | 16 | 545.66 | 24.22 | 0 | |
| ht_2_EQseq | 2 | Equal | Yes | -269.32 | 4 | 546.75 | 25.31 | 0 | |
| ht_2_EQ | 2 | Equal | No | -272.10 | 4 | 552.31 | 30.87 | 0 | |
| ht_3_EQseq | 3 | Equal | Yes | -269.32 | 9 | 557.13 | 35.70 | 0 | |
| ht_2_ARDseq | 2 | All rates differ | Yes | -247.42 | 30 | 560.27 | 38.83 | 0 | |
| ht_3_EQ | 3 | Equal | No | -272.08 | 9 | 562.66 | 41.22 | 0 | |
| ht_3_SYMseq | 3 | Symmetrical | No | -254.40 | 27 | 567.17 | 45.73 | 0 | |
| ht_2_ARD | 2 | All rates differ | No | -240.63 | 42 | 576.16 | 54.72 | 0 | |
| ht_1_EQ | 1 | Equal | No | -288.76 | 1 | 579.53 | 58.09 | 0 | |
| ht_3_ARD | 3 | All rates differ | No | -219.25 | 66 | 599.30 | 77.86 | 0 | |
| ht_3_ARDseq | 3 | All rates differ | Yes | -247.42 | 48 | 605.32 | 83.88 | 0 | |

| (D) Model ranking for Diet | | | | | | | | | |
|----------------------------|-----------------|------------------|------------|----------------|------------|--------|-------|-------|--|
| Model | Rate categories | Transition type | Sequential | Log Likelihood | Parameters | AICc | ΔAICc | ωAICc | |
| diet_2_ARDseq | 2 | All rates differ | Yes | -195.73 | 10 | 412.06 | 0 | 0.98 | |
| diet_2_ARD | 2 | All rates differ | No | -195.63 | 14 | 420.43 | 8.37 | 0.01 | |
| diet_3_ARDseq | 3 | All rates differ | Yes | -192.42 | 18 | 422.76 | 10.70 | 0.01 | |
| diet_1_ARDseq | 1 | All rates differ | Yes | -207.77 | 4 | 423.65 | 11.59 | 0 | |
| diet_1_ARD | 1 | All rates differ | No | -207.73 | 6 | 427.70 | 15.64 | 0 | |
| diet_3_ARD | 3 | All rates differ | No | -193.64 | 24 | 438.72 | 26.66 | 0 | |
| diet_3_SYMseq | 3 | Symmetrical | Yes | -211.12 | 12 | 447.11 | 35.05 | 0 | |
| diet_3_SYM | 3 | Symmetrical | No | -210.18 | 15 | 451.71 | 39.65 | 0 | |
| diet_2_SYMseq | 2 | Symmetrical | Yes | -225.82 | 6 | 463.88 | 51.82 | 0 | |
| diet_2_SYM | 2 | Symmetrical | No | -224.52 | 8 | 465.44 | 53.39 | 0 | |
| diet_2_EQseq | 2 | Equal | Yes | -230.55 | 4 | 469.21 | 57.15 | 0 | |
| diet_2_EQ | 2 | Equal | No | -231.12 | 4 | 470.34 | 58.28 | 0 | |
| diet_3_EQseq | 3 | Equal | No | -227.01 | 9 | 472.52 | 60.46 | 0 | |
| diet_3_EQ | 3 | Equal | No | -227.33 | 9 | 473.16 | 61.10 | 0 | |
| diet_1_EQ | 1 | Equal | No | -244.50 | 1 | 491.00 | 78.95 | 0 | |
| diet_1_EQseq | 1 | Equal | Yes | -245.45 | 1 | 492.91 | 80.86 | 0 | |
| diet_1_SYM | 1 | Symmetrical | No | -244.24 | 3 | 494.55 | 82.49 | 0 | |
| diet_1_SYMseq | 1 | Symmetrical | Yes | -245.42 | 2 | 494.86 | 82.81 | 0 | |

1229 **Table 2.** Model ranking for corHMM analyses for maximum body-size (A), reproductive
1230 strategy (B), habitat (C), and diet (D). The table reports the models applied, the number of rates,
1231 their number of parameters, the log-likelihood, the corrected Akaike Information Criterion
1232 (AICc), the difference of AICc between the best model (lowest AICc) and a given model
1233 (Δ AICc), and the Akaike weight (ω AICc). The best-fitting mode is highlighted in bold.

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(A) Model ranking for Maximum body-size

| Model | Estimated rates | Log Likelihood | Parameters | AICc | ΔAICc | ωAICc |
|------------|-------------------|-----------------|------------|----------------|----------|-------------|
| CTD | Speciation | -1999.03 | 7 | 4012.37 | 0 | 0.88 |
| CTD | Diversification | -1998.94 | 9 | 4016.38 | 4 | 0.12 |
| ETD | Diversification | -2007.41 | 9 | 4033.32 | 20.95 | 0 |
| ETD | Speciation | -2011.77 | 7 | 4037.85 | 25.48 | 0 |
| CTD | Extinction | -2017.93 | 7 | 4050.16 | 37.79 | 0 |
| ETD | Extinction | -2019.37 | 7 | 4053.05 | 40.68 | 0 |
| CR | Constant | -2024.43 | 5 | 4059.03 | 46.66 | 0 |

(B) Model ranking for Reproduction

| Model | Estimated rates | Log Likelihood | Parameters | AICc | ΔAICc | ωAICc |
|------------|-------------------|-----------------|------------|----------------|----------|-------------|
| CTD | Speciation | -1815.61 | 7 | 3645.52 | 0 | 0.92 |
| CTD | Diversification | -1814.95 | 10 | 3650.51 | 4.99 | 0.08 |
| ETD | Diversification | -1823.56 | 10 | 3667.72 | 22.2 | 0 |
| ETD | Speciation | -1832.97 | 7 | 3680.24 | 34.72 | 0 |
| CTD | Extinction | -1833.85 | 7 | 3682.01 | 36.49 | 0 |
| ETD | Extinction | -1834.37 | 7 | 3683.04 | 37.52 | 0 |
| CR | Constant | -1839.21 | 4 | 3686.52 | 41 | 0 |

(C) Model ranking for Habitat

| Model | Estimated rates | Log Likelihood | Parameters | AICc | ΔAICc | ωAICc |
|------------|-------------------|-----------------|------------|----------------|----------|-------------|
| CTD | Speciation | -1980.53 | 18 | 3998.98 | 0 | 0.98 |
| CTD | Diversification | -1980.08 | 22 | 4007.04 | 8.07 | 0.02 |
| ETD | Diversification | -1988.51 | 22 | 4023.9 | 24.92 | 0 |
| ETD | Speciation | -1997.09 | 18 | 4032.1 | 33.12 | 0 |
| CTD | Extinction | -1999.33 | 18 | 4036.59 | 37.61 | 0 |
| ETD | Extinction | -1999.93 | 18 | 4037.79 | 38.81 | 0 |
| CR | Constant | -2007.88 | 14 | 4044.93 | 45.95 | 0 |

(D) Model ranking for Diet

| Model | Estimated rates | Log Likelihood | Parameters | AICc | ΔAICc | ωAICc |
|------------|-------------------|-----------------|------------|----------------|----------|-------------|
| CTD | Speciation | -1945.09 | 9 | 3908.67 | 0 | 0.71 |
| CTD | Diversification | -1943.85 | 11 | 3910.43 | 1.76 | 0.29 |
| ETD | Speciation | -1954.15 | 9 | 3926.79 | 18.12 | 0 |
| ETD | Diversification | -1953.33 | 11 | 3929.38 | 20.71 | 0 |
| CTD | Extinction | -1959.23 | 9 | 3936.97 | 28.29 | 0 |
| ETD | Extinction | -1961.37 | 9 | 3941.22 | 32.55 | 0 |
| CR | Constant | -1964.91 | 7 | 3944.12 | 35.45 | 0 |

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1259 **Table 3.** Model ranking for SecSSE analyses for maximum body-size (A), reproductive
1260 strategy (B), habitat (C), and diet (D). The table reports the models applied, whether the
1261 extinction was estimated, their number of parameters, the log-likelihood, the corrected Akaike
1262 Information Criterion (AICc), the difference of AICc between the best model (lowest AICc)
1263 and a given model (Δ AICc), and the Akaike weight (ω AICc). The best-fitting mode is
1264 highlighted in bold.