estimation methods are refined [3,4]. Furthermore, phylogenetic interpretations of the fossil record do not support an 'explosive' model for the modern avian radiation [5]; the debate is not cut and dried [1,2].

Although some earlier molecular clock studies placed all neornithine divergences deep in the Cretaceous [6,7], recent studies have noted that the accuracy of genetic time estimations are dependent on the establishment of a phylogenetic framework for Neornithes as well as simply knowledge of their numbers and ages [4,5]. Molecular watchmakers accept that, given knowledge of the neornithine record, most internal calibrations are problematic [4]. I do, however, wish to echo Feduccia's assertion [1] that the other 'major problem' inherent to this discussion is assignment of fossil fragments from the Cretaceous to modern orders on the basis of little or no evidence [8,9]. Irrespective of which side of the K–T boundary is being considered, convincing placement of a fossil within a clade of Neornithes requires characters that are demonstrably diagnostic (via cladistic methods) to the lineage in question [5]. The waters have been muddied considerably in this respect as referrals of Cretaceous fossil bones to modern clades on the basis of informally evaluated characters and intuitive systematic assessments have been commonplace [8,9]. Feduccia glosses over the fact that there are large numbers of well dated and phylogenetically constrained fossil modern birds known from rocks of Eocene age and younger – the placement of these taxa within the tree of Neornithes (as it is developed by neontologists) corroborates some clade divergences before the K–T boundary [5], which is less discordant with recent molecular clock estimates. It is time, therefore, to move beyond the current debate.

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'Big bang' for Tertiary birds? A reply

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In a recent Opinion article in *TREE* [1], Feduccia maintains his support for an explosive radiation of modern (neornithine) birds from a late Cretaceous shorebird-like ancestor. However, we think the relevant data do not show this and that Feduccia does not clarify the exact composition of his 'transitional shorebirds'.

Feduccia's 'big bang' theory [2] has moved tinamous, ratites, waterfowl and flamingos to the base of the neornithine radiation [3]. However, he does not take into account attempts to address the transitional charadriiform hypothesis with a molecular phylogenetic approach [4,5]: he claims that genetic studies focus on taxa (modern charadriiforms, paleognaths and galloanserines) that are not relevant to the source of the modern radiation [1]. If so, then it would be appropriate for Feduccia to specify the relevant taxa rather than referring 'transitional' shorebirds, 'paleognaths' and 'some other' lineages [1] to the base of the neornithine radiation.

Because no Cretaceous fossil flamingos, ratites or tinamous have yet been found, Feduccia favors an ecological concept [6] over a direct interpretation of the fossil record. Several fossils from the Cretaceous [7,8] do point to Mesozoic neornithines, but Feduccia does not take into account those with limited character diagnosis [3].

Feduccia also claims that the temporal discrepancy between molecules and fossils indicates that either the molecular or fossil-bird tempo is wrong [1,3]. It might be that neither data set is wrong; they might simply reflect different signals. A Cretaceous origin for many neornithine clades [4,5] should not be interpreted as direct support for the presence of modern albatrosses or pelicans alongside more archaic birds [1]. It is plausible that the diversification of major bird clades did take place near the Cretaceous–Tertiary (K–T) boundary, as indicated for various mammals [9]. Molecular studies at this scale are still limited, and we can only guess whether the patterns observed in disparate lineages (Cretaceous ratites, passerines and anseriforms) document the exception or the rule [4,5]. Hence, neither clocks nor fossils undisputedly confirm whether crown neornithines passed 'unblemished'

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[3] through the K–T boundary. Molecular [4,5], morphological [10] and fossil data [7,8] all indicate that the early history of modern birds began in the Cretaceous and did not involve 'transitional shorebirds'.

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Letters Response

Response to Dyke, and van Tuinen *et al.*: 'Big bang' for Tertiary birds?

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The idea for the 'big bang' model had its origin in 1975 from discussions with the late Berkeley biochemist Allan Wilson, who showed an interest in my early Tertiary mosaic fossils, and noted that the timescale for avian evolution could be quite short, based on small molecular differences among modern birds. The current model poses three basic questions: (1) was there a 'big bang' for Tertiary birds and mammals? (2) was there a late Cretaceous phylogenetic fuse?; and (3) was the Cretaceous–Tertiary (K–T) extinction event devastating for birds? Contra Dyke [1], fossil evidence overwhelmingly supports a Tertiary 'big bang' for birds, mammals, teleost fish, and probably every group of modern vertebrates [2]. As for birds, there is none of truly modern aspect (or any ratites) before the K–T boundary (archaic neornithines are present) and most modern orders are present in abundance by the Eocene, some 10 million years later (many have mosaic skeletons and are basal to their lineage). This phenomenon can only be described as an explosive evolutionary event.

Dyke's letter [1] relates primarily to question 2; was there a phylogenetic fuse in the late Cretaceous? But, even if true, the earlier drifting of continents played no role in modern bird evolution and distribution. Misidentifications of bony fragments and the miscalibration of clocks render this question very difficult. Also, most molecular clock studies are simply off by twofold [3]. Question 3 is also difficult to answer, but a devastating extinction event for birds is concordant with their being the first indicators of an environmental disaster, the veritable 'miner's canary'; it is amazing that any bird survived. There is also a major K–T faunal turnover for birds and mammals, and the explosive model has gained support from studies that also show a diversity bottleneck for insects and plants [4].

Van Tuinen *et al.* [5] have responded to a point related to the above issue; namely, assuming a K–T cataclysm, which taxa constituted the avian K–T bottleneck? This question has nothing to do with the proposition of an early Tertiary 'big bang', but, assuming a bottleneck, it would be of great interest to identify the avian equivalent of the mammalian insectivores. I suggested [2] that 'transitional shorebirds' might be good candidates, because their fossils (although fragmentary) are abundant in the late Cretaceous–early Paleocene, and their skeletons are largely mosaic, with numerous plesiomorphic features. A major difficulty is that van Tuinen *et al.* [5] do not seem to understand the meaning of 'transitional shorebird'. Olson and Parris ([6], and references therein) use the term to recognize taxa with mosaics of gruiform and charadriiform characters. This loose grouping includes a miscellany of birds in the form-family Graculavidae (*Graculavus*, *Telmatornis* and *Paleotringa*, etc.), and others. Graculavid-like birds were widespread from the Late Cretaceous through the early Paleogene [7], and the charadriiform-like *Cimolopteryx* was the most diverse and abundant group of closely related Mesozoic neornithine species, ranging from the mid-Campanian through the late Maastrichtian, and into the Paleocene [8]. (Likewise, the widespread early Paleogene volant paleognaths, the lithornithids, are suitable ratite ancestors.) Van Tuinen *et al.* [5] urge that I specify relevant taxa, which I have done before and now. Why do van Tuinen *et al.* [5,9] not

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