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Xing Xu[a] & Diego Pol[b]
[a] Key Laboratory of Evolutionary Systematics of VertebratesInstitute of Vertebrate Paleontology & Paleoanthropology, Chinese Academy of Sciences, 142 Xiwai Street, Beijing 100044, China
[b] [b]CONICET, Museo Paleontológico Egidio Feruglio, Avenida Fontana 140, Trelew 9100, Chubut, Argentina
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# *Archaeopteryx*, paravian phylogenetic analyses, and the use of probability-based methods for palaeontological datasets

Xing Xu[a]* and Diego Pol[b]

[a]*Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology & Paleoanthropology, Chinese Academy of Sciences, 142 Xiwai Street, Beijing 100044, China;* [b]*CONICET, Museo Paleontológico Egidio Feruglio, Avenida Fontana 140, Trelew 9100, Chubut, Argentina*

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*Archaeopteryx*, which has often been considered the earliest avialan, is an iconic species, central to our understanding of bird origins. However, a recent parsimony-based phylogenetic study shifted its position from within Avialae, the group that contains modern birds, to Deinonychosauria, the sister-taxon to Avialae. Subsequently, probability-based methods were applied to the same dataset, restoring *Archaeopteryx* to basal Avialae, suggesting these methods should be used more often in palaeontological studies. Here we review two key issues: arguments recently advocated for the usefulness of probability-based methodologies in the phylogenetic reconstruction of basal birds and their close relatives, and support for different phylogenetic hypotheses. Our analysis demonstrates that *Archaeopteryx* represents a challenging taxon to place in the phylogenetic tree, but recent discoveries of derived theropods including basal avialans provide increased support for the deinonychosaurian affinities of *Archaeopteryx*. Most importantly, we underscore that methodological choices should be based on the adequacy of the assumptions for particular kinds of data rather than on the recovery of preferred or generally accepted topologies, and that certain probability methods should be interpreted with caution as they can grossly overestimate character support.

**Keywords**: *Archaeopteryx*; Avialae; Deinonychosauria; parsimony-based methods; probability-based methods

## Introduction

*Archaeopteryx* has been considered the most primitive and earliest known bird ever since its discovery, and has been placed at the base of Avialae in nearly all numerical phylogenetic analyses (Gauthier 1986). However, Xu *et al*. (2011) recently challenged this phylogenetic hypothesis and placed *Archaeopteryx* within Deinonychosauria, a nearly globally distributed, highly diverse group of predatory dinosaurs ranging from approximately 40 to 1100 cm in body length (Britt *et al.* 2001; Hu *et al.* 2009), varied in general morphology (e.g. short- to long-armed), and utilizing a range of locomotor systems (terrestrial to flying forms) (Xu *et al.* 2003; Hu *et al.* 2009; Zheng *et al.* 2010). This new phylogenetic result significantly impacts our understanding of various issues related to the origins of birds, such as the structural transformation to the highly flight-adapted avialan body-plan, the ecological origin of the group, and the origin of flapping flight (Hecht *et al.* 1985). For example, the alternative systematic positions of *Archaeopteryx* bear differently on the evolution of avialan cranial kinesis (Chiappe *et al.* 1999), given that *Archaeopteryx* differs from other known basal avialans in lacking a postorbital bar (Wellnhofer 2009); the removal of *Archaeopteryx*, most probably a predatory animal (Wellnhofer 2009), from the base of Avialae, has major implications for assessing different scenarios regarding the ecological origin of Avialae and of flapping flight (Ostrom 1974, 1976). Consequently, this new phylogenetic result has gained much attention and received immediate comments (Lee & Worthy 2012; Witmer 2011; Turner *et al.* 2012). One of these comments questioned the deinonychosaurian affinities of *Archaeopteryx* by applying probability-based methods to the dataset of Xu *et al.* (2011). Given the importance of the systematic position of *Archaeopteryx* for understanding the origin of birds and the arguments that probability-based methods are more useful in palaeontological phylogenetic analyses, we believe that it is important to evaluate whether the arguments of Lee & Worthy (2012) are valid.

Some taxonomic issues associated with the definition of major clades related to basal birds and their close relatives require clarification (Fig. 1). Traditionally the vernacular term ‘birds’ has been equivalent to the technical taxon ‘Aves’, originally proposed to include all living birds (Linnaeus 1758). However, discoveries of fossil birds, particularly Mesozoic ones, required the expansion of Aves to include extinct birds, and *Archaeopteryx* has been placed within Aves since its discovery in 1861 (von Meyer 1861). Aves has been explicitly defined (Gauthier 1986) as the least

*Corresponding author. Email: xingxu@vip.sina.com

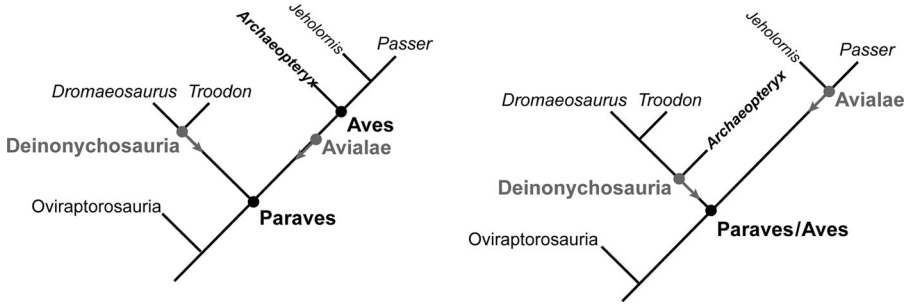


**Figure 1.** Major paravian clades under traditional and new paravian phylogeny.



inclusive clade containing *Passer domesticus* (Linnaeus, 1758) and *Archaeopteryx lithographica* (von Meyer, 1861), and this definition is followed here. The other important taxa are Avialae and Paraves. The former is defined as the most inclusive clade containing *Passer domesticus* (Linnaeus, 1758) but not *Dromaeosaurus albertensis* (Matthew & Brown, 1922) or *Troodon formosus* (Leidy, 1856), and the latter is defined as the least inclusive clade including *Passer domesticus* (Linnaeus, 1758) and *Dromaeosaurus albertensis* (Matthew & Brown, 1922). Recent studies demonstrate that basal members of Avialae and Paraves have feathers and other characteristics implying flight capability (Forster *et al.* 1998; Xu *et al.* 2003, 2011; Makovicky *et al.* 2005), and thus besides Aves, both Avialae and Paraves are also proper technical taxa equivalent to birds.

## Systematic position of *Archaeopteryx* and the choice of phylogenetic methods

*Archaeopteryx* has been considered to be a basal avialan in most phylogenetic studies because it possesses many derived features that were previously known only among avialans (Gauthier 1986; Sereno 1999; Holtz 2000; Norell *et al.* 2001; Turner *et al.* 2007; Hu *et al.* 2009; Choiniere *et al.* 2010; Senter *et al.* 2012). However, some previous studies noted derived similarities shared by *Archaeopteryx* and dromaeosaurids (Paul 1988; Forster *et al.* 1998; Mayr *et al.* 2007). Noteworthy are two previously published parsimony-based analyses (Forster *et al.* 1998; Mayr *et al.* 2005) that recovered a monophyletic group comprised of *Archaeopteryx* and some unenlagiid theropods, which are considered to be basal dromaeosaurids in most recent studies (Makovicky *et al.* 2005; Turner *et al.* 2007; Xu *et al.* 2011; Senter *et al.* 2012), though to be basal avialans in some other studies (Novas & Puerta 1997; Forster *et al.* 1998; Agnolín & Novas 2011; O'Connor *et al.* 2011). Furthermore, some recent studies were unable to confirm the avialan affinity of *Archaeopteryx* (Mayr *et al.* 2005; Naish *et al.* 2011).

Interestingly, while recently discovered basal avialans such as scansoriopterygids and sapeornithids increase the morphological distance between *Archaeopteryx* and other basal avialans (Zhang *et al.* 2008; Hu *et al.* 2010; Xu *et al.* 2010), on the other hand, newly discovered basal deinonychosaurs (Xu *et al.* 1999, 2000, 2002; Makovicky *et al.* 2005; Novas & Pol 2005; Turner *et al.* 2007; Hu *et al.* 2009; Novas *et al.* 2009) decrease the morphological distance between *Archaeopteryx* and derived non-avialan theropods. Many features previously used to support the avialan status of *Archaeopteryx* (particularly those features related to flight capability), have now been demonstrated to characterize a more inclusive group including deinonychosaurs, or have appeared in other non-avialan taxa (Xu *et al.* 2010; Carr *et al.* 2011). This has resulted in a decrease in the number of unique features shared by *Archaeopteryx* and Avialae that are absent among deinonychosaurs and has led to the suggestion that *Archaeopteryx* may be a deinonychosaur rather than an avialan (Xu *et al.* 2010). A few recent phylogenetic analyses have retrieved *Archaeopteryx* outside Avialae (e.g. Naish *et al*. 2011; Xu *et al*. 2011). In particular, the parsimony-based analysis of Xu *et al*. (2011) recovered *Archaeopteryx* as a basal deinonychosaur, supporting earlier morphological observations (Xu *et al*. 2010).

Recently, Lee & Worthy (2012) applied probability-based methods to the dataset of Xu *et al.* (2011) and recovered *Archaeopteryx* as a basal avialan with strong statistical support. These authors conducted two types of probabilistic analyses: maximum likelihood and Bayesian analysis. In both analyses they assumed all characters evolved through a homogeneous Markov model, in which all transformations between character states have equal probability. This is known as the Mk model (Lewis 2001) and is a generalized version of the simplest model developed for nucleotide substitutions (JC model; Jukes & Cantor 1969). Both analyses also incorporated the gamma distribution (Yang 1996) to account for variations in rates among characters. In the maximum likelihood analysis Lee & Worthy (2012) assessed statistical support using character bootstrap (Felsenstein 1985), and in the Bayesian analysis they used

the frequency of clade recovery in the topologies found during the Monte Carlo Markov Chain (MCMC) as an estimate of the posterior probability of each clade (see Huelsenbeck *et al*. 2001).

Arguably, the most important difference with parsimony analysis is that in these probability-based methods each branch of the tree has a given 'length' that is equally applied to all characters in order to determine the probability of change along that branch. The branch length is a combination of rate of evolution and time, and is a structural parameter because it is homogeneously applied to the entire dataset. When the gamma distribution is incorporated character rates are allowed to vary but in a homogeneous way across branches, so that the ratio of the length of any two branches in the tree remains constant for all categories of character rates. In maximum likelihood analyses the length of each branch is optimized for each topology to maximize the likelihood of the tree (i.e. the probability of the data being generated by the model, the topology and the branch lengths). In Bayesian analyses the branch lengths are randomly changed during the MCMC, as much as any other parameter of the model (including topology). Tuffley & Steel (1997) noted that the results of a parsimony analysis can be reproduced by a maximum likelihood approach in which each character has its own set of branch lengths, meaning that along the same branch of the tree the probability of change of one character is completely independent of the probability of change in other characters. In sum, the homogeneity versus heterogeneity in the evolutionary rates of different characters is one of the key differences between the probability-based and parsimony approaches.

Lee & Worthy (2012) concluded that their analysis suggested that probability-based methods can be useful and should be used more often in palaeontological phylogenetic analyses. We discuss several of the arguments related to the contribution of Lee & Worthy (2012) in support of this claim, commenting on the interpretation of topological results, the adequacy of different methods, the role of measures of nodal support, and their specific concerns on the role of homoplastic characters related to the alternative positions of *Archaeopteryx*.

## Topological results and choice of phylogenetic methods

As noted in the original study by Xu *et al*. (2011), character support for the deinonychosaurian affinities of *Archaeopteryx* is relatively low, as measured by Bremer and bootstrap values in the parsimony analysis. Given this scenario it is not surprising that by varying the assumption of the analysis (i.e. the method), poorly supported regions of the tree will change – poorly supported clades represent grouping hypotheses that are not robust. For instance, a phenetic analysis of the original dataset (with mean number of pairwise character difference and a heuristic search using minimum evolution or least-squares objective functions) also provides a tree that shows a more orthodox placement of *Archaeopteryx*, but this can hardly be considered a reason for deciding that these methods are appropriate for palaeontological phylogenetic analyses. The inadequacy of phenetic methods for reconstructing the evolutionary history of a group of organisms in comparison with parsimony has been most clearly demonstrated by Farris (1979, 1980, 1982), who showed the superiority of parsimony in terms of descriptive efficiency, information content and explanatory power. While it is interesting to note that different methods produce different results concerning the systematic position of *Archaeopteryx*, highlighting the murky boundary between birds and other derived theropods (Lee & Worthy 2012), the recovery of a preferred topological result is irrelevant for recommending the use of a phylogenetic method.

If the recovery of traditional topological results was indeed relevant for considering the usefulness of a method for morphological phylogenetics, there are other aspects of the results of Lee & Worthy (2012) that are highly unorthodox in comparison with previous phylogenies. For example, as also recently noted by Turner *et al.* (2012), the probability-based analysis did not recover a monophyletic Tyrannosauroidea, a clade recovered by nearly all recently published analyses (Gauthier 1986; Sereno 1999; Holtz 2000; Norell *et al.* 2001; Turner *et al.* 2007; Hu *et al.* 2009; Choiniere *et al.* 2010). Also, these analyses did not recover a close relationship between *Archaeopteryx* and *Wellnhoferia*, taxa that have been considered synonymous by many authors (Senter & Robins 2003; Wellnhofer 2009). The support values of the probability-based analyses in favour of the paraphyletic arrangement of the pair *Archaeopteryx* and *Wellnhoferia*, however, are extremely low for both maximum likelihood and Bayesian analysis. Nonetheless, these are unusual results for a coelurosaurian phylogeny, but as noted above the choice of a phylogenetic method should not be based on the result of orthodox or unorthodox topologies.

## Assumptions and choice of phylogenetic methods

When deciding which phylogenetic method is going to be used, it is critical to ask what we are willing to assume about the nature of the data being analysed (morphological characters in this case). It has long been debated whether parsimony or probability-based methods are better for phylogenetic reconstruction. Probability-based methods are widely used in molecular systematics and they have been demonstrated to be superior to other methods under some

specific circumstances (i.e. when characters evolve under a homogeneous Markov model) (Huelsenbeck & Hillis 1993; Huelsenbeck 1995; Swofford *et al*. 2001; Felsenstein 2004; Huelsenbeck *et al*. 2011). However, even in ideal cases in which the evolutionary model perfectly fits the assumed model of the probabilistic method, there are particular cases or biases that affect the efficiency of both maximum likelihood (Pol & Siddall 2001) and Bayesian analyses (Pickett & Randle 2005; Goloboff & Pol 2005).

A relevant point here is that when the analysed data deviates from the homogeneity imposed by the homogeneous Markov model, probability-based methods that assume such models can be severely affected (e.g. leading to statistical inconsistency) (Chang 1996). In fact, parsimony has been shown to perform better in simulations where characters evolve heterogeneously (Kolaczkowski & Thornton 2004; Goloboff & Pol 2005; Simmons *et al*. 2006), which is a reasonable scenario for morphological character evolution. Although popularity is not a criterion to judge scientific methods, it is worth noting that the vast majority of recent morphological phylogenetic studies have used parsimony, clearly demonstrating the lack of acceptance of homogeneous Markov models among morphologists and particularly among palaeontologists (but see below). The incorporation of some degree of rate heterogeneity in probability-based methods, such as the gamma distribution, allows rates to vary across the phylogeny and usually explains the data significantly better than when assuming a single constrained rate (Yang 1996). Such an approach has been followed by Lee & Worthy (2012) and some other morphologists in Bayesian analyses applied to morphological datasets (Müller & Reisz 2006; Smith & Kear 2013). Admittedly, this could help to address some issues, but the available probability-based methods cannot accommodate many other heterogeneous conditions (i.e. heterotachy; see Kolaczkowski & Thornton 2004). Along these lines, Clarke & Middleton (2008) proposed the use of data partitioning, as well as the inclusion of autapomorphies (see also Müller & Reisz 2006), as a better way to estimate rates of change for morphological characters in Bayesian analyses.

Furthermore, the performance of probability-based methods in cases in which there are abundant missing entries in the dataset (an inherent property of palaeontological data matrices) is poorly understood. Analyses of both simulated and empirical datasets demonstrate that probability-based methods can be severely affected by abundant missing data (Goloboff & Pol 2005; Lemmon *et al.* 2009; Simmons 2011, 2012). There are disagreements about these problems (see Wiens & Morrill 2011) and numerous issues still need to be investigated. Furthermore, the extent of these problems in empirical studies of palaeontological matrices has not yet been investigated. Nonetheless, these studies suggest a cautionary interpretation of the application of probability-based methods for analysis of palaeontological data with copious (and usually non-randomly distributed) missing entries.

## The role of measures of nodal support

Different methods have different ways of evaluating the robustness of the recovered clades and these measures aim to assess the confidence, credibility, or simply the strength of the analysed data for supporting the monophyly of a given clade, depending on the phylogenetic method (e.g. likelihood, Bayesian, parsimony) and the interpretation of these procedures (Felsenstein 1985; Farris *et al.* 1996; Giribet 2003; Goloboff *et al.* 2003). Posterior probability is the measure of credibility of the recovered clades in Bayesian analyses and bootstrap values are widely used to estimate nodal support in various other phylogenetic methods (including parsimony and maximum likelihood). Posterior probability and bootstrap percentage are two different metrics, and they are neither tightly correlated (Douady *et al.* 2003; Wilcox *et al.* 2003) nor directly comparable (Simmons *et al.* 2004). Several studies have demonstrated that the posterior probability values of Bayesian analyses are consistently higher than bootstrap values and overestimate nodal support (Douady *et al.* 2003; Han 2010), whereas bootstrap values are usually overly conservative (Douady *et al.* 2003; Wilcox *et al.* 2003). As noted by Simmons *et al*. (2004), however, the magnitude by which Bayesian values overestimate support can be markedly large and therefore should not be considered as a good indicator of the reliability of recovered clades.

The analyses conducted by Lee & Worthy (2012) resulted in relatively high support for the avialan affinities of *Archaeopteryx* (73% bootstrap) in the case of the likelihood analysis and a posterior probability of 1 in the case of the Bayesian analysis. Despite these measures indicating a strong statistical support for the avialan affinities of *Archaeopteryx*, Lee & Worthy (2012) concluded that both positions of this taxon remain plausible and that their results do not demonstrate that *Archaeopteryx* belongs to Avialae rather than Deinonychosauria. They further acknowledged that the posterior probability of 1 in the case of the Bayesian analysis may not be meaningful since Bayesian inference can greatly overestimate support if the models implemented are inadequate for the data. Given this situation it is hard to understand the major conclusion of Lee & Worthy (2012): that these methods can be useful and should be used more often in morphological phylogenetics. This is particularly the case for the Bayesian analyses and the posterior probabilities derived from them, if the assumed model is acknowledged to be inadequate and if the method can grossly overestimate nodal support. Irrespective of the actual phylogenetic position of *Archaeopteryx*, it is the use of parsimony and its measures of support that are informing us that both positions remain plausible rather than the misleading

information provided by the Bayesian posterior probabilities. In this case, the bootstrap frequencies of the maximum likelihood analysis provide intermediate values between the bootstrap frequencies of the parsimony analysis and the Bayesian posterior probabilities. Although the method of character resampling is the same in the bootstrap under parsimony and maximum likelihood, the assumptions of each method are not, and therefore support measures are not expected to be necessarily similar (especially if the model assumed for the likelihood analysis is inadequate, as suggested by Lee & Worthy 2012).

## Homoplastic characters and choice of phylogenetic methods

In comparing the probability- and parsimony-based methods applied to the same dataset on coelurosaurian phylogeny, Lee & Worthy (2012) found that the deinonychosaurian status of *Archaeopteryx* is supported by more synapomorphies but that these characters are more homoplastic than those supporting the avialan affinities of *Archaeopteryx* (which are fewer but less homoplastic). An important issue related to this argument is the role of homoplasy for assessing the reliability of characters and the choice of a phylogenetic method.

Homoplasy is common among theropod dinosaurs (Holtz 2001), but the parsimony method is not systematically affected simply by a large number of homoplasies (Farris 1983). There are well known but very specific circumstances under which homoplasies can lead parsimony to reconstruct erroneous phylogenies (i.e. long-branch attraction; see Felsenstein 1978). This would be a problem if homoplasies are concentrated on particular branches and all characters evolve under a homogeneous process, although this is hardly applicable to morphological characters. Moreover, it has been empirically demonstrated that highly homoplastic characters can contribute to recovering clades at different hierarchical levels in parsimony analyses (Kallersjo *et al.* 1999).

A key point is that the lack of homoplasy in characters that support the traditional position of *Archaeopteryx* is not justification for choosing a probabilistic method. Several parsimony methods have been proposed for down-weighting homoplastic characters, favouring the grouping information provided by non-homoplastic characters, such as implied weights (Goloboff 1993, 1995; Goloboff *et al.* 2008). If a researcher aims to use a method that down-weights homoplastic characters in favour of non-homoplastic characters, there are methodological options that do not require the use of "models that are inadequate", p. 302 (as stated by Lee & Worthy 2012) for the analysed data. Running the dataset of Xu *et al.* (2011) with parsimony under implied weights in TNT (Goloboff *et al.* 2008) places *Archaeopteryx* at the base of Avialae in all most parsimonious trees, a point also recently noted by Turner *et al.* (2012). This result is the traditional topology (much as the one obtained by probabilistic methods) and is obtained across a relatively broad range of values for the parameter *k* (between 3 and 10; where *k* is the constant that determines the strength used to down-weight homoplasy; see Goloboff 1993). Using milder penalties of homoplasy in the character weighting function (i.e. *k* values larger than 10) retrieves *Archaeopteryx* in the same position as the equally weighted parsimony analysis.

Another relevant point related to this issue is that support measures calculated under parsimony with implied weights (under all values of *k*) indicate the clade that clusters *Archaeopteryx* and avialans is extremely weakly supported. Bootstrap values for the clade formed by *Archaeopteryx* and avialans are low (below 50%), and over 30% of the bootstrap replicates place *Archaeopteryx* together with deinonychosaurs. In the case of Bremer support, the value obtained for the clade that joins *Archaeopteryx* and avialans is the lowest out of all nodes in the tree (i.e. 0.01, measured in differences in fit; see Goloboff 1993). The parsimony analyses, using either equally weighted parsimony or implied weighing, indicate that placing *Archaeopteryx* (and *Wellnhoferia*) at the base of the Avialae or in different positions at the base of Deinonychosauria are all nearly optimal hypotheses in the dataset of Xu *et al*. (2011); this highlights how these methodological approaches accurately reflect the character conflict and the absence of strong support for alternative placements of this iconic taxon.

In sum, if homoplasy is interpreted as an indicator of the reliability of characters for phylogenetic reconstruction, the use of parsimony with implied weights would be a more appropriate methodological choice. Furthermore, rather than assigning a misleading maximum probability value to a poorly supported clade (as in the case of the inclusion of *Archaeopteryx* at the base of Avialae in the Bayesian analysis), the use of parsimony methods at least provides support measures that actually reflect the lack of strong character support for alternative arrangements at the base of Paraves. As noted above, the maximum likelihood approach provides a moderately strong bootstrap support value (73%) for placing *Archaeopteryx* at the base of Avialae, being intermediate between the maximum value obtained in the Bayesian analysis and the low frequencies of this and other topological resolutions of part of the tree in the parsimony bootstrap.

## Support for alternative placements of *Archaeopteryx*

In phylogenetic analyses, the generated cladograms and associated support values for the recovered clades are determined by the dataset used for phylogenetic analysis,

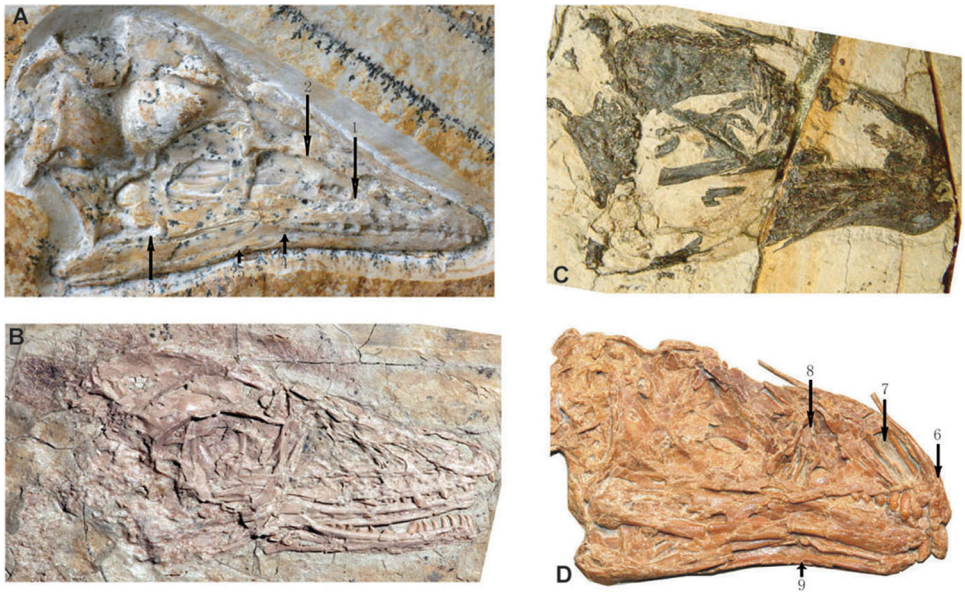


**Figure 2.** Cranial morphologies of selected paravians. **A,** Eichstätt *Archaeopteryx*; **B,** basal dromaeosaurid *Microraptor*; **C,** basal avialan *Jeholornis*; **D,** sapeornithid *Shenshiornis*. 1, Enlarged promaxillary foramen; 2, long lacrimal anterior process; 3, small jugal posterior process; 4, groove widening posteriorly on dentary lateral surface; 5, large splenial lateral exposure; 6, enlarged premaxilla; 7, dorsally located external naris; 8, antorbital fenestra much higher than long; 9, dentary with convex dorsal margin and concave ventral margin.



specifically, the choices of characters, character states, and the taxonomic sample as much as by the methods used for phylogenetic analysis (in this case, parsimony- versus probability-based methods). We underscore that, although the choice of an adequate phylogenetic method for the data at hand is a relevant issue (see above), real progress in determining the currently poorly supported phylogenetic affinities of *Archaeopteryx* will only be achieved through more detailed, extensive, and careful anatomical studies, as well as through the discovery of new taxa with unique combinations of characters.

Because many recent dinosaurian phylogenetic analyses differ from each other in these aspects, the results of these analyses are difficult to compare directly. One way to improve the accuracy of dinosaurian phylogenies is to reduce differences in character choice, character states (Sereno 2007) and OTUs (Graybeal 1998; Hillis 1998), as well as to increase overall matrix size and improve scoring quality. Recent progress in this direction has been made by Turner *et al*. (2012) in a review of paravian phylogeny, in which some character scorings relevant to the phylogenetic position of *Archaeopteryx* and other maniraptorans (e.g. *Epidendrosaurus*, *Epidexipteryx*) of the dataset published by Xu *et al*. (2011) are discussed (Turner *et al*. 2012, p. 139).

Here we compare character support for alternative placements of *Archaeopteryx*, discuss the character evidence that suggests the deinonychosaurian affinity of *Archaeopteryx* (Figs 2–4), and finally note the simpler scenario in terms of major structural and ecological transformations of the deinonychosaurian hypothesis.

Lee & Worthy (2012) stated that evenly spaced anterior teeth are unique to *Archaeopteryx* and birds (character 89), whereas in fact this is the plesiomorphic condition present in all theropods except for *Xiaotingia*, *Anchiornis* and troodontids (Makovicky & Norell 2004). This character does indeed provide information against grouping *Archaeopteryx* with *Xiaotingia* and *Anchiornis* (i.e. Archaeopterygidae), but does not provide any specific information regarding the avialan affinities of *Archaeopteryx* (e.g. either at the base of Deinonychosauria or at the base of Avialae). The only homoplasy-free character in the data matrix of Xu *et al*. (2011) that provides information for placing *Archaeopteryx* within Avialae is the presence of flattened plate-like proximal chevrons (character 122). However, the scoring of this character in the data matrix of Xu *et al*. (2011), which was derived from the matrix of Senter (2007), might be problematic; based on our recent observations, the most anterior chevrons are rod-like in at least the Munich and Solnhofen *Archaeopteryx* specimens (Fig. 2C).

To clearly state the characters that provide support for a basal deinonychosaurian placement of *Archaeopteryx* against its traditionally accepted basal avialan position, we note the following features that are distributed across the skeleton. Several of these characters are uniquely shared by *Archaeopteryx* and deinonychosaurs among maniraptoran theropods (indicated by asterisks): a groove that widens posteriorly on the lateral surface of the dentary* (Character 72; Fig. 2A); a humerus with a proximodistally elongate internal tuberosity (Fig. 3D, E); manual phalanx IV-2

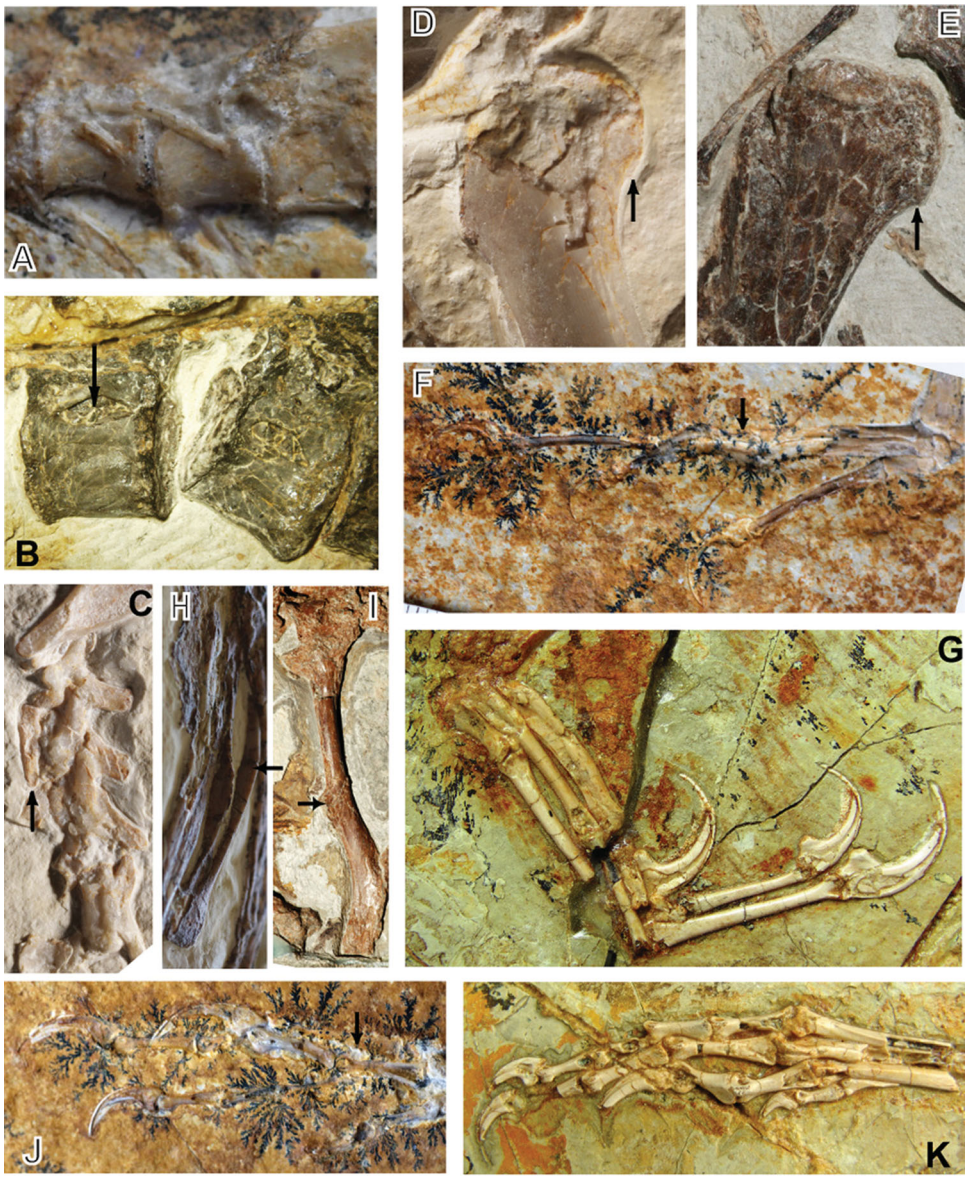


**Figure 3.** Postcranial morphologies of selected paravians. **A,** posterior dorsals of Eichstätt *Archaeopteryx*; **B,** posterior dorsals of basal avialan *Jeholornis*; **C,** anteriormost caudals of Munich *Archaeopteryx*; **D,** humerus proximal end of Munich *Archaeopteryx*; **E,** humerus proximal end of basal dromaeosaurid *Microraptor*; **F,** manus of Eichstätt *Archaeopteryx*; **G,** manus of basal deinonychosaurian *Xiaotingia*; **H,** pubes of Solnhofen *Archaeopteryx*; **I,** pubis of basal dromaeosaurid *Microraptor*; **J,** pedal digits of Eichstätt *Archaeopteryx*; **K,** pedal digits of basal deinonychosaurian *Xiaotingia*.

considerably shorter than IV-1 (Fig. 3F, G); manual phalanx IV-3 longer than IV-1 and IV-2 combined (Fig. 3F, G); an ilium with a shallow and tapered posterior end (Fig. 4); pubic mid-shaft laterally expanded (Fig. 3H, I); a very short, uniquely shaped ischium with a distally placed dorsal process* (Characters 167 and 306; Fig. 4D–G); and distal ends of pedal phalanges II-1 and II-2 strongly expanded anteriorly and ungual II enlarged* (Character 323; Fig. 4J, K). Furthermore, *Archaeopteryx* and basal deinonychosaurs (i.e. basal troodontids and basal dromaeosaurids) share the following set of characters that are unique among paravians and their closest outgroup (Oviraptorosauria), although we note that some of them are absent in derived dromaeosaurids: a low anterior end of the rostrum; a large promaxillary fenestra (Fig. 2A, B); a large antorbital fenestra (Character 365; Fig. 2A, B); a T-shaped lacrimal with a long anterior process (Character 372; Fig. 2A, B); a jugal that does not contact the postorbital (Fig. 2A, B); a small mandibular fenestra (Character 367; Fig. 2A); a coracoid with the anterior edge expanded ventral to the glenoid

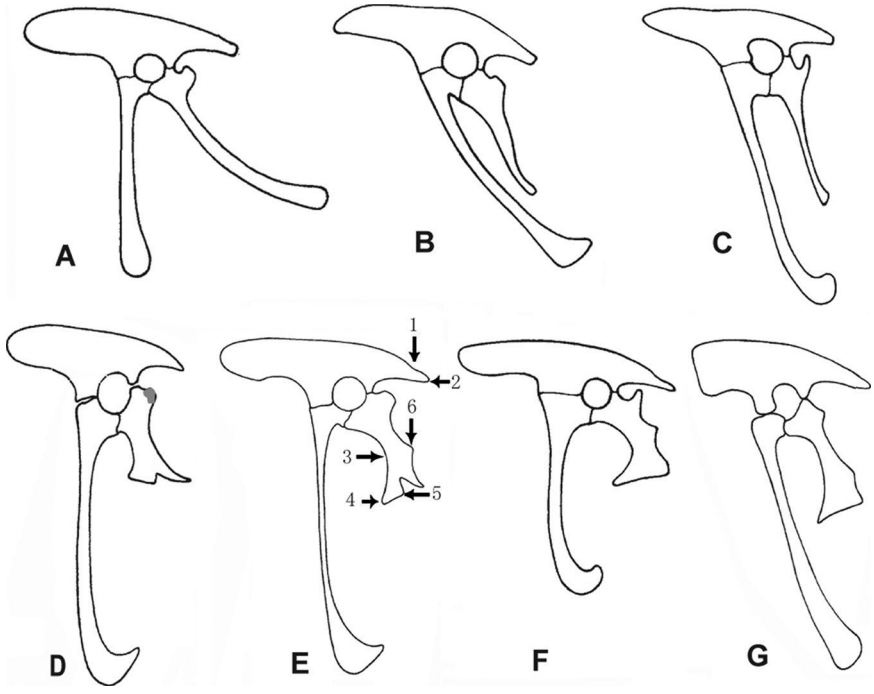


**Figure 4.** Pelvis of selected paravians. **A,** basal avialan *Epidexipteryx*; **B,** basal avialan *Jeholornis*; **C,** basal avialan *Sapeornis*; **D,** basal deinonychosaurian *Anchiornis*; **E,** *Archaeopteryx*; **F,** basal dromaeosaurid *Rohonavis*; **G,** basal troodontid *Sinovenator*. 1, Concavity on posterodorsal margin of ilium; 2, tapered iliac posterior end; 3, short and broad ischium; 4, distally located obturator process; 5, quadrangular obturator process; 6, posterodorsal process on ischium.



fossa (Character 134); and a slender metatarsus that has a length/midshaft diameter ratio greater than eight (Character 335). *Archaeopteryx* also appears to have a laterally exposed splenial, as in Deinonychosauria (Fig. 2A, B), and a concavity on the posterodorsal margin of the ilium, as in some basal dromaeosaurids (Fig. 4). Unique within Coelurosauria, the obturator process of the ischium is quadrangular in both *Archaeopteryx* and *Anchiornis* (Fig. 4).

Features of the soft tissue preserved in several fossil specimens provide further character support. Traditionally, because soft tissue is rarely preserved, it provided very little informative phylogenetic information. However, recent discoveries of feathered non-avialan and avialan dinosaurs from China make it possible to use soft tissue information in phylogenetic reconstructions. For example, *Archaeopteryx*, *Anchiornis* and the basal troodontid *Jinfengopteryx* share a unique frond-like feathery tail in which rectrices are attached to both sides along the entire length (Ji *et al.* 2005; Hu *et al.* 2009; Wellnhofer 2009); the basal dromaeosaurid *Microraptor* is more similar to these taxa than basal avialans in regards to this feature (Xu *et al.* 2003). In comparison, oviraptorosaurs and basal avialans including *Jeholornis* have a fan-shaped feathery tail in which rectrices are restricted to the distal portion of the long bony tail. Furthermore, a recent study suggests that *Archaeopteryx* and *Anchiornis* have elongate coverts, differing from the much shorter ones in most other birds including *Confuciusornis* (Longrich *et al.* 2012). This feature is likely to be unique to the Deinonychosauria and to provide further support for the deinonychosaurian affinity of *Archaeopteryx*.

On the other hand, *Archaeopteryx* lacks many features seen in other basal avialans (Figs 2, 3A, B), including the scansoriopterygids, considered to be more basal than *Archaeopteryx* within Avialae in many studies (Zhang *et al.* 2008; Choiniere *et al.* 2010; Senter *et al.* 2012): a large premaxilla; a highly positioned external naris; an antorbital fenestra much higher than long; a short nasal; a dentary with convex dorsal margin and concave ventral margin; and posterior dorsals with large pneumatic foramina. All these characters imply extra steps in the dataset when *Archaeopteryx* is placed within Avialae; in comparison, there are fewer features shared by *Archaeopteryx* and Avialae that are absent in other theropods (Xu *et al.* 2011).

In addition to the phylogenetic characters discussed above, the hypothesis that *Archaeopteryx* is a basal deinonychosaurian implies a simpler scenario for the major changes in the structural and dietary evolution of coelurosaurs. Trees supporting deinonychosaurian affinities of *Archaeopteryx* suggest that the gracile and shallow cranium of *Archaeopteryx* and deinonychosaurs evolved at the base of the Deinonychosauria from the primitive condition (short and deep cranium) seen in oviraptorosaurs and basal avialans; cranial kinesis (indicated by loose contact

between the jugal and postorbital and the squamosal and quadratojugal, respectively) evolved at the base of the Deinonychosauria from the primitive akinetic skull seen in other maniraptorans (Chiappe *et al.* 1998; Xu & Norell 2004), including basal avialans (e.g. scansoriopterygids and sapeornithids) (Zhang *et al.* 2008; Hu *et al.* 2010). Placing *Archaeopteryx* within Avialae implies a more complex scenario for these major transformations.

In terms of dietary evolution, some recent studies have suggested that most coelurosaurian theropods were primarily herbivorous (Zanno & Makovicky 2011). All known basal avialans retain features that suggest a herbivorous diet; however, deinonychosaurs have features suggesting a reversal to the plesiomorphic carnivorous diet of basal theropods. The deinonychosaurian status of *Archaeopteryx* is compatible with a single ancestral diet change at the base of Deinonychosauria, given that *Archaeopteryx* is considered to have been insectivorous (Ostrom 1974; Wellnhofer 2009), whereas placing *Archaeopteryx* within Avialae requires two independent changes towards carnivory, in Deinonychoauria and in *Archaeopteryx*. However, it should be noted that other authors have inferred a high degree of dietary plasticity in Maniraptora, considering many coelurosaurians to be omnivorous (Barrett 2000); furthermore, even among herbivorous coelurosaurians, dietary habits were likely not uniform and there is evidence for dietary specialization, such as a probable follivorous diet in therizinosaurs (Barrett 2000) and a granivorous diet in the basal avialans *Jeholornis* and *Sapeornis* (Zhou & Zhang 2002, 2003).

## Discussion

We emphasize that shifting the systematic position of *Archaeopteryx* does not weaken the significance of this taxon, which remains unique both historically and evolutionarily (Witmer 2011). The morphology of the most basal taxa in a given clade is arguably the most critical for inferring the plesiomorphic condition and evolutionary origins of both the clade in question and its sister taxon. Even when it is positioned at the base of Deinonychosauria, *Archaeopteryx* provides significant information on the divergence between deinonychosaurs and avialans, and is a key taxon for understanding the origins of Avialae. However, a basal deinonychosaurian status of *Archaeopteryx* would indicate that the taxon sheds more light on the evolution of the lineage leading to *Velociraptor* than on the evolution of the lineage leading to extant birds, given that under this scenario *Archaeopteryx* is a basal member of a side branch in the evolutionary history of the birds. If the coelurosaurian phylogeny of Xu *et al.* (2011) is accepted, some recently discovered basal avialans such as scansoriopterygids and sapeornithids, which differ from *Archaeopteryx* in many respects, will probably become more important for the reconstruction of the primitive condition of Avialae. For example, although the relative length and thickness of the forelimbs of the scansoriopterygids *Epidendrosaurus* and *Epidexipteryx* are suggestive of flight capability, some other features are inconsistent with the presence of powered flight in at least these two taxa: *Epidendrosaurus* has an extremely long tail that is more than three times as long as the trunk, and *Epidexipteryx* appears to have no large pennaceous feathers associated with the forelimbs. In contrast, the deinonychosaurian *Archaeopteryx* and *Rahonavis* provide information on experimental trials in flight capability in an evolutionary side branch near the origin of the birds, though some recent studies have questioned the flight capabilities of *Archaeopteryx* (Nudds & Dyke 2010).

Admittedly the deinonychosaurian status of *Archaeopteryx* is poorly supported, as measured by different support measures in several kinds of parsimony analysis, and an avialan position of *Archaeopteryx* is only marginally suboptimal. However, the shifting of *Archaeopteryx* to Deinonychosauria is a result of the wealth of new anatomical information and the unexpected combination of characters in newly discovered feathered dinosaurs closely related to the origin of Avialae. The new information extracted from these dinosaurs has yet to be fully appreciated and further detailed anatomical studies may provide further character support for defining the deinonychosaurian affinities of *Archaeopteryx*.

We find no compelling reasons in the argument given by Lee & Worthy (2012) to support the recommendation that probability-based methods should be used more often in palaeontological and morphological studies. The utility of these methods for analysing this type of data certainly deserves further exploration as there are numerous issues that are not well understood (Goloboff & Pol 2005; Lemmon *et al.* 2009; Simmons 2011, 2012; Wiens & Morrill 2011). However, at the moment and for this particular case we found worrisome the recovery of exceedingly high support values that mask the existing character conflict regarding the phylogenetic position of *Archaeopteryx*, which is particularly marked in the case of the posterior probabilities of Bayesian analyses. Retrieving a more orthodox phylogenetic placement of *Archaeopteryx* is certainly not a reason for preferring one method over another, and if homoplasy is taken as a measure of reliability for characters in phylogenetic reconstruction we note there are variants of parsimony that have been developed for such purpose (e.g. Goloboff 1993, 1997).

It has been widely accepted that phylogenetic accuracy can be improved by adding characters and OTUs, and the placement of *Archaeopteryx* within the Deinonychosauria is a result of both adding new characters and the addition of a key taxon, *Xiaotingia*. However, some other recent phylogenetic analyses support the traditional placement of *Archaeopteryx* within Avialae (Agnolín & Novas 2011;

Senter *et al.* 2012; Turner *et al*. 2012), and the conflictive placements are at least in part due to different scorings which have been discussed in detail in these studies (Agnolín & Novas 2011; Turner *et al*. 2012). Future theropod phylogenetic work will benefit from these types of study, including a more explicit discussion and documentation of character scorings (e.g. comparative illustrations or measurements are necessary for each scoring). Such approaches will help to achieve progress and consensus in morphological systematic studies and will provide the necessary basis for resolving the controversial phylogenetic affinity of *Archaeopteryx* and understanding the origins of birds.



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