

Precocial ancestry of placental mammals

Arun R. Chavan^{1,*}, Mihaela Pavlicev², Günter P. Wagner^{2,3,4}

¹ Department of Immunobiology, Yale University School of Medicine, New Haven, CT, USA

² Department of Evolutionary Biology, University of Vienna, Vienna, Austria

³ Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, USA

⁴ Hagler Institute for Advanced Studies, Texas A&M University, College Station, TX, USA

* Correspondence to: arun.chavan@yale.edu

ORCiD: ARC ([0000-0002-0518-4713](#)), MP ([0000-0001-8439-9351](#)), GPW ([0000-0002-3097-002X](#))

1 Abstract

Mammals exhibit two distinct reproductive strategies: altriciality, where neonates are highly underdeveloped, and precociality, where neonates are well-developed. The neonatal developmental state of deep nodes in mammalian phylogeny remains unresolved. Here, we use phylogenetic comparative methods to reconstruct the evolutionary history of neonatal maturity in mammals and demonstrate that the eutherian ancestor likely gave birth to precocial neonates. This finding contradicts the prevailing view that precociality evolved multiple times within the eutherian lineage. We contextualize this result with three lines of evidence. First, recent fossil evidence suggests that precocial life history traits arose early in therian evolution. Second, altricial eutherian neonates are markedly more developed at birth compared to altricial non-eutherians, suggesting a precocial ancestry in eutherian evolution. Third, reproductive traits that enable prolonged pregnancy originated in the stem lineage prior to the eutherian ancestor. Based on these findings, we propose an alternative model for the evolutionary history of precociality in mammals.

Keywords: altricial, precocial, eutherian, placental mammal, neonate, gestation

15 2 Introduction

16 Mammalian neonatal maturity spans a spectrum from altricial to precocial (Portmann, 1945).
17 Altricial neonates (e.g., murine rodents), born highly underdeveloped, are often hairless and unable
18 to thermoregulate or move independently. They typically do not open their eyes for days after birth
19 and require extensive parental care for early survival. In contrast, precocial neonates (e.g.,
20 ruminants) are far more developed. They are born with fur, can open their eyes, move
21 independently shortly after birth, and require significantly less parental care.

22 Although neonatal maturity in mammals exists along a continuum, it follows a notably bimodal
23 pattern as illustrated by the distribution of gestation length relative to body mass (Martin &
24 MacLarnon, 1985; **Supp. Figure 1**). Most species fall distinctly into either the altricial or precocial
25 category, with relatively few occupying the intermediate states. This bimodal pattern suggests that
26 altriciality and precociality represent two distinct reproductive strategies.

27 Understanding the evolutionary history of neonatal maturity is pivotal for uncovering broader
28 patterns in mammalian life history evolution. The divergence between these reproductive
29 strategies results from selection on a suite of developmental, physiological, and life history traits.
30 These include litter size, growth rate, neonatal body mass relative to the adult (Derrickson, 1992;
31 Grunstra et al., 2019), relative allocation of resources between gestation and lactation (Künkele &
32 Trillmich, 1997), and mating system (Zeveloff & Boyce, 1980). Because these traits are
33 interdependent (Danis et al., 2025), the adoption of an altricial or precocial strategy accordingly
34 influences their evolutionary trajectories.

35 Evolutionary history of neonatal maturity has been a source of debate not only in mammals but
36 also across other amniotes (Starck & Ricklefs, 1998; Werneburg et al., 2016). Due to the lack of
37 definitive fossil correlates of neonatal maturity, investigation of the evolution of this trait remains
38 speculative. With the exception of a few studies (Ferner et al., 2017; O’Leary et al., 2013;
39 Werneburg et al., 2016), the inference of ancestral states has been predominantly narrative rather
40 than analytical. The prevailing view is that neonates were altricial at deeper nodes in mammalian
41 phylogeny, including the mammalian, therian, and eutherian (placental) ancestors, with
42 precociality evolving multiple times within the eutherian lineage. While the altriciality of the
43 therian ancestor has been extensively debated from contrasting perspectives (Lillegraven, 1975;
44 Lillegraven et al., 1987; Renfree, 1993; Smith, 2001; Smith & Keyte, 2020; White et al., 2023),
45 the altriciality of the eutherian ancestor has received little scrutiny.

46 Here, we reconstruct the evolutionary history of neonatal maturity using phylogenetic comparative
47 methods with a dataset of 420 mammalian species and a modern phylogenetic framework that
48 accounts for phylogenetic uncertainty. Our results suggest that the eutherian ancestor was precocial
49 rather than altricial. We discuss this result in the context of recent fossil and comparative evidence
50 and propose an alternative model for the evolution of mammalian reproductive mode.

51 3 Results

52 3.1 Inferred ancestral state for eutherian mammals is precocial

53 Neonatal maturity data for 420 mammals (**Supp. Table 1**) were compiled from Case (1978) and
54 PanTHERIA (Jones et al., 2009). Case (1978) provides detailed information for 150 mammals, but
55 with a taxonomic representation skewed toward primates and other boreoeutherian species. To
56 address this bias, additional data from PanTHERIA were incorporated, producing a more balanced
57 dataset representing 21 of 27 mammalian orders and 16 of 19 eutherian orders (**Supp. Table 2**).

58 Ancestral state reconstruction was performed using stochastic character mapping (Bollback, 2006;
59 Huelsenbeck et al., 2003; Revell, 2025). Phylogenetic uncertainty was accounted for by using a
60 sample of 100 phylogenetic trees from a distribution of possible trees (Upham et al., 2019) and
61 running ancestral state reconstruction on each. Three models of trait evolution — equal rates (ER),
62 symmetric (SYM), and all rates different (ARD) — were fitted to the data. To account for model
63 uncertainty, 1,000 stochastic character histories were generated using parameters estimated from
64 all three models, with the number of histories per model determined by their respective model
65 weights. Posterior probability of character states at each node was calculated by integrating over
66 the 1,000 stochastic character maps. The same analysis was performed on the consensus tree for
67 visualization.

68 The ARD model provided the best fit to the data across all 100 sampled trees by a wide margin
69 (**Supp. Figure 2**). The mean model weight for ARD across the trees was 0.989, compared to 0.003
70 for the ER model and 0.009 for the SYM model. Consequently, the majority of character histories
71 were generated using the ARD model parameters.

72 As expected, the ancestral states for Prototheria (monotremes) and Metatheria (marsupials) are
73 consistently altricial in all sampled trees, with mean posterior probabilities of 0.93 and 0.94,
74 respectively (**Figure 1**). For Theria and Mammalia, the ancestral states are ambiguous but lean
75 toward altriciality. For the therian ancestor, the mean posterior probabilities are 0.6 for altriciality
76 and 0.36 for precociality, while for the mammalian ancestor, they are 0.69 and 0.28, respectively.

77 Surprisingly, the eutherian ancestor is reconstructed as precocial in all sampled trees but one
78 (**Figure 1b**), with mean posterior probabilities 0.02 for altriciality and 0.98 for precociality. This
79 result contradicts the prevailing assumption that the eutherian ancestor gave birth to altricial
80 neonates.

81 4 Discussion

82 4.1 Sensitivity of ancestral state reconstruction

83 The ancestral state reconstruction described above is sensitive to taxon sampling. Data from Case
84 (1978), biased toward boreoeutherian taxa, produce an altricial reconstruction of the eutherian

85 ancestral state when used exclusively (**Supp. Figure 3**). However, expanding the taxonomic
86 coverage shifts the estimated ancestral state toward precocial.

87 The reconstruction is also influenced by model choice. For Case (1978) data alone, the ER model
88 is the best fit across all 100 trees, with mean model weights of 0.52 for ER, 0.33 for SYM, and
89 0.15 for ARD (**Supp. Figure 4**). Moreover, among the 100 trees, there is an apparent positive
90 association between the ER model weight and the posterior probability of an altricial ancestral
91 state for the eutherian node (**Supp. Figure 5a**). In the full dataset, the only tree for which the
92 eutherian node is reconstructed as altricial also has the highest weight for the ER model among all
93 trees (**Supp. Figure 5b**). Forcing character histories to be generated exclusively under the ER
94 model with the full dataset reconstructs the eutherian ancestral state as altricial (**Supp. Figure 6**).
95 Note, however, that the ER model provides the poorest fit for the full dataset.

96 In summary, using the full dataset with a balanced taxonomic sampling and following the model
97 weights dictated by their fit strongly supports a precocial eutherian ancestral state.

98 4.2 Previous estimates of the eutherian ancestral state for neonatal maturity

99 The prevailing notion of an altricial eutherian ancestor stems, in part, from a long-held bias that
100 marsupial reproductive strategies are a steppingstone toward more advanced eutherian strategies.
101 Altricity of the eutherian ancestor, as a result, is often assumed rather than inferred. This
102 assumption is reinforced by the scattered distribution of precociality on eutherian phylogeny
103 (Derrickson, 1992). However, this pattern may be illusory as the most speciose eutherian groups,
104 such as Rodentia and Carnivora, tend to be altricial (**Supp. Table 1**).

105 The studies that have estimated the ancestral state using comparative methods tend to support an
106 altricial eutherian ancestor, but their inference carries substantial uncertainty.

107 Werneburg et al (2016) estimated the eutherian ancestor's age at eye opening and age at fur
108 development to be 25 and 24 days after birth, respectively, suggesting an altricial condition.
109 However, the authors note that the eutherian ancestor's inferred values had the broadest confidence
110 intervals, even exceeding those of older nodes. Notably, the 70% confidence intervals for eye
111 opening and fur development overlap with those for gestation length (**Supp. Figure 7**). It cannot,
112 thus, be conclusively inferred from these estimates that eye opening and fur development happened
113 after birth in the eutherian ancestor.

114 O'Leary et al (2013) inferred that the eutherian ancestor had hairless neonates with closed eyes
115 and a litter size of one. While hairlessness and closed eyes are associated with altricity, the litter
116 size of one is often associated with precocial neonates. The reconstruction suggests that these
117 neonates, even if altricial, were not as altricial as the clearly altricial eutherians.

118 Ferner et al (2017) consider the possibility that both the eutherian and mammalian ancestors were
119 precocial. However, they favor an altricial eutherian ancestor due to marginally better parsimony

support, and similarly, an altricial mammalian ancestor based on prior evidence, such as the small size of Mesozoic mammals. While small mammals do tend to produce altricial neonates, it is not a necessary association. For instance, elephant shrew and spiny mouse are precocial, whereas bears and anteaters are altricial. The analysis by Ferner et al (2017) underscores the ambiguities inherent to inferring ancestral neonatal traits in mammals.

4.3 Evidence inconsistent with ancestral precociality

Our inference that the eutherian ancestor was precocial, likely requiring a long gestation, appears to conflict with the understanding of early eutherian reproductive physiology.

Eutherian pregnancy depends on sustained circulating progesterone levels, with the corpus luteum serving as the source early in gestation. However, eutherian gestation far exceeds the length of the luteal phase in a non-pregnant ovarian cycle. This extended, or “trans-cyclic” (Chavan et al., 2016), gestation is supported by a variety of “maternal recognition of pregnancy” mechanisms, which either extend the lifespan of the corpus luteum or activate an extra-ovarian source of progesterone, or both (Basanta & Pavlicev, 2025; Swaggart et al., 2015).

Divergent mechanisms of maternal recognition of pregnancy suggest that trans-cyclic gestation evolved independently in major eutherian lineages. That is, the eutherian ancestor had an intra-cyclic pregnancy (Basanta & Pavlicev, 2025; Chavan et al., 2016). A challenge with an ancestral intra-cyclic pregnancy is that extending its duration would also prolong the non-pregnant ovarian cycle. This is due to the luteal phase and pregnancy being serial homologs, which are expected to evolve in a correlated manner. Prolonged non-pregnant cycles would reduce the reproductive rate, posing a selective disadvantage (Basanta & Pavlicev, 2025). Through variational decoupling of the luteal phase from gestation, eutherian lineages could explore gestation lengths unbounded by the ovarian cycle. However, this decoupling was absent in the eutherian ancestor.

This leaves us with two seemingly incompatible results: (i) the eutherian ancestor gave birth to precocial neonates, likely requiring a long pregnancy, and (ii) ancestral eutherian pregnancy, being intra-cyclic, was constrained to a short duration that could not be extended without incurring a selective cost.

The resolution lies in the notion that the selective disadvantage of a long sterile ovarian cycle is not realized in species that have induced ovulation or breed seasonally (Basanta & Pavlicev, 2025). The eutherian ancestor is indeed inferred to have been an induced ovulator, with spontaneous ovulation evolving later (Pavlicev & Wagner, 2016). This ancestral condition would have allowed the eutherian stem lineages to prolong pregnancy without incurring the selective cost. Ancestral eutherian pregnancy could have been intra-cyclic yet long enough for the development of a precocial neonate.

154 **4.4 Evidence consistent with ancestral precociality**

155 Even if one does not accept our inference at face value (Griffith et al., 2015), ancestral precociality
156 emerges as a plausible biological model in light of recent body of evidence.

157 *4.4.1 Reproductive traits enabling prolonged pregnancy predate the eutherian ancestor*

158 Giving birth to precocial neonates requires a long pregnancy, a hallmark of eutherian mammals
159 made possible by several evolutionary innovations. The evolution of embryo implantation (Griffith
160 et al., 2017), facilitated by the modification of maternal inflammatory reaction (Chavan et al.,
161 2017; Stadtmauer & Wagner, 2019) through the origin of decidual stromal cells (Chavan et al.,
162 2020; Erkenbrack et al., 2018), enabled the establishment of a sustained fetal-maternal interface.
163 The timing of these evolutionary events has been traced to the stem eutherian lineage, suggesting
164 that the eutherian ancestor's reproductive biology could support prolonged pregnancies.

165 *4.4.2 Precociality evolved early in mammalian evolution*

166 Funston et al (2022) reconstructed the life history of an early Paleocene mammal *Pantolambda*
167 *bathmodon* using paleohistology and geochemical analysis of dentine and enamel. Its reproductive
168 mode resembled that of extant precocial eutherians, with the estimated gestation length of 207
169 days and a short suckling period of 31–56 days. Although the precise phylogenetic placement of
170 *Pantolambda* remains unresolved (either related to Cetartiodactyla or a stem-group eutherian), it
171 is clearly an early eutherian lineage (~62 million years old), providing evidence for precocial life
172 history traits arising early in eutherian evolution.

173 Histology of long-bone fossils of multituberculates — a stem therian lineage — suggests that they
174 had prolonged prenatal growth and abbreviated postnatal growth (Weaver et al., 2022), a pattern
175 similar to eutherians but not marsupials. The patterns of cranial development across extant
176 mammals and their ancestral state reconstruction also show that the ancestral therian condition
177 resembled eutherian mammals more than marsupials (White et al., 2023, 2024). These studies
178 suggest that the extreme altriciality of marsupials is a derived trait (Renfree, 1993; Smith, 2001;
179 Smith & Keyte, 2020), and raise the possibility that eutherian-like reproductive traits — long intra-
180 uterine development and precocial neonates — may have evolved early in therian evolution.

181 **4.5 A model for the evolutionary history of eutherian precociality**

182 Our results and other evidence lead us to propose an alternative model for the evolutionary history
183 of eutherian precociality, departing from the traditional narrative in three ways: (i) precociality
184 arose early in therian evolution, (ii) marsupial altriciality is a derived trait, and (iii) eutherian
185 ancestor likely gave birth to precocial neonates.

186 Precociality could have evolved early in mammalian phylogeny in two contexts: either in an
187 oviparous mode prior to the mammalian ancestor, or in a viviparous mode in the therian stem
188 lineage. If the latter, viviparity was likely achieved via egg retention. In this mode, a strategy

189 observed in many squamate lineages (Blackburn, 2006), the egg is retained in the maternal
190 reproductive tract until the embryo is near hatching, allowing extended gestation and precocial
191 development. Crucially, the presence of an eggshell separates fetal and maternal tissues,
192 preventing the maternal inflammatory reaction that would trigger early parturition (Wagner et al.,
193 2014).

194 The viviparity seen in crown-group Theria likely evolved later along the therian stem lineage via
195 early hatching in utero (Wagner et al., 2014). In this mode, the early loss of the eggshell or the
196 zona pellucida leads to physical contact between fetal membranes and uterine endometrium
197 causing an attachment-induced inflammatory reaction, precipitating parturition. This mechanism,
198 culminating in birth shortly after early hatching, inherently resulted in extreme altriciality. We
199 propose that this highly altricial state, derived from more precocial early therian lineages, became
200 the ancestral condition for crown-group Theria and was subsequently retained and exaggerated in
201 the marsupial lineage. Marsupials, in turn, evolved a suite of compensatory mechanisms to support
202 adequate postnatal development (Smith & Keyte, 2020).

203 In the eutherian stem lineage, the inflammatory response from embryo attachment was modified
204 into implantation (Griffith et al., 2017) through the evolution of decidual cells (Chavan et al.,
205 2020). This allowed for the evolution of prolonged gestation and a re-emergence of precociality in
206 the eutherian stem lineage. An indirect support for precociality in the eutherian stem lineage is
207 provided by the observation that even the most altricial eutherian mammals are more developed at
208 birth than the least altricial marsupials (Ferner et al., 2017; Halley, 2017; Szdzuy & Zeller, 2009;
209 **Figure 2**). This implies that eutherian altriciality is not a direct continuation of the extreme
210 altriciality of the therian ancestor but derived from a precocial intermediate state in the eutherian
211 stem. Given its substantial length (60–90 million years), there were plausibly multiple transitions
212 between precociality and altriciality along the eutherian stem lineage. The developmental state of
213 the ancestral eutherian neonates — whether precocial or secondarily altricial (thus still more
214 developed than marsupial neonates) — then depends on the most recent transition immediately
215 preceding the crown-group Eutheria node (**Figure 3**).

216 Additional fossil data closer to the eutherian ancestor node will be necessary for a more direct
217 evaluation of models of neonatal maturity. In the meantime, we encourage consideration of a
218 precocial ancestry as a plausible scenario in eutherian evolution.

219 Our proposed model deviates from the simplistic narrative of mammalian reproductive evolution
220 as a linear progression from an assumed primitive state to the derived states observed today. We
221 believe that mammalian reproductive evolution is inherently non-parsimonious, shaped by an
222 interplay of life history trade-offs, genomic conflict, pleiotropy among reproductive traits,
223 anatomical and physiological constraints, and the origin of novel cell types and organs that break
224 ancestral constraints and reshape the variational landscape. A deeper mechanistic understanding

225 of these underlying processes and their evolution is critical for making sense of the complex
226 evolutionary history of mammalian reproduction.

227 5 Methods

228 5.1 Data

229 Neonatal maturity data were collected from two sources: Case (1978) and PanTHERIA (Jones et
230 al., 2009). Case (1978, Appendix 2) provides data on the developmental maturity at birth for 150
231 mammals scored on seven traits: body hair present, teeth present, open eyes, open auditory meatus,
232 the ability to right itself when lying on its back, the ability to move forward, and formed claws.
233 Species meeting at least 6 of the 7 criteria were classified as “precocial”, while those that did not
234 meet at least 6 criteria were classified as “altricial”. Intermediate states were classified as “semi-
235 altricial” or “semi-precocial”. Extremely altricial marsupials and monotremes were classified as
236 “fetal”. We simplified this classification to three categories: altricial (fetal, altricial, semi-altricial),
237 intermediate (semi-precocial), and precocial (precocial).

238 The variables “age at eye opening” and “litter size” from PanTHERIA were used to classify species
239 by neonatal maturity status. All monotremes in the dataset had missing values for age at eye
240 opening. After filling in the missing values for monotremes, 348 species (338 eutherians, 8
241 marsupials, 2 monotremes) had data for both variables. We followed the criteria of Martin and
242 McLarnon (1985) with some modifications. Species with an age at eye opening more than 5 days
243 were classified as altricial regardless of their litter size since this is a direct measure of maturity.
244 Species with eyes open at birth and litter size under 1.5 were classified as precocial. Species with
245 age at eye opening between 0 and 5 days, and litter size between 1.5 and 3 were classified as
246 intermediates. All other species falling outside these bounds were manually classified based on
247 literature.

248 The union of these two datasets was used as the final dataset. For species that are represented in
249 both datasets, classification from Case (1978) was preferred over PanTHERIA. This dataset was
250 filtered to remove species not represented in the phylogeny used for the analysis. The final dataset
251 contains 420 species: 293 altricial, 115 precocial, and 12 intermediate (**Supp. Table 1**). The
252 taxonomic coverage of all mammalian orders in the dataset can be found in **Supp. Table 2**.

253 5.2 Phylogeny

254 Phylogenetic framework from Upham et al (2019) was used for ancestral state reconstruction. We
255 downloaded a sample of 100 trees from a credible set of 10,000 trees that capture uncertainties in
256 inferences of tree topology and branch lengths (“Mammals birth-death node-dated DNA-only trees
257 (4098 species, set of 10k trees”), from <http://vertlife.org/phylosubsets/>. The trees were pruned to
258 the subset of species present in the neonatal maturity dataset. The consensus phylogeny was also
259 downloaded for visualization.

260 **5.3 Ancestral state reconstruction**

261 Ancestral state reconstruction was performed using stochastic character mapping (Bollback, 2006;
262 Huelsenbeck et al., 2003; Revell, 2025) with ‘phytools’ version 2.1.1 (Revell, 2024) in R version
263 4.2.3 (R Core Team, 2023). The reconstruction was run on all 100 trees sampled from the credible
264 set to account for phylogenetic uncertainty as well as on the consensus tree. Results from the latter
265 were used for visualization of ancestral states on the phylogeny.

266 We fit three models using the ‘phytools::fitMk()’ function: equal rates (ER), symmetrical (SYM),
267 and all rates different (ARD). We compared the model fits using ‘stats::anova()’. To account for
268 model uncertainty, we generated 1,000 stochastic character histories using all three models in
269 proportion of their model weights with the function ‘phytools::simmap()’. Posterior probabilities
270 of ancestral states at all nodes were calculated by summing over all 1,000 stochastic character
271 histories with the function ‘base::summary()’.

272 **6 Data and code availability**

273 Neonatal maturity data and the sample of 100 phylogenies from Upham et al (2019) used in this
274 study are available as supplementary files. Code to reproduce all analyses is available at
275 <https://github.com/archavan/precocity>.

276 **7 Acknowledgements**

277 We thank D. Stadtmauer, M. Srivastav, and I. Dhingra for their critical reading of an earlier version
278 of this manuscript.

279

8 Figures

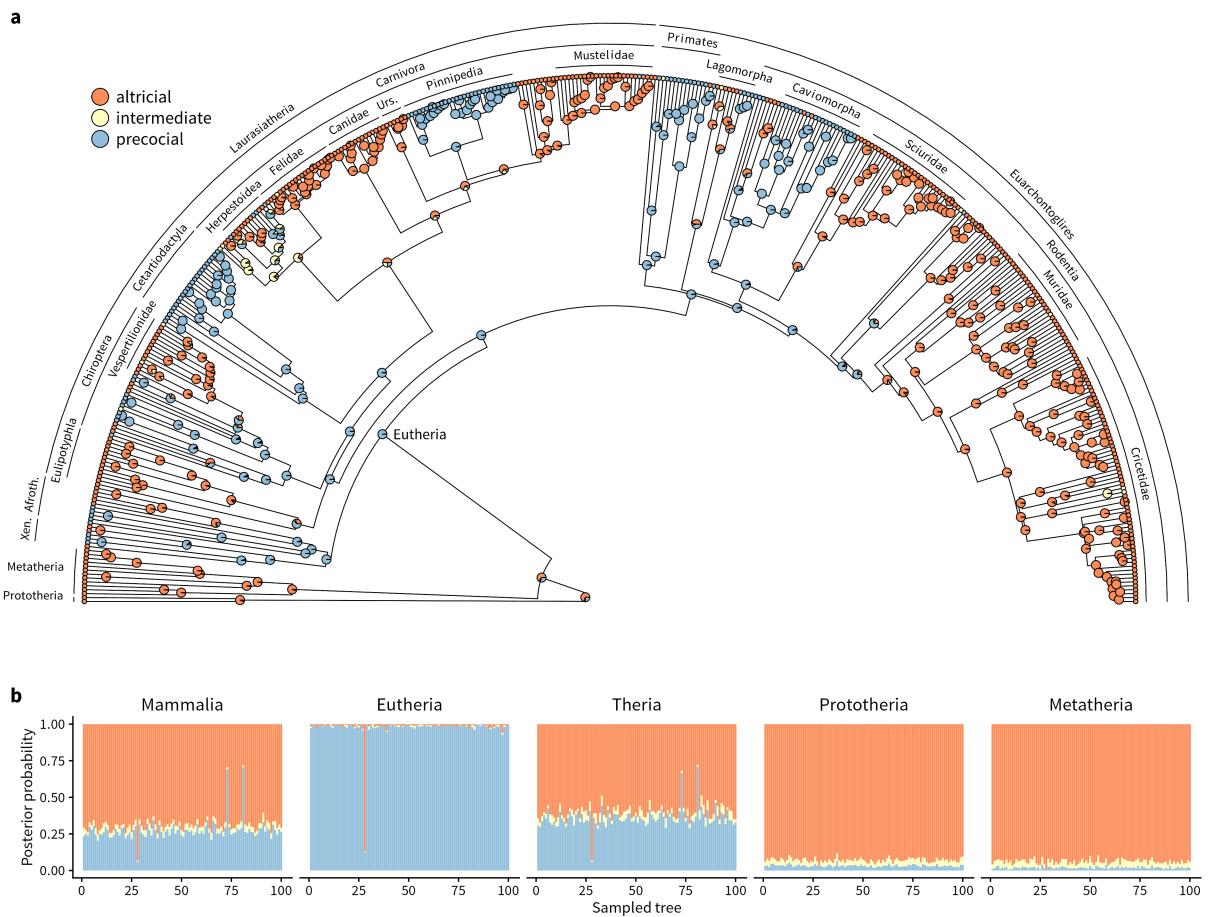


Figure 1: Ancestral state reconstruction of neonatal maturity using stochastic character mapping. **(a)** Consensus phylogeny from Upham et al (2019) showing neonatal maturity data at tips and posterior probabilities of ancestral states at internal nodes. **(b)** Ancestral states at key nodes in the mammalian phylogeny. Posterior probabilities of neonatal maturity states at the given node are plotted on the Y-axis for each of the 100 sampled phylogenies represented on the X-axis. Xen = Xenartha, Afroth = Afrotheria, Urs = Ursidae.

280

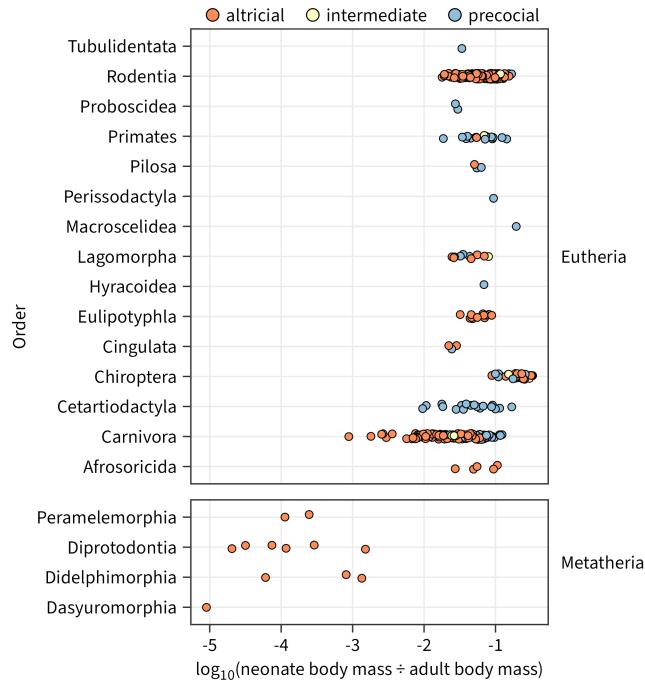


Figure 2: Altricial eutherian neonates are more developed than marsupials. Species with available adult and neonatal body mass data in PanTHERIA (Jones et al., 2009) are used. Log₁₀-transformed relative neonatal body mass (RNB) is used as a proxy for developmental maturity at birth. Higher the RNB, greater the degree of maturity. Median log₁₀(RNB) for altricial eutherians and marsupials is -1.30 and -3.94 , respectively, a difference of more than two orders of magnitude.

281

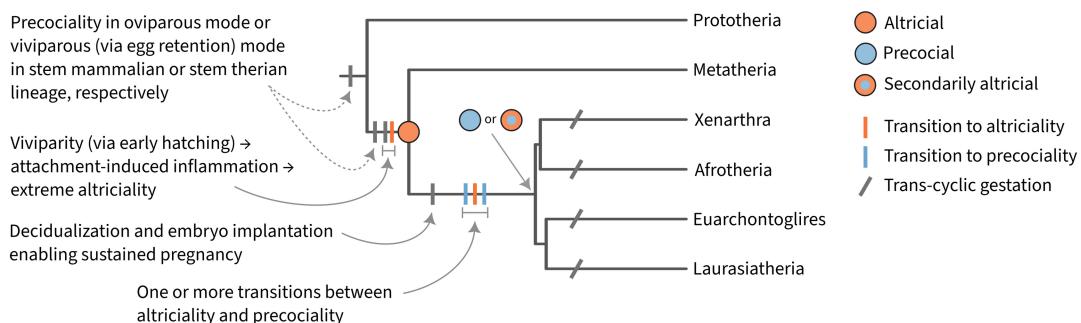


Figure 3: Model for the evolution of precociality in mammals. The key elements are an early evolution of precociality in mammalian phylogeny, reversal to altriciality in the therian stem lineage driven by early-hatching and attachment-induced inflammation, and re-evolution of precociality in the eutherian stem lineage enabled by the origin of decidual cells and embryo implantation.

282

283 **9 References**

- 284 Basanta, S., & Pavlicev, M. (2025). The Shifting Role and Regulation of the Corpus Luteum in
285 Vertebrate Reproduction: A Synthetic Review. *The Quarterly Review of Biology*, 100(3),
286 189–231. <https://doi.org/10.1086/737357>
- 287 Blackburn, D. G. (2006). Squamate Reptiles as Model Organisms for the Evolution of
288 Viviparity. *Herpetological Monographs*, 20, 131–146.
- 289 Bollback, J. P. (2006). SIMMAP: Stochastic character mapping of discrete traits on phylogenies.
290 *BMC Bioinformatics*, 7(1), 88. <https://doi.org/10.1186/1471-2105-7-88>
- 291 Case, T. J. (1978). On the evolution and adaptive significance of postnatal growth rates in the
292 terrestrial vertebrates. *The Quarterly Review of Biology*, 53(3), 243–282.
293 <https://doi.org/10.1086/410622>
- 294 Chavan, A. R., Bhullar, B.-A. S., & Wagner, G. P. (2016). What was the ancestral function of
295 decidual stromal cells? A model for the evolution of eutherian pregnancy. *Placenta*, 40,
296 40–51. <https://doi.org/10.1016/j.placenta.2016.02.012>
- 297 Chavan, A. R., Griffith, O. W., Stadtmauer, D. J., Maziarz, J., Pavlicev, M., Fishman, R., Koren,
298 L., Romero, R., & Wagner, G. P. (2020). Evolution of embryo implantation was enabled
299 by the origin of decidual stromal cells in eutherian mammals. *Molecular Biology and
300 Evolution*, msaa274. <https://doi.org/10.1093/molbev/msaa274>
- 301 Chavan, A. R., Griffith, O. W., & Wagner, G. P. (2017). The inflammation paradox in the
302 evolution of mammalian pregnancy: Turning a foe into a friend. *Current Opinion in
303 Genetics & Development*, 47, 24–32. <https://doi.org/10.1016/j.gde.2017.08.004>
- 304 Danis, T., Lin, D., Caetano, D. S., Funston, G. F., & Rokas, A. (2025). Gestation length both
305 shapes and is shaped by other life history traits in terrestrial eutherian mammals.
306 *Evolution Letters*, qraf028. <https://doi.org/10.1093/evlett/qraf028>
- 307 Derrickson, E. M. (1992). Comparative reproductive strategies of altricial and precocial
308 eutherian mammals. *Functional Ecology*, 6(1), 57. <https://doi.org/10.2307/2389771>
- 309 Erkenbrack, E. M., Maziarz, J. D., Griffith, O. W., Liang, C., Chavan, A. R., Nnamani, M. C., &
310 Wagner, G. P. (2018). The mammalian decidua evolved from a cellular stress
311 response. *PLoS Biology*, 16(8), e2005594. <https://doi.org/10.1371/journal.pbio.2005594>
- 312 Ferner, K., Schultz, J. A., & Zeller, U. (2017). Comparative anatomy of neonates of the three
313 major mammalian groups (monotremes, marsupials, placentals) and implications for the
314 ancestral mammalian neonate morphotype. *Journal of Anatomy*, 231(6), 798–822.
315 <https://doi.org/10.1111/joa.12689>
- 316 Funston, G. F., dePolo, P. E., Sliwinski, J. T., Dumont, M., Shelley, S. L., Pichevin, L. E.,
317 Cayzer, N. J., Wible, J. R., Williamson, T. E., Rae, J. W. B., & Brusatte, S. L. (2022).
318 The origin of placental mammal life histories. *Nature*, 610(7930), 107–111.
319 <https://doi.org/10.1038/s41586-022-05150-w>
- 320 Griffith, O. W., Blackburn, D. G., Brandley, M. C., Van Dyke, J. U., Whittington, C. M., &
321 Thompson, M. B. (2015). Ancestral state reconstructions require biological evidence to
322 test evolutionary hypotheses: A case study examining the evolution of reproductive mode
323 in squamate reptiles. *Journal of Experimental Zoology Part B: Molecular and
324 Developmental Evolution*, 324(6), 493–503. <https://doi.org/10.1002/jez.b.22614>

- 325 Griffith, O. W., Chavan, A. R., Protopapas, S., Maziarz, J., Romero, R., & Wagner, G. P. (2017).
326 Embryo implantation evolved from an ancestral inflammatory attachment reaction.
327 *Proceedings of the National Academy of Sciences*, 201701129.
328 <https://doi.org/10.1073/pnas.1701129114>
- 329 Grunstra, N. D. S., Zachos, F. E., Herdina, A. N., Fischer, B., Pavličev, M., & Mitteroecker, P.
330 (2019). Humans as inverted bats: A comparative approach to the obstetric conundrum.
331 *American Journal of Human Biology*, 31(2), e23227. <https://doi.org/10.1002/ajhb.23227>
- 332 Halley, A. C. (2017). Minimal variation in eutherian brain growth rates during fetal
333 neurogenesis. *Proceedings of the Royal Society B: Biological Sciences*, 284(1854),
334 20170219. <https://doi.org/10.1098/rspb.2017.0219>
- 335 Huelsenbeck, J. P., Nielsen, R., & Bollback, J. P. (2003). Stochastic mapping of morphological
336 characters. *Systematic Biology*, 52(2), 131–158.
337 <https://doi.org/10.1080/10635150390192780>
- 338 Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., Safi, K., Sechrest,
339 W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R.,
340 Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A., Rist, J., ... Purvis, A. (2009).
341 PanTHERIA: A species-level database of life history, ecology, and geography of extant
342 and recently extinct mammals. *Ecology*, 90(9), 2648–2648. <https://doi.org/10.1890/08-1494.1>
- 344 Künkele, J., & Trillmich, F. (1997). Are Precocial Young Cheaper? Lactation Energetics in the
345 Guinea Pig. *Physiological Zoology*, 70(5), 589–596. <https://doi.org/10.1086/515863>
- 346 Lillegraven, J. A. (1975). Biological considerations of the marsupial-placental dichotomy.
347 *Evolution*, 29(4), 707. <https://doi.org/10.2307/2407079>
- 348 Lillegraven, J. A., Thompson, S. D., McNab, B. K., & Patton, J. L. (1987). The origin of
349 eutherian mammals. *Biological Journal of the Linnean Society*, 32(3), 281–336.
350 <https://doi.org/10.1111/j.1095-8312.1987.tb00434.x>
- 351 Martin, R. D., & MacLarnon, A. M. (1985). Gestation period, neonatal size and maternal
352 investment in placental mammals. *Nature*, 313(5999), 220–223.
353 <https://doi.org/10.1038/313220a0>
- 354 O'Leary, M. A., Bloch, J. I., Flynn, J. J., Gaudin, T. J., Giallombardo, A., Giannini, N. P.,
355 Goldberg, S. L., Kraatz, B. P., Luo, Z.-X., Meng, J., Ni, X., Novacek, M. J., Perini, F. A.,
356 Randall, Z. S., Rougier, G. W., Sargis, E. J., Silcox, M. T., Simmons, N. B., Spaulding,
357 M., ... Cirranello, A. L. (2013). The Placental Mammal Ancestor and the Post-K-Pg
358 Radiation of Placentals. *Science*, 339(6120), 662–667.
359 <https://doi.org/10.1126/science.1229237>
- 360 Pavlicev, M., & Wagner, G. P. (2016). The Evolutionary Origin of Female Orgasm. *Journal of*
361 *Experimental Zoology Part B: Molecular and Developmental Evolution*, 326(6), 326–
362 337. <https://doi.org/10.1002/jez.b.22690>
- 363 Portmann, A. (1945). Die Ontogenese des Menschen als Problem der Evolutionsforschung.
364 *Verhandlungen Der Schweizerischen Naturforschenden Gesellschaft*, 1, 44–53.
365 <https://doi.org/10.5169/seals-90447>
- 366 R Core Team. (2023). *R: a language and environment for statistical computing* [Manual]. R
367 Foundation for Statistical Computing. <https://www.R-project.org/>

- 368 Renfree, M. B. (1993). Ontogeny, Genetic Control, and Phylogeny of Female Reproduction in
369 Monotreme and Therian Mammals. In F. S. Szalay, M. J. Novacek, & M. C. McKenna
370 (Eds.), *Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes,*
371 *Early Therians, and Marsupials* (pp. 4–20). Springer. https://doi.org/10.1007/978-1-4613-9249-1_2
- 373 Revell, L. J. (2024). phytools 2.0: An updated R ecosystem for phylogenetic comparative
374 methods (and other things). *PeerJ*, 12, e16505. <https://doi.org/10.7717/peerj.16505>
- 375 Revell, L. J. (2025). Ancestral State Reconstruction of Phenotypic Characters. *Evolutionary*
376 *Biology*. <https://doi.org/10.1007/s11692-025-09645-y>
- 377 Smith, K. K. (2001). The evolution of mammalian development. *Bulletin of the Museum of*
378 *Comparative Zoology*, 156, 119–135.
- 379 Smith, K. K., & Keyte, A. L. (2020). Adaptations of the Marsupial Newborn: Birth as an
380 Extreme Environment. *The Anatomical Record*, 303(2), 235–249.
381 <https://doi.org/10.1002/ar.24049>
- 382 Stadtmauer, D. J., & Wagner, G. P. (2019). Cooperative Inflammation: The Recruitment of
383 Inflammatory Signaling in Marsupial and Eutherian Pregnancy. *Journal of Reproductive*
384 *Immunology*, 102626. <https://doi.org/10.1016/j.jri.2019.102626>
- 385 Starck, J. M., & Ricklefs, R. E. (Eds.). (1998). *Avian growth and development: Evolution within*
386 *the altricial-precocial spectrum*. Oxford University Press.
- 387 Swaggart, K. A., Pavlicev, M., & Muglia, L. J. (2015). Genomics of Preterm Birth. *Cold Spring*
388 *Harbor Perspectives in Medicine*, 5(2), a023127–a023127.
389 <https://doi.org/10.1101/cshperspect.a023127>
- 390 Szdzuy, K., & Zeller, U. (2009). Lung and metabolic development in mammals: Contribution to
391 the reconstruction of the marsupial and eutherian morphotype. *Journal of Experimental*
392 *Zoology Part B: Molecular and Developmental Evolution*, 312B(6), 555–578.
393 <https://doi.org/10.1002/jez.b.21228>
- 394 Upham, N. S., Esselstyn, J. A., & Jetz, W. (2019). Inferring the mammal tree: Species-level sets
395 of phylogenies for questions in ecology, evolution, and conservation. *PLOS Biology*,
396 17(12), e3000494. <https://doi.org/10.1371/journal.pbio.3000494>
- 397 Wagner, G. P., Kin, K., Muglia, L., & Pavlicev, M. (2014). Evolution of mammalian pregnancy
398 and the origin of the decidual stromal cell. *The International Journal of Developmental*
399 *Biology*, 58(2–4), 117–126. <https://doi.org/10.1387/ijdb.130335gw>
- 400 Weaver, L. N., Fulghum, H. Z., Grossnickle, D. M., Brightly, W. H., Kulik, Z. T., Mantilla, G. P.
401 W., & Whitney, M. R. (2022). Multituberculate Mammals Show Evidence of a Life
402 History Strategy Similar to That of Placentals, Not Marsupials. *The American Naturalist*,
403 200(3), 383–400. <https://doi.org/10.1086/720410>
- 404 Werneburg, I., Laurin, M., Koyabu, D., & Sánchez-Villagra, M. R. (2016). Evolution of
405 organogenesis and the origin of altriciality in mammals. *Evolution & Development*, 18(4),
406 229–244. <https://doi.org/10.1111/ede.12194>
- 407 White, H. E., Tucker, A. S., Fernandez, V., Miguez, R. P., Hautier, L., Herrel, A., Urban, D. J.,
408 Sears, K. E., & Goswami, A. (2023). Pedomorphosis in the ancestry of marsupial
409 mammals. *Current Biology*, 33(11), 2136–2150.e4.
410 <https://doi.org/10.1016/j.cub.2023.04.009>

411 White, H. E., Tucker, A. S., & Goswami, A. (2024). Divergent patterns of cranial suture fusion
412 in marsupial and placental mammals. *Zoological Journal of the Linnean Society*, 203(2),
413 zlae060. <https://doi.org/10.1093/zoolinnean/zlae060>

414 Zeveloff, S. I., & Boyce, M. S. (1980). Parental Investment and Mating Systems in Mammals.
415 *Evolution*, 34(5), 973–982. <https://doi.org/10.2307/2408002>

416