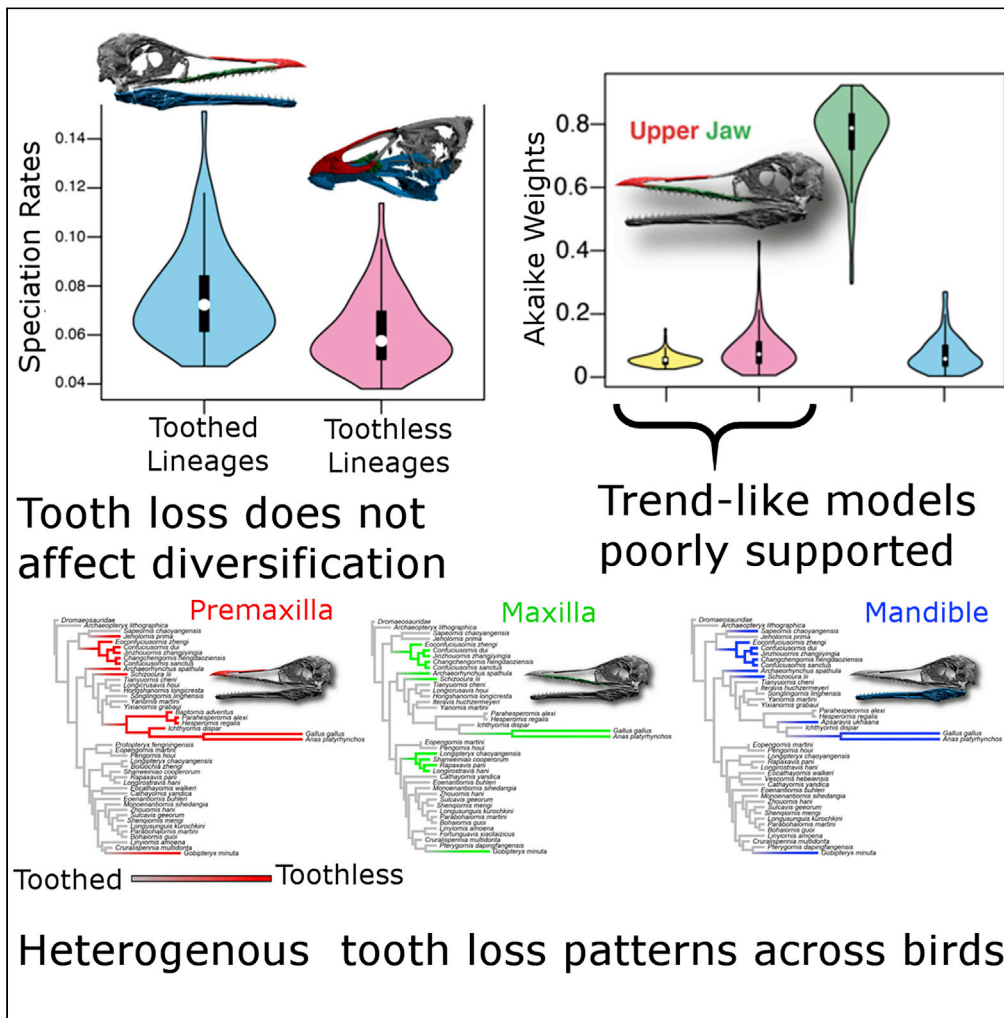


Article

Macroevolutionary dynamics of dentition in Mesozoic birds reveal no long-term selection towards tooth loss



Neil Brocklehurst,
Daniel J. Field

neil.brocklehurst@earth.ox.ac.uk

HIGHLIGHTS

The evolutionary processes underlying tooth loss in Mesozoic birds are debated

Analyses reveal no long-term selective pressure or trend toward toothlessness

Tooth loss was likely a result of local selective pressures on individual lineages

The transition to crown bird toothlessness occurred later than previously hypothesized

Brocklehurst & Field, iScience
24, 102243
March 19, 2021 © 2021 The Author(s).
<https://doi.org/10.1016/j.isci.2021.102243>



Article

Macroevolutionary dynamics of dentition in Mesozoic birds reveal no long-term selection towards tooth loss

Neil Brocklehurst^{1,3,*} and Daniel J. Field²

SUMMARY

Several potential drivers of avian tooth loss have been proposed, although consensus remains elusive as fully toothless jaws arose independently numerous times among Mesozoic avialans and dinosaurs more broadly. The origin of crown bird edentulism has been discussed in terms of a broad-scale selective pressure or trend toward toothlessness, although this has never been quantitatively tested. Here, we find no evidence for models whereby iterative acquisitions of toothlessness among Mesozoic Avialae were driven by an overarching selective trend. Instead, our results support modularity among jaw regions underlying heterogeneous tooth loss patterns and indicate a substantially later transition to complete crown bird edentulism than previously hypothesized (~90 mya). We show that patterns of avialan tooth loss adhere to Dollo's law and suggest that the exclusive survival of toothless birds to the present represents lineage-specific selective pressures, irreversibility of tooth loss, and the filter of the Cretaceous-Paleogene (K–Pg) mass extinction.

INTRODUCTION

The toothless beak is among the most characteristic features of the crown bird bauplan, and toothlessness has been hypothesized to increase the evolvability of crown bird jaws, partially underlying their sensational morphological disparity (Louchart and Viriot, 2011). Numerous potential drivers of avialan tooth loss have been proposed, including selection for flight-related weight reduction (Dilger, 1957; Feduccia, 1998; Proctor and Lynch, 1998) (though see [Zhou et al., 2019; Lautenschlager et al., 2013]), selection for rapid developmental rates precluding tooth formation (Yang and Sander, 2018), dietary shifts favoring alternative modes of food processing (Louchart and Viriot, 2011; Lautenschlager et al. 2013; Wang et al., 2017; Ksepka, et al., 2019), and selection for preening efficacy (Naish 2014; Mayr 2016). However, consensus remains elusive, as fully toothless jaws arose independently numerous times among Mesozoic avialans and dinosaurs more broadly (Louchart and Viriot, 2011; Dilger, 1957).

The origin of crown bird edentulism has been discussed in terms of a trend or selection toward toothlessness (Dilger, 1957; Zhou et al., 2019; Lautenschlager et al., 2013; Yang and Sander, 2018), implying an overarching selective pressure favoring edentulism throughout avialan evolutionary history as opposed to localized selection acting on subsidiary lineages as interpreted in other studies (O'Connor, 2019, 2020). For example, Zhou et al. (2019) justified their assumption of overarching selection favoring tooth loss in Avialae on the basis that it evolved numerous times independently: "Tooth loss occurred independently in several early avian lineages (Zhou and Zhang, 2006; Zhou et al., 2009; Davit-Béal et al., 2009), suggesting that reduction and eventual disappearance of the dentition might have conferred some broadly applicable selective advantage" (Zhou et al., 2019, pg 39). However, no studies had previously tested whether avialan edentulism was associated with increased rates of diversification (i.e., higher speciation rates and/or lower extinction rates), as would be predicted by overarching directional selection for a toothless bill through the Mesozoic, nor had they evaluated whether patterns of tooth loss across Avialae actually follow trend-like patterns. Such an interpretation does not align with other clades in which edentulism has arisen numerous times independently, such as crown mammals (Davit-Béal et al. 2009), which have never been suggested to exhibit a generalized trend toward edentulism.

The hypothesis of long-term selection or a trend toward edentulism in Avialae can be tested in two ways: identifying a shift in diversification rates associated with tooth loss could indicate selection for

¹Department of Earth Sciences, University of Oxford, South Parks Road, Oxford, UK

²Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, UK

³Lead contact

*Correspondence: neil.brocklehurst@earth.ox.ac.uk

<https://doi.org/10.1016/j.isci.2021.102243>



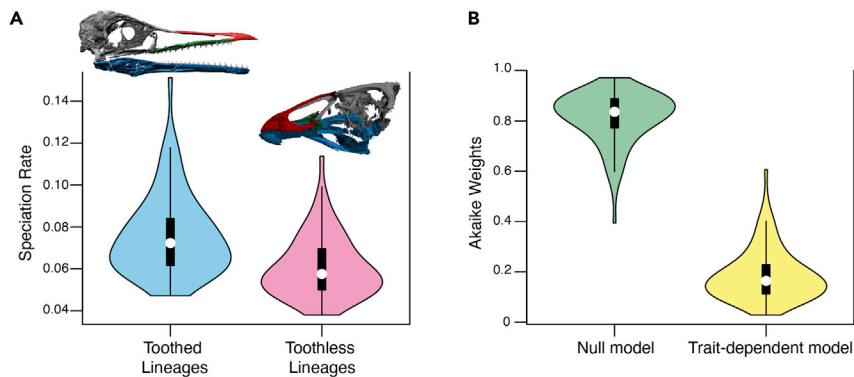


Figure 1. Results of state-dependent diversification analyses

(A) Violin plots showing speciation rates of toothed and toothless avialan lineages through the Mesozoic inferred from FiSSE analysis. Width of violins indicates the density of speciation rate values inferred from 100 time-calibrated trees. (B) Violin plots showing support for Null (no connection between diversification rates and presence or absence of teeth) and Trait-dependent (diversification rates depend on presence/absence of teeth) models inferred from HiSSE analysis. Width of the violin indicates the density of Akaike weights scores inferred from the 100 trees. *Ichthyornis* (toothed stem avialan) skull model modified from (Field et al., 2018b), and *Asteriornis* (toothless crown bird) skull model modified from (Field et al., 2020).

toothlessness on a broad phylogenetic scale [Jablonski, 2008; Rabosky and McCune, 2010], whereas demonstrating that regional losses of teeth within the jaws are more likely to lead to further losses of teeth would support the progression of edentulism throughout the jaws in a trend-like manner. We apply state-dependent diversification methods and evolutionary modeling to show that tooth loss had a negligible impact on avialan diversification, providing no evidence for a link between toothlessness and accelerated cladogenesis. We also found no evidence for models whereby iterative acquisitions of toothlessness among Mesozoic Avialae were driven by an overarching selective trend.

RESULTS AND DISCUSSION

No long-term selection toward toothlessness in Avialae

State-dependent diversification (SDD) methods (FiSSE [Rabosky and Goldberg, 2017]) and HiSSE [Beaulieu & O'Meara, 2016]) reject the hypothesis that edentulism provided a selective advantage throughout the evolutionary history of Avialae (operationally defined here as the clade uniting *Archaeopteryx* and crown birds). Speciation rates inferred by FiSSE were higher in toothed avialans than in toothless avialans (Figure 1A). However, these differences were never significant ($p < 0.05$), implying that diversification rates were not substantially affected by the presence or absence of teeth (Table S2). HiSSE analyses fit a null model better than a state-dependent model, suggesting that avialan patterns of speciation and extinction were unrelated to tooth loss (Figure 1B). These results are consistent when considering transitions to complete toothlessness, as well as transitions to regional edentulism in the premaxilla, maxilla, and dentary (Figures S1–S6). We confirmed that these results are not an artifact of incomplete sampling with a taxonomic jackknifing approach (Close et al., 2015). Although the range of rate values and Akaike weight scores are greater in jackknifed datasets, we still obtained overwhelming support for a null model over a trait-dependant model of diversification (Figure S7) and found no significant difference between speciation rates of toothed versus toothless taxa (Figure S8).

We also found no evidence for a general trend toward edentulism throughout avialan evolutionary history. Loss of teeth in one region of the upper jaw (e.g., premaxilla) did not increase the likelihood of tooth loss in another region of the jaw (e.g., maxilla), and vice versa. Instead, model fits supported the premaxilla and maxilla as discrete modules with largely independent trajectories with respect to tooth loss and tooth retention (Figure 2A), which is understandable in light of the differing populations of primordia, tissues, and cells from which these elements arise (Helms and Schneider, 2003; Schneider and Helms 2003; Wang et al., 2020a). The independent patterns of tooth loss in the premaxilla and maxilla provide evidence against strong directional selection driving transitions to toothlessness across avialans. Although there are several instances of tooth-loss in the premaxilla coinciding with that in the maxilla (e.g., Confuciusornithidae, *Gobipteryx*, *Schizooura*), there are also numerous instances where the evolution of toothlessness in one region occurred independently of the other (e.g., *Jeholornis*, Longipterygidae), or

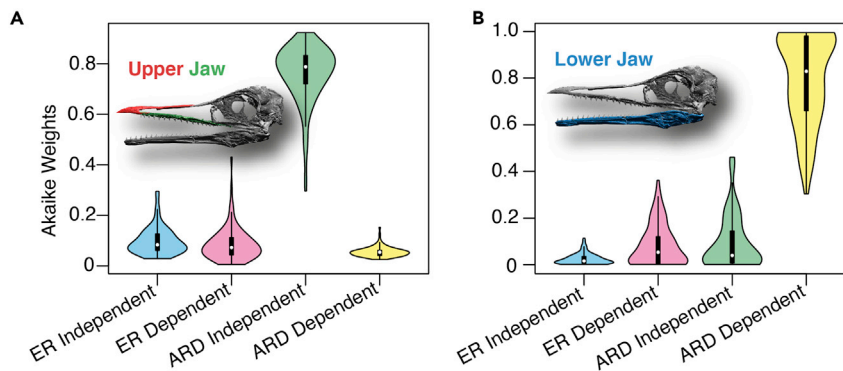


Figure 2. Violin plots showing support for models of dependent (integrated) versus independent (modular) evolution of discrete dental characters

Width of the violin indicates the density of Akaike weights scores inferred from the 100 trees. ER: Equal Rates; ARD: All rates different

(A) Results for degree of integration of presence/absence of teeth in the premaxilla (red bone) and maxilla (green bone).

(B) Results for degree of integration of presence/absence of teeth in the anterior and posterior portions of the dentary (blue bone). *Ichthyornis* skull models modified from (Field et al., 2018b)

where the evolution of toothlessness in one region preceded that in the other by more than 30 million years (Ornithurae). These idiosyncratic patterns, combined with the results of our model-fitting analyses, indicate that transitions toward regional or complete tooth loss in Avialae reflect lineage-specific patterns, rather than a broad-scale trend toward toothlessness across Avialae.

In contrast to the largely modular behavior of the anterior and posterior regions of the upper jaw, the anterior and posterior regions of the lower jaw exhibit tighter integration, most likely because the only ancestrally tooth-bearing element (the dentary) comprises a single bone derived from paired mandibular primordia during embryonic development (Schneider and Helms 2003) (Figure 2B). However, several avialan fossils illustrate that teeth may be present or absent throughout the entire lower jaw, or in either the anterior or posterior region of the dentary (e.g., *Jeholornis* only exhibits teeth in the anterior portion of the dentary [Zhou and Zhang 2002]), demonstrating that, although more integrated than the upper jaw, the lower jaw may exhibit comparable patterns of regional edentulism (Figure 2B).

Idiosyncratic trajectories toward full edentulism are observed across Avialae. For example, within Enantiornithes, instances of maxillary tooth loss preceding premaxillary tooth loss are observed (Figure 3) and are further substantiated by the recent description of the probable latest Cretaceous enantiornithine *Falcatakely* (O'Connor et al., 2020). By contrast, the route to neornithine toothlessness began with the loss of premaxillary teeth from otherwise fully toothed jaws: Hesperornithes and *Ichthyornis* (the immediate outgroups to Neornithes) exhibit only maxillary teeth in the upper jaws (Figure 3). However, this directionality is not universal among ornithuromorphs; taxa within Schizoouridae appear to have lost their maxillary teeth first (*Schizooura* is entirely edentulous, whereas *Mengciusornis* exhibits only premaxillary teeth) (Wang et al., 2020b).

The origin of crown bird edentulism has been discussed in terms of a broad-scale selective pressure or trend toward toothlessness (Dilger, 1957; Zhou et al., 2019; Lautenschlager et al., 2013; Yang and Sander, 2018), although the hypothesis of such dynamics underlying the origin of crown bird toothlessness has not been quantitatively tested. In light of our results, we contend that the numerous iterative transitions to toothlessness in Avialae reflect selection on a phylogenetically localized scale combined with an underlying developmental propensity for tooth loss, instead of the outcome of long-term directional selection.

We posit that explorations of the evolutionary dynamics of Mesozoic avialan edentulism have been unduly biased by the fact that all crown birds are toothless. Indeed, the ubiquity of edentulism in crown birds—characterizing all >10,000 living species, and the entirety of the neornithine fossil record going back to the latest Cretaceous (Field et al., 2020)—appears to be a mere artifact of survival. Avian survivorship to the present day was strongly influenced by the end-Cretaceous mass extinction 66.02 Ma (Clyde et al., 2016), a single event through which only Neornithes are known to have survived (Feduccia, 1995; Longrich

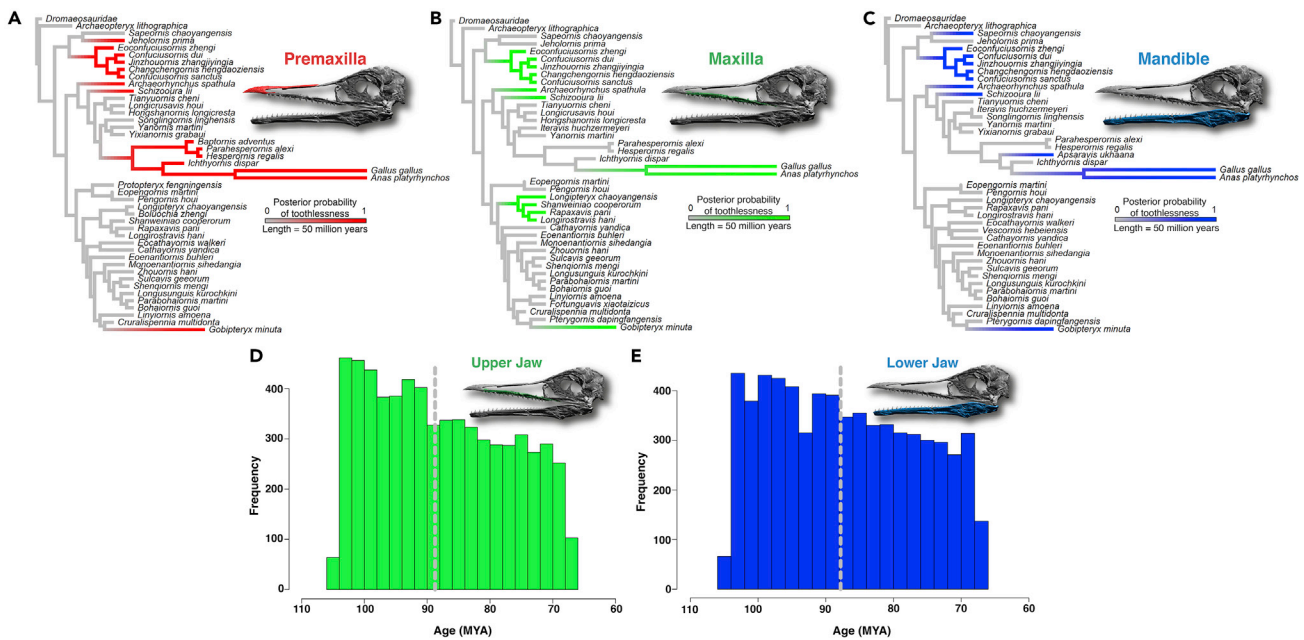


Figure 3. Evolution of complete tooth loss in ancestrally tooth-bearing jaw bones across Avialae

(A–C) Maximum clade credibility trees with branch colors corresponding to the proportion of stochastic maps indicating a toothless state along phylogenetic branches through time. (A) Results for premaxilla; (B) results for maxilla; (C) results for dentary.

(D and E) Histogram indicating estimates of the point in Earth history when the transition to toothlessness homologous with that of crown birds took place in various jaw bones: (D) the maxilla (the last tooth-bearing bone in the upper jaw along the neornithine stem lineage) and (E) the dentary (lower jaw). Dashed vertical lines represent median age estimates for these transitions. *Ichthyornis* skull models modified from (Field et al., 2018b)

et al., 2011; Prum et al., 2014; Field et al., 2018a). Although the toothless bill of avian survivors may have been well suited to exploiting resources such as insects and seeds in the extinction's aftermath (Larson et al., 2016; Field et al., 2018a), the fact that only toothless avialans have persisted to the present day appears to have more to do with patterns of extinction and survival across the end-Cretaceous mass extinction event—which may have been unrelated to dentition—than with any long-term directional trend toward avialan edentulism throughout the Mesozoic.

Timing the origin of crown bird toothlessness

Crown birds comprise a single clade (Neornithes) to the exclusion of all known toothed avialans, and their present-day edentulism presumably reflects a single evolutionary transition to toothlessness in the Late Cretaceous (Meredith et al., 2014a). Our median estimate for the timing of the transition to full edentulism in the upper and lower jaws homologous with the condition in crown birds is slightly less than 90 mya (Figure 3). The median age estimate for the transition to a toothless maxilla homologous with that of crown birds is 88.46 mya (range of estimates = 104.33–67.25, with a skew toward earlier ages), and the median age estimate for the transition to a toothless dentary homologous with that of crown birds is 87.55 mya (range = 104.28–67.19, with a similar skew). Both of these are substantially younger than previous estimates (116 mya [Meredith et al., 2014a]).

Dollo's law and edentulism

Dollo's law (Gould, 1970) posits that complex features lost through evolutionary change are unlikely to be re-acquired in the same form. Tooth loss has been cited as a conspicuous example of Dollo's law: of the numerous avialan lineages that have evolved complete edentulism, none are thought to have undergone a reversal to a toothed state (Louchart and Viriot, 2011; Collin and Miglietta, 2008) (although complete dentition in Enantiornithes optimized as an evolutionary reversal in at least one parsimony analysis [Turner et al., 2012], this inference has been interpreted as unlikely to be accurate [Mayr 2016]). In a notable non-avian example, teeth are thought to have re-evolved in the previously toothless dentary of the frog *Gastrotheca guentheri* (Wiens 2011). However, unlike the situation in crown birds, the ancestral condition for *G. guentheri* was not complete edentulism, because frogs maintain teeth in their upper jaw. Despite independently acquiring tooth-like projections formed by the

Table 1. Instantaneous transition probabilities of tooth loss in different regions of the jaw

	Model	Transition probabilities		To			
		From		0 0	0 1	1 0	1 1
Premaxilla maxilla	Independent ARD	0 0		–	0.016	0.016	0
		0 1		0	–	0	0
		1 0		0	0	–	0.016
		1 1		0	0	0	–
Anterior dentary posterior dentary	Dependent ARD	0 0		–	0.029	0.238	0
		0 1		0	–	0	0.052
		1 0		0	0	–	0
		1 1		0	0	0	–

Inferred for the best models of evolution of toothlessness in each region of the jaw, fit to the maximum clade credibility tree. Character score of 0 = presence of teeth; 1 = absence of teeth. ARD: All rates different.

rhamphotheca and sometimes the underlying jaw bones several times (e.g., Pelagornithidae, mergansers [Anatidae: Mergini], plantcutters [*Phytotoma*: Cotingidae] (Louchart et al., 2013, 2018; Kennedy, 1948; Kirwan and Green 2012), crown birds have never reacquired teeth. *Talpid*² mutant chicks can develop tooth buds (Harris et al., 2006), illustrating that at least some birds retain the genetic underpinnings of tooth development, but this is a lethal mutation. Indeed, the genome of the red junglefowl shows that genes necessary for enamel formation have been lost, precluding the full development of teeth (International Chicken Polymorphism Map Consortium, 2004).

Our model-fitting analyses support the irreversibility of tooth loss across Avialae (Figure 2, Table 1): Patterns of toothlessness across avialan phylogeny best fit models of evolution where transitions from a toothless to a toothed state have instantaneous transition probabilities of zero (Table 1). Stochastic mapping across our maximum clade credibility tree under the best-fitting evolutionary model suggests at least five independent transitions to complete edentulism among the taxa sampled in our phylogeny (Figures 3A–3C): preceding the origin of Confuciusornithidae, within Enantiornithes, separately along the lineages leading to the ornithuromorphs *Archaeorhynchus* and *Schizooura*, and preceding the origin of crown birds (Neornithes). Indeed, *Mengciusornis*—a recently described Cretaceous ornithuromorph inferred to be a close relative of *Schizooura*—exhibits teeth in its premaxilla (Wang et al., 2020b), helping to corroborate our inference that the transition leading to toothlessness in *Schizooura* occurred independently from that of *Archaeorhynchus*. Additional potentially independent transitions to toothlessness among taxa not sampled in our phylogeny include the ornithuromorph *Eo granivora* (Zheng et al., 2018), and the ornithothoracine *Xinghaiornis* (Wang et al., 2013).

Notably, our stochastic mapping approach did not identify any probable reversals from a toothless state to a toothed state in the premaxilla, maxilla, or dentary throughout avialan evolutionary history. Although repeated independent acquisitions of pointed jaw projections such as pseudoteeth provide *prima facie* evidence for the selective benefit of tooth-like projections in some neornithine subclades subsequent to tooth loss (Louchart et al. 2013, 2018), these instances have never led to a reversal to a toothed state. As such, avian edentulism adheres to the expectations of Dollo’s law.

Limitations of the study

Limitations of the present study are primarily related to the nature of the Mesozoic avialan fossil record. All fossil records are incomplete, and that of Mesozoic birds has been shown to be biased by incomplete preservation and heterogeneous human sampling (Brocklehurst et al., 2012). The incompleteness of many Mesozoic avialan specimens (Brocklehurst et al., 2012) imposes limits on the methods we were able to use to evaluate evidence for sustained selective pressures or trends throughout avialan evolutionary history. With precise information on tooth numbers for a greater proportion of Mesozoic avialans it would have been possible to treat tooth number as a continuous character, enabling exploration of selective pressure toward tooth loss in the context of an Ornstein-Uhlenbeck model (in which a trait is drawn to an adaptive peak), or explicit testing of continuous trend-like models. However, as most of the taxa investigated here are represented by variably incomplete fossil remains, requiring such precise counts of tooth numbers would have necessitated the exclusion of many taxa from our analyses. Instead, discrete characters

representing presence or absence of teeth in particular regions were generated, with SDD methods used to assess selection and analyses of character interdependence applied to assess trends. We consider this approach to represent a satisfactory compromise in light of the available data.

SDD methods have been shown to be impacted by incomplete sampling (Harvey and Rabosky, 2018; Fitz-John et al., 2009). However, by using a taxonomic jackknifing approach (where analyses were repeated on a dataset from which taxa were removed at random [Close et al., 2015]), we illustrated that variations in our taxon sample did not induce substantial changes in our results. We therefore consider our sample adequate to support robust conclusions on state-dependent diversification.

Conclusions

It may be tempting to assume that the origin of neornithine edentulism reflects the culmination of an overarching selective pressure or general evolutionary trend toward toothlessness across Avialae. However, transitions to toothlessness in all or part of the jaw evolved via alternative pathways among Mesozoic avialans (Figure 3), and these do not appear to have been associated with increased speciation rates or reduced extinction rates (Figure 1). It is clear that the apparently irreversible transition to neornithine edentulism reflects only one of several transitions to toothlessness throughout the Mesozoic evolutionary history of Avialae, Theropoda, and Reptilia more broadly (Louchart, and Viriot, 2011; Dumont et al., 2016; Pérez-Moreno et al., 1994; Ma et al., 2017; Li et al., 2008), and that at least some independently edentulous non-crown avialans were present in the Late Cretaceous (Elzanowski 1977; Chiappe et al., 2001). We suggest that the ubiquity of the toothless beak among Neornithes simply reflects the sole survival of this single edentulous avialan subclade across the end-Cretaceous mass extinction event, and that neornithine survival may have had little to do with any specific advantages conferred by toothlessness. This interpretation emphasizes the potential for historical contingencies to govern the origin of some of the most ubiquitous morphological patterns observable in the modern world.

METHODS

All methods can be found in the accompanying [transparent methods supplemental file](#).

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2021.102243>.

ACKNOWLEDGMENTS

We thank Albert Chen for helpful comments and Juan Benito for assistance with figures. N.B.'s research was supported by Deutsche Forschungsgemeinschaft grant no. BR 5724/1-1p. D.J.F.'s research is supported by UKRI Future Leaders Fellowship MR/S032177/1 and Royal Society Research Grant RGS/R2/192390.

AUTHOR CONTRIBUTIONS

Conceptualization, N.B., D.J.F.; methodology, N.B.; data, D.J.F.; analysis, N.B.; writing, N.B. and D.J.F.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: June 15, 2020

Revised: December 16, 2020

Accepted: February 25, 2021

Published: March 19, 2021

REFERENCES

- Beaulieu, J.M., and O'Meara, B.C. (2016). Detecting hidden diversification shifts in models of trait-dependent speciation and extinction. *Syst. Biol.* 65, 583–601.
- Brocklehurst, N., Upchurch, P., Mannion, P.D., and O'Connor, J. (2012). The completeness of the fossil record of Mesozoic birds: implications for early avian evolution. *PLoS One* 7, e39056.
- Chiappe, L.M., Norell, M., and Clark, J. (2001). A new skull of *Gobipteryx minuta* (Aves: Enantiornithes) from the cretaceous of the Gobi Desert. *Am. Mus. Novitat.* 3346, 1–15.
- Close, R.A., Friedman, M., Lloyd, G.T., and Benson, R.B. (2015). Evidence for a mid-Jurassic adaptive radiation in mammals. *Curr. Biol.* 25, 2137–2142.
- Clyde, W.C., Ramezani, J., Johnson, K.R., Bowring, S.A., and Jones, M.M. (2016). Direct

- high precision U–Pb geochronology of the end-Cretaceous extinction and calibration of Paleocene astronomical timescales. *Earth Planet. Sci. Lett.* 452, 272–280.
- Collin, R., and Miglietta, M.P. (2008). Reversing opinions on Dollo's law. *Trends Ecol. Evol.* 23, 602–609.
- Davit-Béal, T., Tucker, A.S., and Sire, J.-Y. (2009). Loss of teeth and enamel in tetrapods: fossil record, genetic data and morphological adaptations. *J. Anat.* 214, 477–501.
- Dilger, W.C. (1957). The loss of teeth in birds. *The Auk* 74, 103–104.
- Dumont, M., Tafforeau, P., Bertin, T., Bhullar, B.A., Field, D., Schup, A., Strilisky, B., Thivichon-Prince, B., Viriot, L., and Louchart, A. (2016). Synchrotron imaging of dentition provides insights into the biology of *Hesperornis* and *Ichthyornis*, the “last” toothed birds. *BMC Evol. Biol.* 16, 178.
- Elzanowski, A. (1977). Skulls of *Gobiapteryx* (Aves) from the upper Cretaceous of Mongolia. *Acta Paleontol. Pol.* 37, 153–165.
- Feduccia, A. (1995). Explosive evolution in Tertiary birds and mammals. *Science* 267, 637–638.
- Feduccia, A. (1998). *The Origin and Evolution of Birds*, 2nd edition (Yale University Press).
- Field, D.J., Bercovici, A., Berv, J.S., Dunn, R., Fastovsky, D.E., Lyson, T.R., Vajda, V., and Gauthier, J.A. (2018a). Early evolution of modern birds structured by global forest collapse at the end-Cretaceous mass extinction. *Curr. Biol.* 28, 1825–1831.
- Field, D.J., Hanson, M., Burnham, D., Wilson, L.E., Super, K., Ehret, D., Ebersole, J.A., and Bhullar, B.-A.S. (2018b). Complete *Ichthyornis* skull illuminates mosaic assembly of the avian head. *Nature* 557, 96–100.
- Field, D.J., Benito, J., Chen, A., Jagt, J.W., and Ksepka, D.T. (2020). Late Cretaceous neornithine from Europe illuminates the origins of crown birds. *Nature* 579, 397–401.
- FitzJohn, R.G., Maddison, W.P., and Otto, S.P. (2009). Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Syst. Biol.* 58, 595–611.
- Gould, S.J. (1970). Dollo on Dollo's law: irreversibility and the status of evolutionary laws. *J. Hist. Biol.* 3, 189–212.
- Harris, M.P., Hasso, S.M., Ferguson, M.W., and Fallon, J.F. (2006). The development of archosaurian first-generation teeth in a chicken mutant. *Curr. Biol.* 16, 371–377.
- Harvey, M.G., and Rabosky, D.L. (2018). Continuous traits and speciation rates: alternatives to state-dependent diversification models. *Method Ecol. Evol.* 9, 984–993.
- Helms, J.A., and Schneider, R.A. (2003). Cranial skeletal biology. *Nature* 423, 326–331.
- International Chicken Polymorphism Map Consortium (2004). A genetic variation map for chicken with 2.8 million single-nucleotide polymorphisms. *Nature* 432, 717–722.
- Jablonski, D. (2008). Species selection theory and data. *Annu. Rev. Ecol. Evol.* 39, 501–504.
- Kennedy, P.G. (1948). Birds of the countryside Part XIX: mergansers and grebes. *Studies* 37, 75–83.
- Ksepka, D.T., Grande, L., and Mayr, G. (2019). Oldest finch-beaked birds reveal parallel ecological radiations in the earliest evolution of passerines. *Curr. Biol.* 29, 132–134.
- Larson, D.W., Brown, C.M., and Evans, D.C. (2016). Dental disparity and ecological stability in bird-like dinosaurs prior to the end-Cretaceous mass extinction. *Curr. Biol.* 26, 1325–1333.
- Lautenschlager, S., Witmer, L.M., Altangerel, P., and Rayfield, E.J. (2013). Edentulism, beaks, and biomechanical innovations in the evolution of theropod dinosaurs. *Proc. Nat. Acad. Sci. U S A* 110, 20657–20662.
- Li, C., Wu, X.C., Rieppel, O., Wang, L.T., and Zhao, L.J. (2008). An ancestral turtle from the Late Triassic of southwestern China. *Nature* 456, 497–501.
- Longrich, N.R., Tokaryk, T., and Field, D.J. (2011). Mass extinction of birds at the Cretaceous–Paleogene (K–Pg) boundary. *Proc. Nat. Acad. Sci. U S A* 108, 15253–15257.
- Louchart, A., and Viriot, L. (2011). From snout to beak: the loss of teeth in birds. *Trends Ecol. Evol.* 26, 663–673.
- Louchart, A., Sire, J.E., Mourer-Chauviré, C., Geraads, D., Viriot, L., and de Buffrenil, V. (2013). Structure and growth pattern of pseudoteeth in *Pelagornis mauretanicus* (Aves, Odontopterygiformes, Pelagornithidae). *PLoS One* 8, e80372.
- Louchart, A., De Buffrenil, V., Bourdon, E., Dumont, M., Viriot, L., and Sire, J.Y. (2018). Bony pseudoteeth of extinct pelagic birds (Aves, Odontopterygiformes) formed through a response of bone cells to tooth-specific epithelial signals under unique conditions. *Sci. Rep.* 8, 1–9.
- Ma, W., Wang, J., Pittman, M., Tan, Q., Tan, L., Guo, B., and Xu, X. (2017). Functional anatomy of a giant toothless mandible from a bird-like dinosaur: *Gigantoraptor* and the evolution of the oviraptorosaurian jaw. *Sci. Rep.* 7, 1–15.
- Mayr, G. (2016). *Avian Evolution: The Fossil Record of Birds and its Paleobiological Significance* (John Wiley & Sons).
- Meredith, R.W., Zhang, G., Gilbert, M.T.P., Jarvis, E.D., and Springer, M.S. (2014). Evidence for a single loss of mineralized teeth in the common avian ancestor. *Science* 346, 1254390.
- Naish, D. (2014). The fossil record of bird behaviour. *J. Zool.* 292, 268–280.
- O'Connor, J. (2019). The trophic habits of early birds. *Palaeogeogr. Palaeoclim. Palaeoecol.* 513, 178–195.
- O'Connor, J. (2020). The evolution of the modern avian digestive system: insights from paravian fossils from the Yanliao and Jehol biotas. *Palaeontology* 63, 13–27.
- O'Connor, P.M., Turner, A.H., Groenke, J.R., Felice, R.N., Rogers, R.R., Krause, D.W., and Rahantarisoa, L.J. (2020). Late Cretaceous bird from Madagascar reveals unique development of beaks. *Nature* 588, 272–276.
- Pérez-Moreno, B.P., Sanz, J.L., Buscalioni, A.D., Moratalla, J.J., Ortega, F., and Rasskin-Gutman, D. (1994). A unique multitoothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain. *Nature* 370, 363–367.
- Proctor, N.S., and Lynch, P.J. (1998). *Manual of Ornithology: Avian Structure and Function* (Yale University Press).
- Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Lemmon, E.M., and Lemmon, A.R. (2014). A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* 526, 569–573.
- Rabosky, D.L., and McCune, A.R. (2010). Reinventing species selection with molecular phylogenies. *Trends Ecol. Evol.* 25, 68–74.
- Rabosky, D.L., and Goldberg, E.E. (2017). FiSSE: a simple nonparametric test for the effects of a binary character on lineage diversification rates. *Evolution* 71, 1432–1442.
- Schneider, R.A., and Helms, J.A. (2003). The cellular and molecular origins of beak morphology. *Science* 299, 565–568.
- Turner, A.H., Makovicky, P.J., and Norell, M.A. (2012). A review of dromaeosaurid systematics and paravian phylogeny. *Bull. Am. Mus. Nat. Hist.* 371, 1–206.
- Wang, X., Luis, C.M., Fangfang, T., and Qiang, J. (2013). *Xinghaiornis lini* (Aves: Ornithothoraces) from the Early Cretaceous of Liaoning: an example of evolutionary mosaic in early birds. *Acta Geol. Sin* 87, 686–689.
- Wang, S., Stiegler, J., Wu, P., Chong, C.-M., Hu, D., Balanoff, A., Zhou, Y., and Xing, X. (2017). Heterochronic truncation of odontogenesis in theropod dinosaurs provides insight into the macroevolution of avian beaks. *Proc. Nat. Acad. Sci. U S A* 114, 10930–10935.
- Wang, S., Stiegler, J., Wu, P., and Chuong, C.-M. (2020a). Tooth vs. beak: the evolutionary developmental control of the avian feeding apparatus. In *Pennaraptoran Theropod Dinosaurs: Past Progress and New Frontiers*, M. Pittman and X. Xu, eds. (Bulletin of the American Museum of Natural History), pp. 205–228.
- Wang, M., O'Connor, J., Zhou, S., and Zhou, Z.-H. (2020b). New toothed Early Cretaceous ornithomorph bird reveals intraclade diversity in pattern of tooth loss. *J. Syst. Paleontol.* 18, 631–645.
- Wiens, J.J. (2011). Re-evolution of lost mandibular teeth in frogs after more than 200 million years, and re-evaluating Dollo's law. *Evolution* 65, 1283–1296.
- Yang, T.R., and Sander, P.M. (2018). The origin of the bird's beak: new insights from dinosaur incubation periods. *Biol. Lett.* 14, 20180090.

Zheng, X., O'Connor, J., Wang, X., and Zhou, Z. (2018). Reinterpretation of a previously described Jehol bird clarifies early trophic evolution in the Ornithuromorpha. *Proc. R. Soc. B* 285, 20172494.

Zhou, Z.-H., and Zhang, F.-C. (2002). A long-tailed, seed-eating bird from the Early Cretaceous of China. *Nature* 418, 405–409.

Zhou, Z.H., and Zhang, F.C. (2006). A beaked basal ornithurine bird (Aves, Ornithurae) from the Lower Cretaceous of China. *Zool. Scr.* 35, 363–373.

Zhou, Z.H., Li, Z.H., and Zhang, F.C. (2009). A new Lower Cretaceous bird from China and tooth

reduction in early avian evolution. *Proc. Biol. Sci.* 277, 219–227.

Zhou, Y.C., Sullivan, C., and Zhang, F.C. (2019). Negligible effect of tooth reduction on body mass in Mesozoic birds. *Vert PalAs* 57, 38–50.

iScience, Volume 24

Supplemental information

**Macroevolutionary dynamics of dentition
in Mesozoic birds reveal no long-term
selection towards tooth loss**

Neil Brocklehurst and Daniel J. Field

Transparent Methods

KEY RESOURCES TABLE

Reagent or resource	Source	Identifier
Software and algorithms		
MrBayes version 3.2.6	Ronquist & Huelsenbeck (2003)	http://nbisweden.github.io/MrBayes/
R version 3.4.3	R Core Team (2017)	https://www.r-project.org/
Phytools (R package)	Revell (2013)	https://cran.r-project.org/web/packages/phytools/index.html
hisse (R package)	Beulieu & O'Meara (2016)	https://cran.r-project.org/web/packages/hisse/index.html
FiSSE (R function)	Rabosky & Goldberg (2017)	https://onlinelibrary.wiley.com/doi/abs/10.1111/1/evo.13227
BayesTraits	Pagel & Meade (2006)	http://www.evolution.rdg.ac.uk/BayesTraitsV3.0.2/BayesTraitsV3.0.2.html
Other		
Character/taxon matrix of birds	Modified for this study from Field et al. (2018b)	Supplementary Data 1

RESOURCE AVAILABILITY

Lead Contact – Neil Brocklehurst

Materials Availability

This study did not use or generate any new material

Data and Code Availability

The Nexus file employed is presented in the Supplementary Data 1. All analyses were carried out in MrBayes and *R* using functions from packages cited in the text. No novel code was used in this study. Example code and files for use is present in the Supplementary Data 2.

METHOD DETAILS

Phylogeny

The phylogenetic framework for this study was produced using a recent character matrix (Field et al 2018b) from a large-scale analysis of Mesozoic Avialae, containing 67 taxa. Scores were based on original taxonomic descriptions, but in some instances were modified in light of updated observations (the recognition of maxillary teeth in *Jeholornis* [Hu et al. 2019] and the presence of maxillary teeth in *Monoenantiornis* [Hu & O'Connor 2017]). The matrix was analyzed under the Fossilised Birth Death (FBD) model to produce time-scaled topologies. This Bayesian approach integrates both the ages of taxa and their character state information to simultaneously estimate phylogenetic relationships and branch

lengths (Heath et al. 2014). The analysis was implemented in MrBayes 3.2.6 (Ronquist & Huelsenbeck 2003).

To account for uncertainty in the timing of first appearances of fossil taxa, the ages of taxa were represented by a uniform probability distribution covering the full possible age of the formation or assemblage zone in which they first appeared. The avialan root (all taxa in the matrix except the outgroup Dromaeosauridae) was calibrated using an offset exponential prior with a minimum age of 153 MYA (just older than the age of the oldest taxa in the matrix) and a mean age of 160.7 MYA (halfway between the age of the oldest-known avialan and the oldest-known representative of the outgroup, Dromaeosauridae). An internal node calibration was used to constrain the origin of Neornithes (crown birds) to ages consistent with recent molecular estimates: The most recent common ancestor of *Anas* and *Gallus* (the only two neornithines in the dataset) was calibrated using a truncated normal prior, with a minimum age of 66.7 MYA (the age of the near-crown galloanseran *Asteriornis maastrichtensis* (Field et al. 2020), a mean age of 69.1 MYA, and a standard deviation of 8.65 (the latter two parameters taken from the molecular divergence study of Grealy et al. (2017).

Patterns of character evolution were incorporated using the independent gamma rates prior (an uncorrelated clock model where rates are drawn from a gamma distribution). Rate heterogeneity between characters was also modelled as a gamma distribution. The analysis was carried out with two runs containing two chains for 10,000,000 generations, sampling every 1,000. 25% of trees were discarded as burn-in. To ensure that uncertainty surrounding relationships and divergence times was accounted for, a random sample of 100 trees was drawn from the posterior distribution to be the subject of subsequent analyses. Convergence was determined by the potential scale reduction factor approaching 1 (observed value 1.002) and the standard deviation of split frequencies being less than 0.05 (observed value 0.023)

Illustration of evolutionary history

The evolutionary history of edentulism in the three tooth-bearing bones (premaxilla, maxilla, and dentary) was simulated across the maximum clade credibility tree produced under the fossilised birth-death model. This was done using the *simmap* approach [66] implemented in *R* (R Core Team 2017), using functions in the package *phytools* (Revell 2013). This approach fits a continuous-time model of character evolution to a phylogenetic tree to infer transition rates, then simulates character evolution using these rates and the tip states. Following the results of model fitting analyses of character evolution (see below), an All Rates Different model (where rates of change are affected by the direction of transitions) was used to simulate the evolution of edentulism in the three tooth-bearing jaw bones across Avialae. 1,000 such simulations were performed. It should be noted that, due to limited sampling of Neornithes (crown birds) in the phylogenetic dataset, and the resultant long branches leading to the two extant neornithines included (*Anas* and *Gallus*), the stochastic mapping approach sometimes identified independent origins of edentulism in *Gallus* and *Anas* rather than a single transition along the branch leading to Neornithes, as universally accepted. Multiple losses of teeth in Neornithes is contradicted by genetic, developmental, and available fossil evidence (Field et al. 2020; Meredith et al. 2014a,b), thus artefactually-mapped losses along these two extant branches were ignored when calculating the median and range of ages of tooth loss events.

QUANTIFICATION AND STATISTICAL ANALYSIS

Diversification Analyses

State-dependent diversification (SDD) methods (BiSSE and its derivatives) allow identification of variation in speciation and extinction rates relating to discrete characters evolving over a phylogeny (Davis et al 2013). At present, however, such methods are only available for ultrametric trees (trees where each tip has the same age). To obtain an ultrametric topology in order to apply these methods to Mesozoic avialans, the FBD trees were time-sliced at 125 MYA. This point in avialan phylogenetic history includes a broad sample of toothed and toothless avialans, as well as taxa exhibiting regional edentulism (e.g., toothed premaxillae but toothless maxillae). Slicing the tree at 125 MYA ensures sampling of the Chinese Yixian and Jiufotang fossil Lagerstätten, which have produced over 40% of all known Mesozoic avialan species (Brocklehurst et al. 2012) and over half of the taxa included in our phylogeny, maximising the sample size and quality of the fossils included in the SDD analyses.

Associations between toothlessness and diversification patterns were assessed using both HiSSE and FiSSE methods. HiSSE (Beaulieu & O’Meara 2016) is a method that allows comparison of two models: the first being a standard BiSSE model where a trait of interest is linked to speciation and extinction rates, and a null model where the rates are linked to a “hidden” binary trait evolving independently from the trait of interest. The two models are compared using Akaike weights.

FiSSE (Rabosky & Goldberg 2017) is a non-parametric method that estimates speciation rates associated with each character state and compares this with a null model where the character evolves over the tree at random. FiSSE was shown to have lower false positive rates for inferring associations between traits and diversification rates than BiSSE and HiSSE (Rabosky & Goldberg 2017), but can only be used to assess speciation rates, not extinction rates.

Four binary characters relating to the presence/absence of teeth were assessed using these methods. The first related to complete edentulism (i.e. teeth either present or absent throughout both lower and upper jaws). Characters relating to the presence/absence of teeth in the maxilla, in the premaxilla, and in the dentary were also tested individually. For each test, taxa scored as unknown were dropped from the tree. Since numerous Mesozoic avialans show partial edentulism (e.g., teeth absent only in the premaxilla in taxa such as *Ichthyornis* [Field et al. 2018b]), if the status of one of the tooth-bearing bones was unclear, the taxon was scored as unknown for the character relating to complete edentulism. HiSSE analyses were implemented in *R* using the *R* package *hisse* (Beaulieu & O’Meara 2016), while the FiSSE analysis was carried out using the functions published by Rabosky and Goldberg (2017).

Since SDD methods have been shown to be heavily impacted by incomplete sampling (Harvey & Rabosky 2018; FitzJohn et al. 2009), we assessed the influence of this potential bias on our results with a taxonomic jackknifing approach (Close et al. 2015). For 100 analyses on randomly drawn trees, we removed five taxa at random after time-slicing the tree, prior to performing the HiSSE and FiSSE analyses. This was performed 100 times, and results were compared to those from our original trees.

Assessing Modularity and Integration of Tooth-Bearing Bones

The method of Pagel (1995) was used to assess whether loss of teeth in the maxilla and premaxilla were correlated. This approach involves fitting evolutionary models to the observed tree and morphological data from two discrete characters: one (the independent model) where transition rates between two character states are independent of one-another, and one (the dependent model) where transition rates between two character states depend on the state of the other. Both models may be formulated as an Equal Rates model (ER), where

the direction of a transition (0->1 or 1->0) does not affect the rate, or as an All Rates Different model (ARD), where rates of change are affected by a transition's directionality.

We used this method to test for correlated evolution between the presence/absence of teeth in the maxilla and that of the premaxilla, implemented in the *R* package *phytools* [60]. In each case four models were tested: dependent ER, dependent ARD, independent ER and independent ARD. The models were compared using Akaike weights. The same approach was used to assess whether edentulism in the anterior portion of the dentary and the posterior portion of the dentary were correlated. The boundary of the anterior and posterior dentary was set at the boundary between regions of the dentary opposing the premaxillary and maxillary teeth, respectively.

Supplementary Methods and Results, Related to Figure 2

Analysis using BayesTraits

The results of the model-fitting analyses of dental evolution was corroborated using the program *BayesTraits* (Pagel & Meade 2006). This allows the analysis to be carried out in a Markov Chain Monte Carlo framework, that calculates the likelihood of the tested model models across all trees simultaneously, accounting for uncertainty in the phylogeny.

Analysis was run comparing dependent and independent both the upper and lower jaws using 100 trees randomly drawn from the Bayesian posterior distribution, as in the main text. The analyses were run using the MCMC framework, with 10,000,000 iterations, with 25% discarded as burn in. The harmonic means of likelihoods of dependant and independent models were compared using Bayes Factors: double the difference in log likelihoods between two hypotheses.

A similar approach was used to support the irreversibility of tooth loss in birds. For each of premaxillary, maxillary and dentary teeth, two models were compared: one where instantaneous probabilities of loss and gain of teeth were allowed to vary freely, and one where toothless taxa could not transition to toothed i.e. losses were irreversible.

The results obtained corroborate those found using the likelihood model fitting approach described in the main text. Regarding character independence, in the upper jaw the independent model was found to have a log likelihood of -46.16, and the dependent model -50.62. This comparison therefore has a Bayes Factor of 8.92. In the lower jaw, the independent model was found to have a log likelihood of -55.86 and the dependent model -49.96. This comparison therefore has a Bayes Factor of 11.8. Both these Bayes Factors are considered “positive” support (Kass & Raftery 1995) for the superior fit of the independent model in the upper jaw, and the dependent in the lower jaw.

In all three tooth-bearing bones, the irreversibility of tooth loss was supported by the BayesTraits analysis. For the dentary the free model was found to have a log likelihood of -25.63, while the irreversible model had a log likelihood of -15.38. This comparison therefore has a Bayes Factor of 20.7. For the premaxilla, log likelihoods for the two models are respectively -28.46 and -14.24 (Bayes Factor 28.44) and for the maxilla they are -26.73 and -14.72 (Bayes Factor 23.02). All three comparisons are considered to provide “strong” support (Kass & Raftery 1995) for the irreversible model.

2)????????2??1??024??0?0000??01?0?0?000??020?0?0?000021?0?01??10?0?0??02
????????????01????0??0?0000?0?000000021002??0????????(1
2)??03????????0????????110000?0?0?2??0100?0011?0?00?0?00?00100110

Eoconfuciusornis_zhengi (1 2)?231?1(0

1)?0????0????????????1?01??000??100????0?0?00??0??1??0241??0??0?00?0??
000000?020??0000?02(1
2)????????0?00000?100?0??000??01????0?01?00001?0?0000000210020?0?0?0?
??????1000(1 2)????????0?????10????0?00000002?00200?001000??0?00010100100

Jinzhouornis_zhangjiyingia 0023111(1

2)?1????00??1?????????1?11??010??10??????0??0?1110??????240(1 2)0(1
2)?000?0?0?0????????000?02(1 2)10?0?1(0 1 2)10?00000?021020(0
1)0??11?0101??(0
1)??0?01????01?00?000000021002????????????????0??012??10??100?0010??110000(
0 1)00?0?1?0200?0?10?????0?001000011?

Confuciusornis_dui

??23111????????????0????????1??????0??1????????????????(0 1
2)????14?10?0?0?0????????????????????????2(1
2)?0?0??10?0?0?00021????????????01????0??1??0(0
1)00?00?000?0021002????????????????????(0
2)????????1??????10????0?00????0(1 2)00?0010?0????0?0?1000011?

Boluochia_zhengi ?1(1 2)(0

2)??2????????1????????
????????????????(1 2)(1 2)?(1
2)?????20??11010
1???02????????0????????????0(0 1)?100100002??3200?0011??1??????2?20????

Concornis_lacustris

??01??11????????0?01??????11
1110?02?11?00?1?????1112221222111?20?00111??0(0
1)0211?????1????1112????????????0?0?0??30010(0 1)0122?????????11?1?(1
2)?00?0?????????1111??????1110?0010?0(0 1)?0000?001??01131110?0?2??1??

Elsornis_keni ???(0

1)??10?0?1?10????????????????111110002121?00000101011(2 3)22010?11??(1
2)0?0011000000(1 2)0(1 2)0000111??0100(1 2)1?1??31????0?0
1)?01??
1111?121????????

Eoalulavis_hoyasi

??00111200??2?0????????????????0??11
111010211100000010?111?312?0?0010?40?0011110010211001001111111?21?1????????
0??1?01?001????2??0????1?????????????1?1????????????????????????????????
1??1121111????????

Cathayornis_yandica (1 2)0(1

2)0?0????????????????????????000????00?????1??1??1??0???11?2????240?0?0111???

111?0??20??000001?0111?322122311??20?0011?1?010211(0
1)0101111011????110?31100010?(0
1)00013001010122000000??11?????100????12????1????(0
1)?????1?1?????????????????????????????0?1111111?????????

Eocathayornis_walkeri

??0??2?????????????????0??0????000??00????1??????00?????????????????????1
1????02????000000?0????22121311??20??01??1?000???(0
1)????11??10?????0?31??0010??0001200100011?????????????????????????????????
?????????????????????????????????0?111111?????????

Eoenantiornis_buhleri (0

1)010??02?????????????????0?????????00?????????????1?????????????????(0 1
2)????24020?????1?0111110101?11000?001??11122(1 2
3)?2??110?2000?1??1?000?????????????11?????10?31??0000?000012001010122??0?????
?????(1 2)?001????1?????????????????11??0?10?????0??1?0?1110011(2 3)1011?(0
1)?1?0??2

Gobipteryx_minuta 10(1 2)3101200021?10?????????0??0?1??1?(0

1)0??10??10?????1?????????(0 1 2)10??(1
2)401?????????1111?010?1??0?0010??111(2
3)?????????????0?????0?????0?????????11??111?????????0??0?1?00?????20?????????
?????10?03?????????????10(0 1)10?011?110010?100??11?0??1?1?????????2??1?????????

Iberomesornis_romerali

???0??1110??1000001?0(1
2)401010??0??1????0?00?2??0?????????11?(2 3)(1 2)(1 2
3)?????????????0??????1?0??111??11???
??1?0?0?????0??01?0?????????00?100000001?000?0011??11??11?001??1?

Longipteryx_chaoyangensis

?122111????????????????????????????????000??00?01?1??1011?????????2????24??0?01?11?0
1?1110100??000?000?111132(2 3)?21111??20??0110??0002??(0
1)?0?011?1?11?????0?01100000100?0120010001130000??1111011(1 2)11001?0?(1
2)1?10?????0??0?1?1?0?1000000001?32000001??1?1211?1?2?2????0

Longirostravis_hani (0

1)022??1????????????????????????????00??00?01?1??1?????0?????01????24??0?01110?
0111????00?2?000000?0111(1 2 3)2(1 2 3)?224110?20?01??1?000???(0
1)?????????10?????0?31??10?0?(0
1)01012001??0122??0?????1??10?1?11?????0?1?????1?00?????1?11(0
1)?10010??0?2?0100?00?????0?1??111?1?1????0

Neuquenornis_volans

???0??11?????????????????????1?
???021111000?????1?1111230(1
2)?1?1?????0??11?????1?01?01?????11?1??11??31??10?0?(0
1)0001?????????????????????????????????????1110?????????1?????????10??0?1??1?2?00?011001(
1 2)????1??2(1 2)0??1?0???

Pengornis_houi 00(0)
1)01101?0?????0?????0?1?????0000?0?0?????11?2??1??0?1?10?1????240?0(1
2)??0?0?1?11??00?????0?02??11?2?????????????001?0100101??(0
1)?100?1??11?????1(0 2)(2
3)111??0?01001?0010?0??3?????????????????02?01??????1??(0 1)?01(1
2)11?0100100100101200201?00?????011?101?(0 1)011?021

Eopengornis_martini 0000110(0 1)
2)?0?????????????0?????????00000?000?????1??10?0?00?????????24??0?1?????0121110
1000??000?02?00111321?110?1??10?0010010000??10?0001????10?????0??1(0
1)?00?0?010012001010103?????????????????000??????0????100?????0??0001????1??
0101?0012?000111101?1011102?

Protopteryx_fengningensis (1 2)?(1 2)(0 2)1??(0 1)
2)?????????????????????00?????00?????1??????10?????01????14?????0??1??1111?0?
11?(1 2)?200?00?0111322111011?(1
2)10??1????010?????????????11?????????1?000??(0
1)0001100000010??00????11?????????0(1 2)????1?????0?????????????00?0010?00?0(0
1)01?001110011?0100?(0 1)101121?

Rapaxavis_pani (0 1)022??1(0 1)
2)?????????????????????000??0?0??1?1?????1??01??11?1???024??0?0?110?01????
?00?(1 2)?0?001??11?322122411??20?0100?0000??(0
1)0??1111?10??1??0??11?00?010000130011?01230000?0??111101?111?0100?????????0?
0(0 1)?0?11??100?10000?002?0100?0011??0?121011?10110210

Shanweiniaos_cooperorum (0 1)?(1 2)(2
3)?1?????????????????????0?????00?01?????1?????????????????24?????1?1??01?1
1??000(1 2)?000000?011?22(1 2 3)?211?(0
1)?20??1????00?????????11??11??11?????????????????20?11??22?????????1?????1?
??0?????(0 1)0??1?????????110?0000?????1?(0 1)(0 1)?0?0?1(0 1)?10?12?111?1011?210

Vescornis_hebeiensis ?0????2?????????????????????????0000??00(1
2)001?1??21?1??0??1??2????2??????00?01?1??0?02?(1
2)?000001?011?322120111??20?00110??0101?1(0 1)0??1111111?????1(0
2)011010?00(0 1)0?0130010(0 1)01220??0?????????????????????????0??(0
1)?????????00?0010?011?(0 1)201?1011??11121(0 1)11?(0 1)1110?00

Vorona_berivotrensis
??
??
??
2)000100011?21000000?????????????11??????

Schizouralii 0123111(0
1)?????????????????????11?0????10?01??0?(1 2)1?00?00?1??0(3 4 5)?1??(1 2)(3 4)?(1
2)0(1 2)?000??01011?0?1001??(0 1)2?00????11012(2 3)0(1 2)?011??1??1?000??0(1
2)0010(0 1)0??01?0?10?????00?31??0000?001?0(2 3)001010103?0??1(0
1)1??0101?1?0103?????(1 2)?0????(1 2)??????11?010?00001(0
1)2?011000010?1?01?1110?10000001

Piscivoravis_lii

????????????????????1????111?(0

1)????????????????????1211??10111100(3 4)?0?24?20?0001001011?0?0????(2
3)20???0121002301121(1
2)?51?110??1?1?0??0?????1?0?11?????00?31??000110001021010101121000?0???0101
1(1 2)10003?01121101?10022???1?112011100(0 1)110?001100001011001?01???0000000?

Longicrusavis_houi

10(1

2)01?0????????????????????????????00??101??01????11?11?0??20????????????????????10
11100?????(1
2)21100?01210?23?120110?10?110?01?11012021100010001100???0??31110?0001010210
0010101??????11??1??(1 2)?0?????????01?10022(0
1)121?1112011100??10100100?0011??0010101100110000?

Gansus_yumenensis

??121?1?201111004001024?20210000?1
101110010020?320??0012100230210100?10?11001??010130?1???010011100111?0?312?
01110001?131010001221?0011110101011210003001(1 2)?1101?100(1
2)?0?0?211201110010102?021000011??001?10110?010000?

Ichthyornis_dispar

20231?03100?1??11111110111111?01001??100?1011111(0
1)11012011120?4?0102401021000??1101111010010?2210110012?002300??1212?0111001
100101202101101000110021101?3121012101001031111???3100010110?1101121011310
1221101?100221110?2112011202101?2102000001?????10101001?1????0

Hesperornis_regalis

11231101?0021??111111100101111101010???100010101?021001211112004010?13020210
001010?01?00?0010?020??000200?21?0??0011?00?????0?????1000000?????????????
????????????????????????1000121101110012101131021222011101221111121120112?21013
223220102?????0?01?020?0?0?

Parahesperornis_alexi

1123??0??0?1??1111111?010111????01????1??????1?02100121111200?????1?????10001
??0?01?0?0010?0??????????2??????1???
??1021222011101221111???1201?2?2101?223220002?
????????????????20?0?0??

Enaliornis_baretti

????????????????????????11????????????????????21?0??1??2????????????????????
??
??????????1?????1??????2?????1012212011101221111???1201???1101??0120000?????
??????02???????

Baptornis_adventus

1??3?????????????11??0??111?????0??1?0?10101?021001?11112004010?13020?10001
1?0001?0010010?0?????0?????2(1
2)????0112?0????????????1000000????00000100?????????????????????01000121101
1100121011310112120111012211111211201?2?11013221120001????????????02???????

Brodavis_varneri

??021?01?1??1????????????????????????
??
????????????10????1??1100?210113?????2201?1012211111211201?2?1101?221220001????
?????????2???????

Vegavis_iiiai

??2??????????????(5
6)????????????????????1011?00?001??(0
1)20?00?????????????????????1?0??
?01???1?????01??2?????0112110??1?02?2?1???12011???3?1????1???0?????????10?01????
??????

Anas_platyrhynchos

21230113101111111111111111112112111?102100001011?102110121111000601202402021
000201101111010020?22010000121002311100113401110011110003011111010000100111
0123120132111111031011??123110111110101111210113101121101110022201112112011
2013013210220000101110101121010100010

Gallus_gallus

1123111311121111111111111111112112111?102000001011?102110121111001601202402021
000201121111010020?22110000121012311010112201110011110003011111110001100111
0113120132102101131011??121110112110110111210113101121101110022201112112011
2013013220120100101110101121010100010

Fortunguavis_xiaotaizicus

?????0??00??0??0?110200??1?000??02(3
4)?0??1110?01111101001110020??0111122??2??1??300000??10000??1?0001?1??11?
????112211000001001012001000?120?????????01011110012?0?????????1???10???1?11001
0010000?0?02?100011??11?10?1?11100111

Qiliania_graffini

??
??
?????????10????00?10101?2?0003?0??11100?00?110000?11100?001001?11?(0
1)?20?0?1(0 1)??????????1?120021?

Shenqiornis_mengi (0

1)0101102?????????0??????0?1??????000??000??1?1??11?0?01??11??????????0??????
01?11?0?01?(1 2)?010101??011?(2 3)2(1 2 3)?(1 2)(1
2)3?1??20?01101?000?????????1??11?????????01??001010010120010101130000?????01
?111??01?????????0?????????????0?1011??0???(0 1)?0?0?1???(1 2)11211(1
2)01??2?0?21

Sulcavis_georum (0

1)010?0?????????????????????0?????????000??0?0?????1?????11?????11?(1
2)????24?1010110?01????0?010(1 2)?0(0 1)0001?0?1113(1 2)(1 2
3)?????????????01????010?????????1??11??(0 1)???0?(0 2)1??0(0 1)(0
1)0?00?0120010101120?00?(0 1)?????????(1
2)10?????????????0?00?0?01??110010010?0(1 2 3)?0101?0011??11211(1 2)011110012?

Bohaiornis_guoi ?0(1

2)01102?0?????????????0?????????1000??000??0011?????1?120?1?110(0 1 2
3)????24000?01101?0111110?01020?0(0 1)0101?0?11122(1 2
3)?21311??30?001??100001?10?0?011??11?????10?0110000010010120010101230000????
??01011(1 2)?000?0?1????0?0?0?0?0?10?1100100100?01?(0
1)0101?0?11??10121021111000121

Parabohaiornis_martini (0

1)0201102?0?????????????????????????000??000??0?1??01??200??110(1
2)01?124?0?01101101?1110?01?11?010101?0111132(1 2 3)?20311?(3 4
5)30?001??10000101010001110111?????10?01??000010010120010101230000??0?0101011
(1 2)1100000?????0?0?00?00010?100010010??01200101?0?11??1112102111100022?

Longsunguis_kurochkini ?0(1

2)01?02?0?????????????????????????000??000??01?1??(1 2)?1??20??1110(1 2
3)????24?00?0110?01111101020??010001?0111?32(1 2 3)????1???(2
3)00001??10000??10?00011??11?????10?01??0000100101?00101012200?????????01011(1
2)?000?????1?100?0?00?00010?100?1??000?1??010100?1?????112102011?100221

Zhouornis_hani (0

1)0101?01?0?????????????????????0??1000??000??0??11?(1
2)?1??20??110?????24?0?0?1?0??011111010101??020101?0111132(1 2
3)?2?3110?0?000??10000??10?00011??11?????10?31??000010010120010101220000????
???????(1
2)?00000??1?1?0?1?00?0?01??110010010??01??0101?0?11??11121?2011110012?

Dunhuangia_cuii

??111
1?0?02120?02??0?1?11?(2 3)2(1 2
3)?2121??200?0?10??000?????0001?????1?????0?31100000100101200100012??????????
??0?1?1021?????????

Hongshanornis_longicresta

?020?10?????????1?????????????????00??101?0?0?????????????????1??????24??????01?01
01110010????(0 1)211?0?0121?12??2201(1
2)?210?110?????10??2??0?0??11?????????31??00?0?00?02100010101?????????0?01(
1 2)????3?????????0?(1 2)??????1120?0?00?0?0?0200?00111100101011001100001

Archaeornithura_meemannae

??(2 3)??0(1
2)4??1110001?0101110010110?221100?0?2101230(1
2)?111??????0??10010?02????0100?????????0??(2 3)1??0(1
2)?0?000?02100010101?0?????????01001(1 2)??03?????2?0?0?1?0????2?0?1110?1?01???(0
1)?0100?001111?0101011?01100001

Parahongshanornis_chaoyangornis

??1?
??0?10????(0
1)211??01210123022011??10??10??1?010?0?0??01??11?????????31??01?0?0001021000

10101?0????????10??(1
2)??003??????0???00??????1???11?0????1??0100?0011?001?1011?0110000?

Tianyuornis_cheni

1020??0????????????????????000????01?01?1????????????????4??????11?1
0??0?10??22?????1210123?22111??10?1100??010??0??01?0?11??????(2
3)1??0??0?000102100010101????????????????????????????1??(1
2)??12??111011?01??(0 1)?01?0?0?11??001?1011?0110000?

Pterygornis_dapingfangensis

????1?02????1??????????0??000????00?01?111(1
2)?1??011?110211?12?000??1101??1??0?02??1?000001?0?????2(1 2
3)12?21?0??0?001?0100001?1000001100?110000110?31??0000100101?00?????2??????
?????????????011?0????1?0?1??1?1100100110101?0010110?????0?1?1021?1?1????0

Cruralispennia_multidonta (0

1)0?0??02??????????????0????????000????0?????1????????0?112??????2??00????0(0
1)??1?1??01011??00?001??????2(2
3)12201??10000110??0001??????????10??0????(2
3)1??00??0??0120??0??2200????????0101110003??????????1??????????1100?00?00??
?????????????1?100221??2??1?

Bellulornis_rectusunguis

??1?00?(2 3
4)??2?01?11000??1011?0?10?10?020????0?11?12(2 3)0(1
2)2211?????110000?0100100????01??1000??00?3100000000001021010001031??10?1??
010?12100??0102?????1?02?0??1?112010120??02?0200?00?0??001?0011?1010?00?

Monoenantiornis_sihedangia

?0?0??1??????????????????0??0??000????00?????1????????0??1??1112?2?????1?0??1
??110??1??0?0000010??11??231200000????10100??0001010????1100011????00????0??
0100101200000??12????????????????0000????????????1?0111??1?0?10?1??0100?2?0?0
?11??1?1?101012000012?

Linyiornis_amoena

10101?02?0??????????????000????0?0?01?1??10?1?2?1?0110101??24??020?0??
0111110101(1 2)1?0020001?00111(2 3)2(1 2 3)?(1
2)??1?????00100??01021100??111011110011?012100000010010120010??22000??0010
?0101?1100??0012?0??1?0?10?001?110010010??0?0?0201?0011??11121021111100210

;

END;

begin mrbayes;

charset morph_ordered= 1 3 8 28 31 43 51 56 67 69 70 72 74 92 107 117 159 168 176 183
193 205 213 214 216 219 222 229 233 234 249 261;

ctype ordered: morph_ordered;

lset coding=variable rates=gamma ngammacat=4;

calibrate

Dromaeosauridae=fixed(167.7)

Archaeopteryx_lithographica=fixed(152.1)

Jeholornis_prima=uniform(122.5,125.5)

Sapeornis_chaoyangensis=uniform(122.5,125.5)

Confuciusornis_sanctus=uniform(122.5,125.5)

Changchengornis_hengdaoziensis=uniform(122.5,125.5)

Eoconfuciusornis_zhengi=uniform(125.5,130.7)

Jinzhouornis_zhangjiyingia=uniform(122.5,125.5)

Confuciusornis_dui=uniform(122.5,125.5)

Boluochia_zhengi=fixed(120)

Concornis_lacustris=uniform(122.5,125.5)

Elsornis_keni=uniform(71,75)

Eoalulavis_hoyasi=uniform(122.5,125.5)

Cathayornis_yandica=uniform(119.6,121)

Eocathayornis_walkeri=uniform(119.6,121)

Eoenantiornis_buhleri=uniform(122.5,125.5)

Gobipteryx_minuta=uniform(83.6,70.6)

Iberomesornis_romerali=uniform(122.5,125.5)

Longipteryx_chaoyangensis=uniform(119.6,121)

Longirostravis_hani=uniform(122.5,125.5)

Neuquenornis_volans= uniform(83.6,70.6)

Pengornis_houi=uniform(119.6,121)

Eopengornis_martini=uniform(125.5,130.7)

Protopteryx_fengningensis=uniform(125.5,130.7)

Rapaxavis_pani=uniform(119.6,121)
Shanweiniaocoooperorum=uniform(122.5,125.5)
Vescornis_hebeiensis= uniform(122.5,125.5)
Vorona_berivotrensis=fixed(72.1)
Schizoouralii=uniform(119.6,121)
Jianchangornis_microdonta=uniform(119.6,121)
Archaeorhynchus_spathula=uniform(122.5,125.5)
Songlingornis_linghensis=uniform(119.6,121)
Apsaravis_ukhaana= uniform(83.6,70.6)
Yanornis_martini=uniform(119.6,121)
Patagopteryx_defarrariisi= uniform(83.6,70.6)
Iteravis_huchzermeyeri=uniform(122.5,125.5)
Yixianornis_grabau=uniform(122.5,125.5)
Piscivoravis_lii=uniform(119.6,121)
Longicrusavis_houi=uniform(122.5,125.5)
Gansus_yumenensis=uniform(119.6,121)
Ichthyornis_dispar=fixed(94.3)
Hesperornis_regalis=fixed(84.9)
Parahesperornis_alexi=fixed(84.9)
Enaliornis_baretti=fixed(113)
Baptornis_adventus=fixed(89.3)
Brodavis_varneri=uniform(80.5,81.5)
Vegavis_ii=fixed(68)
Anas_platyrhynchos=fixed(0)
Gallus_gallus=fixed(0)
Fortunguavis_xiaotaizicus=uniform(119.6,121)
Qiliania_graffini=uniform(119.6,121)
Shenqiornis_mengi=fixed(122.5)
Sulcavis_georum=uniform(119.6,121)
Bohaiornis_guoi=uniform(119.6,121)

```
Parabohaiornis_martini=uniform(119.6,121)
Longusunguis_kurochkini=uniform(119.6,121)
Zhouornis_hani=uniform(119.6,121)
Dunhuangia_cuii= uniform(119.6,121)
Hongshanornis_longicresta=uniform(122.5,125.5)
Archaeornithura_meemannae=uniform(125.5,130.7)
Parahongshanornis_chaoyangornis= uniform(119.6,121)
Tianyuornis_cheni=uniform(122.5,125.5)
Pterygornis_dapingfangensis=uniform(119.6,121)
Cruralispennia_multidonta=uniform(125.5,130.7)
Bellulornis_rectusunguis=uniform(119.6,121)
Moenantiornis_sihedangia=uniform(122.5,125.5)
Linyiornis_amoena=uniform(119.6,121)
;
constraint ingroup = 2-.;
constraint node1 = Anas_platyrhynchos Gallus_gallus;
prset clockvarpr=igr;
prset igrvarpr=exp(10);
prset clockratepr = normal(0.0025,0.1);
prset brlenspr = clock:fossilization;
prset samplestrat = random;
prset speciationpr = uniform(0,10);
prset extinctionpr = beta(1.0,1.0);
prset fossilizationpr = beta(1.0,1.0);
calibrate ingroup = offsetexponential(153,160.7);
calibrate node1= truncatednormal(66,69.1,8.65);
prset nodeagepr = calibrated;
prset topologypr = constraints(ingroup,node1);
mcmc ngen=10000000 nruns=2 nchains=2 samplefreq=1000 printfr=1000;
end;
```

Supplementary Table 1: presence (0) and absence (1) of teeth in each region for each taxon, related to Figure 3

	Premaxilla	Maxilla	Dentary Front	Dentary Back
Dromaeosauridae	0	0	0	0
Archaeopteryx_lithographica	0	0	0	0
Jeholornis_prima	1	0	0	1
Sapeornis_chaoyangensis	0	0	1	1
Confuciusornis_sanctus	1	1	1	1
Changchengornis_hengdaoziensis	1	1	1	1
Eoconfuciusornis_zhengi	1	1	1	1
Jinzhouornis_zhangjiyingia	1	1	1	1
Confuciusornis_dui	1	1	1	1
Boluochia_zhengi	0	?	?	?
Concornis_lacustris	?	?	?	?
Elsornis_keni	?	?	?	?
Eoalulavis_hoyasi	?	?	?	?
Cathayornis_yandica	0	0	0	0
Eocathayornis_walkeri	0	?	0	0
Eoenantiornis_buhleri	0	0	0	0
Gobipteryx_minuta	1	1	1	1
Iberomesornis_romerali	?	?	?	?
Longipteryx_chaoyangensis	0	1	0	1
Longirostravis_hani	0	1	0	1
Neuquenornis_volans	?	?	?	?
Pengornis_houi	0	0	0	0
Eopengornis_martini	0	0	0	0
Protopteryx_fengningensis	0	?	0	?
Rapaxavis_pani	0	1	0	1
Shanweinia_cooperorum	0	1	?	?
Vescornis_hebeiensis	?	?	0	0
Vorona_berivotrensis	?	?	?	?
Schizoouralii	1	1	1	1
Jianchangornis_microdonta	?	?	?	?
Archaeorhynchus_spathula	1	1	1	1
Songlingornis_linghensis	0	?	0	0
Apsaravis_ukhaana	?	?	1	1
Yanornis_martini	0	0	0	0
Patagopteryx_defarrariisi	?	?	?	?
Iteravis_huchzermeyeri	1	0	1	0
Yixianornis_grabau	0	?	0	1
Piscivoravis_lii	?	?	?	?
Longicrusavis_houi	0	0	?	?
Gansus_yumenensis	?	?	?	?
Ichthyornis_dispar	1	0	0	0
Hesperornis_regalis	1	0	0	0

Parahesperornis_alexi	1	0	0	0
Enaliornis_baretti	?	?	?	?
Baptornis_adventus	1	?	?	?
Brodavis_varneri	?	?	?	?
Vegavis_iiiai	?	?	?	?
Anas_platyrhynchos	1	1	1	1
Gallus_gallus	1	1	1	1
Fortunguavis_xiaotaizicus	?	0	?	?
Qiliania_graffini	?	?	?	?
Shenqiornis_mengi	0	0	0	0
Sulcavis_geeorum	0	0	0	0
Bohaiornis_guoi	0	0	0	0
Parabohaiornis_martini	0	0	0	0
Longsunguis_kurochkini	0	0	0	0
Zhouornis_hani	0	0	0	0
Dunhuangia_cuii	?	?	?	?
Hongshanornis_longicresta	0	0	?	?
Archaeornithura_meemannae	?	?	?	?
Parahongshanornis_chaoyangornis	?	?	?	?
Tianyuornis_cheni	0	0	0	1
Pterygornis_dapingfangensis	?	0	0	0
Cruralispennia_multidonta	0	0	0	0
Bellulornis_rectusunguis	?	?	?	?
Monoenantiornis_sihedangia	0	0	0	1
Linyiornis_amoena	0	0	0	1

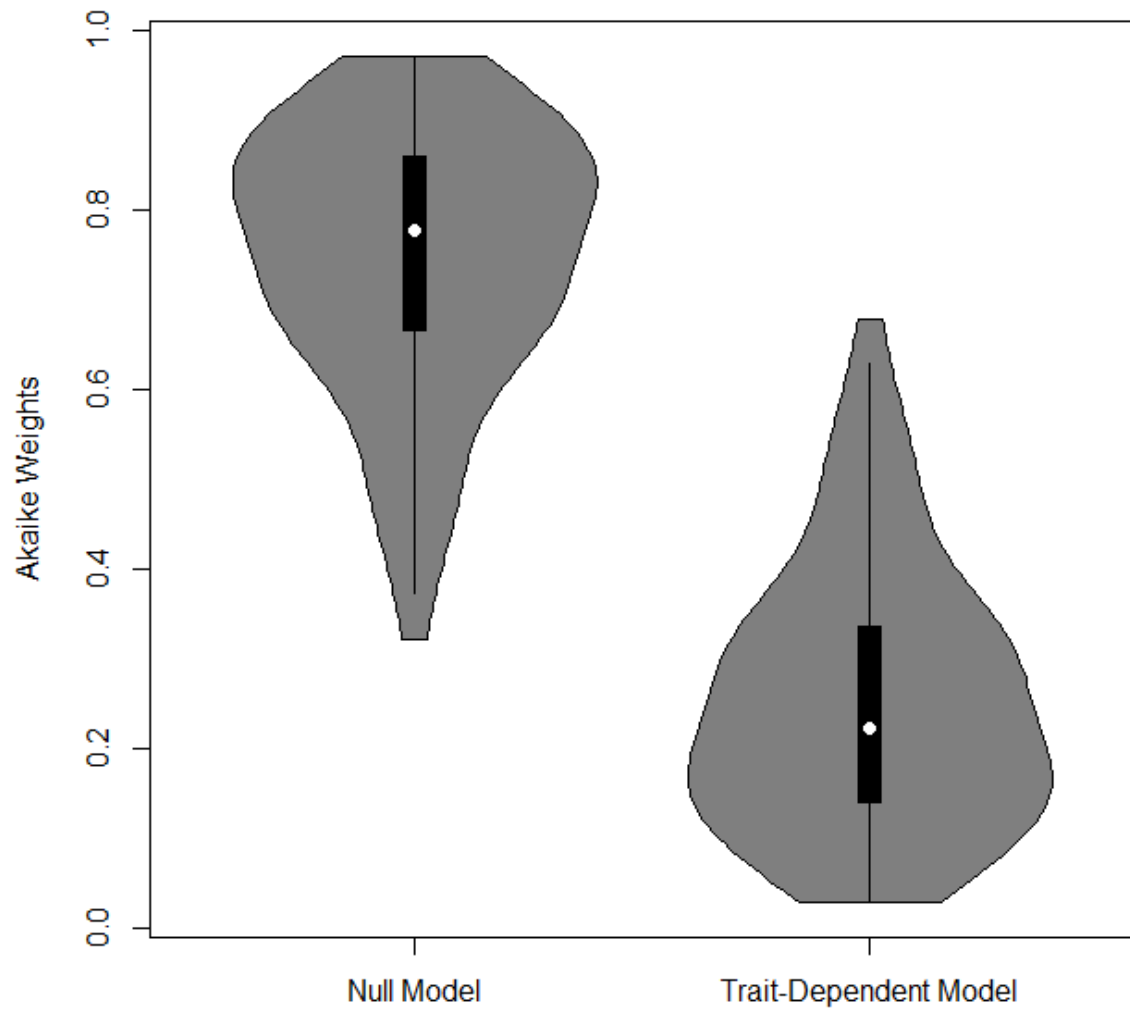
Supplementary Table 2: Results of the FiSSE analysis applied to 100 trees drawn at random from the posterior probability distribution, related to Figure 1

Speciation Rate – Toothed	Speciation Rate – Toothless	P value
0.086024	0.089621	0.603397
0.107096	0.082567	0.380619
0.11096	0.084708	0.203796
0.094652	0.068403	0.237762
0.092332	0.074374	0.263736
0.097617	0.091067	0.396603
0.097617	0.091067	0.396603
0.091368	0.076957	0.396603
0.098663	0.0852	0.422577
0.096911	0.098419	0.494505
0.100169	0.06982	0.361638
0.107234	0.104999	0.462537
0.108935	0.084771	0.417582
0.078928	0.068228	0.364635
0.075532	0.0695	0.42957
0.104152	0.086815	0.363636
0.094742	0.068378	0.321678
0.082491	0.071308	0.305694
0.112526	0.095164	0.451548
0.151171	0.102014	0.326673
0.091758	0.058491	0.25974
0.091758	0.058491	0.25974
0.110055	0.119541	0.549451
0.080993	0.094992	0.72028
0.105751	0.075127	0.308691
0.093947	0.076483	0.278721
0.091828	0.072225	0.367632
0.090337	0.066149	0.372627
0.075633	0.065714	0.40959
0.093144	0.078281	0.317682
0.126846	0.065586	0.282717
0.090083	0.115389	0.817183
0.090083	0.115389	0.817183
0.103542	0.079229	0.378621
0.080159	0.069286	0.423576
0.096189	0.067056	0.346653
0.109171	0.084724	0.432567
0.096109	0.100053	0.568432
0.075356	0.074598	0.482517
0.080195	0.062362	0.302697
0.120289	0.083842	0.372627
0.092103	0.087522	0.446553
0.105502	0.093916	0.47952

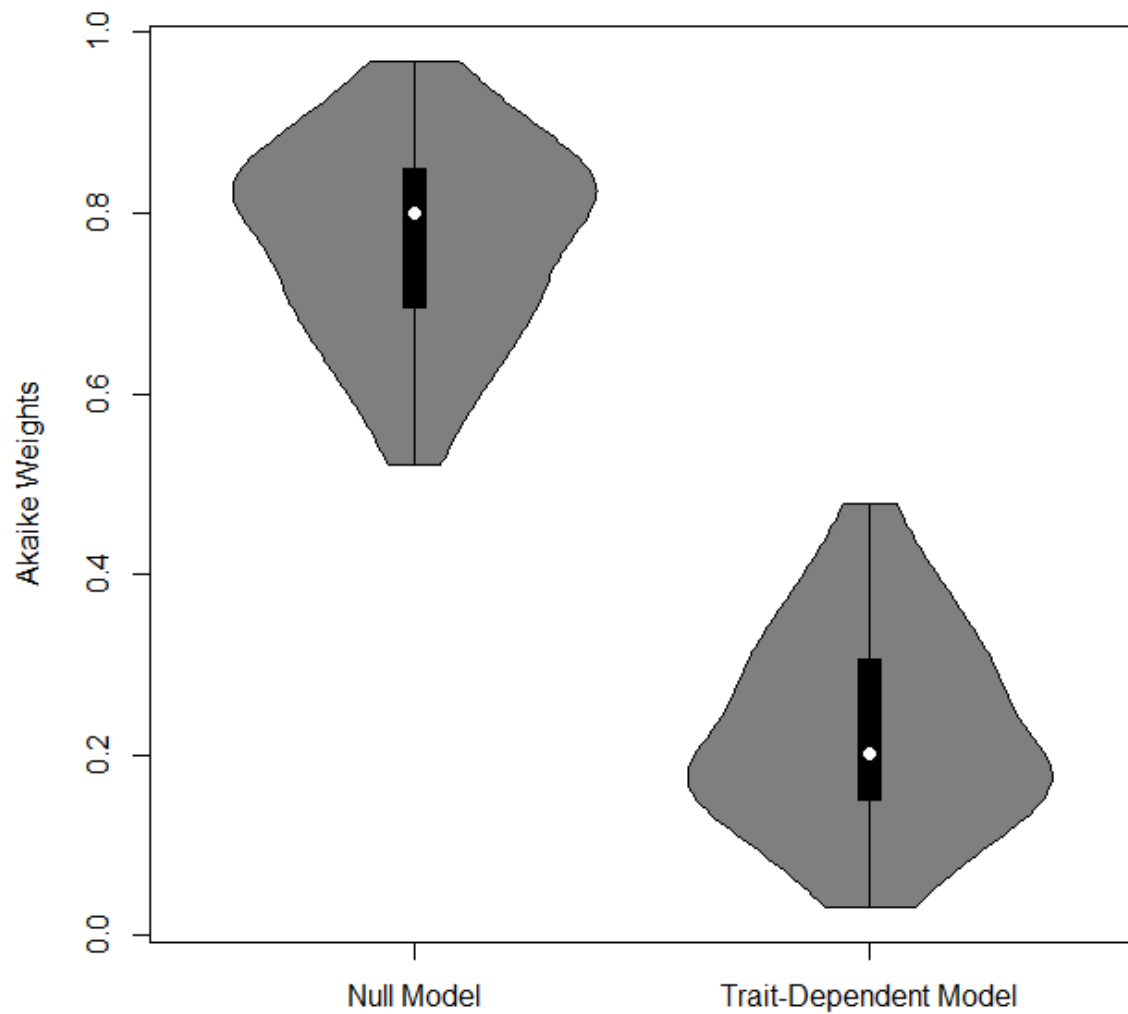
0.067167	0.100557	0.845155
0.082238	0.10036	0.655345
0.088526	0.069881	0.358641
0.082816	0.08978	0.593407
0.079322	0.06882	0.321678
0.078983	0.065927	0.232767
0.093982	0.094521	0.524476
0.072987	0.07734	0.565435
0.093303	0.068958	0.375624
0.092503	0.085212	0.437562
0.127764	0.077737	0.304695
0.118788	0.093869	0.402597
0.090877	0.07213	0.234765
0.083614	0.072496	0.351648
0.097278	0.082458	0.276723
0.08601	0.078021	0.423576
0.108564	0.067375	0.256743
0.083178	0.065875	0.375624
0.117171	0.089113	0.422577
0.095653	0.080566	0.410589
0.171196	0.116266	0.348651
0.08134	0.105813	0.725275
0.09658	0.091652	0.434565
0.096757	0.078842	0.336663
0.078831	0.133738	0.944056
0.07082	0.071832	0.535465
0.080628	0.080408	0.488511
0.101646	0.073328	0.380619
0.097614	0.070178	0.334665
0.080519	0.074131	0.384615
0.079329	0.066572	0.345654
0.140617	0.07343	0.200799
0.114839	0.071124	0.255744
0.083247	0.078033	0.428571
0.083261	0.077338	0.353646
0.0887	0.06087	0.316683
0.110657	0.091383	0.401598
0.100915	0.083733	0.395604
0.120027	0.092288	0.351648
0.082873	0.067063	0.377622
0.082873	0.067063	0.377622
0.077202	0.084545	0.65035
0.103555	0.069429	0.3996
0.130745	0.077154	0.347652
0.088894	0.074997	0.437562
0.07805	0.064411	0.311688

0.084145	0.076094	0.394605
0.081022	0.112672	0.831169
0.088762	0.057983	0.214785
0.081977	0.068777	0.387612
0.13897	0.075633	0.254745
0.103073	0.098303	0.472527
0.078556	0.063686	0.311688
0.133101	0.098954	0.445554
0.104208	0.078722	0.356643
0.106368	0.072226	0.233766
0.100084	0.106976	0.537463

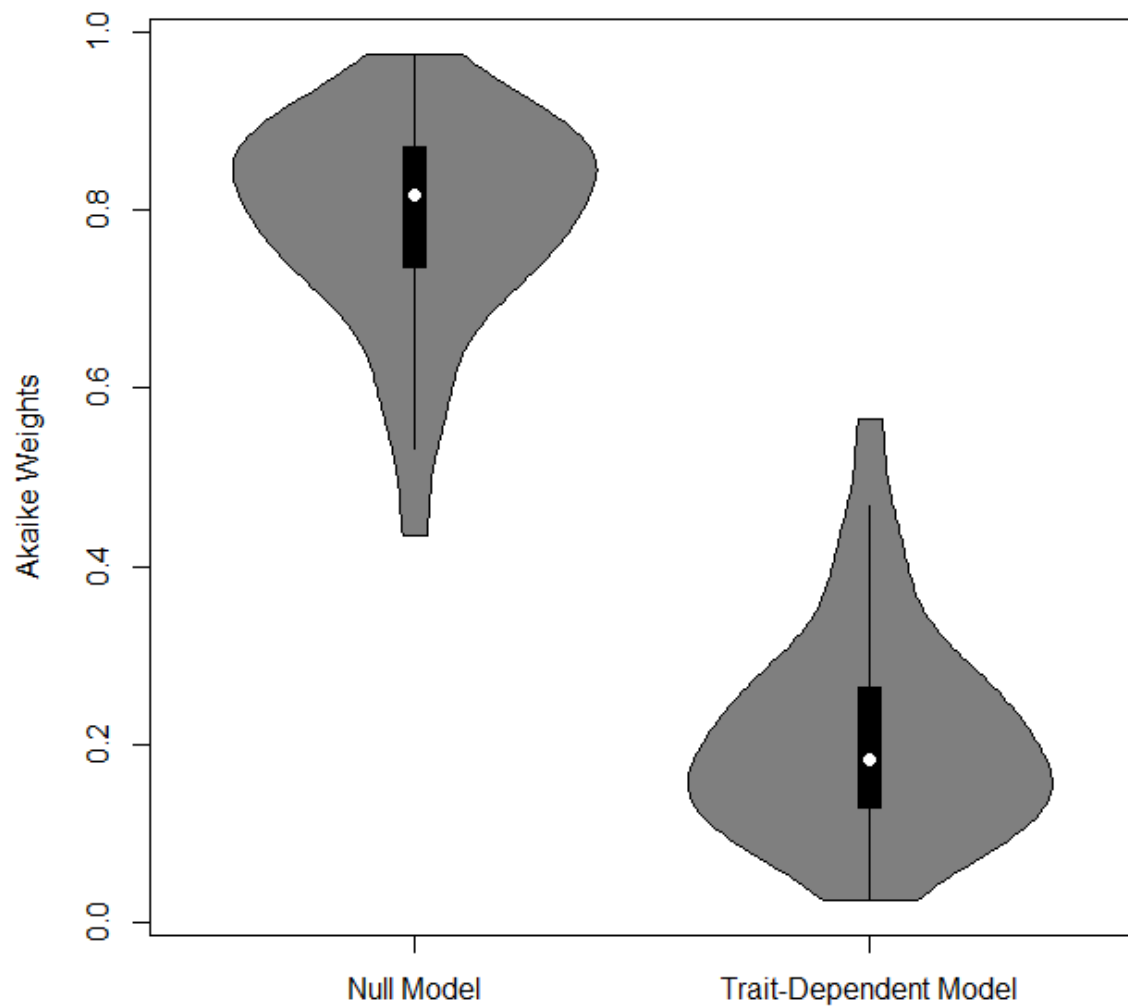
Supplementary Figure 1: Violin plots showing support for Null (no connection between diversification rates and presence/absence of teeth) and Trait dependent (diversification rates depend on presence/absence of teeth) models inferred from HiSSE analysis of 100 time calibrated trees, using premaxillary teeth only, related to Figure 1



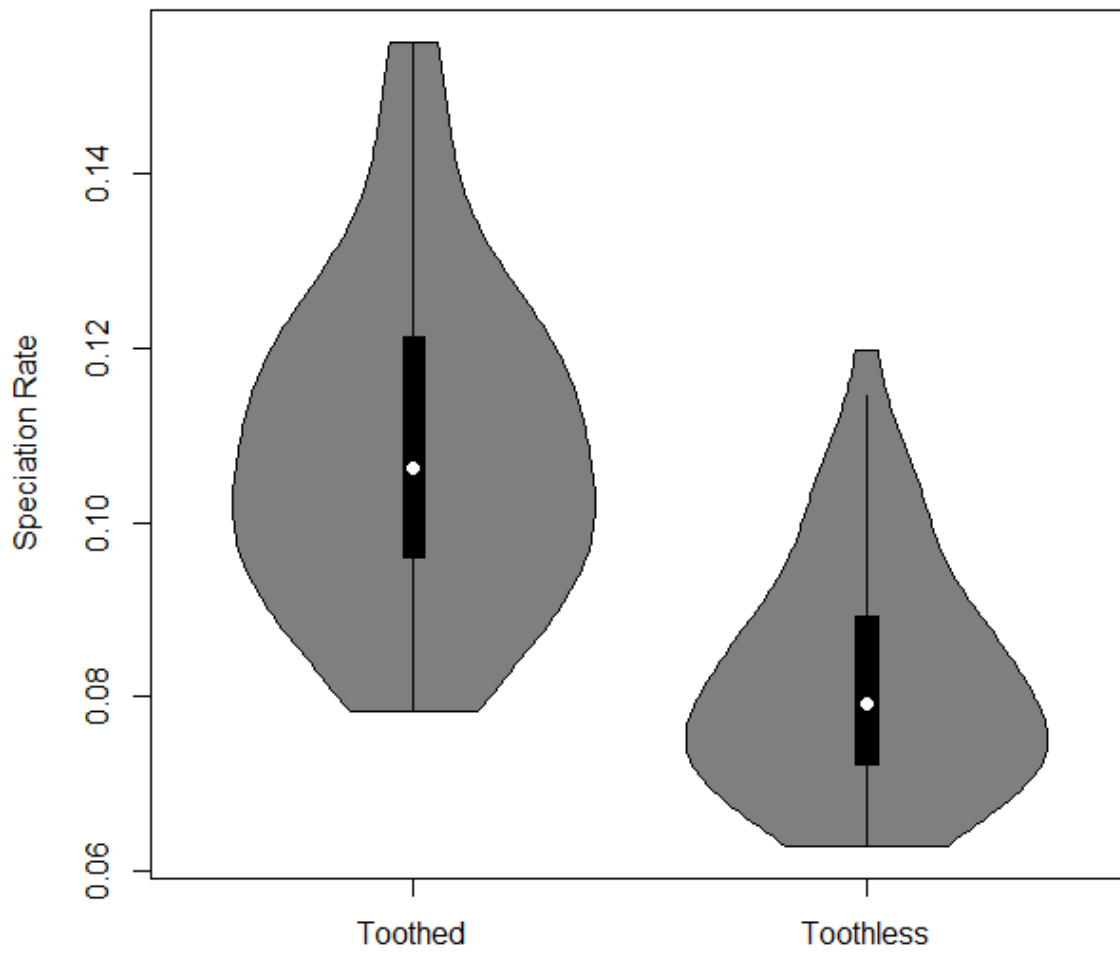
Supplementary Figure 2: Violin plots showing support for Null (no connection between diversification rates and presence/absence of teeth) and Trait dependent (diversification rates depend on presence/absence of teeth) models inferred from HiSSE analysis of 100 time calibrated trees, using maxillary teeth only, related to Figure 1



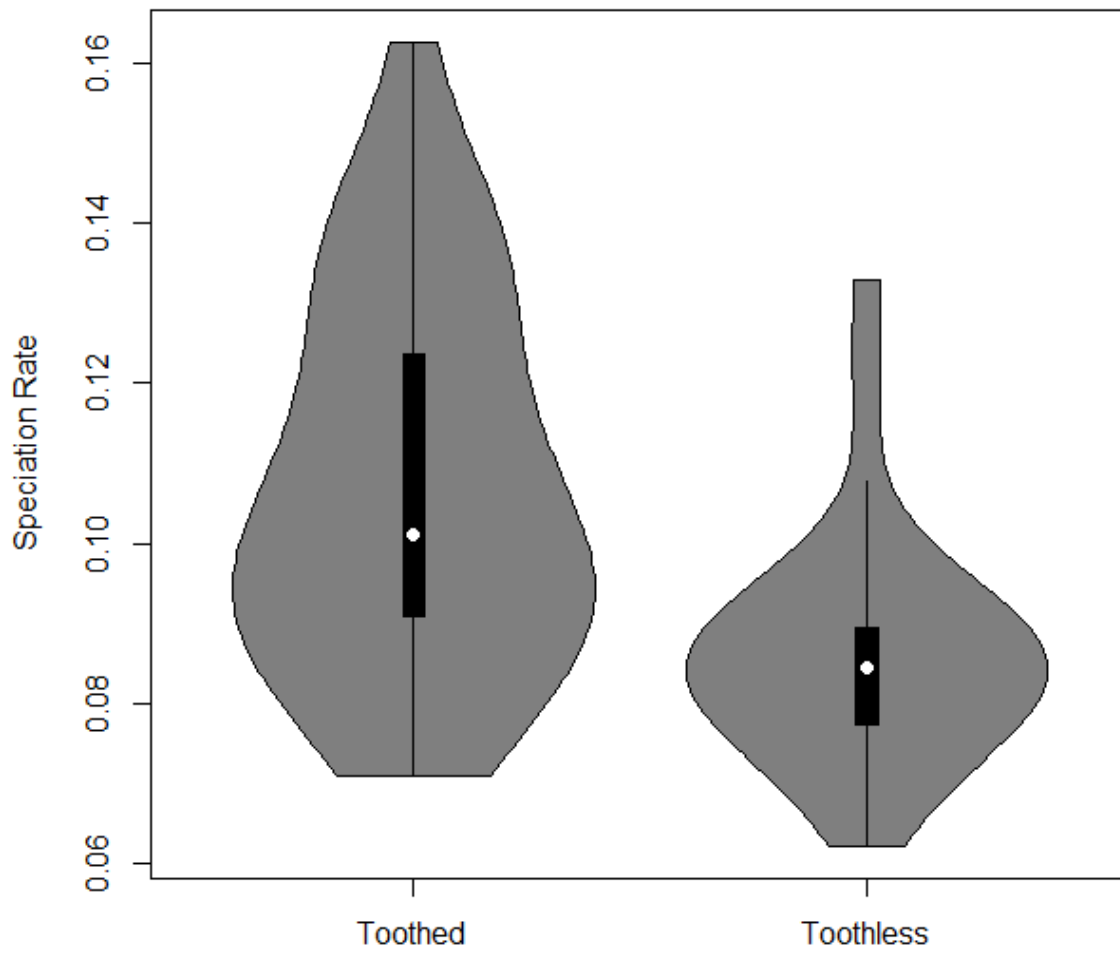
Supplementary Figure 3: Violin plots showing support for Null (no connection between diversification rates and presence/absence of teeth) and Trait dependent (diversification rates depend on presence/absence of teeth) models inferred from HiSSE analysis of 100 time calibrated trees, using dentary teeth only, related to Figure 1



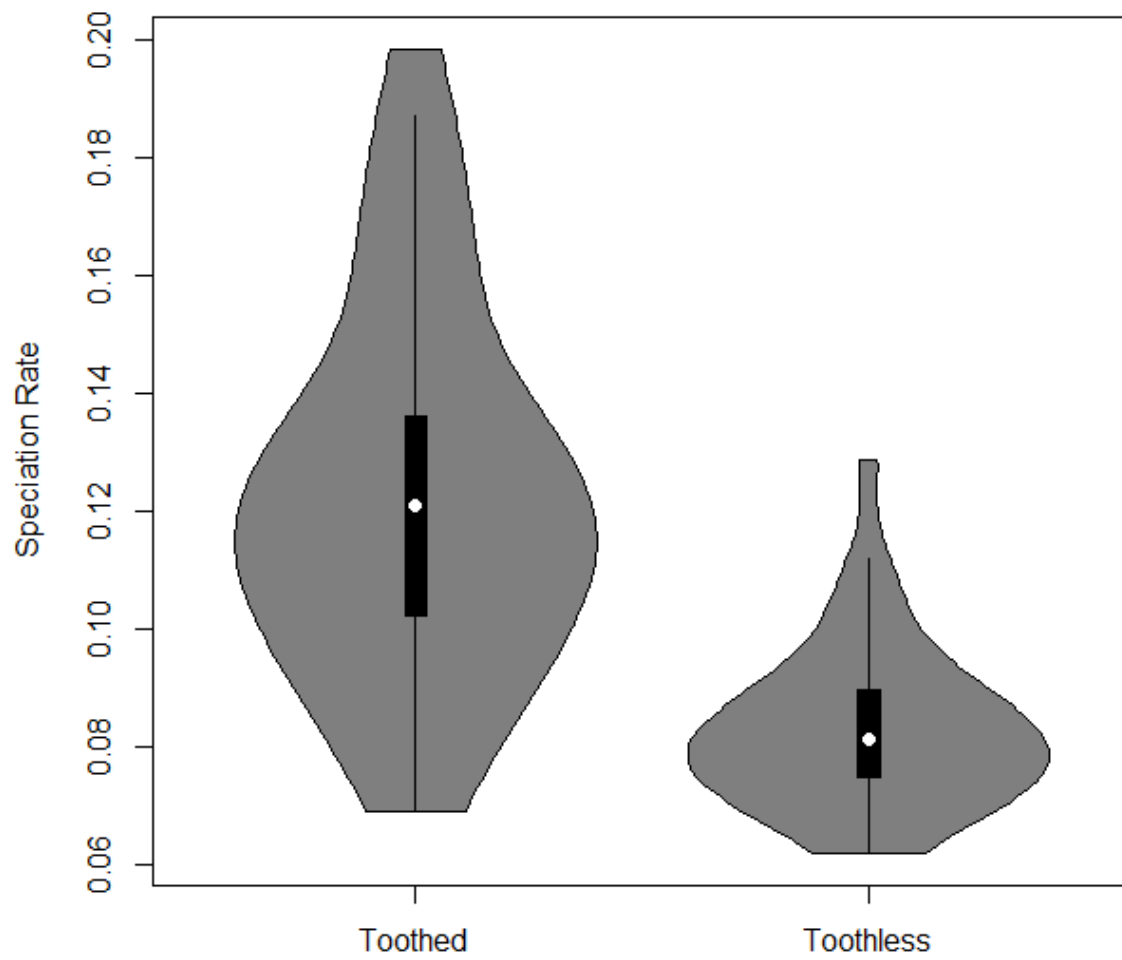
Supplementary Figure 4: Violin plots showing support for speciation rates for birds with and without premaxillary teeth, inferred from FiSSE analysis of 100 time calibrated trees, related to Figure 1



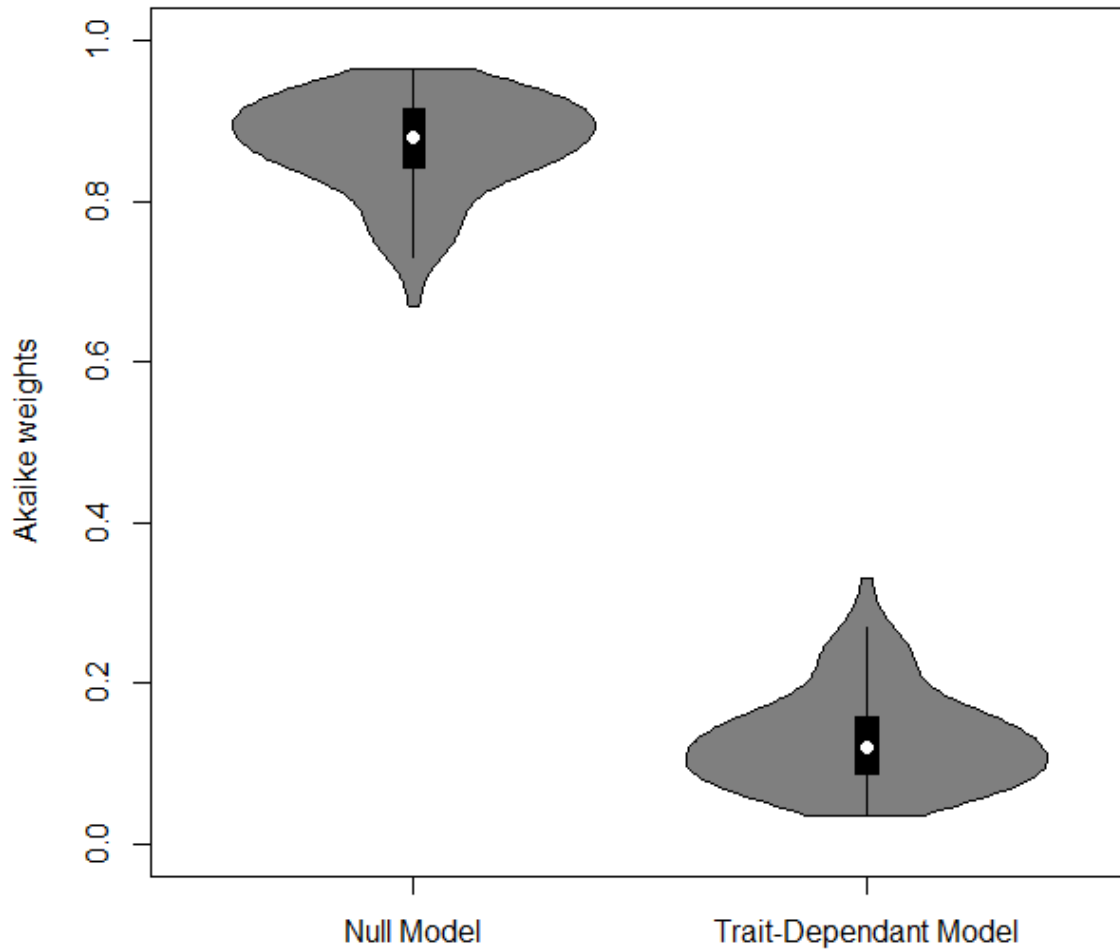
Supplementary Figure 5: Violin plots showing support for speciation rates for birds with and without maxillary teeth, inferred from FiSSE analysis of 100 time calibrated trees, related to Figure 1



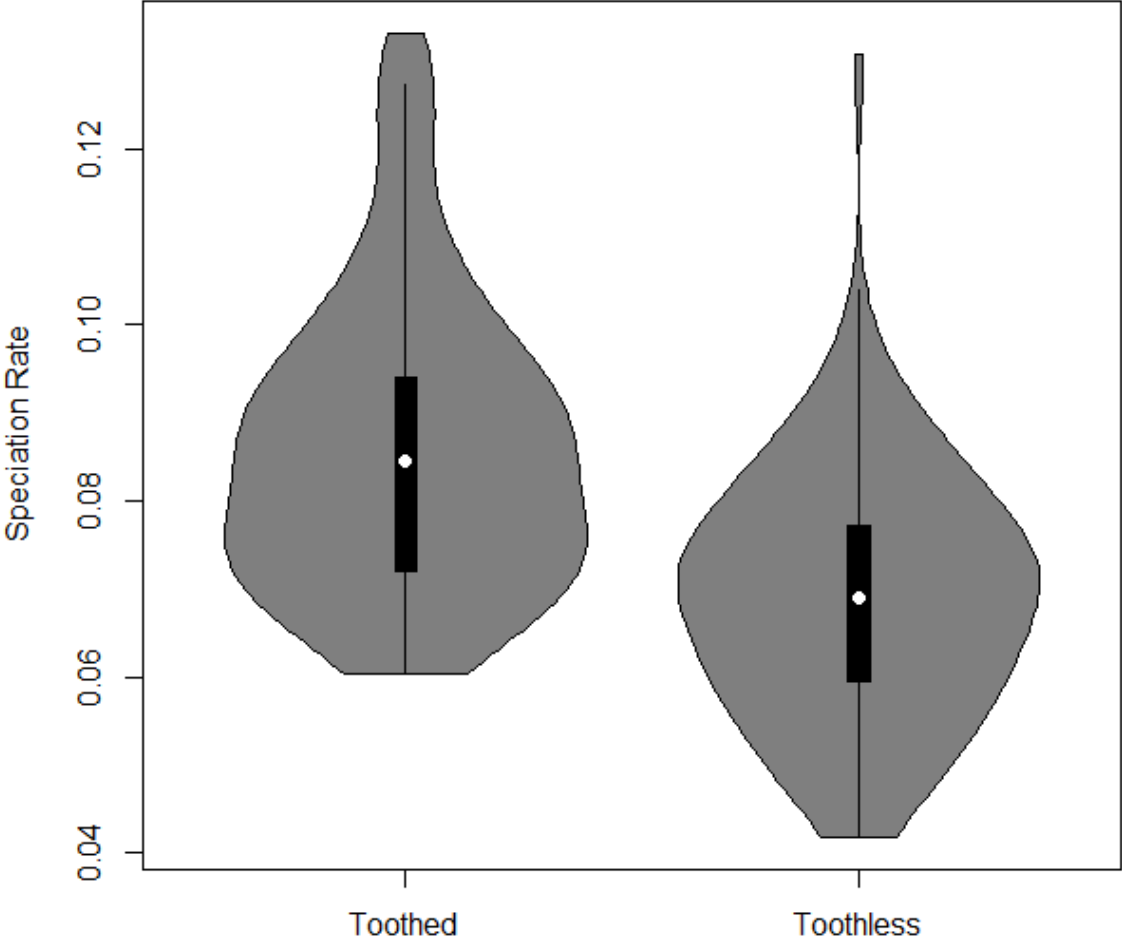
Supplementary Figure 6: Violin plots showing support for speciation rates for birds with and without dentary teeth, inferred from FiSSE analysis of 100 time calibrated trees, related to Figure 1



Supplementary Figure 7: Violin plots showing support for Null (no connection between diversification rates and presence/absence of teeth) and Trait dependent (diversification rates depend on presence/absence of teeth) models inferred from HiSSE analysis of 100 time calibrated trees, following taxonomic jackknifing, related to Figure 1



Supplementary Figure 8: Violin plots showing support for speciation rates for birds with and without teeth, inferred from FiSSE analysis of 100 time calibrated trees, following taxonomic jackknifing, related to Figure 1



Supplementary References

Kass RE, Raftery AE. 1995. Bayes factors and model uncertainty. *J Am Statist Ass* 254, 1-53

Pagel, M. & Meade, A. (2006). Bayesian analysis of correlated evolution of discrete characters by reversible jump Markov Chain Monte Carlo. *Am. Nat.* 167, 808-825