

# Anomalously high variation in postnatal development is ancestral for dinosaurs but lost in birds

Christopher T. Griffin<sup>a,1</sup> and Sterling J. Nesbitt<sup>a</sup>

<sup>a</sup>Department of Geosciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061

Edited by Neil H. Shubin, The University of Chicago, Chicago, IL, and approved November 3, 2016 (received for review August 19, 2016)

Compared with all other living reptiles, birds grow extremely fast and possess unusually low levels of intraspecific variation during postnatal development. It is now clear that birds inherited their high rates of growth from their dinosaurian ancestors, but the origin of the avian condition of low variation during development is poorly constrained. The most well-understood growth trajectories of later Mesozoic theropods (e.g., *Tyrannosaurus*, *Allosaurus*) show similarly low variation to birds, contrasting with higher variation in extant crocodylians. Here, we show that deep within Dinosauria, among the earliest-diverging dinosaurs, anomalously high intraspecific variation is widespread but then is lost in more derived theropods. This style of development is ancestral for dinosaurs and their closest relatives, and, surprisingly, this level of variation is far higher than in living crocodylians. Among early dinosaurs, this variation is widespread across Pangaea in the Triassic and Early Jurassic, and among early-diverging theropods (ceratosaurs), this variation is maintained for 165 million years to the end of the Cretaceous. Because the Late Triassic environment across Pangaea was volatile and heterogeneous, this variation may have contributed to the rise of dinosaurian dominance through the end of the Triassic Period.

ontogeny | variation | dinosaur | Triassic | extinction

In comparison with other reptiles, avian biology is highly unusual, characterized by “hollow” bones and postcranial skeletal pneumaticity, feathers, a unique forelimb digit formula, endothermy, and rapid growth rates. However, these peculiarities initially arose in nonavian dinosaurs (1–7) in a gradual process occurring over tens of millions of years (8, 9). In addition to their extremely rapid rates of growth, avian ontogeny possesses a characteristically low level of morphological variation within a species relative to that of other reptiles. The majority of individuals in a given avian species undergoes the same morphological changes during ontogeny in the same order at similar body sizes (10, 11), whereas their closest living relatives, crocodylians, possess higher variation (10, 12–14). How and when this feature of avian biology evolved is poorly constrained.

This avian style of development must have evolved after its most recent common ancestor with crocodylians but before the origin of Aves. Most studies of the ontogeny of more-derived theropods (15–17) suggest that the low levels of variation that characterize avian ontogeny were present in close nonavian relatives as well. Closer to the origin of Dinosauria, morphological variation within species is widespread (18–26), but whether this variation is the result of taxonomic diversity, ontogeny, sexual dimorphism, or simple individual variation is not clear (22, 23, 27). Furthermore, close dinosaurian relatives or “dinosaur precursors” (e.g., *Silesaurus*, *Asilisaurus*) possess high intraspecific variation in growth sequences [i.e., sequence polymorphism (28)], suggesting that this condition could be ancestral for Dinosauria (21).

In contrast to most of the early dinosaurian record, which rarely preserves greater than a single individual per species (29, 30), the theropod *Coelophysis bauri* is known from the most well-sampled growth series of any nonavian dinosaur preserved as a single population in the same horizon (31). We used this taxon as a lens to interpret development among early dinosaurs, with additional support from another early dinosaur with a well-sampled growth series, *Megapnosaurus rhodesiensis* (24). We used ontogenetic

sequence analysis (OSA) (32) to reconstruct growth sequences of these early dinosaurs, two avian species (*Branta canadensis* and *Meleagris gallopavo*), and a single crocodylian species (*Alligator mississippiensis*), and demonstrate that the earliest dinosaurs developed differently than living archosaurs.

## Results

Our OSAs indicate that both *C. bauri* and *M. rhodesiensis* possessed a high level of intraspecific variation, both in sequence polymorphism and in body size at different levels of morphological maturity (Figs. 1 and 2). Analysis of the 27 ontogenetic characters for *C. bauri* reconstructed 136 equally parsimonious developmental sequences (Fig. 1 and *SI Appendix*, Fig. S4), with the modal sequence representing only 12.57% the support weight of all semaphoronts [unique suites of developmental characters, modified from (33)]. Because of missing data, many sequences were highly unresolved, and so this number of sequences is a lower bound for the amount of variation in the sample during life. OSA for the 10 femoral ontogenetic characters of *C. bauri* resulted in 82 developmental sequences (Fig. 24 and *SI Appendix*, Fig. S7), and for *M. rhodesiensis*, 145 developmental sequences (Fig. 2B and *SI Appendix*, Fig. S8) were reconstructed for 13 femoral characters.

In contrast, the extant birds possess low levels of intraspecific variation relative to early theropods, consistent with other studies (10, 11). The OSA of 36 ontogenetic characters of *B. canadensis* returned 9 equally parsimonious developmental sequences (Fig. 3A and *SI Appendix*, Fig. S9), with a modal sequence possessing 87.22% of the support weight of all semaphoronts combined. The femoral characters in this dataset were poorly resolved, but OSA of the dataset of Tumarkin-Deratzian et al. (11) of 18 femoral characters of *B. canadensis* showed similarly low variation, returning 12 sequences (Fig. 3B and *SI Appendix*, Fig. S10) and a modal sequence consisting of 92% of all combined

## Significance

**Birds—the fastest growing terrestrial vertebrates—develop unlike all other living reptiles. As part of this postnatal developmental mode, birds possess a low amount of intraspecific variation, and the timing of the origin of this low variation is poorly constrained. By studying well-sampled growth series of nonavian dinosaurs and their closest relatives, we were able to identify this transition within Mesozoic theropod dinosaurs. Surprisingly, the earliest dinosaurs and their close relatives possessed an extremely high amount of variation, higher than either crocodylians or birds. This high variation is the ancestral dinosaurian scheme and was lost in more derived nonavian theropods, including *Allosaurus* and *Tyrannosaurus*. High variation could have contributed to the rise of dinosaurian dominance during the Triassic–Jurassic mass extinction.**

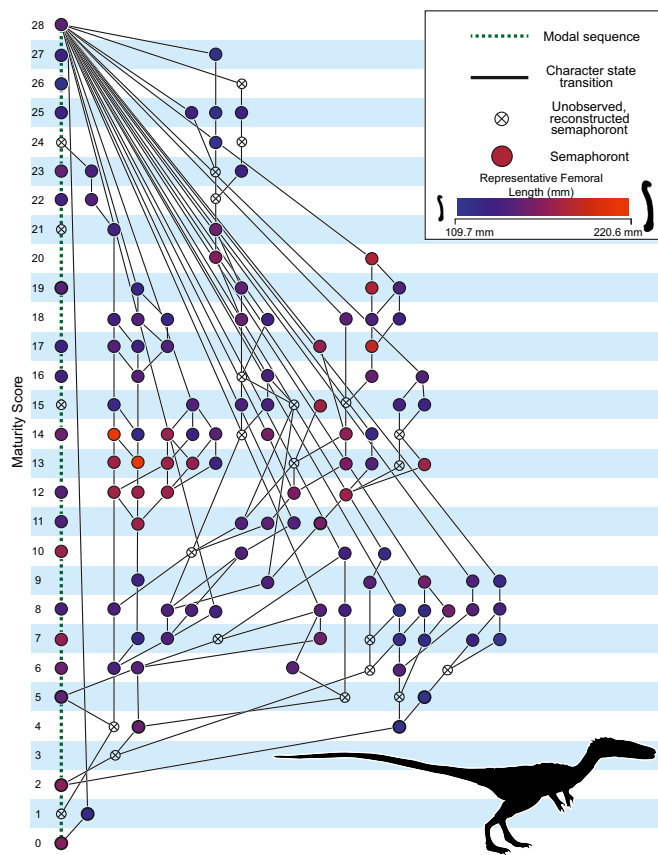
Author contributions: C.T.G. and S.J.N. designed research; C.T.G. performed research; C.T.G. analyzed data; and C.T.G. and S.J.N. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

<sup>1</sup>To whom correspondence should be addressed. Email: ctgriff@vt.edu.

This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1613813113/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1613813113/-DCSupplemental).



**Fig. 1.** OSA reticulating diagram illustrating the 136 reconstructed developmental sequences of the 27 ontogenetic characters of *C. bauri*. Maturity score (*Materials and Methods*) is displayed on the y axis, and semaphoronts lower on the diagram are less morphologically mature than those that are higher. The x axis is dimensionless. Sequences proceed from the least mature (maturity score: 0) to most mature (maturity score: 28) through other semaphoronts along each sequence. The representative femoral length of each semaphoront is indicated by color. See *SI Appendix, Supplementary Text* for details on interpreting OSA reticulating diagrams.

support weights. The OSA of 34 ontogenetic characters of *M. gallopavo* returned four developmental sequences (Fig. 3C and *SI Appendix, Fig. S11*), with the modal sequence possessing 90% of all combined semaphoront support weights.

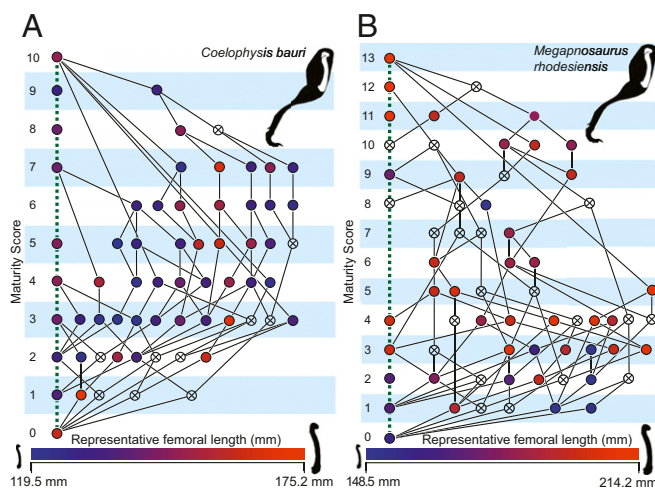
Our analyses of *A. mississippiensis* ontogeny suggested an intermediate level of variation in ontogeny that was lower than that of the early theropods but higher than the level of variation found in living birds. The OSA from Brochu’s postcranial dataset (12) of 22 ontogenetic characters of *A. mississippiensis* returned 234 sequences (Fig. 3D and *SI Appendix, Fig. S12*), with four partially overlapping modal sequences. The combined semaphoronts of all modal sequences possessed 50% of the total weight of all semaphoronts in the analysis. Our two analyses of femoral characters in *A. mississippiensis* reveal a similar trend. The OSA from Brochu’s dataset (12, 13) of 13 femoral characters returned only 3 sequences (Fig. 3E and *SI Appendix, Fig. S13*), with a single modal sequence that represented 85.7% of the combined weight of all semaphoronts in the analysis; and the OSA from the dataset of Tumarkin-Deratzian et al. (14) of 10 femoral characters returned 18 sequences (Fig. 3F and *SI Appendix, Fig. S14*), with a modal sequence representing 88.9% the weight of all semaphoronts.

### Discussion

Compared with birds, *C. bauri* and *M. rhodesiensis* possess a large amount of intraspecific variation, both in suites of character states and in size as related to morphological maturity. The

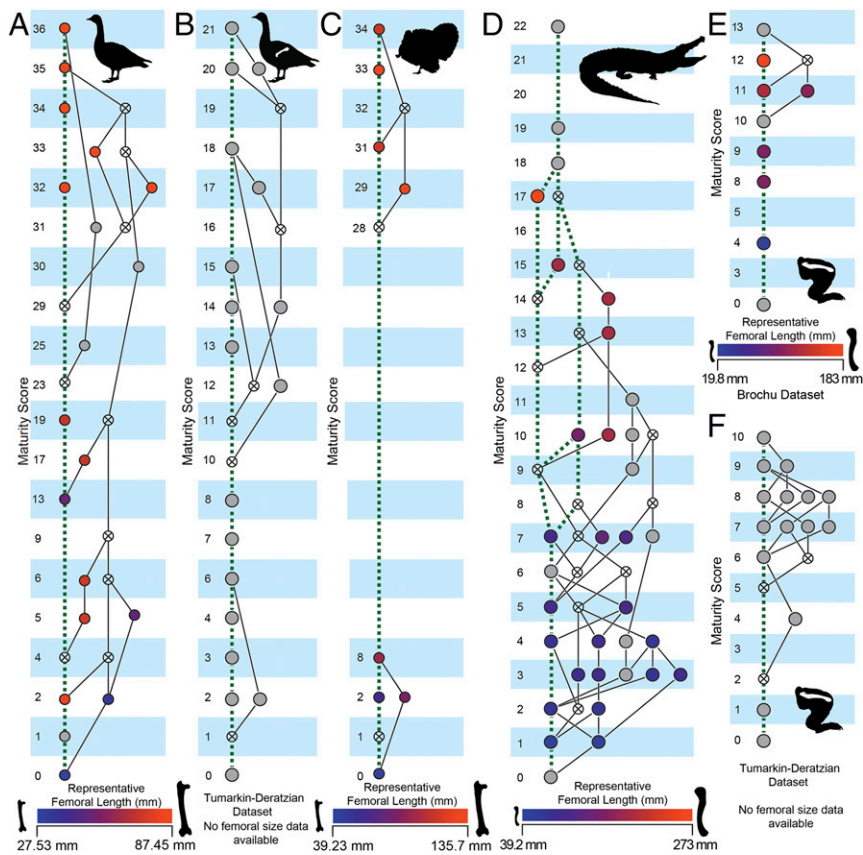
hypothesized mature states of these characters are not attained in a single ontogenetic step but are staggered in appearance in developmental sequences, along which individuals progress toward morphological maturity in a stepwise fashion. Instead of a single path of semaphoronts leading from the least to most mature, semaphoronts of both *M. rhodesiensis* and *C. bauri* are arranged along many developmental sequences (Figs. 1 and 2). Additionally, although size is often used as a proxy for degree of skeletal maturity in many studies (20, 24, 34–41), size correlates poorly with morphological maturity, as quantified by maturity score in OSA, even though OSA may reconstruct missing data as present and thus raise the maturity score higher than a strict scoring of the individual would give (Figs. 1 and 2). Therefore, skeletally mature individuals could possess a range of sizes. The large number of developmental pathways reconstructed by OSA suggests that sequence polymorphism is a widespread aspect of the postnatal development of these two early theropods. This variation has been interpreted as sexual dimorphism (e.g., ref. 24), but our data do not support this possibility (*SI Appendix, Supplementary Text and Fig. S1*). The large number of conflicting developmental pathways consisting of semaphoronts with suites of character states that preclude their belonging in other developmental pathways strongly suggests that variation in the relative order of these developmental characters is widespread throughout the populations of these early dinosaurs. Future histological analyses may help to determine whether this lack of correspondence between size and morphological maturity is an expression of how body size is related to ontogenetic age, and although these analyses are outside the scope of the current study, histological data were unhelpful in resolving this problem in silesaurids because of a lack of histological indicators of ontogenetic age in these taxa (21).

High levels of intraspecific variation are present in many early dinosaurs, particularly theropods. In addition to *Megapnosaurus* and *Coelophysis*, variation previously interpreted as a gracile/robust dichotomy and explicitly compared with the variation found in these taxa has a wide distribution among early-diverging theropods, including other early neotheropods [the “Shake-N-Bake” coelophysoid (42); “*Syntarsus kayentakatae*, *Dilophosaurus wetherilli* (26, 42, 43)], large ceratosaurs [*Ceratosaurus nasicornis* (44)], and small ceratosaurs [*Masiakasaurus knopfleri* (19, 27)]. Most of these studies have been limited to relatively small sample sizes because of a lack of specimens available (usually a maximum of



**Fig. 2.** OSA reticulating diagrams for femora of early theropods. (A) Diagram illustrating the 82 reconstructed developmental sequences of the 10 femoral ontogenetic characters of *C. bauri*. (B) Diagram illustrating the 145 reconstructed developmental sequences of the 13 femoral ontogenetic characters of *M. rhodesiensis*. Representative femoral length for each semaphoront is indicated by color. This figure follows the key in Fig. 1.





**Fig. 3.** OSA reticulating diagrams for extant archosaurs. (A) Diagram illustrating the 9 reconstructed developmental sequences of the 36 ontogenetic characters of *B. canadensis*. (B) Diagram illustrating the 12 reconstructed developmental sequences of the 18 femoral characters of *B. canadensis*. Data are from ref. 11. (C) Diagram illustrating the 4 reconstructed developmental sequences of the 34 ontogenetic characters of *M. gallopavo*. (D) Diagram illustrating the 234 reconstructed developmental sequences of 22 postcranium-wide ontogenetic characters of *A. mississippiensis*. Data are from ref. 12. (E) Diagram illustrating the 3 reconstructed developmental sequences of 13 femoral ontogenetic characters of *A. mississippiensis*. Data are from refs. 12 and 13. (F) Diagram illustrating the 18 reconstructed developmental sequences of 20 femoral ontogenetic characters of *A. mississippiensis*. Data are from ref. 14. Representative femoral length for each semaphoront is indicated by color. This figure follows the key in Fig. 1.

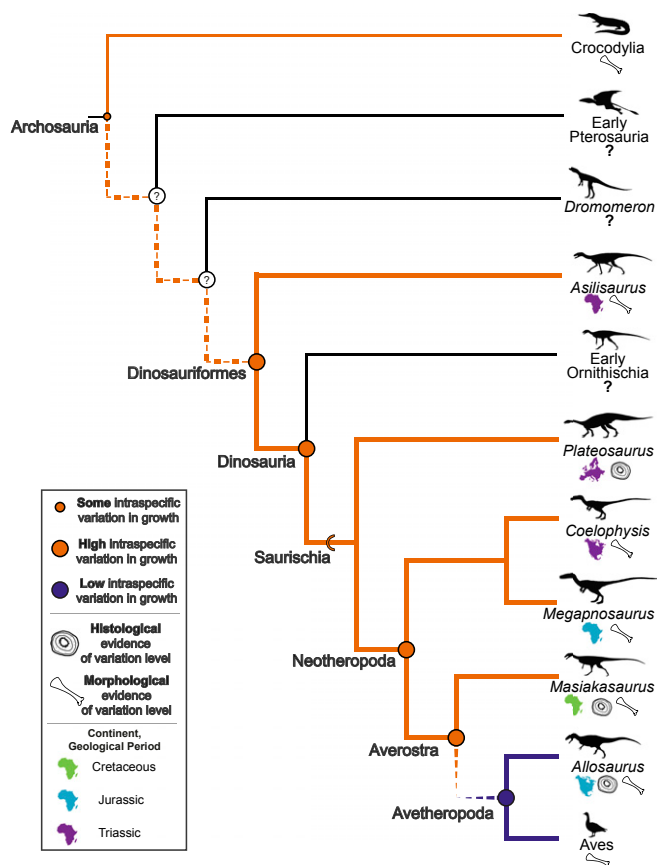
$n = 2-7$ ), with only a few (3–6) bone scars evaluated. Our results of analyses from large sample sizes of *Coelophysis* and *Megapnosaurus* ( $n = 174$  and 43, respectively) indicate that similar variation between individuals of early theropods is the result of a similarly high level of intraspecific variation in development.

Outside Dinosauria, *Silesaurus opolensis* and *Asilisaurus kongwe* possess variation in femoral scars not fully attributable to size. In the case of *Silesaurus*, this variation was interpreted as sexual dimorphism (23), following the earlier interpretation of variation in *Megapnosaurus* (24). *A. kongwe* possesses similar variation in femoral scars, but these exist on a spectrum and do not cleanly split into a clear robust/gracile dichotomy, although similarly sized femora may possess a variety of ontogenetic character states. Instead of sexual dimorphism, the variation in *A. kongwe* was interpreted as individual variation in developmental patterns that produced morphological differences between individuals (21).

These silesaurids and early-diverging theropods phylogenetically bracket Sauropodomorpha and Ornithischia; therefore, similar variation in early-diverging members of these groups should also be present, although the early ornithischian record is exceptionally poor (29). The Triassic sauropodomorphs *Thecodontosaurus antiquus* and *Melanorosaurus readi* have been interpreted as possessing robust/gracile variation in similarly sized limb elements (18, 45), but given our interpretation of a similar ostensible dichotomy in early theropods, these taxa probably possess similar levels of variation in growth patterns. As predicted by our results, along with some morphological variation in *Plateosaurus engelhardti* (46), histological analysis of a large sample of limb elements ( $n = 33$ ) of *Plateosaurus* demonstrated that size and histological maturity are poorly correlated in this taxon (22, 25). Given the wide distribution of this individual variation in ontogenetic patterns among early-diverging dinosaurs and their closest relatives, this observation suggests that this high variation in both developmental sequence and in body size at skeletal maturity is the ancestral dinosaurian condition (Fig. 4).

In contrast to that of early dinosaurs, the extant archosaurs in our study (*B. canadensis*, *M. gallopavo*, *A. mississippiensis*) showed lower levels of variation. The avian taxa analyzed possessed an extremely low number of reconstructed developmental sequences, with the majority of specimens represented by semaphoronts on the modal sequences (Fig. 3 A–C), and this level of variation is supported in other Aves (11). *A. mississippiensis* possessed a higher level of intraspecific variation than the birds, but this level was still at a far lower level than that of the early theropods analyzed (Fig. 3 D–F). This lack of variation in the OSA of extant birds may be partly the result of low resolution in the relative timing of some of the characters; because extant birds grow quickly, we were unable to control for the relative timing of several femoral developmental characters, and therefore the OSA reconstructed these femoral characters as maturing in the same developmental “leap.” However, our OSA of a higher-resolution dataset of *B. canadensis* femoral characters (11) showed predictably low variation (Fig. 3B). Given that variation in ontogeny, especially in size as correlated with skeletal maturity, appears to be muted or absent in more derived theropods including several tyrannosaurids (16, 17) and *Allosaurus fragilis* (15, 47–50) (SI Appendix, Supplementary Text and Figs. S2–S4), we suggest that this anomalously high level of individual variation in ontogenetic trends is absent from the clade Avetheropoda (Allosauroidea + Coelurosauria) and is constrained to early-diverging dinosaurs and their closest relatives (Fig. 4).

Although most vertebrate species possess some individual variation in development (32), this normal feature of populations appears to play an exaggerated role in early-diverging dinosauriforms. The specific cause(s) of this variation in ontogenetic patterns is difficult to test with the evidence available because the fossil record does not record most aspects of the life history of individuals (e.g., variation in diet, environmental stress experienced, or hormone levels). However, there is evidence available supporting the dominant cause as intrinsic or extrinsic,



**Fig. 4.** Intraspecific variation in ontogeny is exaggerated in early-diverging dinosauriforms and dinosaurs relative to *A. mississippiensis* and the ancestral archosaurian condition, regardless of period or geographic location, and is absent in more derived theropod dinosaurs, including birds.

or some combination of the two. Developmental plasticity, a change in development in response to environmental variables, is a common source of variation in development in extant reptiles including birds, and is usually interpreted as an expression of variation in nutrient acquisition (e.g., ref. 51). Therefore, developmental plasticity undoubtedly played at least some role in the ontogeny of early dinosaurs. However, the taxa that possess this variation occur across a wide temporal spread [from the Middle Triassic, *A. kongwe* (21), to the Late Cretaceous, *M. knopfleri* (27)], suggesting that this variation was not primarily influenced by external features typical of a certain period or stage (e.g., a more arid or humid environment). The large paleolatitudinal range [from tropical paleolatitudes (e.g., *Asilisaurus*, *Coelophysis*) to high paleolatitudes (e.g., *Megapnosaurus*, *Plateosaurus*)], and varied ecological niches of these taxa (ranging from small- to large-bodied herbivores and carnivores alike) also suggests that this high level of variation is not solely driven by a common environment or ecology shared by all taxa that possess this level of variation. Instead, phylogenetic location is most predictive of high intraspecific variation in development (Fig. 4), and therefore intrinsic factors played the major role in producing this variation in populations, with individuals in a population exposed to roughly similar environments still undergoing different ontogenetic patterns. With body size commonly suggested to be related to extinction risk (52), such a high level of variation within a species may be advantageous in an ecologically unstable environment as in the low latitudes of the Late Triassic (53) and during the extinction(s) that characterized the Late Triassic (54). Therefore, this anomalously high level of intraspecific variation may have contributed to the early success of dinosaurs relative to

many pseudosuchian clades in the latest Triassic and through the End-Triassic Mass Extinction into the Early Jurassic.

## Materials and Methods

**Collection of Ontogenetic Character Data.** We evaluated the state of 29 developmental characters, including 10 femoral characters, in 174 unique specimens of *C. bauri* (with 93 femora); 13 developmental characters in the femora of 43 specimens of *M. rhodesiensis*; 38 characters in 72 individuals of *B. canadensis*, the Canada Goose; and 36 characters in 26 individuals of *M. gallopavo*, the Wild Turkey (see *SI Appendix, Supplementary Text* for details on ontogenetic characters and discussion of potential bias in the *C. bauri* sample; see *SI Appendix, Tables S3–S6* for specimen scores for ontogenetic characters). Characters differ between taxa because differing ontogenetic characters are present in the postcranium of each species. However, these characters are largely bone scars and suture fusions, and are often formed from homologous structures (for example, fusion between the ilium and ischium occurs during ontogeny in all taxa analyzed, but this fusion is independently acquired in early-diverging theropods (26), *Alligator*, and birds), and so are comparable to each other for general ontogenetic trends although they are not all homologous. *B. canadensis* and *M. gallopavo* were chosen as representative taxa for modeling the growth of extant birds for: (i) their slow growth rate relative to many other birds, making the timing of ontogenetic characters more easily resolved; (ii) their phylogenetic position relatively close to the most recent common ancestor of crown group avians (the last common ancestor of paleognaths and neognaths); and (iii) their large numbers in North America, enabling easy access to skeletal growth series with large sample sizes. Because the relative sequence of many avian femoral characters was unresolved in our dataset (and therefore potentially artificially lowering the perceived level of variation), we also analyzed a dataset of femoral characters from 77 individuals of *B. canadensis* taken from Tumarkin-Deratzian et al. (11), most of which possessed redundant suites of character states, to test the level of variation in the sequence of these ontogenetic characters. We measured the maximum proximal/distal widths and maximum lengths of long bones, the anteroposterior widths of acetabula, and the lengths of sacra in *C. bauri* and *M. rhodesiensis* and measured maximum femoral length of both femora in *B. canadensis* and *M. gallopavo*. The specimens of *C. bauri* all were recovered from a single locality, the *Coelophysis* Quarry at Ghost Ranch, New Mexico (37); and all but three specimens of *M. rhodesiensis* come from a single locality near the Chitake River, Zimbabwe (24, 55). Although a taphonomic study has not been undertaken on the *M. rhodesiensis* localities, the *Coelophysis* Quarry is thought to have undergone almost no time averaging and represents individuals buried in only one to two events (31), making the time and geographic averaging on the *C. bauri* sample potentially less than that of the sample of *B. canadensis* and *M. gallopavo*, the skeletons of which do not represent individuals from a single population but were collected from wild populations across Illinois and Wisconsin, over a period of several decades (reposited in the Field Museum of Natural History). The specimens comprising the femoral dataset of *B. canadensis* were collected from wild populations across several northeastern and mid-Atlantic states (11).

The ontogenetic data for *A. mississippiensis* were obtained from published datasets. For the multielemental OSA, we used the postcranium-wide matrix of 22 skeletal characters from Brochu (12); and for the femoral analyses, we included a matrix of 13 femoral characters from Brochu (12, 13) and a matrix of 10 femoral characters from Tumarkin-Deratzian et al. (14). Although these *Alligator* data were originally collected for a method similar to OSA called cladistic ontogeny (12–14) (see *SI Appendix, Supplementary Text* for comparison of OSA and cladistic ontogeny), the characters are skeletal features that appear during ontogeny and are therefore comparable to the characters scored here for early theropods and extant birds. Brochu's (12) postcranium-wide dataset includes 22 semaphoronts (with four redundant specimens eliminated by our methods; see below), and Brochu's (12, 13) femoral dataset included 8 semaphoronts. However, those datasets were compiled by scoring character states of over 100 specimens and then eliminating redundant specimens. Although the number of individual specimens originally scored was not recorded, skeletal measurements of 125 *A. mississippiensis* specimens were reported. Therefore, the low number of individuals reported in these datasets does not accurately represent the number of individuals for which data were collected, because most individuals (>100) possess redundant suites of characters. Tumarkin-Deratzian et al. (14) scored femoral characters for 109 specimens, but the majority of those possessed redundant character states. The large sample sizes of individuals of *A. mississippiensis* used in those studies makes us confident that the results of our analyses accurately reflect the level of variation in this taxon. Because Tumarkin-Deratzian et al. (14) did not report femoral lengths

of specimens, we were unable to determine how skeletal maturity related to femoral length for the analysis of that dataset. The specimens from ref. 12–14 were collected from wild populations from Florida and Louisiana. We did not incorporate early-diverging pseudosuchian taxa into our study because growth series for early pseudosuchians are rare, and a sample large enough to test the presence of intraspecific variation among individuals of early pseudosuchians is not available. Additionally, intraspecific variation similar to that seen in early dinosauromorphs has not been reported for early pseudosuchians. The derived pseudosuchian *A. mississippiensis*, along with other extant crocodylians (12, 13), is known from excellent growth series for which ontogenetically variable skeletal characters are well understood, and we used these data to provide insight into the level of intraspecific variation among pseudosuchian archosaurs. See [Datasets 1–9](#) for NEXUS files of individuals used in OSA, and [Datasets 10–13](#) for femoral measurement data.

**Reconstructing Developmental Patterns and Quantifying Variation.** OSA is a parsimony-based, size-independent method of reconstructing all equally parsimonious developmental sequences of discrete ontogenetic character changes in a population and will therefore reconstruct multiple developmental sequences when sequence polymorphism is present in that population.

OSA has normally been used to understand variation and development in extant organisms (32, 56–60), with only a few previously published studies using this method in extinct taxa (21, 61). We followed standard OSA procedure (32) to conduct this analysis. First, we constructed a NEXUS matrix file of irreversible ontogenetic characters and combined all operational taxonomic units (OTUs) (in this case, individuals) with identical suites of character states into single OTUs to identify semaphoronts—unique suites of developmental character states that represent all specimens with those states. To reduce the amount of missing data in the analysis, we eliminated redundancies in character states of specimens by removing those specimens with missing data if all known character states were identical to one or more specimens with fewer missing data using safe taxonomic reduction (62) in the Claddis package (63) in R (64) producing a taxonomically reduced NEXUS file that we used to perform OSA ([Datasets 1–9](#)). Additionally, we also constructed a “reversed” NEXUS file for each file previously constructed, with the coding for mature and immature characters reversed (e.g., “0” becomes “1” for two-state characters, etc.). This step polarizes characters using the most mature outgroup, preventing semaphoronts from falling along developmental paths that do not extend from the least to most mature semaphoronts (see ref. 32 for a more detailed explanation). We then used Phylogenetic Analysis Using Parsimony (\*and Other Methods) (PAUP\*) Version 4.0b10 (65) to optimize these developmental events onto trees by running a heuristic search with the tree-bisection-reconnection algorithm, adding specimens randomly and running 300 replicates. The “normal” dataset was run with the most immature individual as the outgroup semaphoront, and the reversed dataset with the most mature individual was run as the outgroup semaphoront. If completely immature or mature individuals were not present in the dataset, we included “hypothetical” semaphoronts with completely immature/mature character states to provide outgroups to polarize characters; however, all individual character states included in the analysis were observed in the sample. We then visualized the normal and reverse treatment trees returned by PAUP\* in MacClade Version 4.04 (66) using the “trace all changes” function on both ambiguous and unambiguous changes.

We used this information to construct the OSA reticulating-sequence diagrams for each dataset by following the standard OSA procedure (32) ([SI Appendix, Supplementary Text](#)), with a few modifications to analyze our datasets that contained large amounts of missing data. To conservatively estimate the amount of sequence polymorphism, we chose to reconstruct ambiguous changes only along the branch closest to the immature outgroup semaphoront, rather than reconstruct this character change as occurring every place where it was ambiguously reconstructed: essentially, an accelerated transformation (ACCTRAN) treatment. Missing data can create ambiguities that sometimes result in inflated numbers of developmental sequences, because the same set of specimens can form two adjacent semaphoronts, with one semaphoront having reconstructed a missing character(s) as absent and the other as present, with the change linking the two as part of a sequence. In most cases, this merely represents the most parsimonious sequence available for these semaphoronts, because the semaphoront

reconstructed as “mature” is connected with entirely different specimens, meaning the different optimizations of the missing data merely made a developmental sequence that was already parsimonious more resolved than it otherwise would have been. However, in some instances, the mature reconstruction of those same specimens merely linked to a more mature semaphoront that the “immature” reconstruction already linked to via another developmental sequence. In this case, the reconstruction of the missing data adds a sequence of equal resolution that only exists because of missing data. To be conservative in estimating the amount of sequence polymorphism in the population, we eliminated those semaphoronts that represented the same set of specimens and only added sequences because of different optimizations of missing data. We also modified OSA to accommodate a problem not yet encountered in published studies using OSA: because some specimens with large amounts of missing data in the full-body dataset possessed character suites extremely different from other, more complete specimens, the normal treatment placed these specimens in divergent sequences close to the immature outgroup (reconstructing most or all of the missing characters as immature), whereas the reverse treatment did the opposite, placing these specimens close to the mature outgroup, reconstructing most of the missing data as mature characters. Because the two treatments did not overlap for these specimens, the specimens were left “stranded”; that is, without a complete path from the least to most mature semaphoronts. Because the assumptions of OSA require each developmental pathway to connect the two outgroup semaphoronts, we connected the stranded semaphoronts to the least or most mature semaphoronts as needed, resulting in several developmental sequences that are highly unresolved and possess extremely low frequency support weights (see below). Although reconstruction of these specimens as near the immature outgroup and reconstruction of these specimens as near the mature outgroup are both equally consistent with the data, to avoid overestimating the number of potential developmental sequences (and therefore the sequence polymorphism in the sample), we chose to eliminate those stranded semaphoronts and associated developmental pathways that were reconstructed as near the mature outgroup, leaving those same specimens that were also reconstructed as semaphoronts near the immature outgroup. The “raw” OSA diagrams and sequences can be found in [SI Appendix, Figs. S6–S13](#).

Maturity score, which is different from developmental stages as used in embryology, is the number of mature character states attained by a semaphoront. Therefore, semaphoronts may have the same maturity score while possessing differing character states. Frequency support weight—a dimensionless number representing the specimen support for a single semaphoront—was calculated for every semaphoront by the standard OSA procedure (32). A specimen gives a frequency support weight of 1 if it is only represented by a single semaphoront; otherwise, the support weight given by that specimen is divided evenly between all semaphoronts that represent it. The sequence with the most support weight is the modal sequence. The representative femoral length for each semaphoront, resulting in a color for each semaphoront in the OSA reticulating diagram (see key in Figs. 1–3 for color scales for femoral lengths), was determined by the length of the specimen(s) that represented each semaphoront in the reduced NEXUS file so as to not include those specimens with missing data that are represented by multiple semaphoronts. For those semaphoronts for which no representative specimen was available (e.g., the hypothetical immature outgroup semaphoront), the median of the femoral lengths of all specimens placed in that semaphoront was used as the representative femoral length.

**ACKNOWLEDGMENTS.** We thank M. Carrano, M. Stocker, L. Freeman, M. Colbert, M. McLain, K. Padian, D. Barta, R. Irmis, the Virginia Polytechnic Institute and State University (VT) Paleobiology Group, and the VT Integrative and Organismal Biology Group for discussions and our two reviewers for their helpful reviews, which greatly improved the manuscript. We thank the curators and staff of all museum collections visited ([SI Appendix, Supplementary Text](#)). We were supported by the VT Department of Geosciences Charles E. and Francis P. Sears Research Scholarship, the VT Graduate Student Assembly Research Development Grant, a Jurassic Foundation Research Grant, a Geological Society of America Graduate Student Research Grant, and an National Science Foundation (NSF) Graduate Research Fellowship (all awarded to C.T.G.), as well as NSF EAR 1349667 (awarded to S.J.N.).

- Benson RBJ, Butler RJ, Carrano MT, O'Connor PM (2012) Air-filled postcranial bones in the theropod dinosaurs: Physiological implications and the ‘reptile’-bird transition. *Biol Rev Camb Philos Soc* 87(1):168–193.
- Eagle RA, et al. (2011) Dinosaur body temperatures determined from isotopic ( $^{13}\text{C}$ - $^{18}\text{O}$ ) ordering in fossil biominerals. *Science* 333(6041):443–445.

- Erickson GM, Rogers KC, Yerby SA (2001) Dinosaurian growth patterns and rapid avian growth rates. *Nature* 412(6845):429–433.
- Norell MA, Xu X (2005) Feathered dinosaurs. *Annu Rev Earth Planet Sci* 33:277–299.
- O'Connor PM, Claessens LPAM (2005) Basic avian pulmonary design and flow-through ventilation in non-avian theropod dinosaurs. *Nature* 436(7048):253–256.



6. Padian K, de Ricqlès AJ, Horner JR (2001) Dinosaurian growth rates and bird origins. *Nature* 412(6845):405–408.
7. Wagner GP, Gauthier JA (1999) 1,2,3 = 2,3,4: A solution to the problem of the homology of the digits in the avian hand. *Proc Natl Acad Sci USA* 96(9):5111–5116.
8. Brusatte SL, Lloyd GT, Wang SC, Norell MA (2014) Gradual assembly of avian body plan culminated in rapid rates of evolution across the dinosaur-bird transition. *Curr Biol* 24(20):2386–2392.
9. Chiappe LM (2009) Downsized dinosaurs: The evolutionary transition to modern birds. *Evolution: Education and Outreach* 2(2):248–256.
10. Bailleul AM, Scannella JB, Horner JR, Evans DC (2016) Fusion patterns in the skulls of modern archosaurs reveal that sutures are ambiguous maturity indicators for the Dinosauria. *PLoS One* 11(2):e0147687.
11. Tumarkin-Deratzian AR, Vann DR, Dodson P (2006) Bone surface texture as an ontogenetic indicator in long bones of the Canada goose *Branta canadensis* (Anseriformes: Anatidae). *Zool J Linn Soc* 148(2):133–168.
12. Brochu CA (1992) Ontogeny of the postcranium in crocodylomorph archosaurs. Master's thesis (University of Texas, Austin, TX).
13. Brochu CA (1996) Closure of neurocentral sutures during crocodylian ontogeny: Implications for maturity assessment in fossil archosaurs. *J Vertebr Paleontol* 16(1):49–62.
14. Tumarkin-Deratzian AR, Vann DR, Dodson P (2007) Growth and textural ageing in long bones of the American alligator *Alligator mississippiensis* (Crocodylia: Alligatoridae). *Zool J Linn Soc* 150(1):1–39.
15. Bybee PJ, Lee AH, Lamm E-T (2006) Sizing the Jurassic theropod dinosaur *Allosaurus*: Assessing growth strategy and evolution of ontogenetic scaling of limbs. *J Morphol* 267(3):347–359.
16. Carr TD (1999) Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Coelosauria). *J Vertebr Paleontol* 19(3):497–520.
17. Erickson GM, et al. (2004) Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. *Nature* 430(7001):772–775.
18. Benton MJ, Juul L, Storrs GW, Galton PM (2000) Anatomy and systematics of the prosauropod dinosaur *Thecodontosaurus antiquus* from the Upper Triassic of southwest England. *J Vertebr Paleontol* 20(1):77–108.
19. Carrano MT, Sampson SD, Forster CA (2002) The osteology of *Masiakasaurus knopfleri*, a small abelisaurid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. *J Vertebr Paleontol* 22(3):510–534.
20. Colbert EH (1990) Variation in *Coelophysis bauri*. *Dinosaur Systematics: Perspectives and Approaches*, eds Carpenter K, Currie PJ (Cambridge Univ Press, Cambridge, UK), pp 81–90.
21. Griffin CT, Nesbitt SJ (2016) The femoral ontogeny and long bone histology of the Middle Triassic (?late Anisian) dinosauriform *Asilisaurus kongwe* and implications for the growth of early dinosaurs. *J Vertebr Paleontol* 36(3):e1111224.
22. Klein N, Sander PM (2007) Bone histology and growth of the prosauropod Plateosaurus engelhardti MEYER, 1837 from the Norian bonebeds of Trossingen (Germany) and Frick (Switzerland). *Spec Pap Paleontol* 77:169–206.
23. Piechowski R, Talanda M, Dzik J (2014) Skeletal variation and ontogeny of the Late Triassic Dinosauriform *Silesaurus opolensis*. *J Vertebr Paleontol* 34(6):1383–1393.
24. Raath MA (1990) Morphological variation in small theropods and its meaning in systematics: Evidence from *Syntarsus rhodesiensis*. *Dinosaur Systematics: Perspectives and Approaches*, eds Carpenter K, Currie PJ (Cambridge Univ Press, Cambridge, UK), pp 91–105.
25. Sander PM, Klein N (2005) Developmental plasticity in the life history of a prosauropod dinosaur. *Science* 310(5755):1800–1802.
26. Tykoski RS, Rowe T (2004) Ceratosaurs. *The Dinosauria*, eds Weishampel DB, Dodson P, Osmólska H (Univ of California Press, Berkeley), 2nd Ed, pp 47–70.
27. Lee AH, O'Connor PM (2013) Bone histology confirms determinate growth and small body size in the noasaurid theropod *Masiakasaurus knopfleri*. *J Vertebr Paleontol* 33(4):865–876.
28. Garn SM, Rohmann CG, Blumenthal T (1966) Ossification sequence polymorphism and sexual dimorphism in skeletal development. *Am J Phys Anthropol* 24(1):101–115.
29. Brusatte SL, et al. (2010) The origin and early radiation of dinosaurs. *Earth Sci Rev* 101(1–2):68–100.
30. Langer MC (2004) Basal Saurischia. *The Dinosauria*, eds Weishampel DB, Dodson P, Osmólska H (Univ of California Press, Berkeley), 2nd Ed, pp 25–46.
31. Schwartz HL, Gillette DD (1994) Geology and taphonomy of the *Coelophysis* quarry, Upper Triassic Chinle Formation, Ghost Ranch, New Mexico. *J Paleontol* 68(5):1118–1130.
32. Colbert MW, Rowe T (2008) Ontogenetic Sequence Analysis: Using parsimony to characterize developmental sequences and sequence polymorphism. *J Exp Zool B Mol Dev Evol* 310(5):398–416.
33. Hennig WE (1966) *Phylogenetic Systematics*, trans Davis DD, Zangerl R (Univ of Illinois Press, Urbana, IL), p 263.
34. Bristowe A, Raath MA (2004) A juvenile coelophysoid skull from the Early Jurassic of Zimbabwe, and the synonymy of *Coelophysis* and *Syntarsus*. *Palaeontologia Africana* 40:31–41.
35. Buckley LG, Larson DW, Reichel M, Samman T (2010) Quantifying tooth variation within a single population of *Albertosaurus sarcophagus* (Theropoda: Tyrannosauridae) and implications for identifying isolated teeth of tyrannosaurids. *Can J Earth Sci* 47(9):1227–1251.
36. Carpenter K (2010) Variation in a population of Theropoda (Dinosauria): *Allosaurus* from the Cleveland-Lloyd Quarry (Upper Jurassic), Utah, USA. *Paleontol Res* 14(4):250–259.
37. Colbert EH (1989) The Triassic dinosaur *Coelophysis*. *Mus North Az Bull* 57:1–160.
38. Currie PJ, Peng J-H (1993) A juvenile specimen of *Saurornithoides mongoliensis* from the Upper Cretaceous of northern China. *Can J Earth Sci* 30(10):2224–2230.
39. Heckert AB, et al. (2006) Revision of the archosauriform reptile *Trilophosaurus*, with a description of the first skull of *Trilophosaurus jacobsi*, from the Upper Triassic Chinle Group, West Texas, USA. *Palaeontology* 49(3):621–640.
40. Manzig PC, et al. (2014) Discovery of a rare pterosaur bone bed in a cretaceous desert with insights on ontogeny and behavior of flying reptiles. *PLoS One* 9(8):e100005.
41. Rinehart LF, Lucas SG, Heckert AB, Spielman JA, Celeskey MD (2009) The paleobiology of *Coelophysis bauri* (Cope) from the Upper Triassic (Apachean) Whitaker Quarry, New Mexico, with detailed analysis of a single quarry block. *New Mexico Mus Nat Hist Sci Bull* 45:1–260.
42. Tykoski RS (1998) The osteology of *Syntarsus kayentakatae* and its implications for ceratosaurid phylogeny. Master's thesis (University of Texas, Austin, TX).
43. Tykoski RS (2005) Anatomy, ontogeny, and phylogeny of coelophysoid dinosaurs. PhD dissertation (University of Texas, Austin, TX).
44. Britt BB, Chure DJ, Holtz TR, Jr, Miles CA, Stadman KL (2000) A reanalysis of the phylogenetic affinities of *Ceratosaurs* (Theropoda, Dinosauria) based on new specimens from Utah, Colorado, and Wyoming. *J Vertebr Paleontol* 20:32A.
45. van Heerden J, Galton PM (1997) The affinities of *Melanosaurus*—a Late Triassic prosauropod dinosaur from South Africa. *Neues Jahrbuch Geol Palaontol Monatsh* 12(1):39–55.
46. Weishampel DB, Chapman RE (1990) Morphometric study of *Plateosaurus* from Trossingen (Baden-Württemberg, Federal Republic of Germany). *Dinosaur Systematics: Approaches and Perspectives*, eds Carpenter K, Currie PJ (Cambridge Univ Press, Cambridge, UK), pp 43–51.
47. Smith DK (1998) A morphometric analysis of *Allosaurus*. *J Vertebr Paleontol* 18(1):126–142.
48. Smith DK (1999) Patterns of size-related variation within *Allosaurus*. *J Vertebr Paleontol* 19(2):402–403.
49. Smith DK, Richmond DR, Bybee PJ (1999) Morphological variation in a large specimen of *Allosaurus fragilis*, Upper Jurassic Morrison Formation, eastern Utah. *Vertebrate Paleontology in Utah, Miscellaneous Publications 99-1*, ed Gillette D (Utah Geological Survey, Salt Lake City), pp 135–141.
50. Loewen MA (2009) Variation in the Late Jurassic theropod dinosaur *Allosaurus*: Ontogenetic, functional, and taxonomic implications. PhD Dissertation (University of Utah, Salt Lake City).
51. Starck JM, Chinsamy A (2002) Bone microstructure and developmental plasticity in birds and other dinosaurs. *J Morphol* 254(3):232–246.
52. Lawton JH (1994) Population dynamic principles. *Philos Trans R Soc Lond B Biol Sci* 344(1307):61–68.
53. Whiteside JH, et al. (2015) Extreme ecosystem instability suppressed tropical dinosaur dominance for 30 million years. *Proc Natl Acad Sci USA* 112(26):7909–7913.
54. Tanner LH, Lucas SG, Chapman MG (2004) Assessing the record and causes of the Late Triassic extinctions. *Earth Sci Rev* 65(1):103–139.
55. Raath MA (1977) The anatomy of the Triassic theropod *Syntarsus rhodesiensis* (Saurischia: Podokesauridae) and a consideration of its biology. PhD dissertation (Rhodes University, Grahamstown, South Africa).
56. Cubbage CC, Mabee PM (1996) Development of the cranium and paired fins in the zebrafish *Danio rerio* (Ostariophysi, Cyprinidae). *J Morphol* 229(2):121–160.
57. de Jong IML, Colbert MW, Witte F, Richardson MK (2009) Polymorphism in developmental timing: Intraspecific heterochrony in a Lake Victoria cichlid. *Evol Dev* 11(6):625–635.
58. Mabee PM, Trender TA (1996) Development of the cranium and paired fins in *Betta splendens* (Teleostei: Percomorpha): Intraspecific variation and interspecific comparisons. *J Morphol* 227(3):249–287.
59. Morris Z (2013) Skeletal ontogeny of *Monodelphis domestica* (Mammalia: Didelphidae): Quantifying variation, variability, and technique bias in ossification sequence reconstruction. Master's thesis (University of Texas, Austin, TX).
60. Sheil C, Greenbaum E (2005) Reconsideration of skeletal development of *Chelydra serpentina* (Reptilia: Testudinata: Chelydridae): Evidence for intraspecific variation. *J Zool* 265(3):235–267.
61. Olori JC (2013) Ontogenetic sequence reconstruction and sequence polymorphism in extinct taxa: An example using early tetrapods (Tetrapoda: Lepospondyli). *Paleobiology* 39(3):400–428.
62. Wilkinson M (1995) Coping with abundant missing entries in phylogenetic inference using parsimony. *Syst Biol* 44(4):501–514.
63. Lloyd GT (2016) Estimating morphological diversity and tempo with discrete character-taxon matrices: Implementation, challenges, progress, and future directions. *Biol J Linn Soc Lond* 118(1):131–151.
64. R Core Development Team (2008) R: A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna). Available at [www.R-project.org](http://www.R-project.org). Accessed August 21, 2015.
65. Swofford DL (2003) PAUP\*. Phylogenetic Analysis Using Parsimony (\*and Other Methods) (Sinauer Associates, Sunderland, MA), Version 4.
66. Maddison DR, Maddison WP (2002) MacClade 4: Analysis of phylogeny and character evolution (Sinauer, Sunderland, MA), Version 1.04.