Report

Gradual Assembly of Avian Body Plan Culminated in Rapid Rates of Evolution across the Dinosaur-Bird Transition

Stephen L. Brusatte,[1,*] Graeme T. Lloyd,[2] Steve C. Wang,[3] and Mark A. Norell[4]
[1]School of GeoSciences, University of Edinburgh, Edinburgh EH9 3JW, UK
[2]Department of Earth Sciences, University of Oxford, Oxford OX1 3AN, UK
[3]Department of Mathematics and Statistics, Swarthmore College, Swarthmore, PA 19081, USA
[4]Division of Paleontology, American Museum of Natural History, New York, NY 10024, USA

Summary

The evolution of birds from theropod dinosaurs was one of the great evolutionary transitions in the history of life [1–22]. The macroevolutionary tempo and mode of this transition is poorly studied, which is surprising because it may offer key insight into major questions in evolutionary biology, particularly whether the origins of evolutionary novelties or new ecological opportunities are associated with unusually elevated "bursts" of evolution [23, 24]. We present a comprehensive phylogeny placing birds within the context of theropod evolution and quantify rates of morphological evolution and changes in overall morphological disparity across the dinosaur-bird transition. Birds evolved significantly faster than other theropods, but they are indistinguishable from their closest relatives in morphospace. Our results demonstrate that the rise of birds was a complex process: birds are a continuum of millions of years of theropod evolution, and there was no great jump between nonbirds and birds in morphospace, but once the avian body plan was gradually assembled, birds experienced an early burst of rapid anatomical evolution. This suggests that high rates of morphological evolution after the development of a novel body plan may be a common feature of macroevolution, as first hypothesized by G.G. Simpson more than 60 years ago [25].

Results

The fossil record provides unique insight into major evolutionary transitions: the origins of entirely new body plans and behaviors. In one of the great transitions in the history of life, bipedal carnivorous theropod dinosaurs evolved feathers and wings [1, 2], dramatically reduced their body size [3–6], and gave rise to birds. The dinosaur-bird transition is captured by a rich fossil record that has expanded tremendously in recent years—including thousands of feathered dinosaur specimens from northeastern China found over the past two decades [2]—providing an unparalleled opportunity to dissect a major morphological, behavioral, and paleobiological transformation in deep time. In particular, the dinosaur-bird transition can provide key insight into major questions in contemporary evolutionary biology, particularly whether the origins of evolutionary novelties or new ecological opportunities are

associated with unusually elevated "bursts" of evolution [23, 24]. This hypothesis was first articulated by George Gaylord Simpson in the 1940s [25] and has been the subject of intense debate ever since.

Phylogenetic Analysis

Birds are members of the theropod dinosaur subgroup Coelurosauria, a diverse clade that includes tyrannosauroids and dromaeosaurids, among others [7–14]. Our comprehensive, new phylogenetic analysis is a species-level analysis that includes nearly all Mesozoic coelurosaurs that are known from well-preserved and diagnostic fossils available for study. It is the latest iteration of the Theropod Working Group (TWiG) project, a 20-year program centered at the American Museum of Natural History that has been building progressively larger and more inclusive data sets of coelurosaurian phylogeny based on personal study of specimens. Previous TWiG analyses have focused extensively on the most derived paravian coelurosaurs: birds (technically known as avialans) and their very closest relatives, such as dromaeosaurids and troodontids [8, 9]. Here, for the first time, we incorporate a broad range of more basal (nonparavian) coelurosaurs into a TWiG analysis. Our data set includes 150 coelurosaurs scored for 853 characters, approximately twice the size of previous TWiG data sets (Supplemental Experimental Procedures available online).

Our phylogenetic analysis places birds within the broader framework of theropod evolution (Figure 1; see also Figures S1 and S2). Tyrannosauroids are the most basal major coelurosaurian subgroup; therizinosauroids and alvarezsauroids form a clade with oviraptorosaurs and paravians exclusive of more basal coelurosaurs; therizinosauroids and oviraptorosaurs are not sister taxa; and, for the first time, a TWiG analysis recovers a polytomy between avialans, dromaeosaurids, and troodontids, meaning that the immediate relative of birds cannot be clearly identified. The recently described *Aurornis*, *Xiaotingia*, and *Anchiornis* comprise a clade of basal troodontids, not avialans, as recently proposed [14]. The iconic *Archaeopteryx* is positioned as the basal-most avialan taxon, a "traditional" placement that is in agreement with most previous studies [8–10], not as a closer relative of dromaeosaurids, as was found in a recent series of analyses [11, 12].

Morphological Rates

The anatomical characters compiled for the phylogenetic analysis provide a ready source of data for examining trends in anatomical evolution across the dinosaur-bird transition. Because our data set includes features from throughout the skeleton, it can encapsulate changes in overall anatomy and document the evolution of the entire avian body plan. It complements recent analyses focused on more specific features, such as body size [3–6, 22] and limb measurements [19–21].

Maximum-likelihood analyses of rates of character evolution on the phylogeny, which test whether individual branches or entire clades have significantly different rates than the remainder of the tree [26, 27], identify high rates in birds (avialans) and the internal branches leading toward birds (Figure 2; see also Figure S3). High rates in birds are consistently found under a variety of conditions: in different most-parsimonious
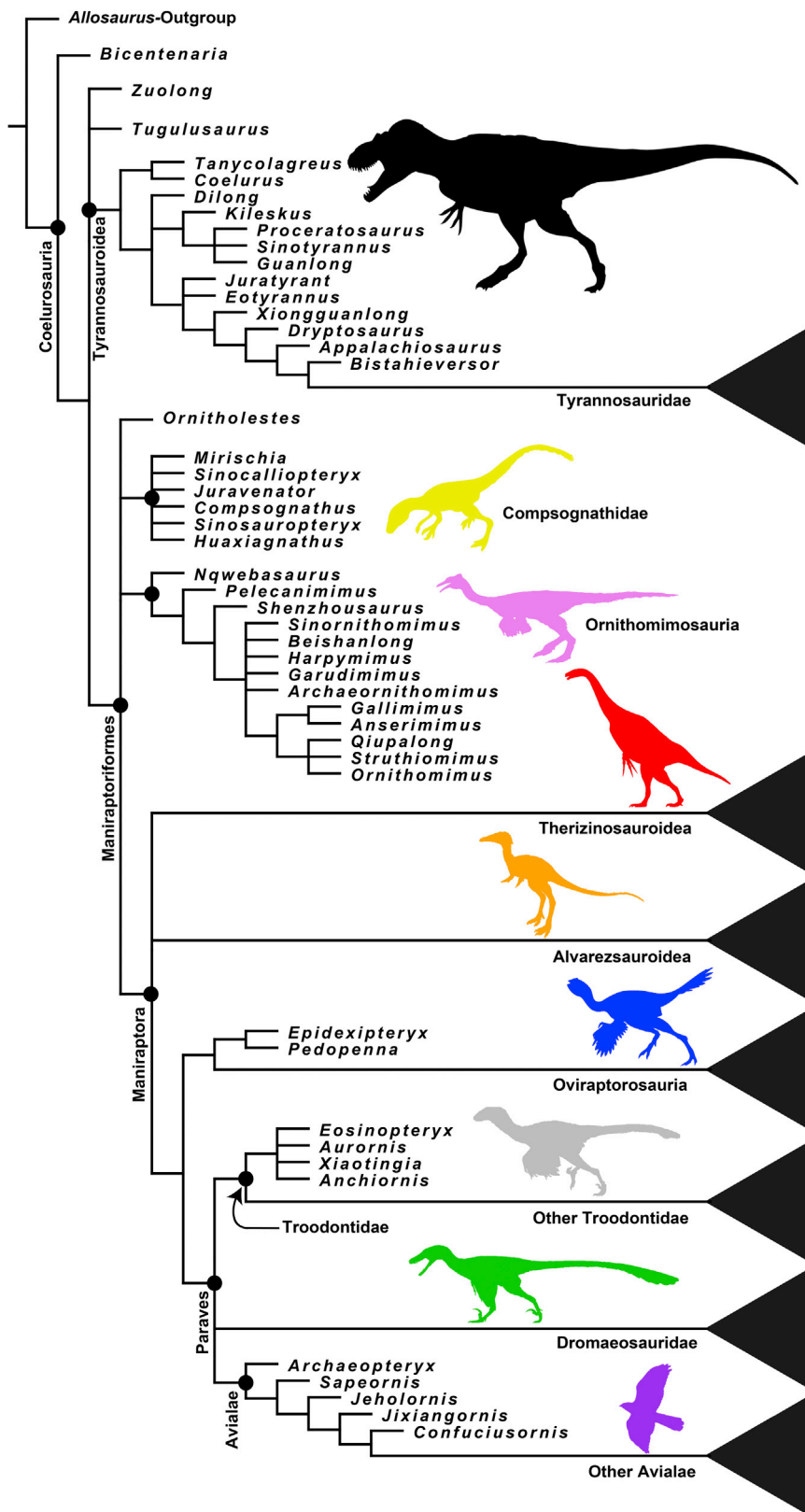
*Correspondence: stephen.brusatte@ed.ac.uk

Figure 1. Phylogenetic Relationships of Coelurosaurian Theropods Based on a Data Set of 152 Taxa Scored for 853 Characters

Strict consensus tree of 99,999 most-parsimonious trees (3,360 steps, consistency index = 0.322, retention index = 0.777). Silhouettes are from http://phylopic.org/. See also Figures S1 and S2 for the full strict reduced consensus tree.

Experimental Procedures and http://dx.doi.org/10.5061/dryad.84t75). This provides robust evidence that birds (and their stem lineage) evolved faster than other theropods and that their origin was associated with an "early burst" of rapid morphological evolution. Previous studies have found significant changes in body size and limb morphology either progressively prior to the origin of birds or within more derived birds [3, 5, 6, 19, 20, 22], but our analysis of the overall phenotype puts the major rate shift at the origin of Avialae itself.

High rates are also common among tyrannosauroids, the only major coelurosaurian subgroup to evolve colossal size (5 tons or more in mass). If genuine, this may suggest that dinosaurs developed gigantism by accelerating rates of morphological evolution, perhaps incongruous with a recent finding that large theropods had slower rates of proportional body size evolution than smaller lineages [6]. However, the high tyrannosauroid rates appear to be artifactual, probably caused by an overinflation of taxa and characters in the data set relevant to these iconic and well-studied theropods. First, high tyrannosauroid rates are not seen in all iterations (based on different branch durations) of the primary analysis, and in some iterations, significantly low rates are recovered. Second, the high tyrannosauroid rates disappear in many of our sensitivity analyses (Supplemental Experimental Procedures and http://dx.doi.org/10.5061/dryad.84t75). This is not the case with the high rates in birds, as these are seen in all branch dating iterations and persist in all sensitivity analyses.

Disparity and Morphospace Occupation

When the character data set is used to calculate disparity, by ordinating all taxa in a morphospace depicting the spread of morphological variability among coelurosaurs [28], there is no firm evidence that birds group separately from other species or have greater disparity than other coelurosaur groups (Figure 3; Tables S1–S3). Although there is separation

trees (MPTs), using different branch dating techniques, when terminal and internal branches are tested separately, and when the phylogeny is subsampled down to a common number of species in each major subgroup (Supplemental
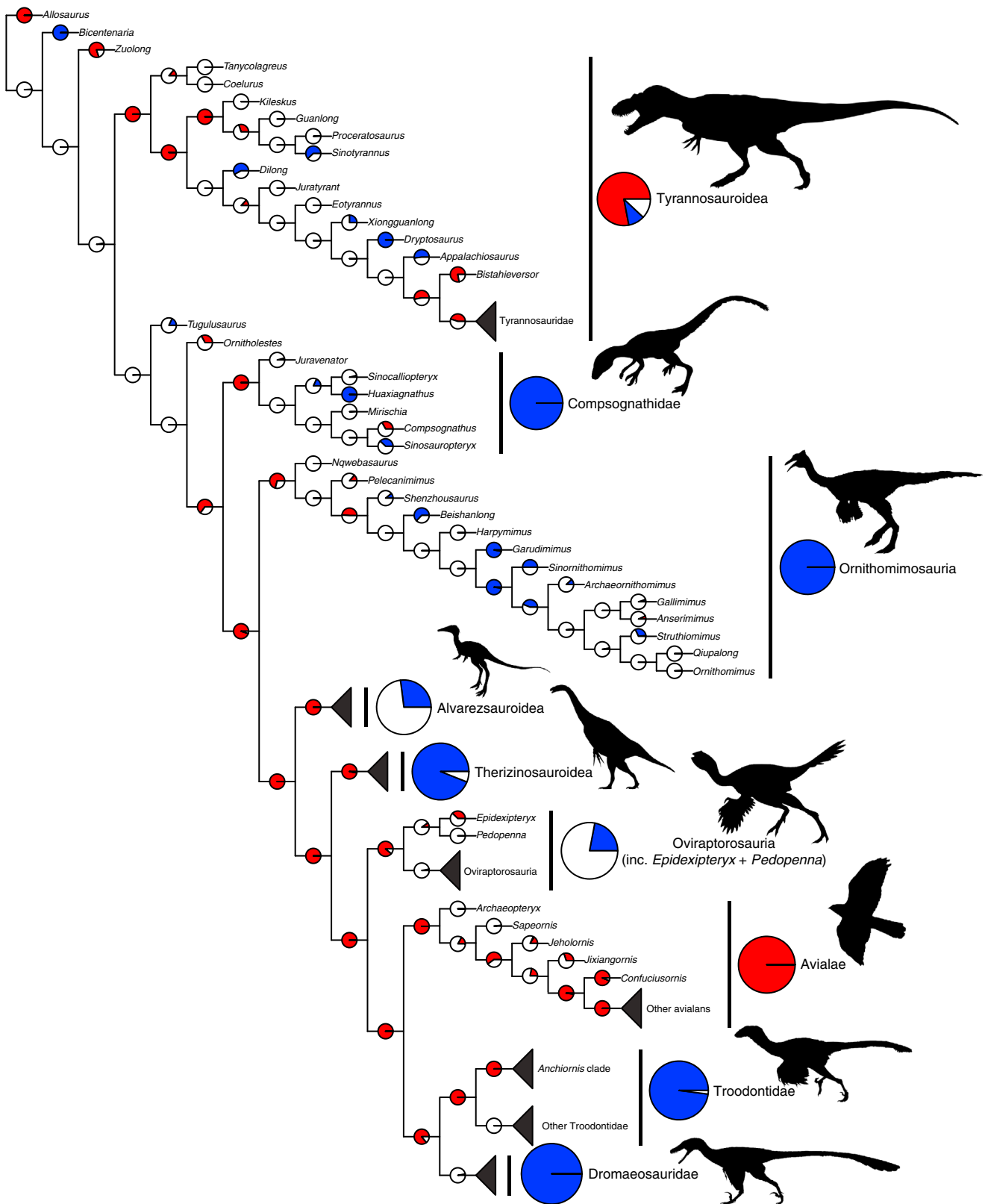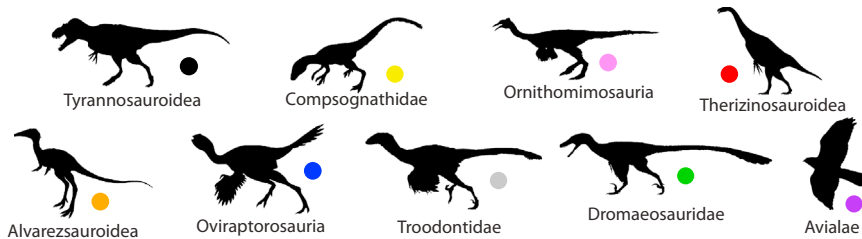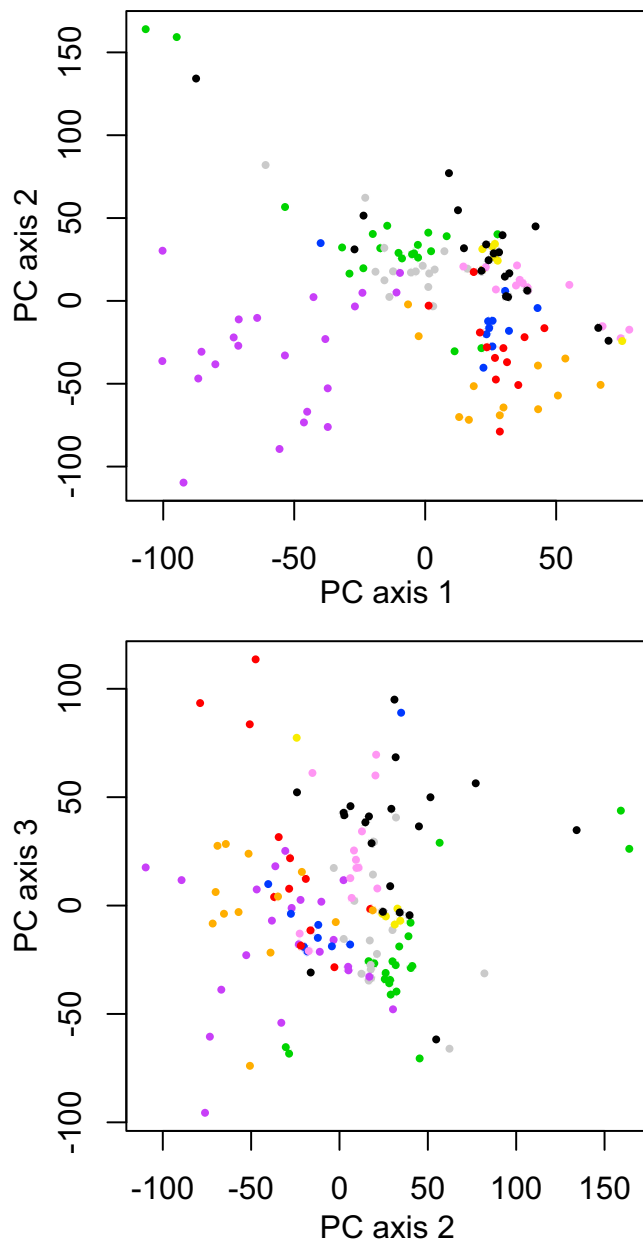
Figure 2. Summary of Results of Two Rate Tests on the First of Ten Randomly Sampled Most-Parsimonious Trees

Clades are collapsed as in Figure 1, with the full tree and all per-branch and clade rate results shown at http://dx.doi.org/10.5061/dryad.84t75. Pie charts along individual branches indicate the proportion of significantly high (red), significantly low (blue), and nonsignificant (white) per-branch rates based on 100 replicates to take into account dating uncertainty. Results for the clade test are shown for the nine major subclades, with the larger pie charts indicating the proportion of high, low, and nonsignificant rates across 100 replicates of dating uncertainty, using the same color scheme. Silhouettes are from http://phylopic.org/. See also Figure S3 for the full clade rate results on our primary tree.

Figure 3. Discrete Character Morphospace of Coelurosaurian Theropods, Depicting the Overall Anatomical Variability of Species

Bivariate plots of principal coordinate axes 2 versus 1 and 3 versus 2 are shown (axes 1–3 account for 4.25% of total variance). Birds are largely distinct from other coelurosaurs on principal coordinate axis 1, but not on axis 2 or 3 (or all subsequent axes). Permutation tests indicate that there is no clear, significant separation between birds and their closest relatives among theropods (Tables S1–S3; Supplemental Experimental Procedures).

demonstrates, for example, that birds and dromaeosaurids are less distinct from each other than are therizinosauroids and oviraptorosaurs, one of the significant comparisons. In other words, birds are not a notable outlier when placed in the context of the entire coelurosaur morphospace. Although birds are clearly distinct compared to all other living vertebrates, the avian bauplan isn't especially distinct relative to other coelurosaurs, particularly their closest relatives.

These results are consistent with many recent phylogenetic studies, ours included (see "Phylogenetic Analysis" in the Results), which find few characters separating Avialae from nonavialan theropods. These results may also help explain why so many alternative phylogenetic analyses have difficulty in placing certain taxa (such as *Anchiornis* and *Archaeopteryx*) consistently in either Avialae or among the clades of nonavialan theropods most closely related to birds [7–14].

Discussion

The rate and disparity results presented here paint a complex picture of the dinosaur-bird transition and the early evolution of birds. In general anatomical terms, birds are a continuum of millions of years of theropod evolution. There is no great jump between nonbirds and birds in morphospace. Instead, those features that today combine to set birds apart from other vertebrates—feathers, wishbones, air sacs, and hundreds more—evolved piecemeal in Mesozoic theropods [18]. Therefore, we surmise that a Mesozoic naturalist would make no immediate distinction between a *Velociraptor*-type animal and an *Archaeopteryx*-type animal. That said, there is an increased rate of morphological evolution associated with the origin of birds, beginning in the stem lineage leading toward birds and continuing throughout most of the avialan portion of Mesozoic coelurosaur phylogeny. This rate does not correspond to a major shift in morphospace occupation, so it does not reflect

of birds and other coelurosaurs on the first principal coordinate axis (which explains only a small portion of overall variance), there is wide overlap on all other axes. Permutation tests, which assess whether the morphospace means of two groups significantly differ from each other over all axes, find birds to be indistinct from their closest paravian relatives (Tables S1 and S2; Supplemental Experimental Procedures). Pairwise comparisons between other coelurosaur subgroups are also generally insignificant, but a few are significant. This

the sudden and simultaneous acquisition of a distinct avian body plan. Instead, it suggests that birds evolved their distinctive features gradually and that once the classic bird-like skeleton was assembled, something was unlocked that allowed birds to evolve rapidly within their fairly indistinct area of morphospace.

There is growing evidence that changes in discrete character evolution, body size, and limb anatomy occurred quickly in the vicinity of the origin of birds, either at the node Avialae, in close avialan outgroups, or beginning with slightly more derived birds [3–6, 19–22]. It is likely that different types of data will pinpoint changes at slightly different positions on phylogeny, but in general, recent studies converge in identifying the dinosaur-bird transition as an abnormally rapid period of morphological evolution. We hypothesize that high rates of morphological change after the development of a novel body plan, whether that development is sudden or gradual, may be a common feature of macroevolution. This is generally consistent with Simpson's theory of adaptive radiations and quantum evolution [25] and a recent study that identified high morphological rates in Cambrian arthropods, after their characteristic bauplans were assembled [29]. It is also consistent with recent studies that found high rates of morphological evolution during the early history of lungfish [27], tetrapods [30], and archosaurs (the larger group containing dinosaurs and crocodiles) [31]. Although such "early bursts" are rarely found in analysis of neontological data [23], improved methods [6, 24, 27] and the deep-time perspective of a good fossil record may show that they are a major driver of evolution and biodiversity.

Experimental Procedures

Phylogenetic Analysis

The phylogenetic analysis includes 152 taxa scored for 853 discrete characters. The analysis is the latest and most inclusive version of the American Museum of Natural History's TWiG data set. This data set has grown iteratively over the past 15 years with the addition of new taxa and characters [8, 9]. The focus of previous TWiG analyses has been paravian theropods (avialans, dromaeosaurids, and troodontids), reflecting long-standing interest in the origin of birds and the relationships of birds and their closest dinosaurian relatives. We added a wealth of new data relevant to nonparavian coelurosaurs, particularly nonmaniraptoran "basal" coelurosaurs (tyrannosauroids, ornithomimosaurs, compsognathids, and singleton taxa). Compared to the most recent TWiG data set [9], this analysis includes 41 new taxa and 379 new characters. As a result, the analysis presented here includes a nearly complete sample of Mesozoic coelurosaurs that have been available to us for personal study. The new taxa include a nearly complete sample of "basal" coelurosaurs and the recently described paravians *Eosinopteryx* [32] and *Aurornis* [14], which are particularly close relatives of birds. The new characters include a number of novel characters pertinent to "basal" coelurosaurs, characters relevant to the ingroup relationships of tyrannosauroids that were previously published by our research group [33], and characters from recent phylogenetic analyses of nonparavian coelurosaur subgroups [34–37]. The character list and data set are provided at http://dx.doi.org/10.5061/dryad.84t75.

The phylogenetic data set was analyzed with equally weighted parsimony in TNT v 1.1 [38]. *Allosaurus* was used as the outgroup to root the tree. The data set was first analyzed under the "New Technology" search options, using sectorial search, ratchet, tree drift, and tree fuse options with default parameters. The minimum length tree was found in ten replicates, a procedure that aims to initially sample as many tree islands as possible. The generated MPTs were then analyzed under traditional tree bisection and reconnection branch swapping, a procedure that aims to more fully explore each tree island. Clade support was assessed via decay indices and jackknife resampling analysis.

Morphological Rates

Rates of discrete character morphological evolution in a phylogenetic context were assessed using likelihood tests conducted in R [27]. The first

of these asks whether an individual branch has a significantly higher or lower rate of evolution than the rest of the tree, and the second asks whether a particular clade has a significantly higher or lower rate than the remainder of the tree. Only Mesozoic coelurosaurs were included in these analyses, which utilized the 853-character discrete data set from the phylogenetic analysis. For each analysis, the tree was time scaled before characters were optimized, using the "equal" branch scaling measure based on the absolute ages of the terminal taxa [31, 39]. After time scaling, ancestral character states were estimated using the likelihood-based rerooting function in the R package phytools [40], which in turn allows the total number of changes along each branch to be recorded. Per-branch rates were calculated based on the total number of changes along the branch, with a correction for missing data, divided by the time duration of the branch [27]. Multiple replicates were used to take into account uncertainty in branch durations, based on uncertainty in the ages of the terminal taxa. Likelihood was then used to assess which branches and clades had higher or lower rates than the rest of the tree, following the protocols of [27].

For our primary analysis, we randomly selected a single MPT and applied the per-branch and per-clade tests using 100 replicates. We followed this with a number of sensitivity tests to gauge how robust the recovered patterns were. The first of these involved randomly selecting nine other MPTs to assess how differences in tree topology affect the rate results. The second examined the effects of different time-scaling algorithms by using a different option, the minimum-branch-length method [39]. The third tested for rate heterogeneity on a tree where branches were scaled to a unit length, to gauge how much of the rate results could be explained solely by the amount of character change (not branch duration). The fourth examined the effect of the number of sampled taxa in each major clade by randomly removing taxa from Alvarezsauroidea, Avialae, Compsognathidae, Dromaeosauridae, Ornithomimosauria, Oviraptorosauria, Therizinosauria, Troodontidae, and Tyrannosauroidea until each one was the same sample size (set at six species, based on the smallest clade, the compsognathids). Finally, the fifth tested for potential bias in rate between terminal and internal branches (such as that due to the lack of sampled autapomorhies) by separating the two branch types and repeating the per-branch and per-clade tests.

Disparity and Morphospace Occupation

In order the test the morphological "distinctiveness" of birds relative to other theropods, we plotted all coelurosaurs in our data set into a multivariate morphospace, which represents the spread of anatomical form in a group [28]. This morphospace is nonphylogenetic (phenetic) in nature and only denotes the total spread of morphological variation in coelurosaurs without any indication of the speed at which this variation accumulates, making our morphospace-based tests distinct from our rate-based tests above. The morphospace was constructed by deriving a Euclidean distance matrix from our 853-character discrete data set, which was then subjected to principal coordinates analysis (PCO; equivalent to multidimensional scaling), a multivariate ordination technique that summarizes information from the distance matrix into a smaller and more manageable set of coordinate axes. The first axis represents those character distances contributing most to the overall variability among coelurosaurs, and each additional axis represents distances of progressively less significance. Each coelurosaur has a score on each axis, which together represent aspects of the overall anatomical form for each taxon.

The "distinctiveness" of avialans relative to other coelurosaurs was tested in three ways. First, we used permutation tests to perform pairwise comparisons of group means in R and PAST [41]. These comparisons tested the equality of multivariate means (based on the 125 recovered PCO axes, which comprise 90% of total variance) of two designated groups (for example, avialans versus deinonychosaurs). The Mahalanobis distance between the two group means was calculated and compared with a null distribution of between-group distances obtained by random permutation of the group labels. Second, we compared Euclidean distances between avialans and their closest relatives (dromaeosaurids and troodontids) with Euclidean distances between several control pairs of coelurosaurian groups that are sister taxa or particularly close relatives. This served to assess whether birds are more distant from their closest relatives in morphospace than are various other pairwise groups of close relatives. The means and distributions of distances for the avialans versus close relative comparisons and the various other coelurosaur close relative comparisons were assessed for statistical significance with t tests and Mann-Whitney-Wilcoxon tests. Third, we tested whether avialans occupied a larger volume of morphospace than other coelurosaurs by calculating four disparity metrics for

the various coelurosaur subgroups (sum and product of the ranges and variances on the PCO axes). These disparity metrics quantify how much morphospace avialans and the other groups occupy. Differences in the disparity metrics between avialans and other coelurosaur groups were tested for significance with a permutation test.

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