Temporal congruence and the origin of birds

Christopher A. Brochu & Mark A. Norell

NOTE

TEMPORAL CONGRUENCE AND THE ORIGIN OF BIRDS

CHRISTOPHER A. BROCHU[1] and MARK A. NORELL[2], [1]Department of Geology, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605, cbrochu@fmppr.fmnh.org; [2]Department of Vertebrate Paleontology, American Museum of Natural History, Central Park West at 79th St., New York, NY 10024

The preponderance of available character evidence indicates that birds evolved from coelurosaurian theropod dinosaurs (Ostrom, 1976; Gauthier, 1986; Holtz, 1994; Sereno, 1997; Padian and Chiappe, 1998; Forster et al., 1998; Makovicky and Sues, 1998). Critics of this perspective have been quick to point out potential problems based on assumptions of process from developmental biology, ecology, and functional expectations (Feduccia and Wild, 1993; Burke and Feduccia, 1997; Ruben et al., 1997; Feduccia and Martin, 1998). One often cited piece of counterevidence is the so-called "temporal paradox," in which the closest hypothesized dinosaurian relatives of birds are said to appear later in the fossil record than do birds (Feduccia, 1996; Hou et al., 1996; Feduccia and Martin, 1998; Thomas and Garner, 1998). Here we show that the "temporal paradox" exists only as a local artifact caused by a failure to consider all relevant portions of the tree concurrently. When entire trees are empirically evaluated, stratigraphic data are most congruent with a hypothesis joining birds with theropod dinosaurs.

The temporal paradox argument has been addressed philosophically (e.g., Padian and Chiappe, 1998). The temporal paradox argument assumes that stratigraphic order should overturn a well-corroborated phylogeny for a group with a fragmentary fossil record; it confuses the concepts of "ancestor" and "sister taxon"; and it ignores or dismisses fragmentary remains that may close the stratigraphic gap between first birds and their closest nonavian theropod relatives (Jensen and Padian, 1989; Chure, 1994; Zhao and Xu, 1998). But despite these philosophical problems, the temporal paradox argument continues to appear in reviews of the issue. We thus decided to address it empirically. This gives us the opportunity to highlight the importance of quantitative approaches to addressing phylogenetic debates and the necessity of considering a whole tree rather than a single node in isolation.

Several techniques have been proposed to assess how well a set of first appearance dates corresponds to the predictions of specific phylogenetic hypotheses, including the Stratigraphic Consistency Index (SCI; Huelsenbeck, 1994), the Sum of Minimum Implied Gaps (SMIG; Benton and Storrs, 1994, 1996; see also Fisher, 1991, and Weishampel, 1996, for identical statistics under different names), and the Manhattan Stratigraphic Measure (MSM; Siddall, 1998). The first measures how well the relative sequence of first appearances matches the expected sequence of appearances on a cladogram, while the others evaluate absolute temporal disparity. All metrics are applied globally over entire trees, rather than concentrating locally on a specific node.

SCI is the ratio between the number of nodes consistent with stratigraphy and the total number of nodes on the tree. As SCI diminishes, fit diminishes. SCI is known to be biased toward pectinate trees (Siddall, 1996), but the different trees in this study can be considered isomorphic on the basis of Heard's Imbalance Index (Table 2). SMIG is simply a measure of the sum length of minimum ghost lineages over the entire tree. Smaller SMIG's indicate a better fit of stratigraphy with topology as lengths of ghost lineages are minimized. MSM considers a step matrix comprising the absolute difference between the first appearance dates of any two taxa in the tree. This matrix is optimized as a Sankoff character on two trees, the tree under analysis and a tree that optimizes differences on the matrix. In effect, one is treating the absolute difference between first appearances of taxa as a single multistate character and optimizing it using Wagner parsimony, with the absolute distances among first appearances acting as weights among different character state transformations. One divides the length of the minimal tree by that of the study tree to obtain MSM. Larger MSM ratios are indicative of

a better fit between stratigraphy and a topology. Although both SMIG and MSM will suffer from data set size biases, MSM is thought to avoid some of the problems in other methods with respect to nonindependence of ranked data from a hierarchical pattern by making pairwise comparisons between all ingroup taxa (Siddall, 1998).

To assess the "temporal paradox" in bird origins, comparisons must be made between competing phylogenies. Unfortunately, the temporal paradox argument is invariably made in a phylogenetic vacuum. Stratigraphic shortcomings of a grouping of birds within Dinosauria are pointed out, but no competing phylogeny for the relationships of birds with other amniotes is proposed that better explains both the distribution of character states among ingroup taxa and their stratigraphic ranges. But we can construct alternatives by drawing Avialae adjacent to putative nondinosaurian relatives of birds as proposed in the literature (Fig. 1).

The most common nondinosaurian "alternative" is the "thecodontian" hypothesis, which dates to the early part of the 20th Century (Heilmann, 1926). This is a very difficult hypothesis to characterize phylogenetically, because "Thecodontia" is a paraphyletic assemblage of virtually any archosauriform not obviously belonging to Crocodyliformes, Pterosauria, or Dinosauria (Gauthier and Padian, 1985). For this analysis, we considered several variants of the thecodontian hypothesis that could be constructed from the literature by making birds the sister group to Crocodylomorpha (Walker, 1972, 1977; Martin, 1991), *Euparkeria* (Welman, 1995), *Scleromochlus* (Feduccia, 1996), and Dinosauromorpha (Tarsitano and Hecht, 1980). We also considered the enigmatic archosauromorph reptile *Megalancosaurus*, which was regarded as a possible avian relative by Tarsitano (1991) and Feduccia and Wild (1993). These alternatives can be mapped onto a phylogeny for archosauromorph reptiles as shown in Figure 1. The base phylogeny is based on work by Gauthier et al. (1988), Sereno (1991), Sereno and Arcucci (1994a, b), Parrish (1993), Renesto (1994), and Merck (1997).

Other alternatives have been proposed, such as *Longisquama, Sharovipteryx,* and *Cosesaurus* (see Padian and Chiappe, 1998, for review), but these involve problematic taxa of uncertain diapsid affinity. Because we could not construct alternative cladograms including them, they were not considered in this analysis. It should also be borne in mind that the alternatives we considered have generally been considered bird relatives and not ancestors per se. In fact, Feduccia (1996) regarded *Longisquama, Megalancosaurus,* and *Scleromochlus* as parts of a radiation that, in combination, preserved features in common with birds.

We compare the stratigraphic implications these alternatives make against those of a placement of birds within Dinosauria (Fig. 1E). Minor differences remain among current analyses of theropod phylogeny, so four different topologies were analyzed (Fig. 1A–D). They are referred to as H (Holtz constraint; Holtz, 1994), S (Sereno constraint; Sereno, 1997), F (Forster constraint; Forster et al., 1998) and M (Makovicky and Sues constraint; Makovicky and Sues, 1998). A few taxa, such as *Ornitholestes* and *Compsognathus,* were not common to all four analyses, but were considered important both for their stratigraphic position in the Late Jurassic and their phylogenetic position within Theropoda. Hence, when missing from a tree, they were added by hand based on their placement in the other trees. A few problematic taxa were not included, such as Therezinosauroidea and the new feathered theropods (Ji et al., 1998) because they are not fully described, highly labile in recent analyses, and would greatly complicate subsequent calculations. Some authors (e.g., Gauthier, 1986; Brinkman and Sues, 1987; Novas,
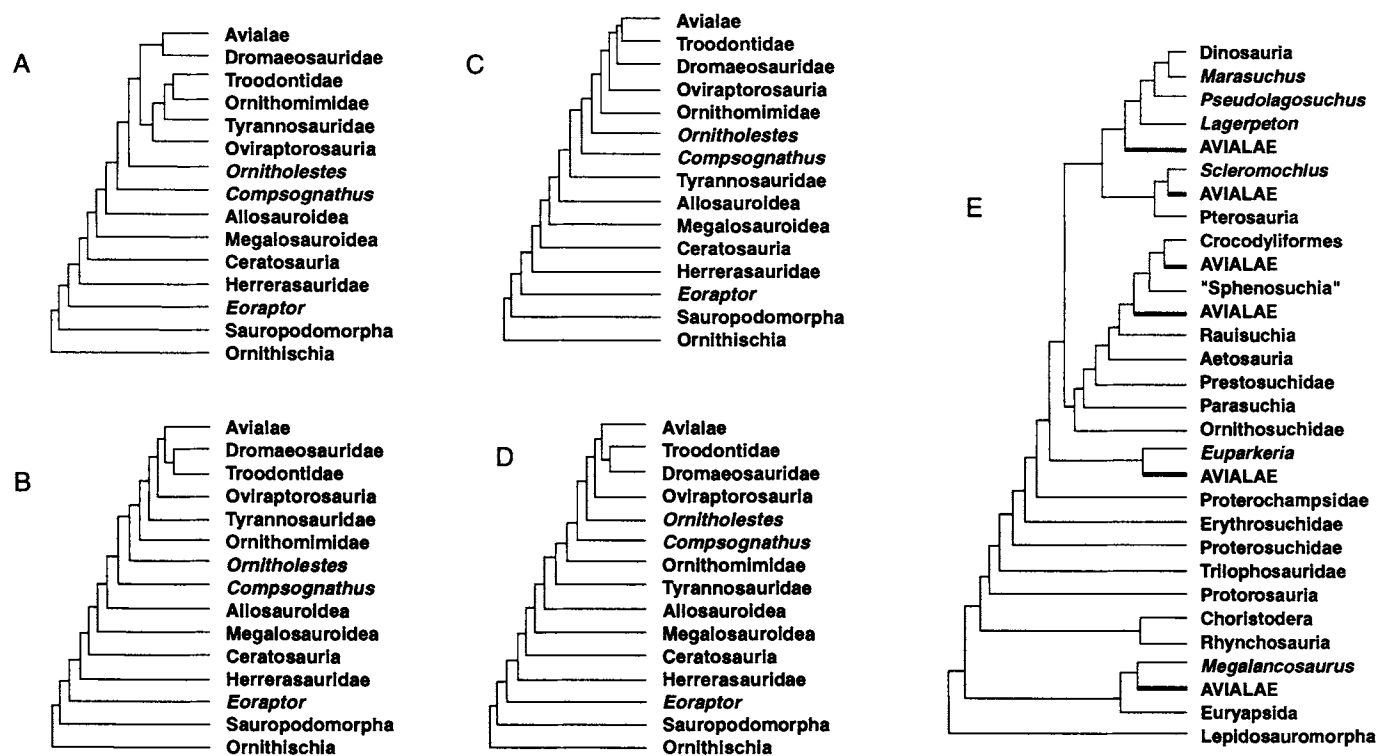
FIGURE 1.   Constraint trees used in this study. **A**, dinosaur phylogeny based on Holtz (1994); **B**, dinosaur phylogeny based on Sereno (1997); **C**, dinosaur phylogeny based on Forster et al. (1998); **D**, dinosaur phylogeny based on Makovicky and Sues (1998); **E**, phylogeny of non-dinosaurian archosauromorphs, with nondinosaurian placements for birds (Avialae) indicated. Trees simplified from Gauthier et al. (1988), Sereno (1991), Sereno and Arcucci (1994a, b), Parrish (1993), and Merck (1997). Because of computational limitations, six taxa considered in SCI and SMIG calculations (*Compsognathus, Eoraptor,* Herrerasauridae, *Marasuchus, Pseudolagosuchus,* and Choristodera) were not included in calculation of MSM.

1992; Padian and May, 1993) have suggested a position for *Eoraptor* and Herrerasauridae outside Dinosauria; alternate placements of these two taxa do not alter the results obtained here.

Absolute ages for fossil taxa were used when available, but most often first appearances were calibrated to the midpoint of their first appearance stage. Absolute times were taken from Harland et al. (1990), and first appearances of taxa were obtained as shown in Table 1. In a few cases (e.g., Euryapsida, Lepidosauromorpha, Protorosauria), the precise stage of first appearance was not known, but a portion of a period (e.g., Early Triassic, Late Permian) could be specified. The midpoint of the given chronostratigraphic unit was used to calibrate the first appearance datum for each taxon, as indicated in Table 1. Calibrations were based as much as possible on nondental remains that unequivocally belong to their respective groups; we acknowledge that fragmentary remains are known that can draw several of these groups back in time (e.g., Jensen and Padian, 1989; Chure, 1994). Measures of relative (SCI) and absolute (SMIG, MSM) disparity are shown in Table 2 and, graphically, in Figure 2.

SCI is essentially unable to distinguish among the different scenarios (Table 2, Figure 2). Most SCI values for nondinosaurian trees under the H or F constraints are equivalent to those of their respective dinosaurian trees, and with the S or M trees most are actually lower than the dinosaurian tree. Relative consistency increases only if the H or F trees are used, and if birds are close to either *Euparkeria* or *Megalancosaurus,* with an improvement of only one out of 35 nodes (Table 2). The node linking birds to their sister taxon is stratigraphically consistent under all nondinosaurian scenarios, but such scenarios often create new inconsistencies elsewhere in the tree that did not exist under the dinosaurian constraint. Hence, relative consistency is generally invariant—local disparity may be eliminated, but net global disparity does decrease and may increase.

The H tree (SMIG=407.6) matches the absolute temporal pattern better than the others, although the difference between it and either the S or M trees (SMIG=419.9) is very small (2.9%; Table 2). These trees match stratigraphy better than the F tree (SMIG=440.6), with the H tree requiring 7.5% less missing record and the others 4.7%.

The minimum ghost lineage separating birds from their nearest dinosaurian relative is short. Based on the presence of dromaeosaurids in the Barremian (Kirkland et al., 1993), the minimum ghost lineage is only 20.9 my long in the H, S, and M constraints; and based on the oldest troodontid non-dental remains in the Aptian (Barsbold et al., 1987; Russell and Dong, 1993), the minimum ghost lineage is 30.6 my under the F constraint. These contrast with the much longer ghost lineages of up to 75 my implied by some applications of the temporal paradox argument (e.g., Hinchliffe, 1997).

All of the trees that exclude birds from Dinosauria had higher SMIG values than their respective dinosaurian trees (Table 2). SMIG ranged from 437.9 (birds + Crocodyliformes, S constraint) to 494.2 (birds + *Euparkeria,* M constraint). Regardless of the theropod tree used, a crocodyliform relationship implied less missing record, and a relationship to *Euparkeria* implied the most. Changes from dinosaurian to non-dinosaurian scenarios were most dramatic under the H constraint (10.87% to 16.10%) and least under the F constraint (1.85% to 7.71%).

Comparison of MSM values generally corroborates the results observed with SMIG. The H and S trees (MSM=0.467) had slightly higher values than the F or M trees (MSM=0.438). Trees excluding birds from Dinosauria have lower MSM values (Table 2). MSM for non-dinosaurian scenarios was slightly higher under the S constraint and lower under the F constraint, which was identical to the M constraint in all cases. Although there is a coarse relationship between SMIG and MSM, they are not directly correlated. Relationships with Crocodyliformes fared better under both SMIG and MSM, but whereas the highest SMIG were associated with a relationship to *Euparkeria,* a relationship with *Megalancosaurus* yielded a slightly lower MSM than one with *Euparkeria.* This may result from the pruning of taxa from the MSM analysis such that the two numbers are not directly comparable in this study.

From the data presented in Table 2 and Figure 2, there is no empirical justification for applying stratigraphic arguments against a dinosaurian

TABLE 1. Calibrations for taxa considered in this study.

Taxon	FAD (MY)	Reference
Avialae	148.9	Sereno, 1997
Dromaeosauridae	128.2	Sereno, 1997
Troodontidae	118.3	Sereno, 1997
Oviraptorosauria	112.0	Makovicky and Sues, 1998
Tyrannosauridae	97.0	Sereno, 1997
Ornithomimosauria	137.9	Sereno, 1997
Ornitholestes	148.9	Sereno, 1997
Allosauroidea	182.5	Sereno, 1997
Megalosauroidea	163.7	Sereno, 1997
Ceratosauria	229.2	Sereno, 1997
Eoraptor	227.8	Rogers et al., 1993
Herrerasauridae	227.8	Rogers et al., 1993
Sauropodomorpha	216.5	Sereno, 1997
Ornithischia	229.2	Sereno, 1997
Marasuchus	237.3	Benton, 1995
Pseudolagosuchus	237.3	Benton, 1995
Lagerpeton	237.3	Benton, 1995
Scleromochlus	229.2	Sereno, 1991
Pterosauria	229.2	Sereno, 1991
Ornithosuchidae	229.2	Sereno, 1991
Parasuchia	229.2	Parrish, 1993
Prestosuchus	237.3	Parrish, 1993
Aetosauria	229.2	Parrish, 1993
Rauisuchia	237.3	Parrish, 1993
Sphenosuchia	229.2	Benton, 1995
Cocodyliformes	208.8	Benton, 1995
Euparkeria	243.1	Benton, 1995
Proterochampsidae	237.3	Benton, 1995
Erythrosuchidae	242.7	Benton, 1995
Proterosuchidae	237.3	Benton, 1995
Trilophosauridae	229.2	Benton, 1995
Proterosauridae	250.5	Benton, 1995
Choristodera	216.5	Benton, 1995
Rhynchosauria	243.1	Benton, 1995
Megalancosaurus	216.5	Merck, 1997
Euryapsida	243.1	Merck, 1997
Lepidosauromorpha	250.5	Benton, 1990

TABLE 2. Imbalance Index (Im), Stratigraphic Consistency Index (SCI), Sum of Minimum Implied Gaps (SMIG), and Manhattan Stratigraphic Measure (MSM) for different placements of birds on different dinosaur phylogenies (H, S, F, and M constraints). Expected Im for a tree of 38 taxa is 0.1071.

|	Taxon	Im	SCI	SMIG	MSM
H	Theropod	0.668	0.556	407.6	0.466
	"Thecodont"	0.677	0.556	485.8	0.394
	Scleromochlus	0.652	0.556	477.7	0.394
	Croc.morph	0.656	0.556	477.7	0.394
	Croc.form	0.656	0.556	457.3	0.416
	Euparkeria	0.647	0.583	491.6	0.386
	Megalanc.	0.638	0.583	465.0	0.381
S	Theropod	0.677	0.583	419.9	0.467
	"Thecodont"	0.677	0.556	466.4	0.405
	Scleromochlus	0.652	0.556	458.3	0.405
	Croc.morph	0.656	0.556	458.3	0.405
	Croc.form	0.656	0.556	437.9	0.426
	Euparkeria	0.647	0.583	472.2	0.396
	Megalanc.	0.638	0.583	445.6	0.390
F	Theropod	0.677	0.556	440.6	0.438
	"Thecodont"	0.677	0.556	477.4	0.374
	Scleromochlus	0.652	0.556	469.3	0.374
	Croc.morph	0.656	0.556	469.3	0.374
	Croc.form	0.656	0.556	448.9	0.394
	Euparkeria	0.647	0.583	483.2	0.367
	Megalanc.	0.638	0.583	456.6	0.362
M	Theropod	0.677	0.556	419.9	0.438
	"Thecodont"	0.677	0.528	488.4	0.374
	Scleromochlus	0.652	0.528	480.3	0.374
	Croc.morph	0.656	0.528	480.3	0.374
	Croc.form	0.656	0.528	459.9	0.394
	Euparkeria	0.647	0.556	494.2	0.367
	Megalanc.	0.638	0.556	467.6	0.362
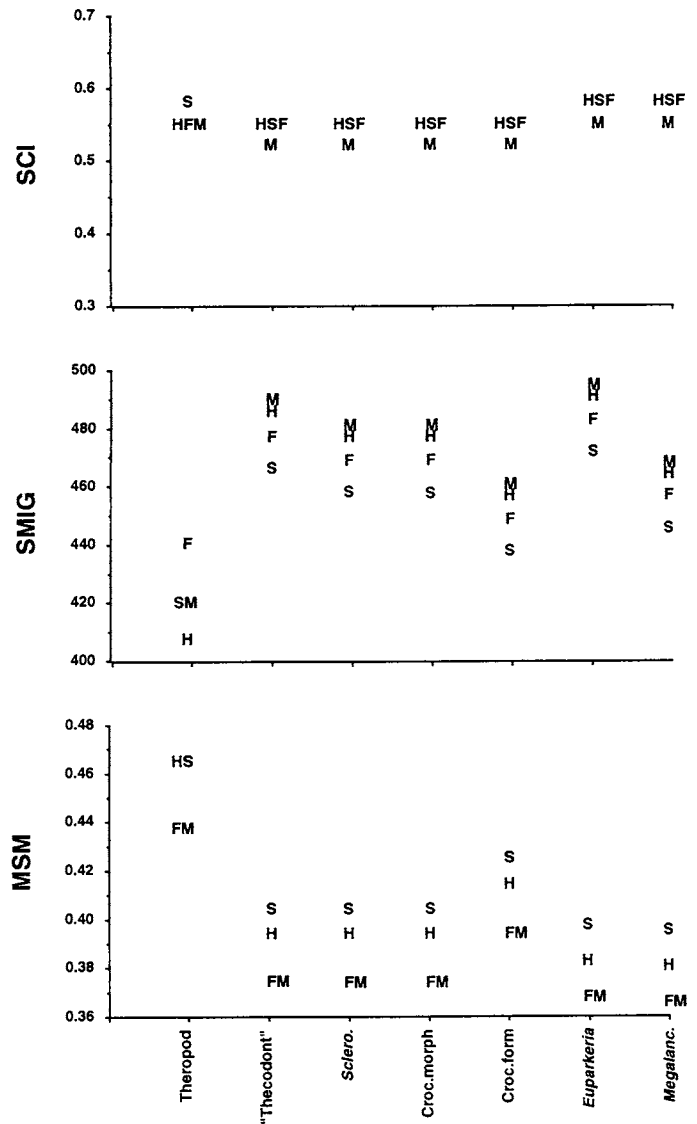
FIGURE 2. SCI, SMIG, and MSM for the Holtz (H), Sereno (S), Forster et al. (F), and Makovicky and Sues (M) constraints for various placements of birds within Archosauromorpha (see Table 2). Competing placements of Avialae are indicated on the X axis; values for each constraint are indicated by capital letters (H, S, F, and M) at each placement. When capital letters are adjacent to each other, indicated constraints have identical values for that placement.

hypothesis for bird origins. Philosophical problems aside, a "temporal paradox" exists only if a single node is examined in isolation from the rest of the tree. Global relative stratigraphic consistency is uniform among all hypotheses, and measures of global absolute disparity strongly favor birds as dinosaurs. Moreover, the magnitude of the ghost lineage on the dinosaurian sister group to birds is much shorter than sometimes reported. Moving birds out of Dinosauria may increase global absolute disparity by as much as 15 percent, with most of the added stratigraphic debt resulting from a longer ghost lineage for birds. We thus conclude that stratigraphy presents no significant paradox to the congruent hypotheses supported by multiple independent character data sets.

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