

However, Mongolia was characterized in the Late Cretaceous by extensive lakes, possibly with marine connections, and by the Campanian it would perhaps be most accurate to describe it as a desert, as in South Africa, with a swampy inland delta⁸. Small, possibly volant hesperornithiforms and *Presbyornis*, a widespread wader with webbed feet, have been found at nearby sites of about the same age⁹.

I consider *Apsaravis* to have little to contribute to our understanding of avian evolution, and its lack of a clear relationship with any kind of modern bird makes its significance ambiguous. If *Apsaravis* is not related to any modern ornithurine, how can it tell us anything important about the evolutionary questions raised by Norell and Clarke?

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Norell and Clarke reply — Given that Feduccia has explicitly stated that there is a near absence of ornithurine birds in Late Cretaceous continental deposits¹ and has speculated that ornithurines may have been more or less restricted to shoreline and marine deposits during this time¹, we do not believe that we misrepresented Feduccia’s hypothesis. We reported the finding of an almost complete skeleton of an ornithurine from Late Cretaceous continental deposits, and do not see how this specimen could have no bearing on Feduccia’s previous arguments.

Feduccia comments that other Mesozoic bird specimens are more, or just as, useful for tackling questions concerning the origin of extant bird lineages. Although all specimens contain some information, we disagree with Feduccia’s current assertion that *Apsaravis* is simply one of a group of “abundant” ornithurine fossils. The specimens he mentions are either not ornithurine or are so poorly preserved that they have not shed much light on their own phylogenetic positions, let alone on broader patterns of avian evolution.

The two “ornithurine” birds *Liaoningornis*

and *Chaoyangia* fall outside Ornithurae in Feduccia’s own work. The explicit cladistic definition of Ornithurae (most recent common ancestor of Hesperornithiformes plus Aves and all descendants²) is less inclusive than Feduccia’s more subjective definition (taxa other than those that are not ‘modern’ enough to be ornithurine). Feduccia’s ‘Ornithurae’ is predicated on the existence of a ‘Sauriurae’ or the paraphyletic group that contains these primitive taxa. The fact that *Apsaravis* and our analyses add to the mounting evidence^{3,4} against sauriurine monophyly has been overlooked in Feduccia’s estimation of the importance of *Apsaravis*.

Other specimens that we did not consider are problematic and underscore the importance of well preserved and phylogenetically placed taxa such as *Apsaravis*. Feduccia did not include the fragmentary *Otogornis*, *Ambiortus* and *Gansus* in his analyses⁵. Although he claims that *Chaoyangia* possesses a “toothed skull”, the holotype actually consists only of a torso and partial hindlimbs. The “toothed skull” belongs to a specimen once referred to as *Chaoyangia*⁵ but later identified as the holotype of *Songlingornis linghensis*⁶. This specimen cannot be referred to *Chaoyangia* (as indeed it has not been⁶) as no element known from the holotype is also represented in the referred specimen.

Although we did not comment on the implications of *Apsaravis* for the timing of the origin of Aves, Feduccia’s conjecture that it cannot inform our understanding of this origin (because it is not part of an extant lineage) is incompatible with his own arguments. In recounting the origin of Aves, he invokes taxa such as ichthyornithiforms and hesperornithiforms, which are not parts of extant lineages. Furthermore, it has been argued⁷ that gap analyses may be consistent with Cretaceous or Tertiary diversification of avian lineages, depending on what model of diversification rate and recovery potential is considered realistic.

Reasoning derived from phylogenetic analysis is a powerful way to test hypotheses of relationships or the evolution of morphology (for example, enantiornithine monophyly and novelties in the flight apparatus). We used a phylogenetic test to assess the idea that transitional ‘shore birds’ gave rise to all extant birds through an ecological bottleneck¹.

If such a bottleneck occurred, then when ecology is bracketed phylogenetically for living birds, ‘shore bird’ morphology and ecology should be basal to the crown clade, as well as in its nearest sister taxa. However, virtually all molecular and morphological evidence places ‘land birds’ (tinamous, ratites, galliforms and anseriforms, for example) at the base of Aves^{8,9}. Charadriiformes, the extant lineage referred to as

shore birds, are placed as derived forms within Aves^{8,9}. Thus, if the ecologies that are basal to the crown clade are bracketed, no support is found for such a bottleneck.

Apsaravis, because of its phylogenetic placement, constrains the inference of the ecologies of the most recent common ancestor of the avian crown clade. We do not understand how an ornithurine with no ‘shore bird’ morphologies, from a dune-field¹⁰, can be interpreted as compatible with Feduccia’s idea¹ of ecological restriction of these taxa to shorelines and marine environments. If *Apsaravis* can simply be assumed, without consideration of phylogenetic tests, to have flown from an unknown nearby lake, then we do not see how Feduccia’s hypothesis is testable.

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Furtive mating in female chimpanzees

Pascal Gagneux, David S. Woodruff & Christophe Boesch
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In this genetic analysis of a community of chimpanzees in the Tai forest, Côte d’Ivoire (carried out in 1994), we concluded that 7 out of 13 offspring were sired by males not found in the mother’s social group. Now a study of paternity using quantified and automated methods shows that the incidence of extra-group paternity is much lower (1 out of 14 offspring; ref. 1). Direct comparison at the only satellite locus re-examined reveals that 10 out of 66 alleles (15%) and 9 out of 33 individuals (27%) were inaccurately genotyped. Possible sources of error in the first study include allelic dropout in the amplification of degraded DNA from field-collected samples of shed hair, inconsistent visual autoradiograph interpretation (stutter bands), contamination and sample mix-up. The new analysis confirms that extra-group paternity can occur in nature, but shows that the social community probably corresponds to the reproductive unit in chimpanzees.

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