

A Comprehensive Phylogeny of Birds (Aves) using Targeted Next Generation DNA Sequencing

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Online Data and Software Archive

A zip archive containing assembled sequence data, newick formatted tree files, code and scripts for generating and analyzing phylogenetic informativeness, and information on probe design and data assembly is available at Zenodo.org:

<http://dx.doi.org/10.5281/zenodo.28343>. R code used for generating tree and supplemental figures is available on request.

Choosing Fossil Calibrations

We elected to employ traditional node-based divergence dating instead of a fossil tip-dating approach^{1,2} due to the lack of a sufficiently extensive and reliable morphological data matrix for extant and fossil crown birds. Our node-dating approach followed the commonly employed method of specifying hard minimum bounds on the age of a divergence using fossils, while applying a ‘soft’ upper bound for date estimates^{3,4}. This approach is based on the premise that the common ancestor of a clade (a node on the phylogeny) cannot be younger than its oldest fossil descendant (a child cannot be older than its parent). As a result, for a given node on the phylogeny (representing a theoretical ancestor α with two descendent lineages), only the oldest known fossil representing one of the descendant lineages of α is used for setting a hard minimum age for that divergence. More recent fossils that represent descendants of α are uninformative, since they are younger than α 's youngest possible age.

In contrast to recently published divergence time analyses for crown birds⁵, we sought to employ Parham *et al.*'s⁶ criteria for best practices for justifying fossil calibrations in the selection of our calibration points. These criteria outline stringent phylogenetic and geochronological criteria that must be met in order for a potential

calibrating fossil to be considered strongly supported. Only fossils that have been phylogenetically placed by apomorphy-based diagnoses or comprehensive phylogenetic analyses have been included here. We provide references to up-to-date apomorphy-based diagnoses or phylogenetic analyses for each taxon listed (all of which are associated with museum specimen numbers), the most exclusive clade to which they can be referred, names of each fossil locality, and minimum-possible geochronological ages for each fossil, inclusive of error⁶. In instances where radioisotopic dates were unavailable and fossils could only be biostratigraphically assigned to geochronological stages, the most conservative approach of selecting the minimum-possible age of the stage, inclusive of error, was implemented⁶.

Our complete list of fossil calibrations comprises 19 fossil taxa, which together document many deep phylogenetic divergences within Neognathae. Although palaeognaths are well represented in Palaeogene fossil deposits in the form of members of the clade Lithornithidae⁷, ambiguity regarding their monophyly and phylogenetic relationships with respect to extant palaeognaths informed our decision to exclude them from this analysis. The restriction of calibration points to Neognathae, and the lack of definitive stem neognaths or stem palaeognaths, rendered it impossible to directly calibrate the root divergence within crown Aves.

The Mesozoic fossil record of crown birds is at best extremely sparse^{8,9}, or possibly completely absent. Although the putative crown anseriform *Vegavis iaai* has often been used as a Late Cretaceous (66.5 Ma¹⁰) calibration point for Anseriformes, Neognathae, or crown Aves, recent phylogenetic analyses have cast doubt on the relationships of this taxon, and its placement within the avian crown group¹¹. As a result, we decided not to include this fossil in our full analysis; however, we have conducted an additional sensitivity analysis to assess the robustness of our results to the exclusion/inclusion of the *Vegavis* calibration (see below).

In certain instances, multiple closely related extant clades exhibited Palaeogene stem group representatives deriving from similarly aged sediments. For example, the stem potoo (Pan-Nyctibiidae), *Paraprefica kelleri*, is dated at 47.5Ma, whereas the stem oilbird (Pan-Steatornithidae), *Prefica nivea*, is dated at 51.66Ma¹²⁻¹⁴. In this instance, the phylogenetic divergence between Nyctibiidae and Steatornithidae was calibrated using the older fossil (*Prefica nivea*), and the stem nyctibiid was not used. Similar logic resulted in, for example, the exclusion of the stem leptosomid *Plesiocathartes kelleri* in favor of the older stem representative of the Coraciidae + Brachypteraciidae clade *Primobucco mcgrewi*^{15,16}.

Additional Dating Analysis using *Vegavis* Calibration

Since *Vegavis* may represent a *bona fide* crown anseriform, we performed a sensitivity analysis of our dating estimate with ten data partitions that exhibited the lowest declines in phylogenetic informativeness across the tree; otherwise we used the same diagnostic criteria employed in our initial analyses. In order to include *Vegavis*, we substituted our stem galliform calibration (*Gallinuloides*, ~51.66 Ma) for a stem anatid calibration (~66.5 Ma). As in previous fossil calibrations, we used a lognormal

distribution, setting the offset to 66.5 Ma and defined 97.5% of the calibration density to fall more recently than 86 Ma (see comments on defining the soft crown prior for justification of the soft maximum we employ here).

Figure S10 shows the alternative time calibration (including *Vegavis*) for the Bayesian tree with error bars for each node age. Figure S11 compares the posterior distributions of the estimated ages of the avian crown clade with and without the *Vegavis* calibration, and Figure S12 compares the ages of all nodes in the phylogeny with and without *Vegavis*. When *Vegavis* is included, we find that the median posterior estimate of the root age is increased, but only by ~6 million years, pushing the estimate of the age of the avian crown to ~78 Ma (mean: 78.26; median: 78.00; 95% HPD interval: 71.98–84.93)(Fig. S11). However, this is not a significant change; the median estimate of the divergence time falls within the HPD confidence intervals of our initial estimate of the root age without *Vegavis* (mean: 72.72; median: 72.33; 95% HPD interval: 66.96–79.45)(Fig. S11). Examining the differences over the entire tree, we see that the only significant changes to node age estimates are restricted to those within the Galloanserae (Fig. S12); several divergences were pulled significantly closer to the end of the Cretaceous. For example, when *Vegavis* is included, the median age of the oldest split in Galloanserae is necessarily increased to ~72.5 Ma. The median posterior age estimates for most other neoavian nodes were also pushed further back in time by ~2–4 million years as a consequence of including *Vegavis*, but they also fell within the HPD confidence intervals of our analysis excluding *Vegavis* (Fig. S12).

In summary, based on an analysis of the most phylogenetically informative subset of our data using a calibration with *Vegavis*, we are confident that our age estimates are robust to the inclusion or exclusion of this particular calibration. Although crown group ages within Anseriformes are pulled further back in time, the inclusion of *Vegavis* has no significant influence on the HPD confidence for various neoavian subclades. Until more fossils become available, the age estimates of early avian diversification events will remain inherently uncertain.

Detailed Justification of Fossil Calibrations

For every specimen presented below, the clade calibrated represents the most recent common ancestor of the total group noted, and its extant sister taxon. For example, *Pulchrapollia gracilis* (stem Psittaciformes) calibrates the divergence between total group Psittaciformes and total group Passeriformes. For taxa whose phylogenetic and stratigraphic placement have already been discussed in light of best practices for fossil calibrations¹⁷, (e.g. *Limnofregata azygosternon*¹⁸), only brief summaries are presented here.

Clade: Stem Pici (all Piciformes except Bucconidae and Galbulidae)

Taxon: *Rupelramphastoides knopfi*^{19,20}

Cladistic justification: Analyses of discrete morphological characters diagnose *Rupelramphastoides* as a stem group representative of Pici, including the presence of a very large and narrow accessory trochlea for the retroverted fourth toe, a very narrow tarsometatarsal trochlea for the second toe, and marked ulnar papillae for the attachment of the secondary flight feathers⁷. The plesiomorphic absence of an ossified extensor

bridge on the proximal tarsometatarsus, and a mosaic of other features supports a phylogenetic position for *Rupelramphastoides* on the stem of the clade bracketed by Indicatoridae and Picidae, while the presumably plesiomorphic similarity of the tarsometatarsus of *Rupelramphastoides* and crown Ramphastidae support *Rupelramphastoides*' status as a stem group representative of Pici⁷.

Stratigraphy: Frauenweiler south of Wiesloch, Germany¹⁹. Provenance identifiable only to geologic stage (Rupelian); thus youngest possible age of Rupelian inclusive of error is applied (following¹⁷).

Calibration: Minimum age of 28.3 Ma^{21,22}.

Clade: Stem Upupidae + Phoeniculidae

Taxon: *Messelirrisor grandis*^{23,24}

Cladistic justification: Phylogenetic analyses of morphology²⁴.

Stratigraphy: Messel, Germany. A detailed description of the age of the Messel Pit, and the minimum age of the fossils contained within it is presented by¹⁰.

Calibration: Minimum age of 46.6 Ma²⁵.

Clade: Stem Coraciidae + Brachypteraciidae

Taxon: *Primobucco mcgrewi*^{16,26,27}

Cladistic justification: Morphological phylogenetic analysis²⁸, and phylogenetic analyses of combined morphological and molecular data²⁷.

Stratigraphy: Fossil Butte Member of the Green River Formation. The most complete specimen of this taxon¹⁰ derives from the middle unit of the Fossil Butte Member; detailed age justification presented in¹⁰.

Calibration: Minimum age of 51.57 Ma²⁹.

Clade: Stem Psittaciformes

Taxon: *Pulchrapollia gracilis*³⁰

Cladistic justification: Based on phylogenetic analyses of morphological data³⁰⁻³², and combined analyses of morphological and molecular data^{33,34}.

Stratigraphy: Collected from the Walton Member of the London Clay Formation at Walton-on-the-Naze, England. Details regarding the age of the specimen (³⁵⁻³⁷) are summarized by¹⁰.

Calibration: Minimum age of 53.5 Ma¹⁰.

Clade: Stem Fregatidae

Taxon: *Limnofregata azygosternon*^{38,39}

Cladistic justification: Based on analyses of osteological data,³⁹ identified 18 unambiguous synapomorphies of a *Limnofregata* + *Fregata* clade. These are discussed in detail in¹⁸.

Stratigraphy: Fossil Butte Member of the Green River Formation. Several referred specimens have been recovered from the F-2 Facies, in the middle unit of the Fossil Butte Member of the Green River Formation^{18,40,41}. Precise details regarding the dating of these deposits are discussed by¹⁸.

Calibration: Minimum age of 51.58 Ma¹⁸.

Clade: Stem Sphenisciformes

Taxon: *Waimanu manneringi*⁴²

Cladistic justification: Following¹⁰, *Waimanu* was recovered as a total group sphenisciform by multiple analyses using morphology⁴² and combined data^{43,44}.

Stratigraphy: Basal Waipara Greensand, Waipara River, New Zealand. The top of the Waipara Greensand marks the Paleocene-Eocene boundary, and calcareous nannofossils further constrain this locality's age. Detailed age justification presented in¹⁰.

Calibration: Minimum age of 60.5 Ma⁴⁵.

Clade: Stem Gruoidea (Aramidae + Psophiidae + Gruidae)

Taxon: *Parvigrus pohli*^{7,46}

Cladistic justification: Analyses of discrete character data support the position of *Parvigrus pohli* as a stem group representative of the Gruoidea⁴⁶. Morphological support for the gruoid affinities of *P. pohli* include an elongated and narrow sternum lacking deep incisions on its caudal margin, and a medially protruding projection on the proximal end of the first phalanx of the fourth toe^{7,46}. A combination of features observable in *P. pohli* and its extinct relative *Rupelrallus saxoniensis* diagnose *P. pohli* as a stem group gruoid, including the sternal extremity of the coracoid bearing a marked depression, and a lack of coracoid pneumatic foramina. Additionally, the caudal margin of the sternum of *P. pohli* exhibits a pair of shallow incisions, in contrast to the condition observed in crown Gruoidea^{7,46}.

Stratigraphy: Pichovet, Vachères, France. Provenance identifiable only to geologic stage (Rupelian); thus youngest possible age of Rupelian inclusive of error is applied (following¹⁷).

Calibration: Minimum age of 28.3 Ma⁴⁷.

Clade: Stem Phaethontidae

Taxon: *Lithoptila abdouensis*⁴⁸

Cladistic justification: Based on cladistic analyses of morphological data^{39,48}.⁹³ found 10 unambiguous cranial synapomorphies for Phaethontes + *L. abdouensis*¹⁸.

Stratigraphy: Bed IIa, Ouled Abdoun Basin, near Grand Daoui, Morocco. Provenance identifiable only to geologic stage (Thanetian), thus youngest possible age of Thanetian inclusive of error is applied (following¹⁷).

Calibration: Minimum age of 55.6 Ma⁴⁹.

Clade: Stem Apodidae

Taxon: *Scaniacypselus wardi*^{50,51}

Cladistic justification: Phylogenetic analysis of morphology⁵², and combined phylogenetic analyses of morphological and molecular data¹⁰³.

Stratigraphy: Bed R6 of the Rønæs Clay Formation, Denmark⁵³. Provenance identifiable only to geologic stage (Ypresian); thus youngest possible age of Ypresian inclusive of error is applied (following¹⁷). Additional details of the stratigraphic provenance presented in¹⁰.

Calibration: Minimum age of 48.4 Ma⁵⁴⁻⁵⁶.

Clade: Stem Podargidae

Taxon: *Fluvioviridavus platyrhamphus*¹⁴

Cladistic justification: Parsimony analysis of morphology, and combined morphological and molecular data, by ¹⁴. A *F. platyrhamphus* + Podargidae clade was supported by numerous cranial synapomorphies including i) a rim surrounding the external naris that extends anterolaterally onto the dorsal surface of the beak, the absence of pterygoid-basipterygoid contact, and a well rounded posterior portion of the articular portion of the mandible¹⁴. Monophyly of crown group Podargidae to the exclusion of *F. platyrhamphus* was supported by several characters, including posteriorly-projecting lacrimal ‘horns’ at the anterior portion of the orbit, and very long lateral trabeculae and short intermediate trabeculae of the sternum¹⁴.

Stratigraphy: Fossil Butte Member of the Green River Formation; precise details regarding the dating of these deposits are discussed by ¹⁰.

Calibration: Minimum age of 51.58 Ma²⁹.

Clade: Stem Steatornithidae

Taxon: *Prefica nivea*^{12,13,14,53}

Cladistic justification: Discrete analyses of morphological data by ⁷¹, and morphological and combined morphological and molecular phylogenetic analyses by ¹⁴. *P. nivea* shares a distinct mandibular morphology with *S. caripensis*, as well as an extremely short tarsometatarsus and a well-developed temporal fossae with the extant Oilbird, *Steatornis caripensis*. Additionally, these taxa share a distinctly shortened tibiotarsus, approaching the length of the carpometacarpus¹⁴; characters differentiating *P. nivea* and *S. caripensis* include overall body size, and an unfused ilium-synsacrum contact in *P. nivea*^{12,13,57}.

Stratigraphy: Fossil Butte Member of the Green River Formation; precise details regarding the dating of these deposits are discussed by ¹⁸.

Calibration: Minimum age of 51.58 Ma²⁹.

Clade: Stem Threskiornithidae

First: *Rhynchaeites* sp.⁵⁸

Cladistic justification: Following ¹⁸, which lists the full suite of threskiornithid apomorphies exhibited by *Rhynchaeites*, three unambiguous synapomorphies place *Rhynchaeites* with total group Threskiornithidae (an elongate recurved bill; a schizorhinal bill with a dorsoventrally broad basal segment of the ventral bar, and a notarium consisting of at least three fused thoracic vertebrae^{59,60}).

Stratigraphy: Fur Formation. Precise horizon within Fur Formation from which fossil was recovered is unknown, thus the youngest possible radiometric age for these deposits, inclusive of error, is applied. A comprehensive discussion of the age justification for the oldest known specimen of *Rhynchaeites* sp. is presented in ¹⁸.

Calibration: Minimum age of 53.9 Ma⁶¹.

Clade: Stem Coliiformes

First: *Sandcoleus copiosus*^{62,63}

Cladistic justification: Morphological phylogenetic analyses⁶³⁻⁶⁶.

Stratigraphy: Sand Coulee Beds, Willwood Formation. Fossil derives from *Plesiadapis cookei* zone in ⁶⁷, thus youngest possible age of this zone is applied (following ¹⁷). Details of stratigraphic provenance and aging presented in ¹⁰.

Calibration: Minimum age of 56.22 Ma⁶⁷.

Clade: Stem Alcediniformes (Momotidae + Meropidae + Alcedinidae + Todidae)

First: *Quasisyndactylus longibrachis*^{57,68,69}

Cladistic justification: Placement of *Q. longibrachis* as the extinct sister taxon to crown group Alcediniformes enjoys support from analyses of discrete anatomical characters^{57,68,69}. Although a suite of anatomical features align *Q. longibrachis* with crown group Alcediniformes (the proximal end of the first phalanx of the hindtoe bears a lateral projection like all crown alcediniforms), and the cranial anatomy compares favorably with that of crown Todidae¹¹⁹, the plesiomorphic morphology of the furcula supports the assignment of *Q. longibrachis* to the alcediniform stem group^{109,118}.

Stratigraphy: Messel, Germany. A detailed description of the age of the Messel Pit, and the minimum age of the fossils contained within it is presented by¹⁰.

Calibration: Minimum age of 47.5 Ma²⁵.

Clade: Stem Todidae

First: *Palaeotodus cf. itardiensis*⁷⁰

Cladistic justification: The taxon *Palaeotodus* was initially erected to describe material from the early Oligocene Brule Formation of Wyoming (*P. emryi*⁷¹). Additional material belonging to *Palaeotodus* (*P. escampsiensis* and *P. itardiensis*) was described by⁷². A postcranial skeleton identified as *Palaeotodus cf. itardiensis* was described by⁷⁰, and exhibits a substantially elongate and narrow tarsometarsus approaching the length of the humerus¹¹⁹, and the complete absence of a procoracoid process (the former a Todidae + Momotidae synapomorphy, the latter one shared with Todidae)^{7, 120} describes the distal tarsometatarsus as exhibiting a plesiomorphic morphology with respect to crown Todidae, suggesting that *P. cf. itardiensis* represents the extinct sister taxon to the todid crown group.

Stratigraphy: Frauenweiler south of Wiesloch, Germany. Provenance identifiable only to geologic stage (Rupelian); thus youngest possible age of Rupelian inclusive of error is applied (following¹⁷).

Calibration: Minimum age of 28.3 Ma^{21,22}.

Clade: Stem Phalacrocoracidae

First: *Oligocrax stoeffelensis*^{39,73,74}

Cladistic justification: Based on morphological analyses by¹²³. That analysis identified three unambiguous *?Borvocarbo stoeffelensis* + Phalacrocoracidae synapomorphies, discussed by¹⁸. Taxonomy of *?Borvocarbo stoeffelensis* has been changed to *Oligocrax stoeffelensis* following¹²⁴.

Stratigraphy: Enspel Formation. Following¹⁸, The Enspel deposits correspond the Upper Oligocene Mammal Paleogene reference level 28⁷⁵. ⁴⁰Ar/³⁹Ar radiometric dating from basaltic flows bounding the Enspel deposits exhibit ages of 24.56 ± 0.04 to 24.79 ± 0.05 Ma⁷⁵.

Calibration: Minimum age of 24.52 Ma⁷⁵.

Clade: Stem Musophagidae

First: *Foro panarium*^{76,77}

Cladistic justification: Based on Bayesian and parsimony phylogenetic analyses of morphological characters, both unconstrained and constrained to molecular backbone trees by ¹²⁷. That analysis identified *Foro* as sister to Musophagidae with strong statistical support from bootstrap percentages and Bayesian posterior probabilities under all unconstrained and constrained topologies. Although the extant sister taxon to Musophagidae has historically been a topic of controversy, the morphological analysis of ¹²⁷ supports a close relationship between Musophagidae and Cuculidae, a hypothesis strongly supported by the independent phylogenomic dataset presented in the present study (as part of a clade that also includes the Otididae).

Stratigraphy: Fossil Butte Member of the Green River Formation. Following ¹²⁶, the only known specimen derives from the “Thompson Quarry,” northwest of Kemmerer, Lincoln County, Wyoming: NW1/4, SW1/4, sec.22, T22N, R117W (Kemmerer 15-minute quadrangle); 41°44’N, 110°31’W. This site is among the F-2 localities of ⁷⁸. Precise details regarding the dating of these deposits are discussed by ¹⁸.

Calibration: Minimum age of 51.58 Ma²⁹.

Clade: Stem Galliformes

First: *Gallinuloides wyomingensis*⁷⁹

Cladistic justification: Phylogenetic analyses of morphological data^{129,80}, and combined morphological and molecular data¹²⁹. ¹²⁹ performed a series of phylogenetic analyses incorporating variants of a morphological cladistic dataset, and inclusion and exclusion of gene sequence data. In all analyses *Gallinuloides* resolved as a stem galliform, with varying degrees of statistical support. In those analyses six unambiguous synapomorphies were found to support a monophyletic Galliformes to the exclusion of *Gallinuloides*; these synapomorphies are similar to those proposed by ⁸⁰ in support of the same phylogenetic position⁷⁹. These include i) scapus clavicularae of furcula narrow, ii) spina interna of sternum present, iii) apex carinae of sternum shifted caudally, iv) cotyla scapularis of coracoid shallowly excavated, v) incisura capitis of humerus enclosed distally by a ridge, vi) spatium intermetacarpale of carpometacarpus wide⁷⁹.

Stratigraphy: Fossil Butte Member of the Green River Formation; precise details regarding the dating of these deposits are discussed by ¹⁸.

Calibration: Minimum age of 51.58 Ma²⁹.

Clade: Stem Apodiformes

First: *Eocypselus rowei*^{51,81}

Cladistic justification: ^{51,81} conducts two analyses under parsimony, one of a comparative morphological dataset, and one combining these morphological data with genetic data from 4 loci. The position of *Eocypselus* as a total group apodiform was supported by two unambiguous synapomorphies (a short humerus, and an ossified arcus extensorius of the tarsometatarsus), while crown apodiform monophyly was upheld to the exclusion of *Eocypselus* by eight crown group synapomorphies¹³¹.

Stratigraphy: Smith Hollow Quarry, Fossil Butte Member, Green River Formation; precise details regarding the dating of these deposits are discussed by ¹⁸.

Calibration: Minimum age of 51.58 Ma²⁹.

Detailed Phylogenetic Discussion

Particular effort was made to include taxa that would break up long phylogenetic branches and provide the highest likelihood of resolving short internodes at the base of Neoaves. We also sampled multiple species within groups whose monophyly or phylogenetic relationships to other birds have been controversial—i.e. multiple species of tinamous (4 sp.), nightjars (3 sp.), hummingbirds (3 sp.), turacos (2 sp.), cuckoos (4 sp.), pigeons (5 sp.), sandgrouse (2 sp.), mesites (2 sp.), rails (3 sp.), storm petrels (3 sp.), petrels (3 sp.), storks (2 sp.), herons (3 sp.), hawks (3 sp.), hornbills (2 sp.), mousebirds (2 sp.), trogons (2 sp.), kingfishers (2 sp.), barbets (2 sp.), seriemas (2 sp.), falcons (4 sp.), parrots (5 sp.), and suboscine passerines (28 sp.).

Here, we discuss our phylogenetic results (Figs. 1, S1) in detail, and we describe points of congruence and discordance with previous hypotheses of avian phylogeny from the published literature.

Congruent with all recent studies, the concatenated phylogeny places the palaeognaths as the sister group to the rest of living birds, and the flying tinamous (Tinamidae) within the flightless ratites^{82–86}. However, these studies have placed tinamous in various positions: as sister group to a cassowary (*Casuarius*), emu (*Dromaius*), and kiwi (*Apteryx*) clade^{82,83}, as sister to all extant palaeognaths except ostrich (*Struthio*)⁸⁵, or in the same position but as the sister group to the extinct moas⁸⁴. Our tree places tinamous as the sister group to a cassowary-emu clade (Casuariiformes) (Fig. 1). The phylogenetic relationships among the Galloanserae (Fig. 1) are exactly congruent with Hackett *et al.*⁸².

Within the monophyletic Neoaves, we identify five main clades which are each the successive sister groups to the rest of Neoaves (Fig. 1). A clade including Caprimulgiformes and Apodiformes, called Strisores (or Caprimulgimorphae⁵), is resolved as the sister to the rest of Neoaves (Fig. 1, brown). The interrelationships we recover within this clade are novel: the nightjars (Caprimulgidae), a Neotropical oilbird-potoo clade, the frogmouths (Podargidae), and the owlet-nightjars (Aegothelidae) form four successive sister groups to the monophyletic swifts (Hemiprocnidae + Apodidae) and hummingbird (Trochilidae) clades. Within nightjars, our placement of *Eurostopodus* as sister group to *Caprimulgus* and *Chordeiles* is congruent with Barrowclough *et al.*⁸⁷. We also confirm the monophyly of swifts (*Chaetura* and *Streptoprocne*, Apodidae) with respect to the crested swifts (Hemiprocnidae). Congruent with a recent comprehensive, multilocus phylogeny of the hummingbirds⁸⁸, *Topaza* and *Phaethornis* form a clade that is sister to *Archilochus* (Fig 1).

The next neoavian clade is a novel clade that consists of two recently identified monophyletic groups, which we call Columbaves (Fig. 1, purple). The first subclade includes the turacos (*Tauraco* and *Corythaeola*, Musophagidae), the bustards (*Ardeotis*, Otididae), and the cuckoos (*Tapera*, *Centropus*, *Cuculus*, and *Coccyzus*, Cuculidae). A turaco-bustard-cuckoo clade was previously identified by Jarvis *et al.*⁵ and called the Otidimorphae. Jarvis *et al.*⁵ found weak support for a turaco and bustard clade (BS= 0.55) with cuckoos as their sister group. However, we find strong support for the placement of

turacos as the sister group to a clade of bustards and cuckoos. Within the cuckoos, our phylogeny is exactly congruent with Sorenson and Payne⁸⁹.

Within the Columbaves, the sister group to the Otidimorphae consists of pigeons (Columbidae) as the sister group to an Old World clade consisting of monophyletic radiations of sandgrouse (Pteroclididae) and the Malagasy mesites (Mositornithidae). This clade was identified by Hackett *et al.*⁸², and confirmed by Jarvis *et al.*⁵ and called the Columbimorphae. Within the Columbimorphae, Hackett *et al.*⁸² placed mesites and pigeons as sister groups, but our phylogeny agrees with Jarvis *et al.*⁵ in placing mesites and sandgrouse in a clade with pigeons as their sister group. Jarvis *et al.*⁵ proposed that the Otidimorphae was the sister group to the caprimulgiform+apodiform clade (Caprimulgimorphae), and that the Columbimorphae was related to flamingos and grebes. Our results do not support these proposed phylogenetic relationships.

Within pigeons, our phylogeny is congruent with the result of Johnson and Clayton⁹⁰ and Pereira *et al.*⁹¹, except for our placement of *Columbina* as the sister group to the *Columba-Leptotila* clade instead of as the sister to all other columbids. This is one of the few areas of discordance between our Bayesian and our ML phylogenies; our ML topology is congruent with the placement of *Columbina* in Johnson and Clayton⁹⁰ and Pereira *et al.*⁹¹ (Fig. S1).

The next neoavian clade consists of the core Gruiformes (Fig. 1, yellow) *sensu stricto* as previously proposed by Hackett *et al.*⁸² and others. Among the gruiforms, we find phylogenetic interrelationships that are entirely consistent with Hackett *et al.*⁸². There are two monophyletic superfamilies. The Gruoidea consists of the trumpeters (Psophiidae) as the sister group to the limpkin (Aramidae) and the cranes (*Grus* and *Balearica*, Gruidae). Within the Ralloidea, we confirm that the flufftails (*Sarothrura*, Sarothruridae) are more closely related to the sungrebes (Heliornithidae) than they are to other rails (*Rallus*, *Porphyrio*, and *Micropygia*, Rallidae).

Our results confirm the existence of a diverse, waterbird clade (Fig. 1, blue), similar to, but more expansive in composition than, that previously proposed^{5,82,92}. This clade, which we call Aequorlornithes, includes all diving birds, wading birds, shorebirds, and two small, eclectic, aquatic bird clades. Briefly stated, we find that the clade of (Shorebirds+(Flamingos+Grebes)) is the sister group of the clade of (all diving and wading birds +(Sunbittern+Tropicbirds))(Fig. 1). Within the charadriiform clade, the interrelationships in our Bayesian tree are exactly congruent with those found by Hackett *et al.*⁸². Our Bayesian results are completely congruent with the charadriiform phylogeny of Baker *et al.*⁹³, except for the relationships among terns (*Sterna*), gulls (*Chroicocephalus*), and skimmers (*Rynchops*). Our Bayesian tree has (gulls +(terns +skimmers)), whereas Baker *et al.*⁹³ found (terns+(gulls+skimmers)). Interestingly, this is one of three areas of discordance between our Bayesian and ML results, and our ML tree agrees with the Baker *et al.*⁹³ topology.

We confirm the monophyly of the clade including diving and wading birds^{5,82,92} (called Aequornithia⁹⁴), and we confirm the placement of the sunbittern-tropicbirds clade

(Phaethontimorphae) as the sister group to Aequornithia. Hackett *et al.*⁸² placed the Kagu (*Rhynochetos*), as sister to the sunbittern (*Eurypyga*). Unfortunately, we were not able to obtain tissue of *Rhynochetos* to test this hypothesis.

Within Aequornithia, our phylogeny is exactly congruent with Jarvis *et al.*⁵, and closely follows Hackett *et al.*⁸². Loons (*Gavia*) are the sister group to the rest of Aequornithia, which is composed of two main clades. Within the Procellariimorphae⁵, the penguins (*Spheniscus*) are the sister group to the monophyletic tubenoses (Procellariiformes). Our extensive sampling establishes new relationships within tubenoses beyond Hackett *et al.*⁸². *Contra* Hackett *et al.*, we place albatross (Diomedidae) as the sister group to all other tubenoses. We confirm that the storm petrels are paraphyletic with respect to other petrels. *Oceanites* and *Pelagodroma* (Oceanitidae) and *Oceanodroma* (Hydrobatidae) are successive sister groups to the rest of the petrels. Lastly, the traditional petrels are paraphyletic with respect to the diving petrels (*Pelecanoides*); *Pelecanoides* is more closely related to *Pterodroma* than are *Puffinus* or *Fulmarus* (respectively). These novel relationships are not congruent with previous studies^{95,96}. However, the alternative resolutions have not been highly supported in these previous studies^{95,96}.

The sister group to Procellariimorphae has been called the Pelecanimorphae⁵. Within this clade, our results are very similar to Hackett *et al.*⁸² but with some differences between our Bayesian and ML topologies. Both trees agree with Hackett *et al.*⁸² in the relationships of (frigatebirds+(boobies+(anhingas+cormorants))). The sister group to this clade has the same composition in our Bayesian and ML trees and Hackett *et al.*⁸², but with some variation in topology among them. Our Bayesian tree places ibis as sister group to the rest. Our ML tree and Hackett *et al.*⁸² place ibis as the sister group to herons. Our Bayesian tree, our ML tree, and Hackett *et al.*⁸² find three different resolutions of the relationships among the Shoebill (*Balaeniceps*), pelicans (*Pelecanus*), and Hamerkop (*Scopus*). Our Bayesian tree finds (*Scopus*+(pelicans+*Balaeniceps*)). The ML tree places (*Balaeniceps*+(pelicans+*Scopus*)). Hackett *et al.*⁸² found (pelicans+(*Balaeniceps*+*Scopus*)).

Our results confirm the monophyly of a comprehensive clade of landbirds (Fig. 1, green), Telluraves⁸³, which has been supported by many recent studies^{82,83,85,92,97}. However, we find that the sister group to this land bird clade is the enigmatic Hoatzin (*Opisthocomus hoazin*), and we call this new, more comprehensive clade Inopinaves (*inopina*= unexpected). Based on this phylogenetic position and our fossil calibration, *Opisthocomus* is the most ancient (~64 myo), living bird lineage that is represented today by only a single extant species. Thus, *Opisthocomus* is the longest 'long branch' in the avian tree, which has obviously contributed to the great challenges of placing it confidently within avian phylogeny.

Within Telluraves, we find that hawks and relatives (Accipitriformes *sensu stricto*⁸²) is the sister group to the remaining members of the landbird clade (congruent with Kimball *et al.*'s⁸⁵ 49-locus species-tree; Fig. 5B), and not the sister group to the clade of owls, mousebirds, cuckoo-roller, trogons, bucerotiforms, coraciiforms, and piciforms^{5,82,83,85,97}. Consequently, 'Afroaves'⁵ is not monophyletic in our analysis. We

call this new clade of landbirds, excluding Accipitriformes, Eutelluraves. Within the accipitriforms, we uncover the same relationship as many previous studies: (New World vultures+(secretarybird+(Osprey+hawks))^{5,82,83,85,97,98}. Within the hawks (Accipitridae), our topology is congruent with Griffiths *et al.*⁹⁸. We also confirm the monophyly of the New World vultures (Cathartidae).

Eutelluraves consists of two well supported clades with increasingly well established interrelationships. Congruent with recent studies, we find that owls are the sister group to the diverse clade Coraciimorphae, comprised of (mousebirds+(cuckoo roller+(trogons+(bucerotiforms+(coraciiforms+ piciforms))^{5,82,83,85,97}. Within each of these groups, our phylogeny is closely congruent with Hackett *et al.*⁸², except that we find bee-eaters (*Merops*) to be the sister group to the rollers (*Coracias*) and ground-rollers (*Atelornis*), instead of the sister group to all other coraciiforms. The hornbills are the sister group to hoopoes and wood hoopoes. The coraciiforms (*sensu stricto*) form a clade that is the sister group to the monophyletic piciforms. Within the piciforms, honeyguides (Indicatoridae) are sister to woodpeckers (Picidae)^{82,99}, the wrynecks (*Jynx*) are the sister group to all other woodpeckers⁹⁹, and the Asian, African, and Neotropical barbets share successively closer relationships to the Neotropical toucans¹⁰⁰.

The last major clade of the land bird assemblage, called Australavis¹⁰¹ or Australaves⁵, is comprised of seriemas (Cariamidae), falcons (Falconidae) and parrots (Psittaciformes) as the successive sister groups to the monophyletic perching birds (Passeriformes). This topology has been identified consistently in several recent studies^{5,82,83}. We confirm the monophyly of the extant seriemas (*Chunga+Cariama*). Within the falcons, our tree is exactly congruent with Griffiths *et al.*¹⁰² Within the parrots (Psittaciformes), our topology– (*Nestor*+(*Probosciger*+(*Barnardius*+*Psittrichas*)+(*Psittacus*+*Deropterys*)))– is largely congruent with Wright *et al.*¹⁰³, except for the placement of *Psittrichas fulgidus*. Wright *et al.*¹⁰³ found (*Barnardius*+(*Psittrichas*+(*Psittacus*+*Deropterys*))), but their placement of *Psittrichas* was among the most poorly supported relationships in their analysis.

Congruent with previous morphological¹⁰⁴ and molecular^{5,82,83,85} phylogenetic analyses of the passerines, the New Zealand wrens (*Acanthisitta*) are the sister group to the suboscine and oscine clades (Fig. 1). Within the Old World suboscines, our placement of the Malagasy asities (*Neodrepanis*) as sister to Asian *Eurylaimus* is congruent with previous morphological¹⁰⁵ and molecular¹⁰⁶ phylogenies. Congruent with Moyle *et al.*¹⁰⁶, we identify an exclusive clade including *Smithornis* and *Calyptomena* broadbills. However, pittas (*Pitta*) are placed within the broadbills as the sister group to the *Smithornis* and *Calyptomena* clade. The monophyly of all broadbills and asities, excluding the pittas, was the lowest supported node in the Moyle *et al.* phylogeny¹⁰⁶ (BS=0.85). This novel placement of *Pitta* should be tested further with greater taxon sampling.

Within the New World suboscines, we identified the two main tracheophone and tyrannoid clades (Fig. 1). The phylogenetic relations among the tracheophones in our tree are largely congruent with Moyle *et al.*¹⁰⁷ and Ohlson *et al.*¹⁰⁸. Congruent with Ohlson *et al.*¹⁰⁸, we find *Melanopareia* to be the sister group to the thamnophilid antbirds. In

contrast, Moyle *et al.*¹⁰⁷ placed *Melanopareia* as sister to all other tracheophones except thamnophilids, but this relationship was poorly supported¹⁰⁷. Furthermore, within antbirds, we find *Myrmornis* to be the sister group to *Terenura callinota* and *Thamnophilus ruficapillus*, whereas Moyle *et al.*¹⁰⁷ placed *Terenura sharpei* as the sister group to all other thamnophilids. Bravo *et al.*¹⁰⁹ place both *T. callinota* and *T. sharpei* in a clade as sister to all other antbirds, putting them in the new genus *Euchrepomis*. Further taxon sampling will be needed to resolve the conflict between our phylogeny and these previous analyses^{107,109}.

Within the tyrannoid suboscines, the relationships are quite similar to recent phylogenies by Tello *et al.*¹¹⁰ and Ohlson *et al.*¹⁰⁸, with a few notable differences. Congruent with several recent studies^{108,111}, the manakins (Pipridae) and cotingas (Cotingidae) are monophyletic, successive sister groups to the rest of the tyrannoids. Within manakins, *Neopelma* is sister to *Cryptopipo* and *Ceratopipra*, which is congruent with all recent phylogenies¹¹²⁻¹¹⁴. The next tyrannoid lineage is a clade including the Sharpbill (*Oxyruncus*) and *Myiobius*—the Onychorhynchini of Tello *et al.*¹¹⁰, or the Onychorhynchidae-Oxyruncidae clade of Ohlson *et al.*¹⁰⁸. The tityrid clade (Tityridae) and *Piprites* are the next successive sister groups to the tyrant flycatcher radiation (Tyrannidae). Within tyrannids, *Rhynchocyclus* (Rhynchocyclinae) and *Hirundinea* (Hirundineinae) are successive sister groups to rest, within which *Elaenia* (Elaeniinae) is the sister group to *Hymenops* (Fluvicolinae) and *Tyrannus* (Tyranninae).

Within the oscine clade, the interrelationships among the 15 oscine passerines sampled are exactly congruent with the phylogeny of Barker *et al.*¹¹⁵. Three Australopapuan lineages comprise the first three successive sister groups to the rest of the oscines. The lyrebirds (*Menura*) are sister group to the rest. A clade including the Australian treecreepers (*Climacteris*) and the bowerbirds (*Sericulus* and *Ptilonorhynchus*) is the next, and the fairy wrens (*Malurus*) are the third. The corvoid clade (*Corvus* and *Lophorhina*) is the sister group to the Passerida clade. Within Passerida, the Sylvioidea (*Poecile*, *Calandrella*, *Pycnonotus*, and *Sylvia*) are sister groups to the Muscicapoidea (*Turdus* and *Regulus*) and the Passeroidea (*Fringilla* and *Spizella*). Within the sylvioids, our topology—(*Poecile*+(*Calandrella*+(*Pycnonotus*+*Sylvia*)))—is exactly congruent with Barker *et al.*¹¹⁵.

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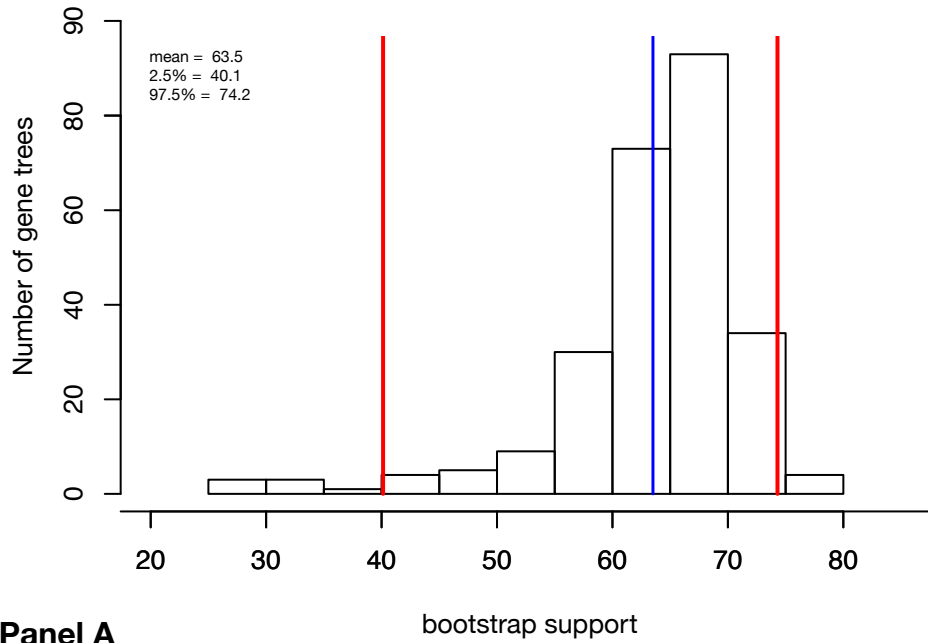
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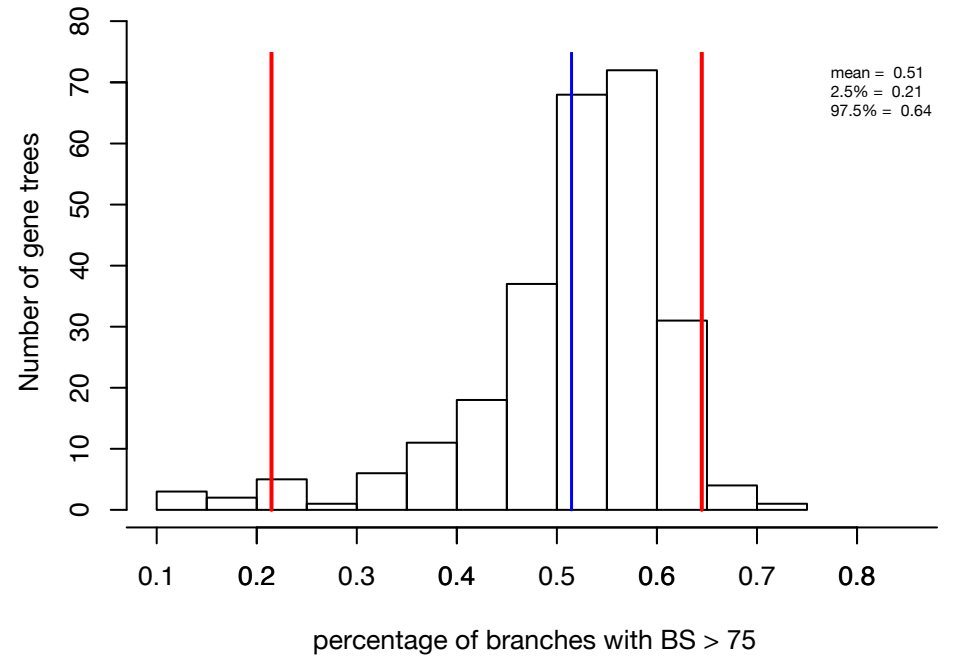
Figure S1

Figure S1. Concatenated RAxML Tree. The RAxML phylogeny estimated using the 75 partition model and 100 bootstrap replicates. Branch lengths are proportional to substitutions/site, and low support nodes are highlighted in yellow. Various clades are colored according to our classification scheme: Palaeognathae (**black/gray**), Galloanserae (**red**), Strisores (**brown**), Columbaves (**purple**), Gruiformes (**yellow**), Aequorlithornithes (**blue**), and Inopinaves (**green**).

Average bootstrap support (unbinned)



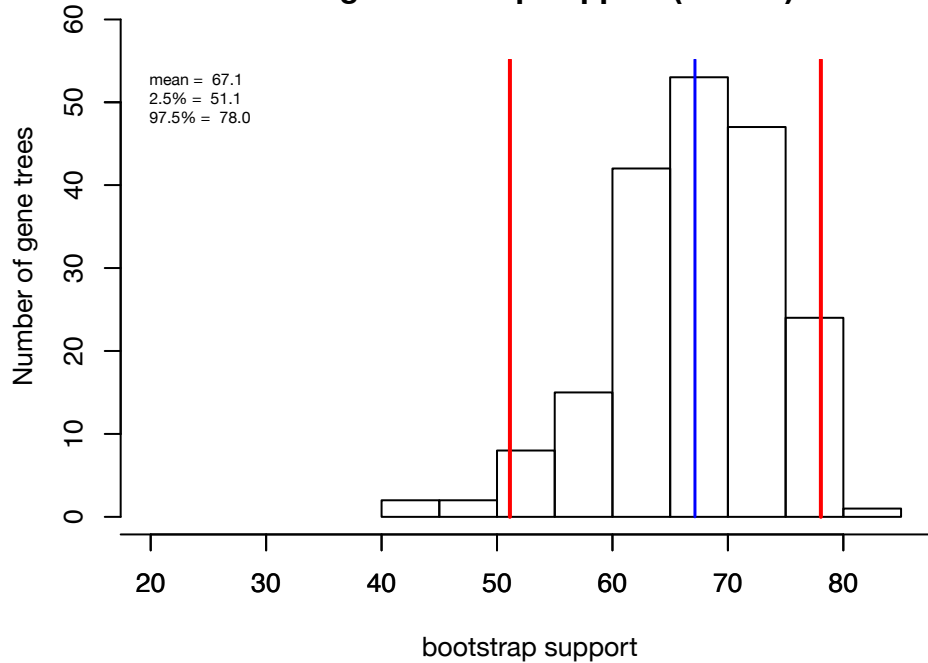
Percentage of highly supported branches (unbinned)



Panel A

Panel B

Average bootstrap support (binned)



Percentage of highly supported branches (binned)

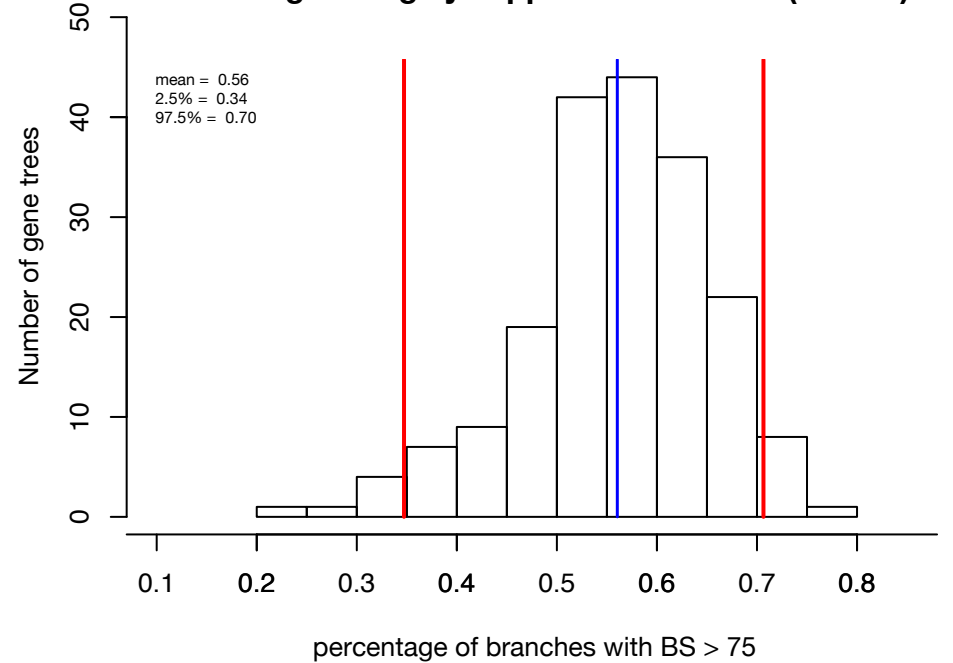


Figure S2

Figure S2. Statistical binning and bootstrap support. Histograms of average bootstrap support and the percentage of highly supported nodes across individual loci. **(A)** distributions for unbinned loci. Most loci have high average bootstrap support (~ 70), and most loci have a high percentage ($\sim 55\%$) of branches with bootstrap support > 75 . **(B)** loci after binning with a bootstrap threshold of 75. Most supergenes have high average bootstrap support (~ 70), but the low-support tail of the distribution **(A)** has been eliminated. Most supergenes have a high percentage ($\sim 60\%$) of branches with bootstrap support > 75 .



Figure S3

Figure S3. Binned ASTRAL Tree. Coalescent species tree generated with the (weighted) binned ASTRAL algorithm, with low support branches collapsed (< 75 bootstrap support). Various clades are colored according to our classification scheme: Palaeognathae (**black/gray**), Galloanserae (**red**) Strisores (**brown**), Columbaves (**purple**), Gruiformes (**yellow**), Aequorlitorithes (**blue**), and Inopinaves (**green**).

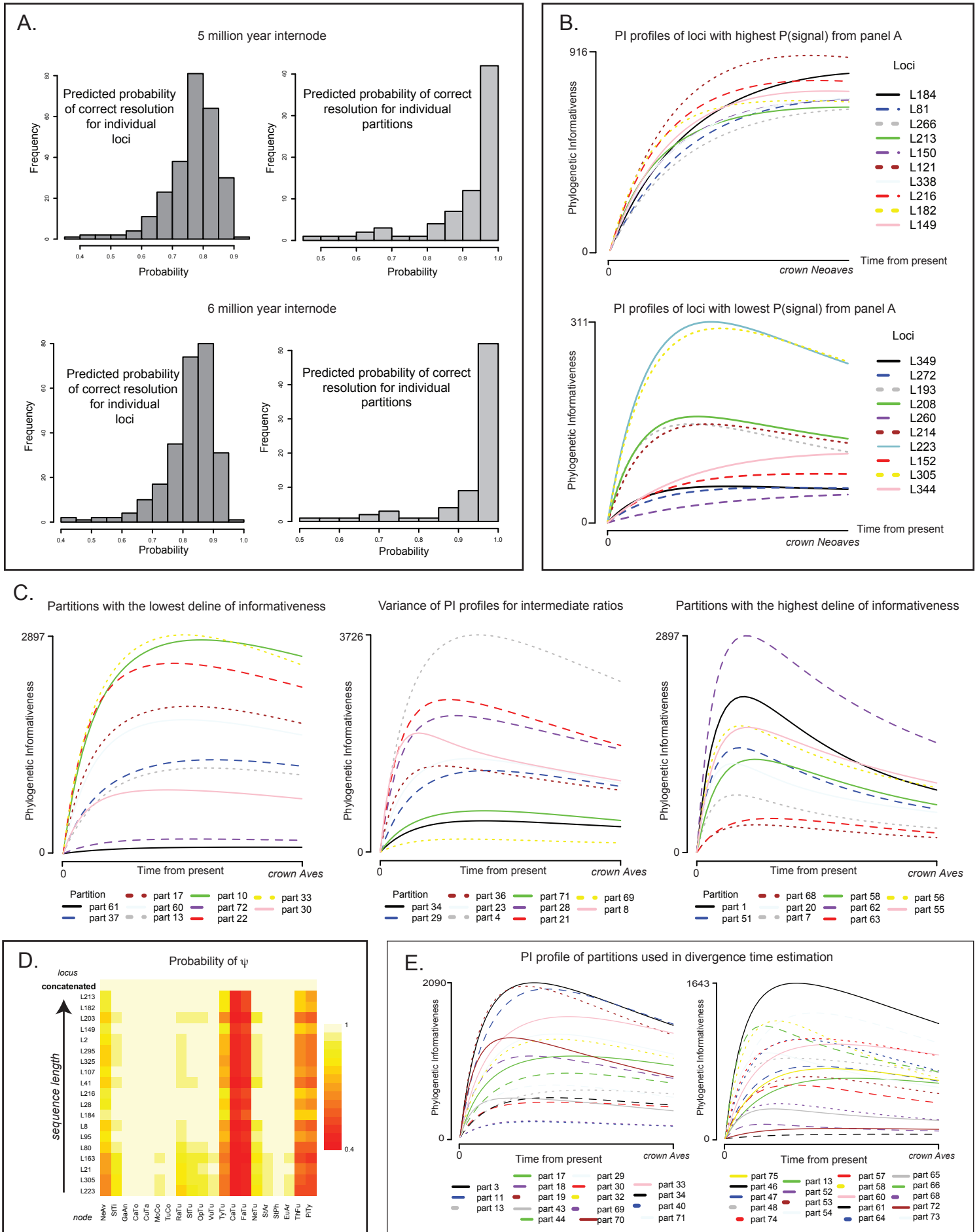


Figure S4

Figure S4. Analyses of phylogenetic informativeness of the loci captured by anchored hybrid enrichment of 198 bird species. **A)** Values of ψ of all individual loci and combinations of loci assigned to partitions by PartitionFinder for the crown of Neoaves given relative divergences corresponding to approximate internode lengths between 5 and 6 million years. **B)** Visualizations of PI profiles for the loci with the highest and lowest values of ψ . **C)** PI profiles for loci that span the variance of ratios in the PI of crown of Neoaves to Crown Aves, with low ratios corresponding to the highest decline in informativeness. **D)** Probability of ψ of individual loci that span the range of locus lengths and the concatenated dataset for focal nodes: NeAv= most recent common ancestor (MRCA) Neoaves; StTi= MRCA of *Struthio* and *Tinamus*; GaAn = MRCA of *Gallus* and *Anas*; CaTo = MRCA of *Caprimulgus* and *Topaza*; CuTa = MRCA of *Cuculus* and *Tauraco*; MoCo = MRCA of *Monias* and *Columba*; TuCo = MRCA of *Tauraco* and *Columba*; RaTu = MRCA of *Rallus* and *Turdus*; StTu = MRCA of *Sterna* and *Turdus*; OpTu = MRCA of *Opisthocomus* and *Turdus*; VuTu = MRCA of *Vultur* and *Turdus*; TyTu = MRCA of *Tyto* and *Turdus*; CaTu = MRCA of *Cariama* and *Turdus*; FaTu = MRCA of *Falco* and *Turdus*; NeTu = MRCA of *Nestor* and *Turdus*; StAr = MRCA of *Sterna* and *Ardea*; StPh = MRCA of *Sterna* and *Phoenicopterus*; EuAr = MRCA of *Eurypyga* and *Ardea*; ThFu = MRCA of *Thamnophilus* and *Furnarius*; and PiTy = MRCA of *Pitta* and *Tyrannus*. **E)** PI profiles of dataset partitions used in divergence time estimation.

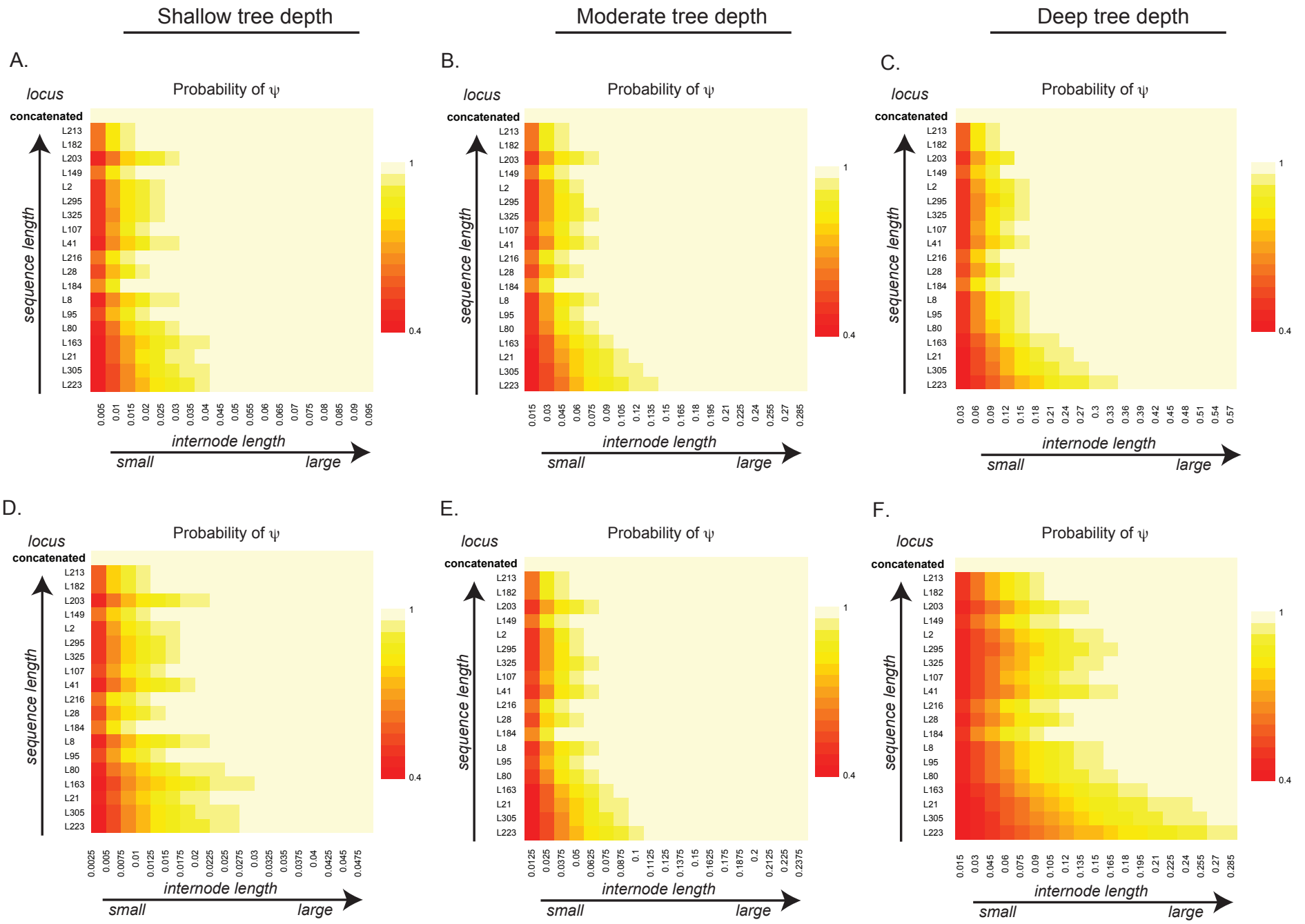


Figure S5

Figure S5. Calculations of ψ values for individual loci sorted by the number of nucleotides that span the range of locus lengths and the concatenated dataset for hypothetical nodes. ψ values were quantified for a range of internode distances across a set range of tree depths: **A)** a shallow divergence occurring at 10% of the total depth, **B)** a divergence occurring at 30% of the total tree depth, **C)** a divergence occurring at 60% of the total tree depth, **D)** a divergence occurring at 5% of the total tree depth, **E)** a divergence occurring at 25% of the total tree depth, and **F)** a divergence occurring at 60% of the total tree depth with a fifty percent reduction in the range of internode distances relative to those in A.

Avian Time Tree

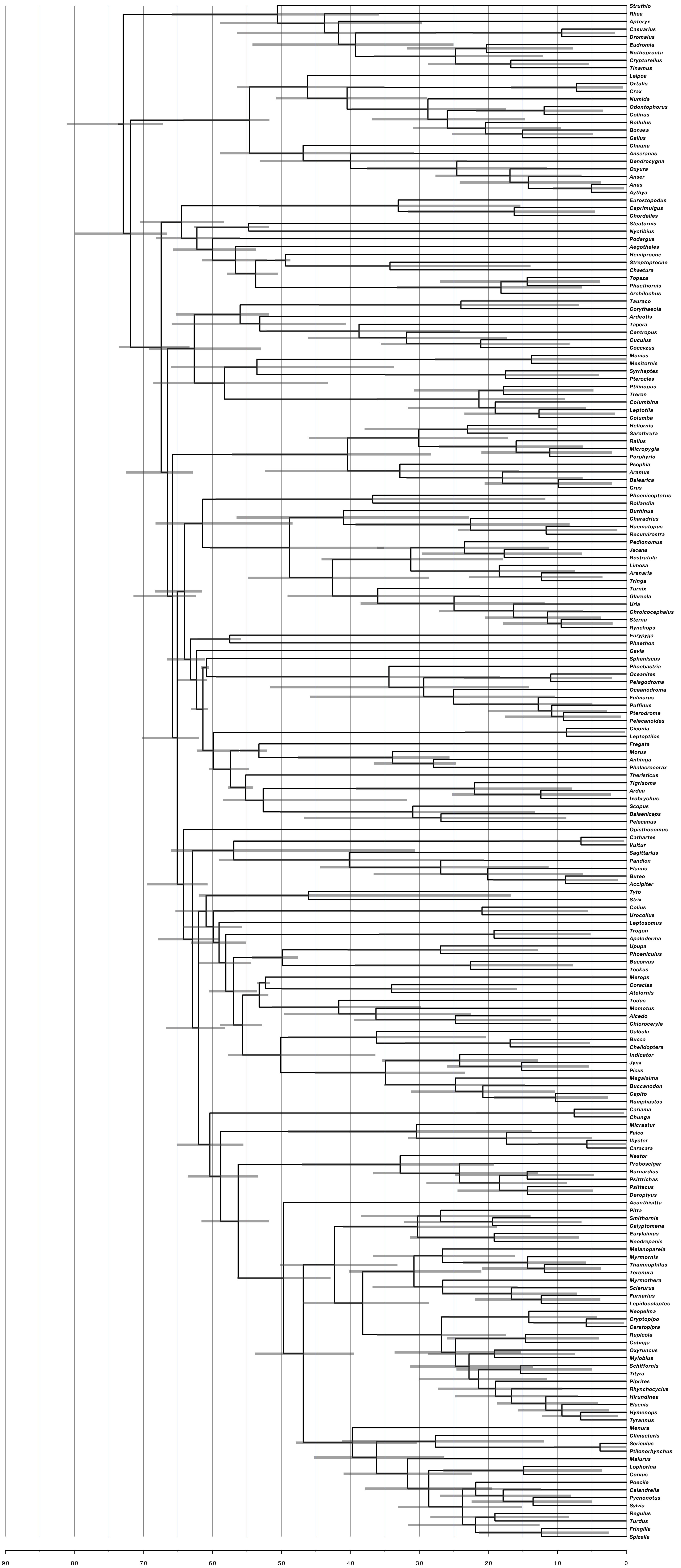


Figure S6

Millions of Years

Figure S6. Time calibrated Bayesian Tree. The final calibrated analysis (median ages) of the ExaBayes topology and 36 data partitions (see supplemental text), shown here with error bars at each node indicating the 95% HPD confidence intervals. For an alternative calibration analysis that includes the fossil *Vegavis*, see Fig. S12.

Distributions of Branching Times

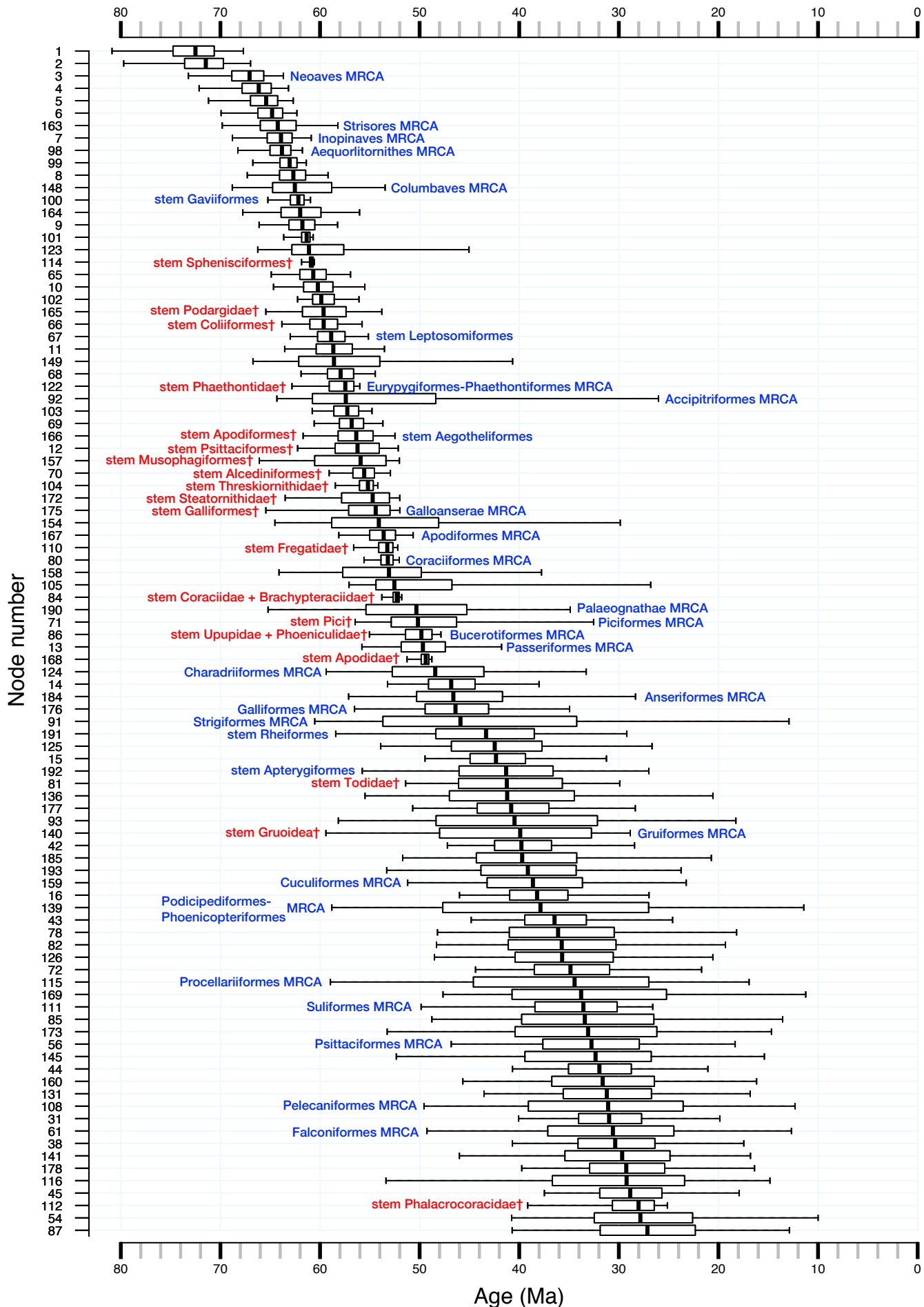


Figure S7 - Page 1

Distributions of Branching Times

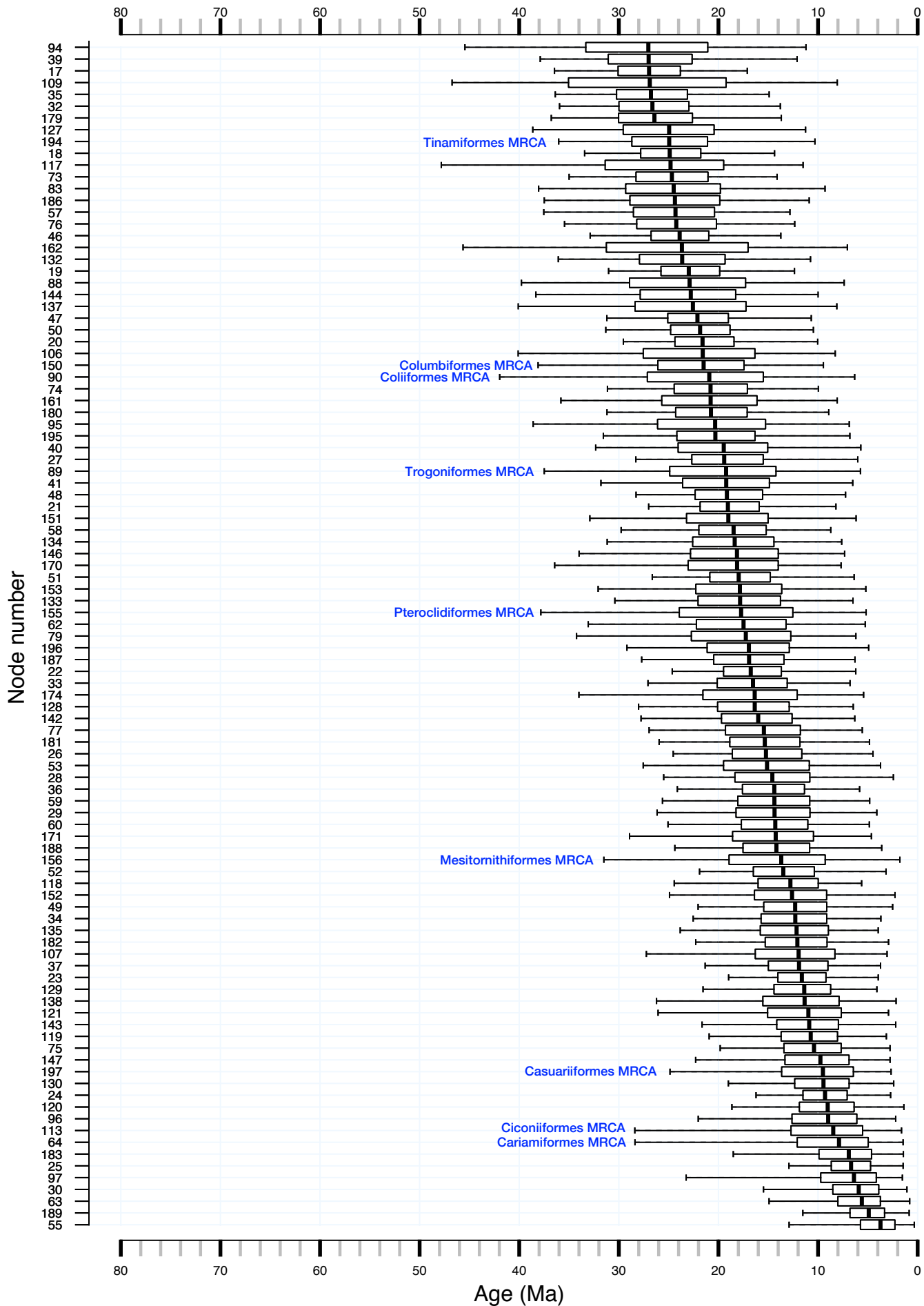
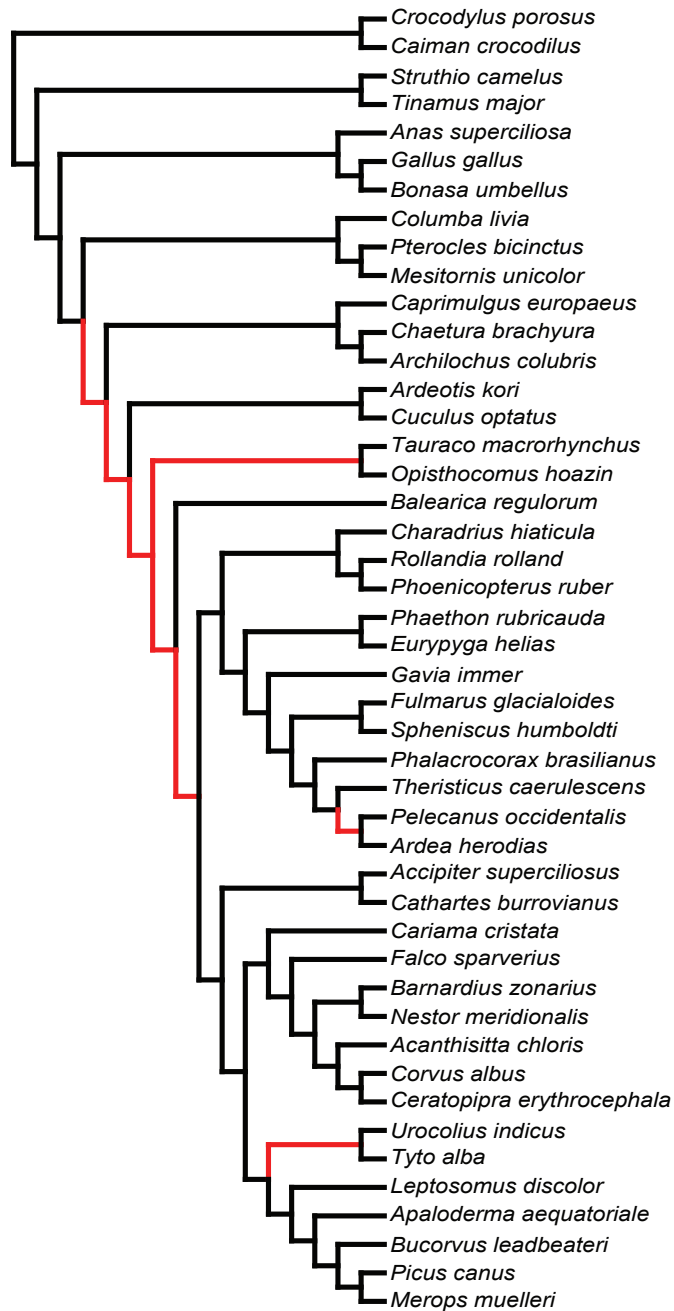


Figure S7 - Page 2

Figure S7. Posterior distributions of estimated node ages. Node numbers on the left margin refer to nodes in the Bayesian tree (Fig. 1). Boxplots represent the posterior distribution of node ages across the summarized distribution of trees from the dating analysis. Whisker lines represent 2.5 and 97.5 percentiles, while the inner box represents the interquartile range and median. Fossil calibrated nodes are labeled in red, and other key nodes at the interordinal level are labeled in blue.

RaxML re-analysis

Lineages sampled to match Jarvis et. al. 2014



Low support branches collapsed (<75)

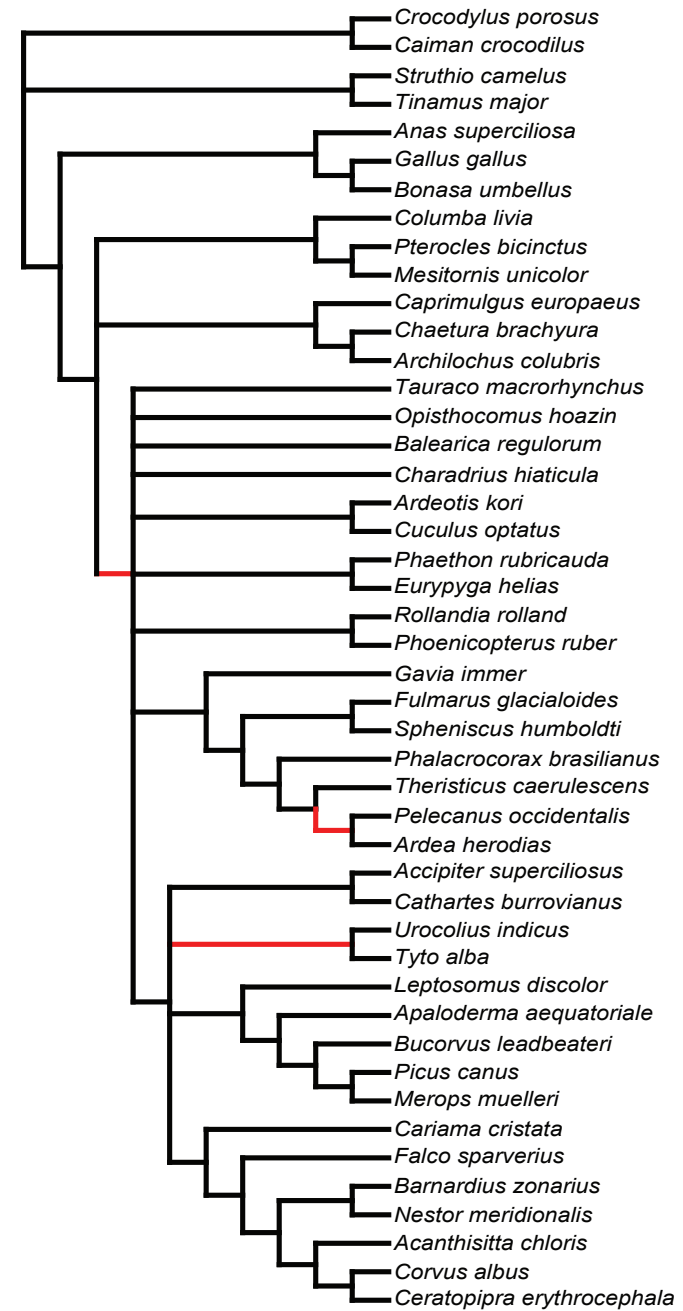


Figure S8

Figure S8. Maximum Likelihood Analysis of the Anchored Enrichment data set pruned to 48 taxa. Phylogenetic hypothesis produced with RaxML from the anchored enrichment data for a reduced sample of 48 species representing the same clades examined in a recent phylogenetic analysis of 48 whole avian genomes⁵. Red lineages mark clades that are incongruent with the Bayesian and ML trees of the full anchored enrichment data set (Fig. 1).

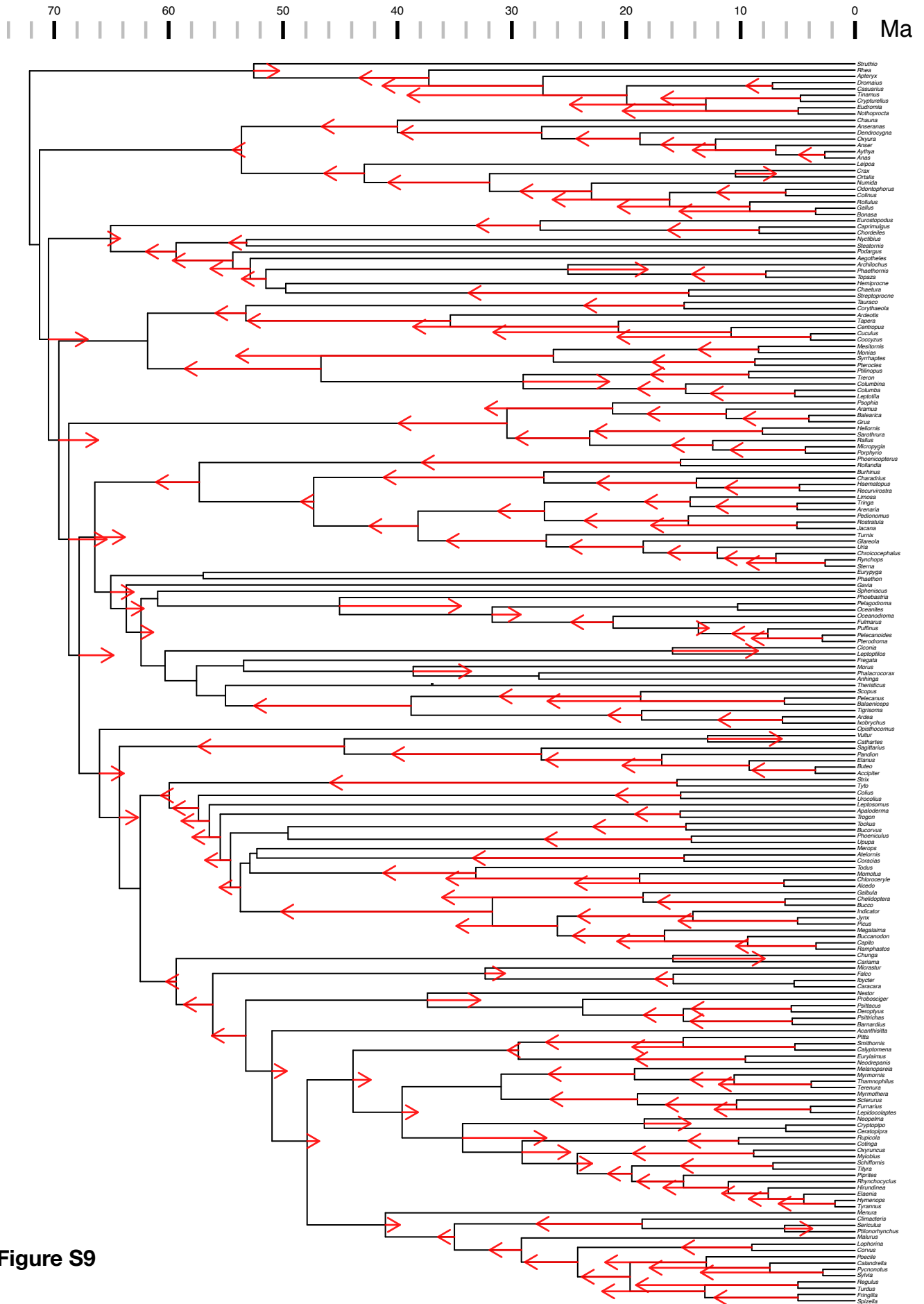


Figure S9

Figure S9. Comparison of Prior and Posterior age estimates. The black base tree is derived from summarizing an MCC tree with median node heights from the distribution of trees generated when only prior calibrations are included in the BEAST analysis (i.e., it is a representation of the effective prior on the entire topology). The red arrows at each node indicate how the estimated divergence times change when our new molecular data is included in the analysis (ie, a representation of the posterior). Arrows pointing to the left indicate posterior ages that are older than their effective prior, and arrows pointing to the right indicate posterior ages that are younger. The posterior divergence time estimates of nodes with no arrows were within 1% of their effective prior.

Avian Time Tree - Testing Vegavis

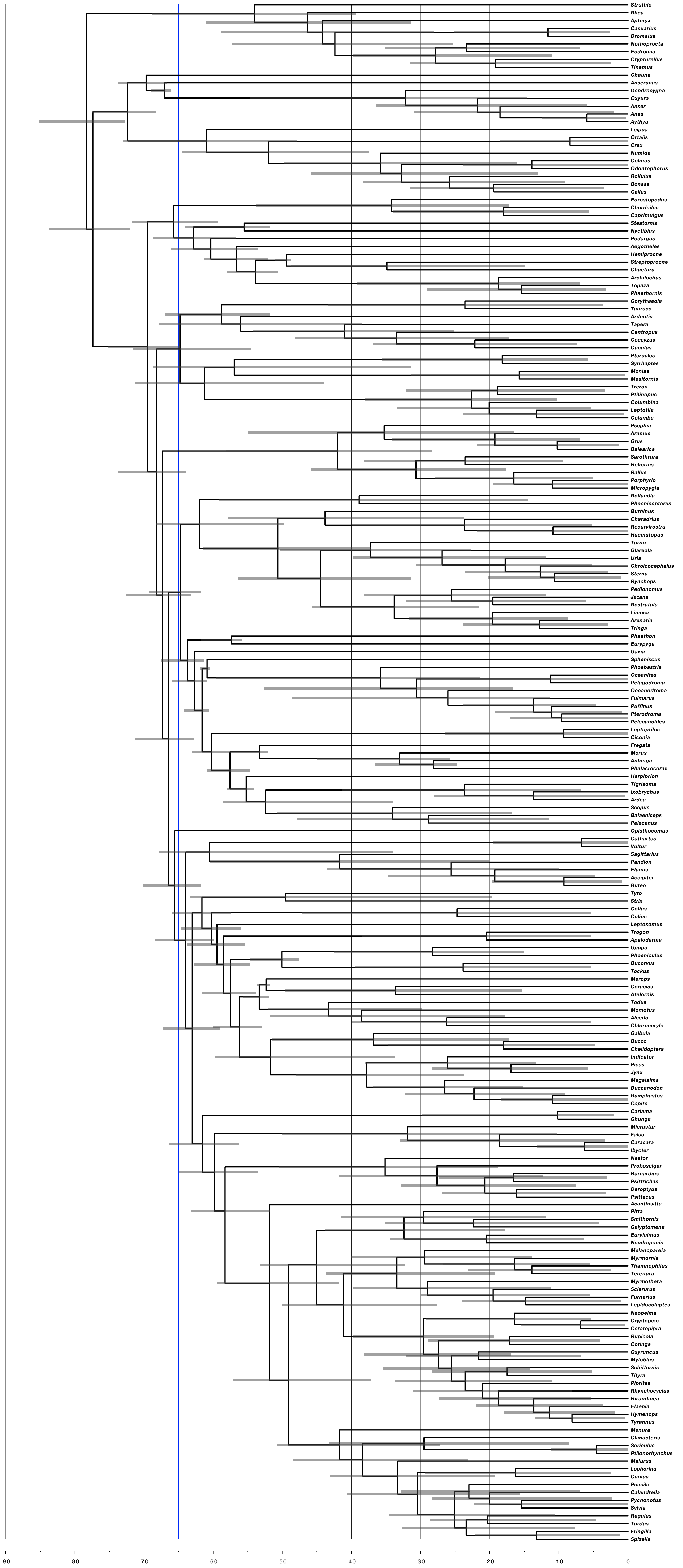


Figure S10

Millions of Years

Figure S10. Alternative Time calibrated Bayesian Tree including *Vegavis* calibration point. A time calibrated sensitivity analysis of the ExaBayes topology and the top ten data partitions (those ten partitions which exhibited the lowest declines in phylogenetic informativeness), shown here with error bars at each node indicating the 95% HPD confidence intervals. This analysis includes the putative stem anseriform *Vegavis* (see supplemental text). For comparison to the primary analysis that excludes *Vegavis*, see Fig S12.

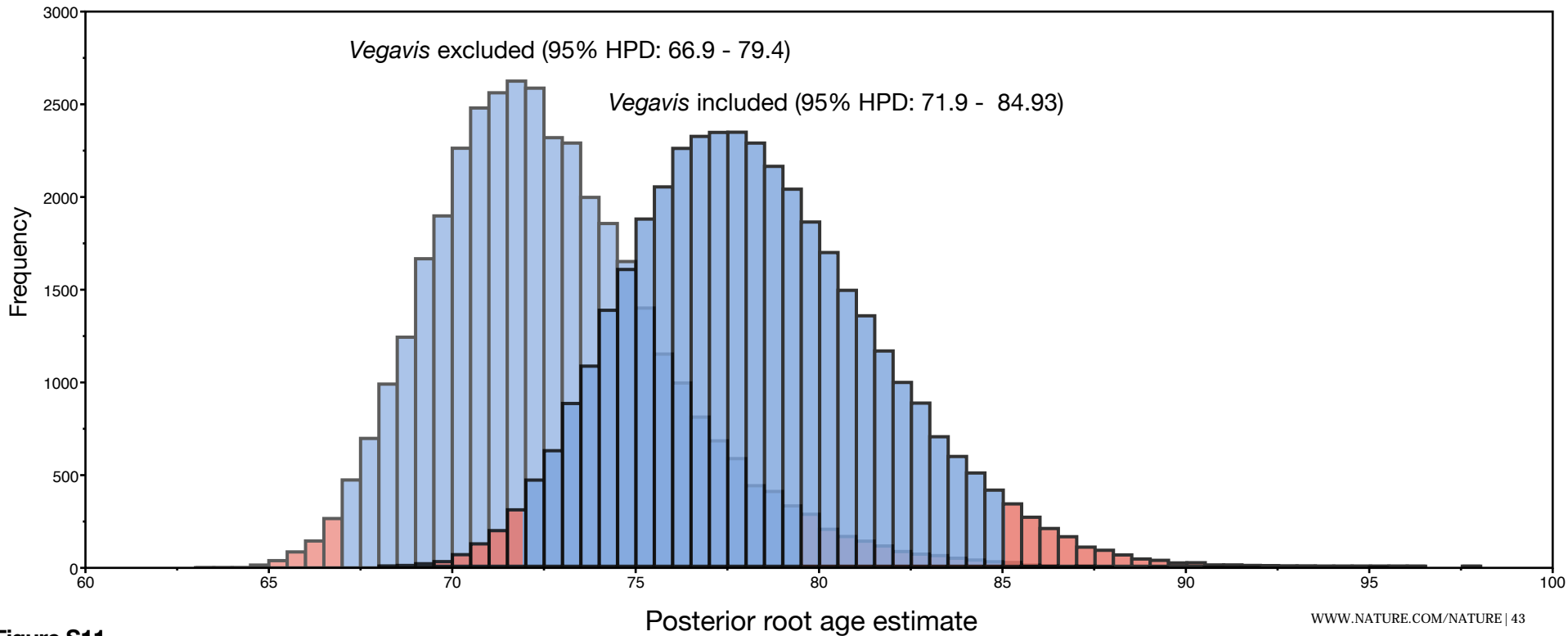


Figure S11

Figure S11. Comparison of Posterior age estimates of the avian crown clade with and without *Vegavis* calibration (see Supplement text). The inclusion of *Vegavis* increased the median estimated age of the avian crown clade by 6.36 MY to 78.26 MY. This revised estimate is not significantly different from our previous analysis (Fig. S6-S7), because it falls within the HPD confidence intervals of our initial estimate of the root age without the *Vegavis* calibration.

Figure S12. Comparison of divergence time estimates without (black) and with (red arrows) *Vegavis* calibration. The black base tree is the time calibrated Bayesian analysis (Fig. S6) which excludes the putative stem Anseriform *Vegavis*. The red arrows at each node indicate how the estimated divergence times change when *Vegavis* is included in the analysis as a calibration point (Fig. S10). For most nodes, ages are increased slightly by the inclusion of *Vegavis*, but significant changes are restricted to the Galloanseres (Fig. S9). The posterior divergence time estimates of nodes with no arrows were within 1% of the analysis excluding *Vegavis*.