Early Paleocene landbird supports rapid phylogenetic and morphological diversification of crown birds after the K–Pg mass extinction

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Evidence is accumulating for a rapid diversification of birds following the K–Pg extinction. Recent molecular divergence dating studies suggest that birds radiated explosively during the first few million years of the Paleocene; however, fossils from this interval remain poorly represented, hindering our understanding of morphological and ecological specialization in early neoavian birds. Here we report a small fossil bird from the Nacimiento Formation of New Mexico, constrained to 62.221–62.517 Ma. This partial skeleton represents the oldest arboreal crown group bird known. Phylogenetic analyses recovered *Tsidiiyazhi abini* gen. et sp. nov. as a member of the Sandcoleidae, an extinct basal clade of stem mousebirds (Coliiformes). The discovery of *Tsidiiyazhi* pushes the minimum divergence ages of as many as nine additional major neoavian lineages into the earliest Paleocene, compressing the duration of the proposed explosive post–K–Pg radiation of modern birds into a very narrow temporal window parallel to that suggested for placental mammals. Simultaneously, *Tsidiiyazhi* provides evidence for the rapid morphological (and likely ecological) diversification of crown birds. Features of the foot indicate semizygodactyly (the ability to facultatively reverse the fourth pedal digit), and the arcuate arrangement of the pedal trochleae bears a striking resemblance to the conformation in owls (Strigiformes). Inclusion of fossil taxa and branch length estimates impacts ancestral state reconstructions, revealing support for the independent evolution of semizygodactyly in Coliiformes, Leptosomiformes, and Strigiformes, none of which is closely related to extant clades exhibiting full zygodactyly.

aves | phylogeny | morphology | fossil | evolution

Mammals recovered rapidly in the aftermath of the Cretaceous–Paleogene (K–Pg) mass extinction (~66 Ma). In North America, mammalian diversity levels began to surpass the benchmarks observed in the latest Cretaceous just a few million years after the extinction (1, 2). The placental mammal radiation is thought to be part of a broader diversification that occurred on a recovering terrestrial landscape dominated by flowering plants (angiosperms) (3, 4).

In contrast to mammals, our understanding of the recovery and radiation of the most diverse clade of tetrapods—birds—is poorly understood. Easily identifiable stem lineage representatives of most major neoavian clades are known by the early Eocene, and in many cases are first recorded in Lagerstätten, such as the Green River and Messel Formations (5, 6). The fossil record of birds in the critical latest Cretaceous–earliest Paleocene interval is less well documented, however. Archaic (non-crown) birds dominate the global Late Cretaceous fossil record, and the only phylogenetically secure record of a Cretaceous crown bird is the anseriform *Vegavis iaai* (7).

In North America, an enigmatic Maastrichtian avifauna is known primarily from isolated elements. Fossils support the presence of at least 17 species, many belonging to archaic taxa, such as Enantiornithes, Hesperornithes, and basal Ornithurae (8).

Other fossils defy precise classification, but none can be convincingly assigned to any clade within crown Aves, and only one taxon identified from the Maastrichtian of North America appears to cross the K–Pg boundary (5, 8). Even fewer early Paleocene birds are known, a situation exacerbated by the fact that stratigraphic resolution remains poor for many marine birds from the Hornerstown Formation of New Jersey and terrestrial birds from the "Bug Creek" sequence in Montana, each of which contains a mixture of Paleocene and Cretaceous fossils (9, 10).

Globally, the published record of early Paleocene birds is limited primarily to "waterbirds" (Aequornithes, *sensu* 11 and Aequorlitornithes, *sensu* 12) including the stem penguin *Waimanu*, an unnamed stem tropicbird, and the aquatic *Australornis* from New Zealand (13–15), and the poorly understood and imprecisely dated *Scaniornis* from Sweden (16). Terrestrial taxa include the enigmatic *Qianshanornis* and *Qinornis* of China (17, 18). None of these can be assigned to any extant ordinal level clade, and the latter may even represent a late surviving archaic taxon from outside crown Aves (17, 19). Thus, the record of birds in the aftermath of the K–Pg mass extinction remains poor compared with that of other terrestrial groups, such as plants, insects, and mammals.

A fossil of a small arboreal species from the early Paleocene of New Mexico provides insight into the initial phases of post-extinction recovery by birds. This associated partial skeleton bears multiple synapomorphies nesting it within total-group Coliiformes (mousebirds), the earliest-diverging lineage within the landbird clade Coraciimorphae (12, 20). Today, Coliiformes are one of the most species-poor ordinal-level clades, with just six species, all restricted to Africa. However, mousebirds were

Significance

Molecular (DNA) studies suggest that birds radiated rapidly in the wake of the Cretaceous–Paleogene mass extinction (66 Ma), diversifying into nearly all the major groups we recognize today. However, fossil evidence for this pattern has been difficult to find because of the poor fossilization potential of small, delicate-boned birds. We report a tiny species of bird from ~62.5 million-year-old rocks in New Mexico. *Tsidiiyazhi abini* (Navajo for "little morning bird") is an ancient species of mousebird (Coliiformes). The fossil provides evidence that many groups of birds arose just a few million years after the mass extinction and had already begun evolving specializations of the foot for different ecological roles.

more diverse and enjoyed a wider geographic distribution, spanning Europe and North America during the Paleogene (21, 22).

Systematic Paleontology

Aves Linnaeus, 1758
   Coliiformes Murie, 1872
   cf. Sandcoleidae Houde and Olson, 1992
   Tsidiiyazhi abini, gen. et sp. nov.

Holotype. NMMNH (New Mexico Museum of Natural History and Science) P-54128: associated partial skeleton including the right articular portion of the mandible, two thoracic vertebrae, pygostyle, partial left and right coracoids, cranial portions of both scapulae, proximal and distal portions of both humeri, proximal end of left radius, distal end of right ulna, processus extensorius of right carpometacarpus, proximal end of right femur, head and shaft of left femur, distal end of right tibiotarsus, proximal and distal ends of left tarsometatarsus, and a pedal phalanx. Several additional fragments cannot be identified to a particular element. All elements were collected within a single 25 cm × 25 cm grid square, share the same color and texture, and fall within the same size range with no duplicate elements.

Etymology. The genus and species names are derived from the Navajo (Diné Bizaad) language, reflecting the discovery of the fossil within ancestral Navajo lands. The genus name is derived from the words "tsidii" for "bird" and "yazhi" for "little," in reference to the fossil's small size. The specific epithet is derived from the Navajo word "abini" for "morning," referencing the early Paleocene age of the taxon. Pronunciation using International Phonetic Alphabet phonetic symbols is as follows: /tsɪdi:jæʒi:/ /ˈɔbɪnɪ/.

Type Locality and Horizon. NMMNH locality L-6898 comprises a relatively thin (<10 cm) muddy siltstone bed of restricted areal extent (<5 m²), representing an exposure of the Ojo Encino Member of the Nacimiento Formation (Fig. 1 and *SI Appendix*, Fig. S1). The site is located on the West Flank of Torreon Wash within the San Juan Basin, in Sandoval County, New Mexico. (Precise location data are on file at NMMNH and available to qualified researchers.) These deposits are assigned to the *Mixodectes pungens* biozone (23), and thus fall within the late Torrejonian (To3) North American Land Mammal Age (24). Furthermore, L-6898 falls within magnetochron C27N (23), constraining the absolute geochronological age to 62.221–62.517 Ma (25). Locality L-6898 also has yielded semi-articulated skeletons of small mammals, as well as disarticulated bones and teeth from mammals, lizards, and a snake (26, 27). This overall area also has produced several arboreal mammal skeletons, including nearly complete and partially articulated skeletons of the

mixodectid euarchontan *M. pungens* and palaechthonid plesiadapiform *Torrejonia wilsoni* (28), and a partial disarticulated skeleton of the cimolestid *Acmeodon secans*.

Diagnosis. *T. abini* is differentiated from all other Coliiformes by the following apomorphies: (*i*) tubercle on the medial face of cranial end of the scapula, (*ii*) strongly developed triangular protuberance at the apex of impressio m. sternocoracoidei of the coracoid, (*iii*) medially displaced distal exit of canalis extensorius of the tibiotarsus, and (*iv*) arcuate arrangement of the metatarsal trochleae. Apomorphies are indicated with asterisks in Fig. 2.

Referral. *T. abini* is assigned to Sandcoleidae (an extinct clade nested within total group Coliiformes) based on the following combination of derived features: (*i*) corpus of thoracic vertebra with large ovoid fossa; (*ii*) fossa pneumotricipitalis of humerus lacking pneumatic foramina; (*iii*) tuberculum supracondylare ventrale of the humerus expanded, forming a large triangular platform approximately equal in width to the condylus ventralis; and (*iv*) presence of a wing-like plantar flange extending from the lateral margin of trochlea metatarsi IV (21, 22). These features are indicated with a "‡" in Fig. 2. An isolated pedal phalanx suggests that *Tsidiiyazhi* had extremely abbreviated proximal phalanges of digit IV, a feature that characterizes Coliiformes and is also observed in Psittaciformes, Strigiformes, Falconiformes, and Accipitriformes. We consider referral of *Tsidiiyazhi* to Sandcoleidae to be the strongest hypothesis, but owing to morphological homoplasy evident within Neoaves as well as the age of the fossil, we consider it plausible that the species may occupy an alternate position as a sister taxon to all other Coliiformes. We denote this uncertainty with a "cf." pending discovery of more complete material.

Description and Comparisons. *T. abini* is a small bird, nearly identical in skeletal dimensions to the extant *Colius striatus* (speckled mousebird; ~50 g). Only a fragment of the skull is preserved. This fragment, the right articular region of the mandible, differs from that in extant mousebirds in that the cotyla lateralis is less bulbous. The processus retroarticularis is short as in the stem mousebird *Sandcoleus*, although it is noteworthy that several stem mousebirds, including *Chascacocolius*, *Masillacolius*, and *Oligocolius*, exhibit an elongate blade-like processus retroarticularis.

A prominent lateral ovoid fossa marks the corpus of the thoracic vertebra, a feature also observed in *Sandcoleus*. The pygostyle of *Tsidiiyazhi* is extremely similar to that of *Sandcoleus*, except for the straighter caudal margin and smaller relative size. It is mediolaterally flattened, lacks the wide expansion of the discus pygostyli seen in advanced mousebirds, and is pierced laterally by a prominent foramen. The discus pygostyli shows a slight expansion at its dorsal and ventral portions, creating a subtle hourglass-like shape in caudoventral view.

The coracoid resembles that of previously described Sandcoleidae in that the processus acrocoracoideus is hooked, forming a sulcus supracoracoideus that lacks pneumatic foramina. The cotyla scapularis is modestly concave, exhibiting a shape intermediate to the deep cup-like cotyla scapularis observed in such taxa as Accipitriformes and the essentially flat cotyla scapularis in most other extant Telluraves ("landbirds", *sensu* 11). A processus procoracoideus and an ovoid foramen nervi supracoracoideus are present. The cranial end of the scapula resembles that of extant mousebirds, except that the acromion, which is subtriangular, has a small ridge near the dorsal margin of the lateral face and lacks the squared, mediolaterally broadened shape present in extant mousebirds. The tuberculum coracoideum is strongly developed as in *Sandcoleus* (poorly developed in *Anneavis* and *Chascacocolius*). A pronounced concavity is present on the caudal face of the humerus at the base of the crista deltopectoralis, which appears to have been strongly developed based on the intact base of this
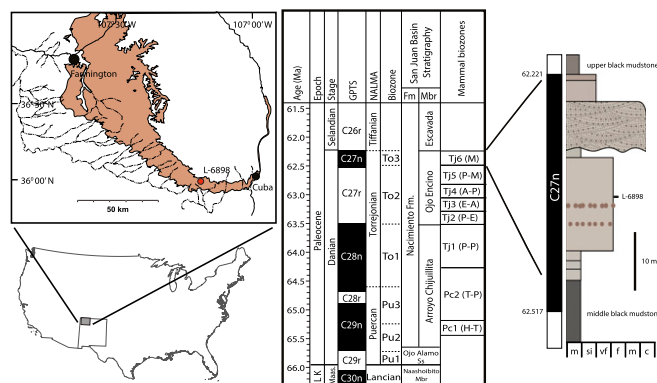
Fig. 1. Geologic map showing Nacimiento Formation sediments (orange), and the location and stratigraphic correlation of the *Tsidiiyazhi abini* holotype locality (NMMNH locality L-6898) (23).
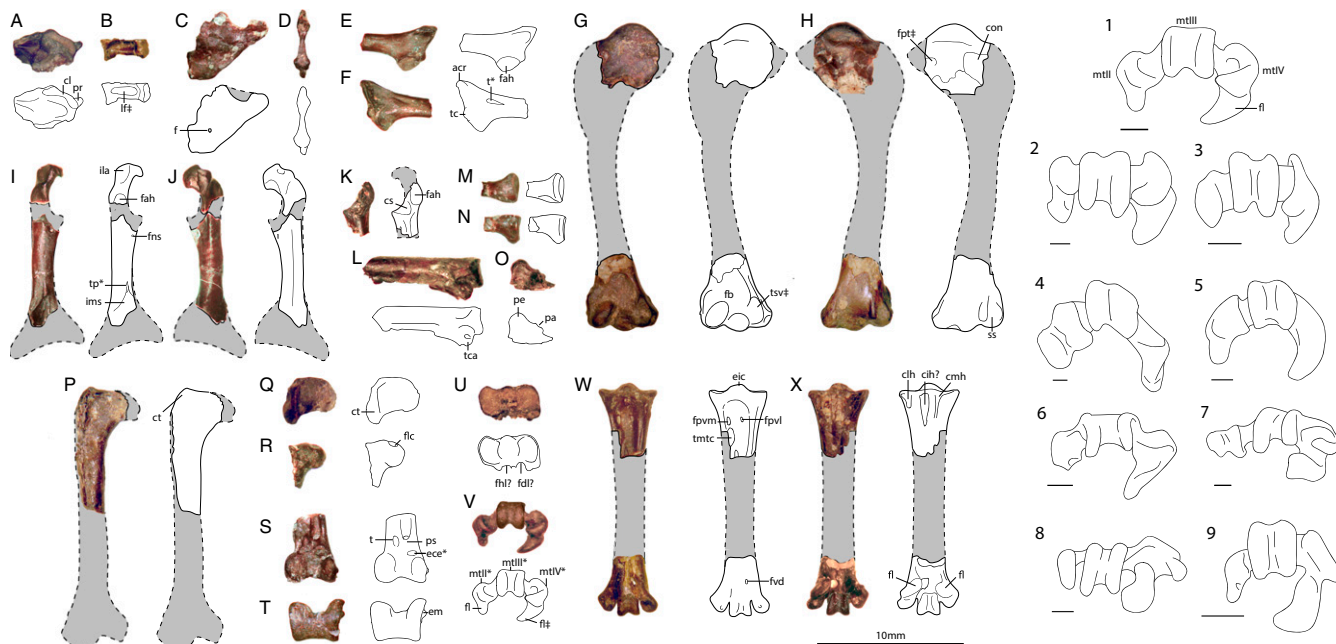
Fig. 2. *Tsidiiyazhi abini* holotype (NMMNH P-54128): (*A*) dorsal view of articular region of mandible, (*B*) lateral view of thoracic vertebral corpus, (*C*) lateral and (*D*) caudal views of pygostyle, (*E*) lateral and (*F*) medial views of right scapula, (*G*) cranial and (*H*) caudal views of right humerus, (*I*) dorsal and ventral (*J*) views of the left coracoid, (*K*) dorsal view of right coracoid, (*L*) ventral view of right ulna, (*M*) dorsal and (*N*) ventral views of left radius, (*O*) dorsal view of right carpometacarpus, (*P*) cranial and (*Q*) proximal views of right femur, (*R*) caudal view of head of left femur, (*S*) cranial and (*T*) distal views of right tibiotarsus, and (*U*) proximal, (*V*) distal, (*W*) dorsal, and (*X*) plantar views of left tarsometatarsus. Comparative line drawings of the distal view of the left tarsometatarsus in (1) *T. abini* (Coliiformes: cf. Sandcoleidae), (2) *Sandcoleus copiosus* (Coliiformes: Sandcoleidae), (3) *Colius striatus* (Coliiformes: Coliidae), (4) *Ogygoptynx wetmorei* (Strigiformes: Ogygoptyngidae), (5) *Otus scops* (Strigiformes: Strigidae), (6) *Pseudasturides macrocephalus* (Psittacopasseres: Pseudasturidae), (7) *Myiopsitta monachus* (Psittaciformes: Psittacidae), (8) *Lybius bidentatus* (Piciformes: Capitonidae), and (9) *Zygodactylus grivensis* (Passeriformes: Zygodactylidae). Illustrations 2 and 3, after ref. 21; 4, after ref. 46; and 5–9, after ref. 34. acr, acromion; chl, crista hypotarsi lateralis; cih, crista intermedialis hypotarsi; cmh, crista medialis hypotarsi; cl, cotyla lateralis; cs, cotyla scapularis; con, concavity at base of crista deltopectoralis; ct, crista trochanteris; ece, exit of canalis extensorius; eic, eminentia intercotylaris; f, foramen; fah, facies articularis humeralis; fb, facies brachialis; fl, flange; flc, fovea ligamentalis capitis; fhl, pathway for tendon of m. hallucis longus; fdl, pathway for tendon of m. flexor digitorum longus; fpt, fossa pneumotricipitalis; fpvl, foramen vasculare proximale laterale; fpvm, foramen vasculare proximale mediale; fvd, foramen vasculare distale; ims, impressio m. sternocoracoidei; lf, lateral fossa; mtlI-IV, trochlea metatarsi II–IV; pa, processus alularis; pe, processus extensorius; pr, processus retroarticularis; ps, pons supratendineus; ss, sulcus scapulotricipitalis; t, tubercle; tc, tuberculum coracoideum; tmtc, tuberositas m. tibialis cranialis; tp, triangular protuberance; tsv, tuberculum supracondylare ventrale. *Apomorphies. ‡Diagnostic features of Sandcoleidae/Coliiformes. (Scale bars: 1–9, 1 mm.)

crest. The sulcus ligamentum transversus and incisura capitalis are well developed, and the crista bicipitalis is weakly inflated. Within the intact portion of the fossa pneumotricipitalis, there is no evidence of any pneumatic foramina or openings into the shaft. The tuberculum supracondylare ventrale expands to form a large triangular surface adjacent to the condylus ventralis, a prominent feature shared with *Sandcoleus* and *Anneavis*. The wide, shallow m. brachialis fossa is bordered on its ventral margin with a well-defined rim, whereas the dorsal margin grades more smoothly into the shaft. A prominent crescent-shaped depression occurs proximal to the condylus dorsalis (well preserved on the left humerus, but less perceptible on the right humerus), a feature observed in crown (and some stem) mousebirds but not previously observed in Sandcoleidae. The process flexorius is poorly developed, and the epicondylus ventralis is marked by a circular pit on its ventral face, with a second pit on the ventral face of the shaft. Neither pit occurs in extant mousebirds, but both pits are present in *Anneavis*. The sulcus scapulotricipitalis is well marked, and the sulcus humerotricipitalis is broad and shallow. The cotyla ventralis of the ulna appears to extend onto the olecranon as in extant and fossil Coliiformes, although the margins are incompletely preserved. The distal end of the ulna differs from extant mousebirds, in that the sulcus intercondylus is flattened across its distal and dorsal faces. An ovoid fossa is positioned along the margo caudalis adjacent to the articular region, and a smaller round fossa is on the ventral face of the strongly developed tuberculum carpale.

The crista trochanteris of the femur projects strongly cranially, but shows very little proximal projection. The caudal face shows a deep, subcircular impressio obturatoria. The distal end of the tibiotarsus lacks the sharp, triangular projection that extends off the lateral face of the shaft in extant mousebirds, and instead bears a pair of low ridges. The pons supratendineus has a strong cranial projecting tubercle, and a small foramen enters the shaft just lateral to this tubercle. Of note, the distal exit of the canalis extensorius is positioned medially, unlike in either sandcoleids (placed near the midline) or extant mousebirds (placed laterally). In distal view, the tibiotarsus is mediolaterally wide, as in other sandcoleids. As in other sandcoleids, the proximal end of the tarsometatarsus has a low, wide eminentia intercotylaris. The fossa infracotylaris dorsalis is deep and pierced by two proximal vascular foramina, and the margins of a well-developed and elongate tuberositas m. tibialis cranialis are intact. Two short hypotarsal crests are present at the medial and lateral edges of the hypotarsus, and the base of a damaged intermediate hypotarsal crest is intact close to midline, on the sides of which are two deep hypotarsal grooves (likely for the tendons of m. flexor hallucis longus and m. flexor digitorum longus). The trochlea metatarsi II is small and squared, in contrast to the grossly enlarged trochlea of many Paleogene stem owls, and bears a pronounced medial plantar flange. The dorsal face of the articular surface of the trochlea lacks a furrow, whereas a deep furrow is present on the plantar face. Trochlea metatarsi III is relatively large, and the plantar projection of the rims of the trochlea are

subequal. Trochlea metatarsi IV has a strong, plantarly directed lateral flange, which is deeply grooved as in *Sandcoleus* and some Strigiformes. An extremely shortened, asymmetrical pedal phalanx appears to represent the proximal phalanx of the fourth digit based on comparisons with articulated stem mousebird specimens.

Phylogenetic Methods

A phylogenetic matrix of 111 morphological characters was assembled and scored for 48 species-level taxa (including 16 fossil taxa), sampling all major lineages of Telluraves (*SI Appendix*). Tinamiformes and Anseriformes were used as outgroups. Because recent molecular studies have yielded topologies that conflict with those based on morphology and with one another, we conducted an unconstrained analysis of the morphological data, as well as analyses using backbone constraints derived from five recently published molecular studies: a 19-loci dataset (29), a genome-based dataset (20), a 1,541-loci UCE dataset (30), a MP retrotransposon dataset (31), and the 259-loci anchored hybrid enrichment dataset (12). To test the impact of more complete fossils on the placement of *Tsidiiyazhi*, we conducted additional analyses excluding all fossil taxa except *Tsidiiyazhi*, with and without the backbone constraints. All analyses were conducted in PAUP*4.a147 (32), using the heuristic search option and 10,000 replicates of random taxon addition, multistate codings treated as uncertainty, and branches of minimum length zero collapsed.

Ancestral character state reconstructions for pedal digit arrangement were conducted in Mesquite 3.01 (33) under the Mk1 maximum likelihood models. Each taxon was scored as anisodactyl, heterodactyl, semizygodactyl, or fully zygodactyl. We tested the impact of topology by performing nine iterative reconstructions (*SI Appendix*, Figs. S14–S22). Topologies tested include the tree from the unconstrained analysis, the tree based on the preferred molecular scaffold (12), and the scaffold tree with the position of Halcyornithidae shifted to consider the hypotheses that these fossils represent stem parrots (34, 35) or stem Psittacopasserae (36). We tested the impact of temporal data by iteratively setting all branch lengths to be equal or to be scaled based on fossil ages and molecular divergence estimates (12). To avoid zero-length branches, each branch leading to a fossil or extinct clade was assigned a 1.0-Ma branch length if the branch otherwise would be zero. Finally, we tested the impact of fossils by performing reconstructions on trees from which all extinct taxa were pruned.

Results

All phylogenetic analyses using the full taxon sample recovered *Tsidiiyazhi* as a stem mousebird. In the four most parsimonious trees (MPTs) from the unconstrained analysis (*SI Appendix*, Fig. S2), *Tsidiiyazhi* is placed in Sandcoleidae. However, the morphology-based tree conflicts with recent molecular results in uniting Passeriformes with a Piciformes + Upupiformes clade and supporting a "raptorial clade" (Accipitriformes, Falconiformes, and Strigiformes). In contrast, recent molecular analyses unite Passeriformes and Psittaciformes and recover the three raptorial groups as separate radiations (12, 20, 29–31). Furthermore, the internal branches separating Coliiformes from other extant avian clades appear to be exceptionally short, and thus mousebirds have proven highly labile, being recovered as sister taxon to Strigiformes (29), core Coraciimorphae (12, 20), Australaves (30), and Afroaves (31) in recent phylogenies. Thus, it is crucial to establish the sensitivity of our placement of *Tsidiiyazhi* to different hypotheses for the higher-level affinities of Coliiformes.

Enforcing our preferred molecular scaffold (12) results in six MPTs (Fig. 3) that are 31 steps longer than those recovered in the unconstrained analysis. This highlights a potentially high level of homoplasy within some morphological characters, including many related to beak shape and pedal digit organization that contribute to the clustering of the raptorial taxa in the morphological tree. Applying the scaffold breaks up the "raptorial clade" and unites Passeriformes + Psittaciformes, but *Tsidiiyazhi* nonetheless retains its position as a stem mousebird. Likewise, *Tsidiiyazhi* retains this position when each of the four alternate molecular scaffolds are enforced (*SI Appendix*, Figs. S6–S13).

The unconstrained analysis excluding all fossils except *Tsidiiyazhi* resulted in the taxon falling into a large polytomy with little resolution among Neoaves (*SI Appendix*, Figs. S3), whereas enforcing

any of the five molecular scaffolds draws *Tsidiiyazhi* back into total group Coliiformes (*SI Appendix*, Figs. S6–S13).

Ancestral state reconstructions are sensitive to inclusion of fossil and temporal data (37, 38). In the present study, a "naïve" reconstruction using the molecular scaffold tree with only extant taxa and no branch length data supports a single origin of semizygodactyly in the most recent common ancestor of Coraciimorphae + Strigiformes, along with two independent origins of full zygodactyly in Piciformes and Psittaciformes (*SI Appendix*, Fig. S17); however, fossil taxa and branch length data have the power to overturn this reconstruction. Inclusion of fossil taxa alters the optimization, revealing support for an independent transition to semizygodactyly within Leptosomiformes, as well as weak support for a gain of full zygodactyly in Psittacopasserae (Psittaciformes + Passeriformes), with a secondary loss on the branch leading to crown Passeriformes (*SI Appendix*, Fig. S19). Furthermore, incorporating branch length data derived from the fossil record and molecular divergence dates results in support for independent origins of semizygodactyly in Strigiformes, Leptosomiformes, and Coliiformes regardless of whether fossil taxa are sampled (*SI Appendix*, Figs. S19 and S20). Finally, if Halcyornithidae is manually shifted to a position as a sister taxon to extant Psittaciformes or to Psittacopasserae, as proposed in previous paleontological work (34–36), support strengthens for a single gain of zygodactyly in Psittacopasserae with a secondary loss in Passeriformes (*SI Appendix*, Figs. S2 and S22). We remain agnostic as to the position of Halcyornithidae, but consider support for multiple origins of semizygodactyly within Telluraves to be robust because it incorporates both morphological data from fossils and branch length estimates.

This series of analyses yields several key observations: (*i*) *Tsidiiyazhi* is well supported as a stem mousebird, falling within total group Coliiformes regardless of which molecular topology is enforced; (*ii*) molecular scaffolds have the potential to "rescue" fossil-inclusive phylogenies from homoplasy within morphological datasets (e.g., by breaking up the cluster of raptorial taxa); and (*iii*) the inclusion of fossils can have a strong positive impact on phylogenetic analyses, here manifested as greater resolution (e.g., four collapsed nodes when all fossils are included vs. seven collapsed nodes when all fossils except *Tsidiiyazhi* are excluded in unconstrained analyses; *SI Appendix*, Figs. S2 and S3), and alternate inferred ancestral states at the base of Coraciimorphae and Psittacopasserae.

Discussion

Tsidiiyazhi has important implications for the timing of the neoavian radiation (a clade that includes nearly 10,000 extant species). Under our preferred tree, *Tsidiiyazhi* pushes the hard minimum fossil ages of the lineages leading to four major landbird clades into the early Paleocene: Australaves, Accipitriformes, Strigiformes, and Cavitaves (Fig. 3). Furthermore, the fossil slightly extends the minimum divergence age of the clades Opisthocomiformes, Aequorlitornithes, Gruiformes, Columbaves, and Strisores because *Tsidiiyazhi* (62.221–62.517 Ma) is older than the stem penguin *Waimanu* (60.5–61.6 Ma; ref. 13). This narrows the post-Cretaceous mass extinction window for the divergences among most major neoavian clades to less than 4 million years, and reinforces the evidence for an explosive radiation of Neoaves during the earliest Cenozoic, alongside rapidly diversifying placental mammals and flowering plants (1, 2, 39). However, the age and phylogenetic placement of *Tsidiiyazhi* go beyond simple confirmation of molecular results, providing enhanced resolution via a stratigraphic data point not obscured by divergence dating confidence intervals, which typically span millions if not tens of millions of years.

The basal placement of Coliiformes within Telluraves and the antiquity of *Tsidiiyazhi* make the specialized foot morphology of this fossil taxon particularly interesting. *Tsidiiyazhi* exhibits morphologies
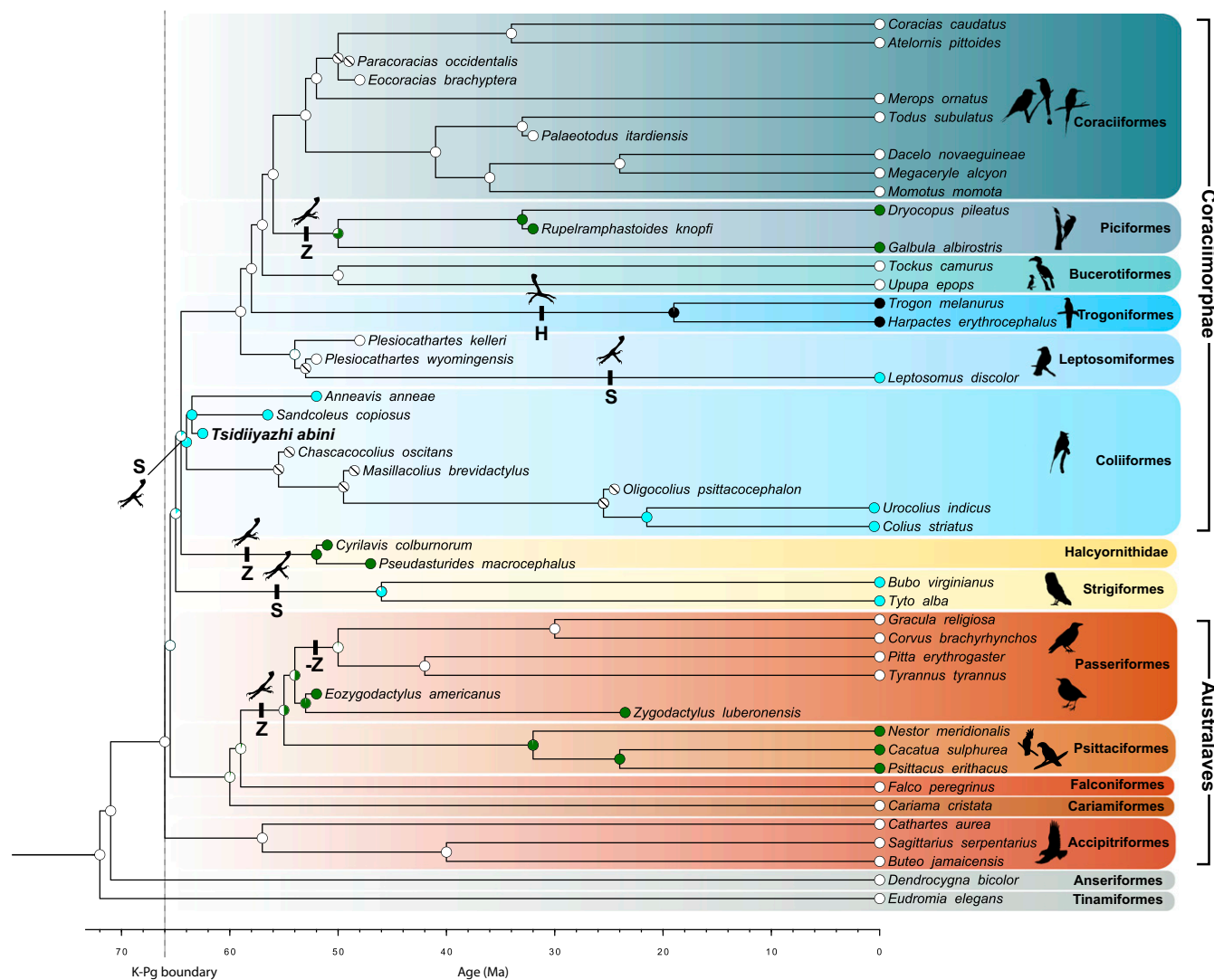
Fig. 3. Phylogeny based on analysis of 111 morphological characters enforcing the preferred backbone constraint (12). Pie charts represent Mk1 likelihood optimization of ancestral state for pedal digit conformation (anisodactyl, white; semizygodactyl, blue; fully zygodactyl, green; heterodactyl, black), with inferred transitions indicated on branches (S, transition to semizygodactyly; Z, transition to zygodactyly; −Z, loss of zygodactyly; H, transition to heterodactyly). Nodes recovered by the phylogenetic analysis but not represented in the reconstruction because of lack of data for fossil taxa are indicated with a slash. Trees and reconstructions from analyses using alternative taxon samples, constraints, and branch lengths are provided in *SI Appendix*.

indicative of semizygodactyly, specifically a grooved, wing-like flange extending from trochlea metatarsi IV and abbreviated proximal pedal phalanges. Semizygodactyl birds have the ability to facultatively reverse digit IV from a cranial direction to a more plantar or caudal direction, a conformation associated with arboreal climbing, as well as with grasping and manipulating objects. Given that Strigiformes, Coliiformes, and Leptosomiformes occupy sequential branches in many recent phylogenies, it would be reasonable to hypothesize that the common ancestor of these groups had a semizygodactyl foot. Indeed, semizygodactyly is reconstructed as the most likely ancestral condition at this node when only extant taxa are considered without branch length data (*SI Appendix*, Fig. S17). Surprisingly, paleontological data instead support a scenario in which semizygodactyly arises independently in Strigiformes, Coliiformes, and Leptosomiformes. This result is influenced by both branch length data and inclusion of the stem couroi *Plesiocathartes*, which lacks semizygodactyl modifications of the tarsometatarsus (40).

Counterintuitively, the fully zygodactyl Psittaciformes and Piciformes appear to share no close phylogenetic relationships with any of the three semizygodactyl clades. Embryologic studies provide evidence for a transitional relationship between the semizygodactyl and fully zygodactyl conditions: a wing-like flange similar to that observed in adult semizygodactyl birds acquires the hooked shape (Sehnenhalter) characteristic of fully zygodactyl birds during embryonic ontogeny (41). However, this intuitive transition from semizygodactyly to full zygodactyly is not observed in any of our ancestral state reconstructions. Psittaciformes nonetheless may have evolved from semizygodactyl ancestors, but this remains uncertain given the unresolved relationships of possible stem parrots, such as the extinct Vastanavidae and *Psittacopes* (35, 36). Interestingly, a complete loss of zygodactyly is supported in our results; crown Passeriformes are strongly supported as the sister taxon to the extinct, fully zygodactyl clade Zygodactylidae, in agreement with recent work (42), and our character state reconstructions are consistent with the previously hypothesized scenario in which songbirds and parrots share a fully zygodactyl ancestor, with subsequent reversion to an anisodactyl condition in the lineage leading to modern songbirds (41, 42). The numerous independent shifts in foot morphology inferred here reinforce our appreciation of the plasticity of digital conformation, which has been linked to

embryonic development and muscle activity (41, 43). These results emphasize how the fossil record may provide insight into a deep region of the avian tree that is opaque to detection by methods that sample only extant taxa, given the major morphological disparity between many stem fossils and their extant relatives.

Tsidiiyazhi provides compelling evidence that less than 4 million years after the K–Pg mass extinction, most (and even possibly all) of the deep phylogenetic divergences in crown birds had already occurred, as had the evolution of specializations such as semizygodactyly and associated diverse ecologies. Extant mousebirds are largely frugivorous, with early members of Coliiformes (e.g., the sandcoleid *Eoglaucidium*) known to have consumed fruits and/or seeds (22). The emerging consensus on neoavian phylogeny suggests a rapid radiation of mousebirds and their relatives, including the largely nocturnal carnivorous owls and a great diversity of insectivorous, herbivorous, and omnivorous members of Telluraves. Although seed consumption is known among archaic Cretaceous birds

(44), it is likely that the diversification of angiosperms in the Paleocene provided both the arboreal habitat and abundant food resources (e.g., fruits and plant-associated insects) to fuel this broader radiation of crown group birds (45). The presence of a stem mousebird in the early Paleocene hints that the origins of not just the morphological specializations among Neoaves, but also the dietary breadth and ecological variation present within this diverse clade, had their origins early in neoavian evolutionary history.

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