

The origin of birds: current consensus, controversy, and the occurrence of feathers

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Abstract

Research in the late 1900s has established that birds are theropod dinosaurs, with the discovery of feather preservation in non-avian theropods being the last decisive evidence for the dinosaur origin of this group. Partially due to the great interest in the origin of birds, more phylogenetic analyses of non-avian theropod dinosaurs have probably been published than for any other group of fossil vertebrates. Despite a lot of uncertainty in the exact placement of many taxa and even some major clades, there is a remarkable consensus about the hierarchical position of birds (here used for the total group, Avialae) within theropod dinosaurs. Thus, birds are part of Paraves, together with such well-known theropod groups as dromaeosaurids and troodontids; Paraves are part of Maniraptora, which furthermore include Oviraptorosauria, Therizinosauroidea and Alvarezsauridae; Maniraptora belong to Maniraptoriformes, which also include Ornithomimosauria; Maniraptoriformes are a subclade of Coelurosauria, to which Tyrannosauroidea and some other basal taxa also belong; Coelurosauria are part of Tetanurae, together with Allosauroidea and Megalosauroidea; finally, Tetanurae are a subclade of Theropoda, which also include Ceratosauria and Coelophysoidea.

Keywords: Theropoda; Avialae; Aves; phylogenetic hierarchy

Introduction

The transition of one major animal "bauplan" into another and the origin of evolutionary novelty has captured the interest and imagination of scientists and the general public alike, ever since the advent of evolutionary thought in the 19th century and its acceptance following the publication of Darwin's epochal book "On the origin of species" (1859). Birds are arguably the most extremely divergent example of a tetrapod bauplan, as they seem fundamentally different from their living reptilian relatives, crocodiles and lepidosaurs, in

almost any respect, from their anatomy, via neurology and physiology to their behaviour. Although recent research has shown that some of these differences are less marked than originally thought (e.g. important aspects of the avian-type flow-through lung are already present in lepidosaurs and crocodiles; Farmer and Sanders 2010; Schachner et al. 2013; see also Cieri and Farmer 2016), many of these evolutionary novelties of birds require complex and changing functional scenarios to explain their selective advantages, especially if many must be seen as exaptations to flight, rather than as consequences of this drastic change in locomotor behaviour. Thus, it is not surprising that the question of the origin of birds and the evolutionary history of their novelties has been a "hot topic" in evolutionary biology and palaeontology in the past 150 years. Understanding these evolutionary events requires a good idea of the interrelationships of bird ancestors, the origin of birds, and the phylogenetic relationships between early members of this clade.

The discovery of the first Mesozoic "bird", *Archaeopteryx lithographica*, only two years after the publication of Darwin's book (Meyer 1861a, b) marks a milestone in our quest of understanding bird origins (although, interestingly, both initial descriptions of this animal came from anti-Darwinists, who came to diametrically opposite conclusions: Andreas Wagner [1862] came to the conclusion that this animal clearly represents a somewhat odd lizard, whereas Richard Owen [1863] concluded that the fossil undoubtedly represented a bird). Especially the preservation of feathers in the limestone slab that contained the skeleton of this taxon was taken as a clear indication that this animal was a transitional fossil of importance for the question of the origin of birds, and soon after the discovery of *Archaeopteryx* (and the discovery of the small theropod dinosaur *Compsognathus* in the same year; Wagner 1861), Darwin's "bulldog" Thomas Henry Huxley published the hypothesis that birds were derived from small theropod dinosaurs (Huxley 1868). However, although this hypothesis fell on fertile ground in the beginning, other possibilities for the ancestry of birds were proposed subsequently, such as the Early Triassic basal archosauromorph *Euparkeria* (Broom 1913).

In his very influential book "The origin of birds", the Danish artist Gerhard Heilmann (1926) summarized the current knowledge on this topic. Although he clearly noticed the many similarities between dinosaurs and birds (especially in *Archaeopteryx*), Heilmann came to the conclusion that birds cannot be derived from dinosaurs, as all dinosaurs then known lacked clavicles, whereas the furcula in birds is generally considered to be derived from a fusion of these bones, which are present in reptiles ancestrally. Heilmann's very detailed and well-illustrated book had a lasting impact on the field and formed the basis for the common consensus for 50 years that birds were derived from some still unknown, probably arboreal, Triassic "Proavis".

In the wake of the "dinosaur renaissance" in the 1960ies and 1970ies, especially the discovery of the dromaeosaurid *Deinonychus* in North America (Ostrom 1969a, b), and a comparison of this taxon with newly discovered (Ostrom 1970, 1972; Wellnhofer 1974) and already known specimens of *Archaeopteryx* led Ostrom (1973, 1976) to revive the hypothesis of the dinosaur origin of birds. Not surprisingly, the hypothesis was met with skepticism (e.g. Martin et al. 1980; Tarsitano and Hecht 1980; Martin 1983), and a sometimes heated debate ensued over the following two and a half decades (see Witmer 2002; Prum 2002 for a summary).

One important aspect that led to the acceptance of the hypothesis of the theropod origin of birds was the advent of new phylogenetic methods, following the publication of Hennig's book "Phylogenetic systematics" in 1966. The cladistic methodology outlined in this work first found acceptance in vertebrate palaeontology in the 1980ies, and in a very influential paper published in 1986, Jacques Gauthier listed a total of 84 nested synapomorphies that supported the inclusion of birds in the theropod dinosaurs. Gauthier's paper was the first of a long list of phylogenetic analyses that support the inclusion of birds in the Theropoda, and our knowledge of this transition and the successive acquisition of avian characters has considerably increased since (see Chiappe 2009; Brusatte et al. 2015; Cau 2018; Agnolin et al. 2019).

The final push for the theropod hypothesis, however, came from the discovery of abundant feathered dinosaurs in the Cretaceous of China, starting in the late 1990ies (Chen et al. 1998; Ji et al. 1998; Xu et al. 1999a, b, 2001), and the subsequent realization that filamentous integumentary structures are widely distributed not only in theropod dinosaurs (Rauhut et al. 2012), but are even found in ornithischians (Zheng et al. 2009; Godefroit et al. 2014, this volume). In some instances, the interpretation of integumentary structures as feathers has been questioned, and the most detailed conflicting analyses interpreted these structures as degraded dermal collagen fibres (e.g. Lingham-Soliar 2003a, b, 2012; Lingham-Soliar et al. 2007) or other tissues (e.g. Lingham-Soliar 2010). However, these studies have been criticised on taphonomic, structural and methodological grounds (e.g. Mayr 2010; Smith et al. 2015; Smithwick et al. 2017), and thus cannot be sustained. Furthermore, the vast array of taxa in which feathers have now been reported plus the great variety of feather types identified (e.g. Xu & Guo 2009) make these alternative interpretations untenable.

Although the opponents of the theropod origin of birds have questioned the cladistic methodology altogether (e.g. Feduccia 1996, 2013), there is no other hypothesis for avian origins that has been formulated in any comparable detail (see Xu et al. 2014; Brusatte et al. 2015; Cau 2018), and the criticism seems to be rather ideological than scientific (Prum 2003; Smith et al. 2015). Thus, in the absence of contrary evidence, the theropod origin of birds can now be regarded as being firmly established, and it is on this background that we will discuss the current consensus and controversies surrounding the origin of birds. For recent reviews of the overwhelming evidence that birds are theropods see e.g. Xu et al. (2014), Brusatte et al. (2015), Smith et al. (2015), Mayr (2017), Cau (2018), and Agnolin et al. (2019).

Current consensus on the phylogeny of theropod dinosaurs and the origin of birds

Since the pioneering work of Gauthier (1986), numerous phylogenetic analyses of the interrelationships of theropod dinosaurs have been published (e.g. Novas 1992; Holtz 1994, 1998; Sereno 1997, 1999; Forster 1999; Rauhut 2003; Smith et al. 2007; Xu et al. 2009; Choiniere et al. 2010; Rauhut et al. 2010; Novas et al. 2015; Wang et al. 2017; Cau 2018), with many more analyses focusing on the different subclades of this clade. Interestingly, several of the main phylogenetic findings of Gauthier (1986) have consistently been confirmed, both in terms of tree topology as well as general taxonomic composition of several major clades, despite widely differing taxon and character sampling. Thus, these aspects of theropod phylogeny can be considered well established and largely uncontroversial.

All phylogenetic analyses including theropod dinosaurs agree that this clade is monophyletic, although there is some controversy as to whether certain basal taxa are members of Theropoda or not. Nevertheless, at least the monophyly of Neotheropoda (the clade including *Coelophysis* and modern birds [Sereno 1998]; the classical Theropoda before the discovery of a number of basal taxa; see Colbert 1964) has never been questioned. Within Theropoda, a number of mainly Late Triassic and Early Jurassic taxa (sometimes included in a single lineage named Coelophysoidea), but also the clade Ceratosauria, which reached the Cretaceous/Paleogene boundary, are consistently found as basal forms outside a more derived clade which was named Tetanurae by Gauthier (1986). The interrelationships of these basal forms are still debated; although basically all phylogenetic analyses agree in the existence of two monophyletic clades, the Coelophysoidea (Fig. X-1A) and the Ceratosauria (Fig. X-1B), the referral of numerous taxa to either one of these clades remains controversial. Furthermore, whereas many early phylogenetic analyses recovered Coelophysoidea and Ceratosauria in a monophyletic clade (for which Gauthier [1986] used the name Ceratosauria; see e.g. Gauthier 1986; Holtz 1994, 1998; Sereno 1997, 1999; but also Allain et al. 2007 as a more recent example), there is an emerging consensus that Ceratosauria represent the sister-taxon to Tetanurae to the exclusion of Coelophysoidea (e.g. Rauhut, 1998, 2003; Forster 1999; Carrano et al. 2002; Smith et al. 2007; Xu et al. 2009; Novas et al. 2015; Wang et al. 2017; Cau 2018) in a clade that was named Averostra by Paul (2002; see also definition by Ezcurra and Cuny 2007).

Whereas Coelophysoidea seems to represent the first successful radiation of theropod dinosaurs in the Triassic and includes both taxa from the Late Triassic and Early Jurassic, the earliest averostrans are Early Jurassic in age (see Dal Sasso et al. 2018), and there is growing evidence that an explosive radiation of this clade in the latest Early to Middle Jurassic might have been triggered by the Pliensbachian/Toarcian extinction event (Pol and Rauhut 2012; Rauhut and Carrano 2016; Rauhut et al. 2016).

The Tetanurae are the main clade of theropod dinosaurs that includes most of the well-known forms and also recent birds. They first occur in the fossil record in the earliest Middle Jurassic, but the clade obviously experienced an explosive radiation soon after its origin, as all major clades, including avialans, are established by the Late Jurassic (Rauhut et al. 2010, 2016; Xu et al. 2010). Basically all recent phylogenetic analyses agree that Tetanurae split in three major lineages early in their evolutionary history, the Megalosauroidea (=Spinosauroidea in older literature), Allosauroidea (Fig. X-1C) and Coelurosauria, although the exact taxonomic composition of the three clades differs somewhat, especially in respect to inclusion or exclusion of basal taxa (e.g. Holtz 1998; Allain 2002; Rauhut 2003; Rauhut & Xu 2005; Smith et al. 2007; Benson 2010a; Benson et al. 2010; Choiniere et al. 2010; Carrano et al. 2012; Novas et al. 2015; Wang et al. 2017; Cau 2018).

Megalosauroids include mainly large-bodied and often heavily built megapredators, such as *Megalosaurus* and *Torvosaurus*, that thrived during the Middle and Late Jurassic (Benson 2010a; Carrano et al. 2012; Rauhut et al. 2016), but also the highly specialized gigantic spinosaurids of the Cretaceous, which include the largest theropod known, *Spinosaurus*, which probably reached a length of 18 m and up to 10 t in body mass (Stromer 1915; Therrien and Henderson 2007; Hone & Holtz 2017). Likewise, allosauroids were also generally large-bodied and megapredatory theropods that originated in the Middle Jurassic and thrived to at least the early Late Cretaceous, culminating in the gigantic carcharodontosaurids (e.g. Brusatte & Sereno 2008; Benson et al. 2010; Carrano et al. 2012).

In contrast to these two major lineages of tetanurans, the third major clade, the Coelurosauria, includes both large and small forms and saw repeated changes in trophic ecology (Zanno & Makovicky 2011). Coelurosaurs include such iconic animals as *Tyrannosaurus rex* or *Velociraptor mongoliensis*, and more phylogenetic analysis of this clade have probably been published than for most other fossil animals (e.g. Makovicky & Sues 1998; Norell et al. 2001, 2006; Xu et al. 2002, 2011, 2015; Makovicky et al. 2003; Senter 2007; Zhang et al. 2008; Choiniere et al. 2010, 2014a; Turner et al. 2012; Agnolin & Novas 2013; Godefroit et al. 2013a, b; Brusatte et al. 2014; Foth et al. 2014; Cau et al. 2015, 2017). Although there are considerable differences in the placement of many taxa and even whole clades within coelurosaurs (see below), there also exists some consensus about the general topology of the coelurosaur family tree. Thus, basically all analyses of the last twenty years agree that Tyrannosauroida is one of the most basal clades. The Tyrannosauroida have recently been found to include not only the well-known, gigantic megapredators of the Late Cretaceous, such as *Tyrannosaurus*, but also several other lineages, reaching back to the Middle Jurassic, such as the rather small-bodied, obviously fleet-footed proceratosaurids (Brusatte et al. 2010; Rauhut et al. 2010; Brusatte & Carr 2016).

The Tyrannosauroida and several other basal taxa and clades are outside a derived clade of coelurosaurs that Holtz (1996) named Maniraptoriformes. The most basal group within this clade are the Ornithomimosauria, generally small to medium-sized theropods with small skulls, long necks and elongate hindlimbs. All derived members of this clade are toothless and were probably omnivorous. Although most members of the Ornithomimosauroida do not exceed 5-6 m in length and weighed less than 600 kg (Benson et al. 2017), the clade also includes the giant *Deinocheirus* that reached more than 11 m in length and more than six tons in weight (Lee et al. 2014).

An important clade within coelurosaurs is the Maniraptora. Originally coined by Gauthier (1986) to include birds (Avialae) and theropods that share characters, especially of the manus, with these that are not present in ornithomimosaurids, the clade has been phylogenetically defined by Holtz (1996) as all coelurosaurs that share a more recent ancestor with birds than with ornithomimids. Ever since the analysis of Gauthier (1986), several clades were consistently found to be maniraptorans, including Oviraptorosauria (Figs. X-1E; X-2A), Troodontidae (Fig. X-2B), Dromaeosauridae (Fig. X-1F), and Avialae (birds), together with some taxa that do not seem to be included in a larger clade, such as the genus *Ornitholestes*. A number of clades that have only more recently been recognized (or firmly established as theropodan, in the case of therizinosaurids), including Alvarezsauridae (Fig. X-1D), Therizinosauria, Scansoriopterygidae, and Anchiornithidae, are usually also found within Maniraptora, although their detailed relationships differ widely between different analyses (see below).

Within Maniraptora, the Troodontidae, Dromaeosauridae and Avialae are united in the clade Paraves, defined as all maniraptorans that are more closely related to extant birds than to Oviraptor (Sereno 1997, 1998). Whereas the recently recognized Anchiornithidae (Xu et al. 2016; Foth & Rauhut 2017) have always also been recovered as Paraves (e.g. Xu & Zhang 2005; Hu et al. 2009, 2018; Xu et al. 2009b, 2011; Godefroit et al. 2013a, b; Foth & Rauhut 2017), the Alvarezsauridae and Scansoriopterygidae have been found to be Paraves only in some, but not all phylogenetic analyses.

Nested within Paraves is the clade Avialae, which is the most-inclusive clade containing extant birds, but not Dromaeosauridae or Troodontidae (Maryańska et al. 2002). Basal members of this clade are Archaeopteryx and Alconavis from the Late Jurassic of Germany (see Rauhut et al. 2019) and the groups Jeholornithidae, Sapeornithidae and Confuciusornithidae, which are all known from the Early Cretaceous of China (e.g. Mayr 2017; Wang & Zhou 2017). The clade that embrace Confuciusornithidae and extant birds including all its descendants are the Pygostylia (Chiappe 2002). This clade contains two major groups, the Enantiornithes and Ornithuromorpha (Euornithes), which are summarized as Ornithothoraces (Sereni 1998; Chiappe 2002). The Enantiornithes are small-bodied, toothed Avialae, which represents the most successful group of stem birds during the Cretaceous in terms of species richness as well as temporal and geographic range (Mayr 2017; Wang & Zhou 2017). According to the foot morphology they were primarily arboreal (O'Connor et al. 2011a), but as indicated by differences in the snout shape, tooth morphology and pedal claw geometry, a certain degree of ecological specializations was present. This includes for instance the long-snouted Longipterygidae (O'Connor et al. 2011b) or the raptorial Bohaiornithidae (Li et al. 2014).

In contrast to Enantiornithes, Ornithuromorpha possesses an enormous ecological diversification in terms of habitat and diet preferences, while their species diversity is lower when compared to their sister taxon. The ecological diversity includes semi-to-fully aquatic, but also ground-dwelling, and even secondary flightless taxa. In contrast to other Avialae, they also show a higher degree of tooth reduction and adaptation to piscivory, omnivory, insectivory and granivory (Mayr 2017; Wang & Zhou 2017). The most successful group of Ornithuromorpha are the Aves (Neornithes), which represents the crown-group of extant birds, and are the only theropod branch that survived the K/T extinction event. The Aves already originated in the Late Cretaceous, showing an initial diversification of the clades Palaeognathae, Galloanseres and Neovaves (Clarke et al. 2005; Brown et al. 2008; Prum et al. 2015; Mayr 2017). However, the actual radiation of crown group birds happened during the early Cenozoic, after the K/T event (Mayr 2009; Prum et al. 2015).

Remaining controversies

Although there is a remarkable consensus in the general hierarchy of theropod interrelationships and the hierarchy levels that most clades belong to, there are numerous controversies about the exact phylogenetic position of numerous taxa and some entire clades. In non-tetanuran theropods, these uncertainties mainly concern the taxonomic composition of the basal clade Coelophysoidea and the question whether Coelophysoidea and Ceratosauria are united in a clade or whether Ceratosauria are closer to Tetanurae. Concerning Coelophysoidea, current hypotheses reach from uniting basically all Late Triassic and the vast majority of Early Jurassic neotheropods in this clade (e.g. Carrano et al. 2005; Allain et al. 2007) to the possibility that a number of Late Triassic and Early Jurassic taxa are more closely related to averostrans (e.g. Rauhut 2003; Smith et al. 2007; Ezcurra & Brusatte 2011; Langer et al. 2014; Ezcurra 2017; Martínez & Apaldetti 2017), including the possibility of another clade of mainly Early Jurassic theropods, the Dilophosauridae (e.g. Smith et al. 2007). In respect to the phylogenetic position of the Ceratosauria, there seems to be a growing consensus that this clade is united with the Tetanurae in a monophyletic Averostrans,

with the last formal analysis finding a Coelophysoidea-Ceratosauria clade being that of Allain et al. (2007), whereas all more recent phylogenies found support for Averostra.

Within basal tetanurans, there is some disagreement on the relationships between the three major lineages, Megalosauroidea, Allosauroidea and Coelurosauria. Thus, whereas most recent analyses found Allosauroidea and Coelurosauria to be sister taxa in a clade named either Avetheropoda or Neotetanurae (see Carrano et al. 2012), to the exclusion of Megalosauroidea (e.g. Allain 2002; Smith et al. 2007; Benson 2010; Benson et al. 2010; Rauhut et al. 2010, 2016; Carrano et al. 2012; Novas et al. 2015; Wang et al. 2017), some analyses found Allosauroidea and Megalosauroidea to be united in a clade called Carnosauria to the exclusion of Coelurosauria (e.g. Rauhut 2003; Rauhut et al. 2012; Cau 2018).

Apart from uncertainties of the placements of several genera within their respective clades, a further important discrepancy in phylogenetic hypotheses of basal tetanurans concerns the placement of the only recently recognized Megaraptora. The first representatives known of this clade were represented by very fragmentary material (Novas 1998; Azuma & Currie 2000; Calvo et al. 2004; Novas et al. 2008), and so their recognition as belonging to a monophyletic clade and an analysis of their phylogenetic relationships only became possible after more complete remains had been found (Serenio et al. 2008; Hocknull et al. 2009). The first work to recognize a monophyletic Megaraptora was Benson et al. (2010), who recovered Megaraptora as part of the Neovenatoridae, the sister taxon to Carcharodontosauridae within the Allosauroidea. This phylogenetic placement was supported by several subsequent analyses (e.g. Carrano et al. 2012; Rauhut et al. 2016), but Novas et al. (2013) argued that Megaraptora were basal coelurosaurs and, more specifically, a mainly Gondwanan radiation of tyrannosauroids. Coelurosaur affinities have been supported by several more recent analyses using new material (Porfiri et al. 2014; Aranciaga Rolando et al. 2019), but the exact position of this interesting clade is still uncertain (e.g. Apesteguía et al. 2016; Coria & Currie 2016; Novas et al. 2016).

Within basal Coelurosauria, an important early clade of uncertain phylogenetic position are the Compsognathidae. This clade might be an early radiation of coelurosaurian theropods that originated in the Late Jurassic at the latest and reached a wide distribution in the Early Cretaceous, although the exact taxonomic composition of the group is also still debated. One problem with the current concept of the Compsognathidae might be that several taxa included in this clade are young juveniles (e.g. *Juravenator*: Chiappe & Göhlich 2010; *Scipionyx*: Dal Sasso & Maganuco 2011), and some of the characters supporting compsognathid monophyly might be ontogenetically variable (see Rauhut et al. 2012). Thus, *Compsognathus* and its closest relatives are found as the most basal larger clade of coelurosaurs in some analyses (e.g. Rauhut 2003; Holtz et al. 2004; Rauhut et al. 2010; Cau 2018), as sister-taxon to Maniraptoriformes (e.g. Senter 2007; Smith et al. 2007; Xu et al. 2009a, 2015; Novas et al. 2012, 2015; Choiniere et al. 2014a; Rauhut et al. 2019), or as basal Maniraptora (e.g. Choiniere et al. 2010; Foth et al. 2014).

Another problematic clade within coelurosaurs are the Alvarezsauridae. Originally thought to be basal birds (e.g. Perle et al. 1993; Novas 1996; Chiappe et al. 1998; Chiappe 2002), most more recent phylogenies have placed these animals as basal maniraptorans (e.g. Clark et al. 2002; Senter 2007; Choiniere et al. 2010, 2014b; Foth et al. 2014; Xu et al. 2018), and Sereno (2001) suggested that alvarezsaurids were the sister taxon to Ornithomimosauria.

The problem with alvarezsaurids was that most first discoveries of this clade were of highly derived members that have a very aberrant morphology (e.g. Perle et al. 1993; Novas 1996, 1997; Chiappe et al. 1998), making their placement within theropods problematic. However, with the recent discovery of more basal forms (Choiniere et al. 2010, 2014b; Xu et al. 2018), our understanding of alvarezsaurid anatomy, phylogeny and evolution is rapidly improving, and a consensus of this clade being basal maniraptorans seems to be emerging, although the exact phylogenetic position at the base of Maniraptora remains unstable.

A similar problem has affected the Therizinosauoidea. As with alvarezsaurids, the first discoveries of therizinosauroids were of highly derived forms (e.g. Maleev 1954; Perle 1979, 1981, 1982; Barsbold & Perle 1980), and even the placement in one of the principle clades of dinosaurs of these animals was at first unclear (see Paul 1984). Only with the discovery of more basal forms became the theropod affinities of therizinosauroids firmly established (Russell & Dong 1994). Since then, this clade has repeatedly been found as the sister taxon of the Oviraptorosauria within the Maniraptora (e.g. Makovicky & Sues 1998; Holtz 1998; Clark et al. 2002; Rauhut 2003; Holtz et al. 2004; Xu et al. 2007; Choiniere et al. 2014a; Cau 2018), although most recent analyses have favoured a more basal position of therizinosauroids, outside the Pennaraptora (Oviraptorosauria + Paraves; e.g. Senter 2007; Zanno 2010; Xu et al. 2011, 2017; Turner et al. 2012; Agnolín & Novas 2013; Brusatte et al. 2014; Foth et al. 2014; Foth & Rauhut 2017; Hu et al. 2018). This problem remains currently unresolved, as highlighted by the analyses presented by Rauhut et al. (2019): whereas an unweighted analysis found a Therizinosauoidea-Oviraptorosauria clade, an implicit weight analysis of the same data matrix found the therizinosauroids outside the Pennaraptora.

Another only recently recognized clade of interesting, bird-like theropods are the Scansoriopterygidae. These animals are so far only known from the early Late Jurassic Yanliao Biota of north-eastern China, from where at least four different taxa have been described (Zhang et al. 2002, 2008; Xu et al. 2015; Wang et al. 2019). Scansoriopterygids are small, bird-like theropods that included volant forms with membraneous wings (Xu et al. 2015; Wang et al. 2019). The clade was originally regarded as a radiation of basal avialans (Zhang et al. 2008), and this has been supported by some subsequent analyses (e.g. Xu et al. 2011; Foth et al. 2014), whereas a number of more recent analyses regarded scansoriopterygids as basal paravians, outside a Avialae-Deinonychosauria split (Xu et al. 2015; Wang et al. 2019). On the other hand, Agnolín & Novas (2013) recovered scansoriopterygids as basal oviraptorosaurs, which was supported by Brusatte et al. (2014) and Rauhut et al. (2019). Thus, more finds and more detailed studies of the known taxa are necessary to resolve the relationships of these interesting animals.

Another area of conflict concerns basal paravian phylogeny. In most analyses of coelurosaur interrelationships, Troodontidae and Dromaeosauridae are recovered as sister groups, forming the monophyletic Deinonychosauria (e.g. Sereno 1997, 1999; Holtz 1998; Clark et al. 2002; Rauhut 2003; Senter 2007; Turner et al. 2012; Rauhut et al. 2019). In contrast, several recent analyses found Troodontidae and Avialae as sister taxa to the exclusion of Dromaeosauridae (e.g., Godefroit et al. 2013b; Choiniere et al. 2014; Foth et al. 2014; Cau 2018). This uncertainty reflects the great similarity of many of these bird-like dinosaurs and is mirrored by the uncertain phylogenetic position of some other basal paravians, such as the anchiornithids, which are considered to be troodontids in some analyses (e.g. Hu et al. 2009; Turner et al. 2012; Godefroit et al. 2013b; Brusatte et al. 2014), basal deinonychosaurs (e.g. Xu et al. 2011, 2015; Wang et al. 2019), or avialans more basal than *Archaeopteryx* (e.g.

Agnolín & Novas 2013; Godefroit et al. 2013a; Foth et al. 2014; Rauhut et al. 2019), apart from occasional other placements within Paraves (e.g. as basal taxon outside the Deinonychosauria-Avialae split; Lefèvre et al. 2017).

These different phylogenetic hypotheses also affected the phylogenetic position of Archaeopteryx, which until today represents a yardstick for early bird evolution. Traditionally, *Archaeopteryx* is a basal member of the Avialae (e.g. Sereno 1999; Rauhut 2003, Senter 2007; Turner et al. 2012; Brusatte et al. 2014; see above), while some recent studies placed *Archaeopteryx* together with *Anchiornis* outside Avialae as sister taxon to Deinonychosauria (e.g. Xu et al. 2011, 2015; Xu & Pol 2014; Godefroit et al. 2013a; Hu et al. 2018; Wang et al. 2019). On the other hand, due to a high level of homoplasy in early Paraves, single studies classified *Rahonavis*, *Balaur* or *Microraptor* to be basal Avialae (e.g. Agnolín & Novas 2011, 2013; Cau et al. 2015, 2017; Foth & Rauhut 2017; Lefèvre et al. 2017), while they are traditionally placed within Dromaeosauridae (see Turner et al. 2012; Brusatte et al. 2013). Further controversies remain regarding the exact relationships between Jeholornithidae, Sapeornithidae, Confuciusornithidae and more derived Ornithothoraces. Many studies found the long-tailed Jeholornithidae to be the sister taxon of a monophyletic clade Pygostylia containing the short-tailed Sapeornithidae and Confuciusornithidae and more derived Ornithothoraces (e.g. Zhou et al. 2008; O'Connor et al. 2009, 2013; Zhang et al. 2014; Wang et al. 2015). This relationship represents the most parsimonious explanation for the tail evolution in the stem line of birds. However, other analyses found Sapeornithidae to be more basal than Jeholornithidae (e.g. Zhou et al. 2010; Turner et al. 2012; Cau et al. 2017; Foth & Rauhut 2017; Agnolín et al. 2019), which is more parsimonious explaining the evolution of the pectoral girdle and sternum. In contrast to basal Avialae, the phylogenetic relationship of the main clades within Ornithothoraces are well supported by various phylogenetic analyses (e.g., Clarke et al. 2006; Zhou et al. 2008; Wang et al. 2015; O'Connor et al. 2016).

The occurrence of feathers in the fossil record of theropod dinosaurs

As feathers are not skeletal tissues, they might only be preserved under exceptional circumstances, such as in Konservat-Lagerstätten. It is therefore not surprising that the fossil record of feathers in general is rather poor, and this is especially also the case for Mesozoic theropods.

The first record of a feather from the Mesozoic was the original isolated feather of Archaeopteryx, which von Meyer (1861a) first announced. More importantly, a skeletal specimen including feather impressions was found in the same year (von Meyer 1861b), and it were primarily the feather impressions that led to the identification of this animal as a bird (Owen 1863). The importance of the feather impressions in this iconic fossil was such that their authenticity was questioned as recently as 1985 (Hoyle et al. 1985), although there is no reasonable doubt that these structures are real (see Rietschel 1985; Charig et al. 1986; Wellnhofer 2008).

For many decades, the feathers of Archaeopteryx were the only known fossil feathers from the Mesozoic. More importantly, although feathers were later occasionally found as carbonized traces in exceptional lagerstätten or preserved in amber (see Davis & Briggs 1995; Kellner 2002; Prado et al. 2016), these were isolated finds of feathers, which did not

allow a taxonomic identification of the animal that they belonged to, and thus provided only limited data on the evolution of these structures. This changed drastically with the discovery of abundant feathered dinosaurs and early birds in the Lower Cretaceous Jehol Biota of China in the 1990ies (e.g. Hou et al. 1995; Chen et al. 1998; Ji et al. 1998; Xu et al. 1999a, b). Since then, feathers have been reported from these deposits and the older (late Middle to early Late Jurassic) Yanliao biota for all major clades of maniraptoran theropods (see Xu, this volume), and for some more basal coelurosaurian taxa, such as the compsognathid *Sinosauroptryx* (Chen et al. 1998) and the tyrannosauroid *Yutyranus* (Xu et al. 2012).

Reports of feathers in non-coelurosaurian theropods, in contrast, are still exceedingly rare, mainly because no such taxa have been found in these exceptional lagerstätten. Most reports of the possible presence of feathers in non-coelurosaurian theropods are therefore debatable. Gierlinski (1997) reported feather-like impressions in a theropod resting trace from the Early Jurassic of North America, and this interpretation was more recently supported by Kundrát (2004). As there are no coelurosaurian theropods known from the Early Jurassic, these traces might not only represent the oldest evidence of feathers, but also indirect evidence for non-coelurosaurian feathers. Although Kundrát (2004) made a good case for these imprints to represent feathers, some uncertainty remains, and another problem is, of course, the difficulty of identifying the trackmaker.

Another indirect evidence for feathers in a non-coelurosaurian theropod was presented by Ortega et al. (2010), who reported bumps on the ulna of the carcharodontosaurid *Concavenator*, which they interpreted as feather quill knobs. However, as argued by Foth et al. (2014) these knobs are in a different position than the quill knobs found in some modern volant birds and are irregularly spaced, casting doubt on this interpretation. Although Cuesta (2017), in a study of probable forelimb myology of *Concavenator*, did not find any evidence for these knobs representing attachments of interosseous ligamentes, as suggested by Foth et al. (2014), their significance remains controversial.

The probably best evidence of feathers in a non-coelurosaurian theropod is provided by the exceptionally preserved holotype specimen of *Sciurumimus albersdoerferi* from the Kimmeridgian Torleite Formation of southern Germany (Rauhut et al. 2012). This specimen does have abundant filament impressions above the base of the tail and shows numerous phosphatized filaments in different parts of the body under UV light (Rauhut et al. 2012; see also Foth et al., this volume). In the case of *Sciurumimus* the question is thus not so much the presence of protofeathers, but there is some uncertainty about its phylogenetic position. Rauhut et al. (2012) recovered this taxon as a basal tetanuran, and probably a megalosauroid, based on an analysis of this taxon in three different phylogenetic matrices. Thus, in this hypothesis, the presence of protofeathers in this taxon extends the record of these structures to at least the base of Tetanurae. However, Godefroit et al. (2013a) recovered *Sciurumimus* as a basal coelurosaur, in which case the origin of protofeathers might well lie within this clade. However, as argued by Rauhut et al. (2012), we strongly suspect that possible coelurosaurian characters in *Sciurumimus* are due to the very early ontogenetic stage of the only known specimen, as heterochrony seems to have played an important role in the evolution of coelurosaurian theropods (e.g. Bhullar et al. 2012; Foth et al. 2016), and thus consider a basal tetanuran placement of this taxon to be more likely.

Conclusions and outlook

Although there is still much debate about many details of the phylogenetic relationships of theropod dinosaurs and thus the origin of birds, there is a remarkable consensus on the backbone structure of the family tree of the ancestors of birds and the relative hierarchical placement of almost all major clades that constitute this tree (Fig. X-3). Thus, disregarding the more problematic (and often smaller) groups, all recent analyses agree that avialans ("birds") are members of the Paraves, together with dromaeosaurids and troodontids; Paraves are a subclade of Maniraptora, together with oviraptorosaurs, therizinosaurids, and alvarezsaurids; Maniraptora is part of Maniraptoriformes, together with ornithomimosaurs; Maniraptoriformes is a subclade of Coelurosauria, together with Tyrannosauroidae; Coelurosauria is part of Tetanurae, together with Megalosauroidea and Allosauroidae; Tetanurae is part of Neotheropoda, together with Ceratosauria and Coelophysoidea (and probably part of Averostra together with Ceratosauria). Thus, this phylogenetic hierarchy forms a solid base for improving our understanding of the evolution of the unique avian body plan (Fig. X-4), as originally lined out by Gauthier (1986) and elaborated in more detail recently by Brusatte et al. (2014), Xu et al. (2014), and Cau (2018). With the discovery of abundant feathered dinosaurs, mainly from the Late Jurassic and Early Cretaceous of China, but also from other areas, the phylogenetic hierarchy outlined above helps us to extend such evolutionary scenarios to the evolution of feathers (Xu 2006, this volume; Xu & Guo 2009) and novel insights into the possible functional context in which these structures evolved.

New discoveries and more detailed studies of key taxa will certainly help to further improve our understanding of theropod phylogeny. However, as there seems to be a trend to increase "birdiness" in several lineages independently, including possible multiple experiments with flight in derived coelurosaurian theropods (e.g. Xu et al. 2003; Foth et al. 2014; Wang et al. 2019). Together with the incomplete preservation of many remains, this marked parallelism - which is also seen in other parts of the theropod family tree (e.g. Rauhut & Pol 2018) - will make detailed reconstructions of the phylogenetic relationships at the origin of birds, in which the relationships of all relevant taxa can be established, difficult, if not impossible. However, such a detailed understanding might not be necessary to improve our understanding of the origin of birds, as the general agreement on the placement of most taxa in the hierarchy leading towards birds provides ample anatomical and functional data for hypothesis formulation and testing.

Likewise, new discoveries of feathered dinosaurs, not only in the now famous Yanliao and Jehol Biota, but also other lagerstätten, such as the limestones of the Solnhofen Archipelago (Chiappe & Göhlich 2010; Rauhut et al. 2012) or in Mesozoic amber (e.g. Xing et al. 2016a, b, 2019), will certainly improve our understanding of feather diversity, evolution and function. Furthermore, the use of novel techniques, such as laser-stimulated fluorescence (e.g. Kaye et al. 2015, 2019), new microscopic or chemical techniques (Schweitzer et al. 1999, 2008), investigations of the role of melanosomes for both feather colouring and structure (see Smithwick & Vinther, this volume, and references therein), and further improvements of methods such as UV photography have a great potential to provide new insights into the preservation and structure of feathers in fossil taxa.

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References

Agnolín, F.L. and Novas, F.E. 2013. Avian ancestors. A review of the phylogenetic relationships of the theropods Unenlagiidae, Microraptoria, Anchiornis and Scansoriopterygidae. Springer, Dordrecht.

Agnolín, F.L., Motta, M.J., Egli, F.B., Lo Coco, G. and Novas, F.E. 2019. Paravian phylogeny and the dinosaur-bird transition: an overview. *Frontiers in Earth Science* 6: 252.

Allain, R. 2002. Discovery of megalosaur (Dinosauria, Theropoda) in the middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. *Journal of Vertebrate Paleontology* 22: 548–563.

Allain, R., Tykoski, R.S., Aquesbi, N., Jalil, N.-E., Manbaron, M., Russell, D.A. and Taquet, P. 2007. An Abelisauroid (Dinosauria: Theropoda) from the Early Jurassic of the High Atlas Mountains, Morocco, and the radiation of Ceratosaurs. *Journal of Vertebrate Paleontology* 27: 610–624.

Benson, R.B.J. 2010. A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. *Zoological Journal of the Linnean Society* 158: 882–935.

Benson, R.B.J., Carrano, M.T. and Brusatte, S.L. 2010. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. *Naturwissenschaften* 97: 71–78.

Brown, J.W., Rest, J.S., Garcia-Moreno, J., Sorenson, M.D. and Mindell, D.P. 2008. Strong mitochondrial DNA support for a Cretaceous origin of modern avian lineages. *BMC Biology* 6: 1–18.

Brusatte, S.L. and Sereno, P.C. 2008. Phylogeny of Allosauroidea (Dinosauria: Theropoda): comparative analysis and resolution. *Journal of Systematic Palaeontology* 6: 155–182.

Brusatte, S.L., O'Connor, J.K. and Jarvis, E.D. 2015. The origin and diversification of birds. *Current Biology* 25: R888–R898.

Brusatte, S.L., Vremir, M., Csiki-Sava, Z., Turner, A.H., Watanabe, A., Erickson, G.M. and Norell, M.A. 2013. The osteology of *Balaur bondoc*, an island-dwelling dromaeosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Romania. *Bulletin of the American Museum of Natural History* 374: 1–100.

Brusatte, S.L., Lloyd, G.T., Wang, S.C. and Norell, M.A. 2014. Gradual assembly of avian body plan culminated in rapid rates of evolution across the dinosaur-bird transition. *Current Biology* 24: 2386–2392.

Carrano, M.T., Sampson, S.D. and Forster, C.A. 2002. The osteology of *Masiakasaurus knopfleri*, a small Abelisauroid (Dinosauria, Theropoda) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* 22: 510–534.

- Carrano, M.T., Benson, R.B.J. and Sampson, S.D. 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 10: 211–300.
- Cau, A. 2018. The assembly of the avian body plan: a 160-million-year long process. *Bollettino della Società Paleontologica Italiana* 57: 1–25.
- Cau, A., Beyrand, V., Voeten, F.A.E., Fernandez, V., Taffereau, P., Stein, K., Barsbold, R., Tsogtbaatar, K., Currie, P.J. and Godefroit, P. 2017. Synchrotron scanning reveals amphibious ecomorphology in a new clade of bird-like dinosaurs. *Nature* 552: 395–399.
- Cau, A., Brougham, T. and Naish, D. 2015. The phylogenetic affinities of the bizarre Late Cretaceous Romanian theropod *Balaur bondoc* (Dinosauria, Maniraptora): dromaeosaurid or flightless bird? *PeerJ* 3: e1032.
- Chen, P., Dong, Z. and Zhen, S. 1998. An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. *Nature* 391: 147–152.
- Chiappe, L.M. 2002. Basal bird phylogeny: problems and solutions. In: Chiappe, L.M. and Witmer, L.M. (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*, 448–472. University of California Press, Berkeley.
- Chiappe, L.M. 2009. Downsized dinosaurs: the evolutionary transition to modern birds. *Evolution: Education and Outreach* 2: 248–256.
- Choiniere, J.N., Xu, X., Clark, J.M., Forster, C.A., Guo, Y. and Han, F. 2010. A basal alvarezsaurid theropod from the Early Jurassic of Xinjiang, China. *Science* 327: 571–574.
- Choiniere, J.N., Clark, J.M., Forster, C.A., Norell, M.A., Eberth, D.A., Erickson, G.M., Chu, H. and Xu, X. 2014. A juvenile specimen of a new coelurosaur (Dinosauria: Theropoda) from the Middle–Late Jurassic Shishugou Formation of Xinjiang, People's Republic of China. *Journal of Systematic Palaeontology* 12: 177–215.
- Cieri, R.L. and Farmer, C.G. 2016. Unidirectional pulmonary airflow in vertebrates: a review of structure, function, and evolution. *Journal of Comparative Psychology B* 186: 541–552.
- Clarke, J.A., Zhou, Z. and Zhang, F. 2006. Insight into the evolution of avian flight from a new clade of Early Cretaceous ornithurines from China and the morphology of *Yixianornis grabaui*. *Journal of Anatomy* 208: 287–308.
- Clarke, J.A., Tambussi, C.P., Noriega, J.I., Erickson, G.M. and Ketchum, R.A. 2005. Definitive fossil evidence for the extant avian radiation in the Cretaceous. *Nature* 433: 305–308.
- Colbert, E.H. 1964. Relationships of the saurischian dinosaurs. *American Museum Novitates* 2181: 1–24.
- Darwin, C.R. 1859. *On the origin of species by means of natural selection*. John Murray, London.
- Ezcurra, M.D. and Cuny, G. 2007. The coelophysoid *Lophostropheus airelensis*, gen. nov.: a review of the systematics of '*Liliensternus*' *airelensis* from the Triassic–Jurassic outcrops of Normandy (France). *Journal of Vertebrate Paleontology* 27: 73–86.
- Farmer, C.G. and Sanders, K. 2010. Unidirectional airflow in the lungs of alligators. *Science* 327: 338–340.

- Feduccia, A. 1996. The origin and evolution of birds. Yale University Press, New Haven.
- Feduccia, A. 2013. Bird origins anew. *The Auk* 130: 1–12.
- Forster, C.A. 1999. Gondwanan dinosaur evolution and biogeographic analysis. *Journal of African Earth Sciences* 28: 169–185.
- Foth, C. and Rauhut, O.W.M. 2017. Re-evaluation of the Haarlem *Archaeopteryx* and the radiation of maniraptoran theropod dinosaurs. *BMC Evolutionary Biology* 17: 236.
- Foth, C., Tischlinger, H. and Rauhut, O.W.M. 2014. New specimen of *Archaeopteryx* provides insights into the evolution of pennaceous feathers. *Nature* 511: 79–82.
- Gauthier, J.A. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Science* 8: 1–55.
- Godefroit, P., Demuynck, H., Dyke, G.J., Hu, D., Escuillié, F. and Claeys, P. 2013a. Reduced plumage and flight ability of a new Jurassic paravian theropod from China. *Nature Communications* 4: 1394.
- Godefroit, P., Cau, A., Hu, D., Escuillié, F., Wu, W. and Dyke, G.J. 2013b. A Jurassic avialan dinosaur from China resolves the early phylogenetic history of birds. *Nature* 498: 359–362.
- Godefroit, P., Sinitsa, S.M., Dhouailly, D., Bolotsky, Y.L., Sizov, A. V, McNamara, M.E., Benton, M.J. and Spagna, P. 2014. A Jurassic ornithischian dinosaur from Siberia with both feathers and scales. *Science* 345: 451–455.
- Heilmann, G. 1926. The origin of birds. Witherby, London.
- Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana.
- Holtz, T.R.J. 1994. The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. *Journal of Paleontology* 68: 1100–1117.
- Holtz, T.R.J. 1998. A new phylogeny of the carnivorous dinosaurs. *Gaia* 15: 5–61.
- Hone, D.W.E. and Holtz, T.R.J. 2017. A century of spinosaurs - a review and revision of the Spinosauridae with comments on their ecology. *Acta Geologica Sinica* 91: 1120–1132.
- Hu, D., Clarke, J.A., Eliason, C.M., Qiu, R., Li, Q., Shawkey, M.D., Zhao, C., D’Alba, L., Jiang, J. and Xu, X. 2018. A bony-crested Jurassic dinosaur with evidence of iridescent plumage highlights complexity in early paravian evolution. *Nature Communications* 9: 217.
- Huxley, T.H. 1868. On the animals which are most nearly intermediate between birds and reptiles. *Annals and Magazine of Natural History* 4: 66–75.
- Ji, Q., Currie, P.J., Norell, M.A. and Ji, S. 1998. Two feathered dinosaurs from northeastern China. *Nature* 393: 753–761.
- Lefèvre, U., Cau, A., Cincotta, A., Hu, D., Chinsamy, A., Escuillié, F. and Godefroit, P. 2017. A new Jurassic theropod from China documents a transitional step in the macrostructure of feathers. *The Science of Nature* 104: 74.
- Li, Z., Zhou, Z., Wang, M. and Clarke, J.A. 2014. A new specimen of large-bodied basal Enantiornithine Bohaiornis from the Early Cretaceous of China and the inference of feeding ecology in Mesozoic birds. *Journal of Paleontology* 88: 99–108.

- Lingham-Soliar, T. 2003a. The dinosaurian origin of feathers: perspectives from dolphin (Cetacea) collagen fibers. *Naturwissenschaften* 90: 563–567.
- Lingham-Soliar, T. 2003b. Evolution of birds: ichthyosaur integumental fibers conform to dromaeosaur protofeathers. *Naturwissenschaften* 90: 428–432.
- Lingham-Soliar, T. 2010. Dinosaur protofeathers: pushing back the origin of feathers into the Middle Triassic. *Journal of Ornithology* 151: 193–200.
- Lingham-Soliar, T. 2012. The evolution of the feather: *Sinosauropteryx*, life, death and preservation of an alleged feathered dinosaur. *Journal of Ornithology* 153: 699–711.
- Lingham-Soliar, T., Feduccia, A. and Wang, X. 2007. A new Chinese specimen indicates that 'protofeathers' in the Early Cretaceous theropod dinosaur *Sinosauropteryx* are degraded collagen fibres. *Proceedings of the Royal Society of London B* 274: 1823–1829.
- Makovicky, P.J. and Sues, H.-D. 1998. Anatomy and phylogenetic relationships of the theropod dinosaur *Microvenator celer* from the Lower Cretaceous of Montana. *American Museum Novitates* 3240: 1–27.
- Makovicky, P.J., Norell, M.A., Clark, J.M. and Rowe, T.B. 2003. Osteology and relationships of *Byronosaurus jaffei* (Theropoda: Troodontidae). *American Museum Novitates* 3402: 1–32.
- Martin, L.D. 1983. The origin and the early radiation of birds. In: Brush, A.H. and Clark, G.A. (eds.), *Perspectives in Ornithology*, 291–338. Cambridge University Press, Cambridge.
- Martin, L.D., Stewart, J.D. and Whetstone, K.N. 1980. The origin of birds: structure of the tarsus and teeth. *The Auk* 97: 86–93.
- Maryańska, T., Osmólska, H. and Wolsan, M. 2002. Avialian status for Oviraptorosauria. *Acta Palaeontologica Polonica* 47: 97–116.
- Mayr, G. 2009. *Paleogene Fossil Birds*. Springer, Berlin.
- Mayr, G. 2010. Response to Lingham-Soliar: Dinosaur protofeathers: pushing back to origin of feathers into the Middle Triassic. *Journal of Ornithology* 151: 523–524.
- Mayr, G. 2017. *Avian evolution*. John Wiley, Chichester.
- von Meyer, H. 1861a. Vogel-Federn und Palpipes priscus von Solnhofen. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde* 1861: 561.
- von Meyer, H. 1861b. *Archaeopteryx lithographica* und *Pterodactylus*. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde* 1861: 678–679.
- Norell, M.A., Clark, J.M. and Makovicky, P.J. 2001. Gauthier, J.A. (ed.), Phylogenetic relationships among coelurosaurian theropods. In: *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom*, 49–67. Yale University, New Haven.
- Norell, M.A., Clark, J.M., Turner, A.H., Makovicky, P.J., Barsbold, R. and Rowe, T.B. 2006. A new dromaeosaurid theropod from Ukhaa Tolgod (Ömnögovi, Mongolia). *American Museum Novitates* 3545: 1–51.

- Novas, F.E. 1992. Phylogenetic relationships of the basal dinosaurs, the Herrerasauridae. *Palaeontology* 35: 51–62.
- Novas, F.E., Salgado, L., Suárez, M., Agnolín, F.L., Ezcurra, M.D., Chimento, N.R., de la Cruz, R., Isasi, M.P., Vargas, A.O. and Rubilar-Rogers, D. 2015. An enigmatic plant-eating theropod from the Late Jurassic period of Chile. *Nature* 522: 331–334.
- O'Connor, J.K., Wang, M. and Hu, H. 2016. A new ornithuromorph (Aves) with an elongate rostrum from the Jehol Biota, and the early evolution of rostralization in birds. *Journal of Systematic Palaeontology* 14: 939–948.
- O'Connor, J.K., Chiappe, L.M. and Bell, A. 2011a. Pre-modern birds: avian divergences in the Mesozoic. In: Dyke, G.J. and Kaiser, G.W. (eds.), *Living Dinosaurs: The Evolutionary History of Modern Birds*, 39–119. John Wiley, Chichester.
- O'Connor, J.K., Chiappe, L.M., Gao, C. and Zhao, B. 2011b. Anatomy of the Early Cretaceous enantiornithine bird *Rapaxavis pani*. *Acta Palaeontologica Polonica* 56: 463–475.
- O'Connor, J.K., Zhang, Y., Chiappe, L.M., Meng, Q., Quanguo, L. and Di, L. 2013. A new enantiornithine from the Yixian Formation with the first recognized avian enamel specialization. *Journal of Vertebrate Paleontology* 33: 1–12.
- O'Connor, J.K., Wang, X., Chiappe, L.M., Gao, C., Meng, Q., Cheng, X. and Liu, J. 2009. Phylogenetic support for a specialized clade of Cretaceous enantiornithine birds with information from a new species. *Journal of Vertebrate Paleontology* 29: 188–204.
- Ostrom, J.H. 1969a. A new theropod dinosaur from the Lower Cretaceous of Montana. *Postilla* 128: 1–17.
- Ostrom, J.H. 1969b. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Peabody Museum of Natural History, Bulletin* 30: 1–165.
- Ostrom, J.H. 1970. *Archaeopteryx*: notice of a 'new' specimen. *Science* 170: 537–538.
- Ostrom, J.H. 1972. Description of the *Archaeopteryx* specimen in the Teyler Museum, Haarlem. *Proceedings Koninklijk Nederlandse Akademie van Wetenschappen, B* 75: 289–305.
- Ostrom, J.H. 1973. The ancestry of birds. *Nature* 242: 136.
- Ostrom, J.H. 1976. *Archaeopteryx* and the origin of birds. *Biological Journal of the Linnean Society* 8: 91–182.
- Owen, R. 1863. On the *Archaeopteryx* of von Meyer, with a description of the fossil remains of a long-tailed species from the lithographic stone of Solenhofen. *Philosophical Transactions of the Royal Society of London* 153: 33–47.
- Paul, G.S. 2002. *Dinosaurs of the air: the evolution and loss of flight in dinosaurs and birds*. The John Hopkins University Press, Baltimore.
- Pol, D. and Rauhut, O.W.M. 2012. A Middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs. *Proceedings of the Royal Society B* 279: 3170–3175.
- Prum, R.O. 2002. Perspectives in ornithology. Why ornithologists should care about the theropod origin of birds. *The Auk* 119: 1–17.

- Prum, R.O. 2003. Are current critiques of the theropod origin of birds science? Rebuttal to Feduccia (2002). *The Auk* 120: 550–561.
- Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Moriarty Lemmon, E. and Lemmon, A.R. 2015. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* 526: 569–573.
- Rauhut, O.W.M. 1998. *Elaphrosaurus bambergi* and the early evolution of theropod dinosaurs. *Journal of Vertebrate Paleontology* 18: 71A.
- Rauhut, O.W.M. 2003. The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology* 69: 1–213.
- Rauhut, O.W.M. and Xu, X. 2005. The small theropod dinosaurs *Tugulusaurus* and *Phaedrolosaurus* from the Early Cretaceous of Xinjiang, China. *Journal of Vertebrate Paleontology* 25: 107–118.
- Rauhut, O.W.M. and Carrano, M.T. 2016. The theropod dinosaur *Elaphrosaurus bambergi* Janensch, 1920, from the Late Jurassic of Tendaguru, Tanzania. *Zoological Journal of the Linnean Society* 178: 546–610.
- Rauhut, O.W.M., Milner, A.C. and Moore-Fay, S. 2010. Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woodward, 1910) from the Middle Jurassic of England. *Zoological Journal of the Linnean Society* 158: 155–195.
- Rauhut, O.W.M., Hübner, T.R. and Lanser, K.-P. 2016. A new megalosaurid theropod dinosaur from the late Middle Jurassic (Callovian) of north-western Germany: implications for theropod evolution and faunal turnover in the Jurassic. *Palaeontologia Electronica* 19: 26A.
- Rauhut, O.W.M., Foth, C., Tischlinger, H. and Norell, M.A. 2012. Exceptionally preserved juvenile megalosauroid theropod dinosaur with filamentous integument from the Late Jurassic of Germany. *Proceedings of the National Academy of Sciences, U.S.A.* 109: 11746–11751.
- Rauhut, O.W.M., Tischlinger, H. and Foth, C. 2019. A non-archaeopterygid avialan theropod from the Late Jurassic of southern Germany. *eLife* 8: e43789.
- Schachner, E.R., Hutchinson, J.R. and Farmer, C.G. 2013. Pulmonary anatomy in the Nile crocodile and the evolution of unidirectional airflow in Archosauria. *PeerJ* 1: e60.
- Senter, P. 2007. A new look at the phylogeny of Coelurosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 5: 429–463.
- Sereno, P.C. 1997. The origin and evolution of dinosaurs. *Annual Review of Earth and Planetary Sciences* 25: 435–489.
- Sereno, P.C. 1998. A rationale for phylogenetic definitions with application to the higher-level taxonomy of Dinosauria. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 210: 41–83.
- Sereno, P.C. 1999. The evolution of dinosaurs. *Science* 284: 2137–2147.

Smith, N.A., Chiappe, L.M., Clarke, J.A., Edwards, S. V, Nesbitt, S.J., Norell, M.A., Stidham, T.A., Turner, A.H., van Tuinen, M., Vinther, J. and Xu, X. 2015. Rhetoric vs. reality: a commentary on “Bird origins anew” by A. Feduccia. *The Auk* 132: 467–480.

Smith, N.D., Makovicky, P.J., Hammer, W.R. and Currie, P.J. 2007. Osteology of *Cryolophosaurus ellioti* (Dinosauria: Theropoda) from the Early Jurassic of Antarctica and implications for early theropod evolution. *Zoological Journal of the Linnean Society* 151: 377–421.

Smithwick, F.M., Mayr, G., Saitta, E.T., Benton, M.J. and Vinther, J. 2017. On the purported presence of fossilized collagen fibres in an ichthyosaur and a theropod dinosaur. *Palaeontology* 60: 409–422.

Stromer, E. 1915. Ergebnisse der Forschungsreisen Prof. Stromers in den Wüsten Ägyptens. II Wirbeltier-Reste der Baharije-Stufe (unterstes Cenoman). 3. Das Original des Theropoden *Spinosaurus aegyptiacus* nov. gen., nov. spec. Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften. Mathematisch-physikalische Klasse 28: 1–32.

Tarsitano, S. and Hecht, M.K. 2008. The reptilian relationships of *Archaeopteryx*. *Zoological Journal of the Linnean Society* 69: 149–182.

Therrien, F. and Henderson, D.M. 2007. My theropod is bigger than yours...or not: estimating body size from skull length in theropods. *Journal of Vertebrate Paleontology* 27: 108–115.

Turner, A.H., Makovicky, P.J. and Norell, M.A. 2012. A review of dromaeosaurid systematics and paravian phylogeny. *Bulletin of the American Museum of Natural History* 371: 1–206.

Wagner, A. 1861. Beiträge zur Kenntnis der urweltlichen Fauna des lithographischen Schiefers. 2. Abt. Schildkröten und Saurier. Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften. Mathematisch-physikalische Klasse 9: 67–124.

Wagner, A. 1862. On a new fossil reptile supposed to be furnished with feathers. *Annals and Magazine of Natural History* 9: 261–267.

Wang, M. and Zhou, Z. 2017. The evolution of birds with implications from new fossil evidences. In: Maina, J.N. (ed.), *The Biology of the Avian Respiratory System*, 1–26. Springer Nature, Cham.

Wang, M., O'Connor, J.K., Xu, X. and Zhou, Z. 2019. A new Jurassic scansoriopterygid and the loss of membranous wings in theropod dinosaurs. *Nature* 569: 256–259.

Wang, M., Zheng, X., O'Connor, J.K., Lloyd, G.T., Wang, X., Wang, Y., Zhang, X. and Zhou, Z. 2015. The oldest record of Ornithuromorpha from the early cretaceous of China. *Nature Communications* 6: 6987.

Wang, S., Stiegler, J., Amiot, R., Wang, X., Du, G., Clark, J.M. and Xu, X. 2017. Extreme ontogenetic changes in a ceratosaurian theropod. *Current Biology* 27: 1–5.

Wellnhofer, P. 1974. Das fünfte Skelettexemplar von *Archaeopteryx*. *Palaeontographica Abt. A* 147: 169–216.

Witmer, L.M. 2002. The debate on avian ancestry: phylogeny, function, and fossils. In: *Mesozoic Birds: Above the Heads of Dinosaurs*, 3–30. University of California Press, Berkeley.

- Xu, X., Zheng, X., Sullivan, C., Wang, W., Xing, L., Wang, Y., Zhang, X., O'Connor, J.K., Zhang, F. and Pan, Y. 2015. A bizarre Jurassic maniraptoran theropod with preserved evidence of membranous wings. *Nature* 521: 70–73.
- Xu, X., Clark, J.M., Mo, J., Choiniere, J.N., Forster, C.A., Erickson, G.M., Hone, D.W.E., Sullivan, C., Eberth, D.A., Nesbitt, S.J., Zhao, Q., Hernandez, R., Jia, C., Han, F. and Guo, Y. 2009. A Jurassic ceratosaur from China helps clarify avian digital homologies. *Nature* 459: 940–944.
- Xu, X. and Guo, Y. 2009. The origin and early evolution of feathers: insights from recent paleontological and neontological data. *Vertebrata Palasiatica* 47: 311–329.
- Xu, X. and Pol, D. 2014. Archaeopteryx, paravian phylogenetic analyses, and the use of probability-based methods for palaeontological datasets. *Journal of Systematic Palaeontology* 12: 323–334.
- Xu, X., Wang, X. and Wu, X. 1999a. A dromaeosaurid dinosaur with filamentous integument from the Yixian Formation of China. *Nature* 401: 262–266.
- Xu, X., Tang, Z. and Wang, X. 1999b. A therizinosauroid dinosaur with integumentary structures from China. *Nature* 399: 350–354.
- Xu, X., Zhou, Z. and Prum, R.O. 2001. Branched integumental structures in *Sinornithosaurus* and the origin of feathers. *Nature* 410: 200–204.
- Xu, X., Ma, Q. and Hu, D. 2010. Pre-*Archaeopteryx* coelurosaurian dinosaurs and their implications for understanding avian origins. *Chinese Science Bulletin* 55: 3971–3977.
- Xu, X., You, H., Du, K. and Han, F. 2011. An *Archaeopteryx*-like theropod from China and the origin of Avialae. *Nature* 475: 465–470.
- Xu, X., Norell, M.A., Wang, X., Makovicky, P.J. and Wu, X. 2002. A basal troodontid from the Early Cretaceous of China. *Nature* 415: 780–784.
- Xu, X., Zhou, Z., Dudley, R., Mackem, S., Chuong, C., Erickson, G.M. and Varricchio, D.J. 2014. An integrative approach to understanding bird origins. *Science* 346: 12532931–10.
- Zanno, L.E. and Makovicky, P.J. 2011. Herbivorous ecomorphology and specialization patterns in theropod dinosaur evolution. *Proceedings of the National Academy of Sciences, U.S.A.* 108: 232–237.
- Zhang, F., Zhou, Z., Xu, X., Wang, X. and Sullivan, C. 2008. A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. *Nature* 455: 1105–1108.
- Zhang, Y., O'Connor, J.K., Di, L., Meng, Q., Sigurdson, T. and Chiappe, L.M. 2014. New information on the anatomy of the Chinese Early Cretaceous Bohaiornithidae (Aves: Enantiornithes) from a subadult specimen of *Zhouornis hani*. *PeerJ* 2: e407.
- Zheng, X., You, H., Xu, X. and Dong, Z. 2009. An Early Cretaceous heterodontosaurid dinosaur with filamentous integumentary structures. *Nature* 458: 333–336.
- Zhou, Z., Clarke, J.A. and Zhang, F. 2008. Insight into diversity, body size and morphological evolution from the largest Early Cretaceous enantiornithine bird. *Journal of Anatomy* 212: 565–577.

Zhou, Z., Zhang, Z. and Li, Z. 2010. A new Lower Cretaceous bird from China and tooth reduction in early avian evolution. *Proceedings of the Royal Society B* 277: 219–227.

Figures

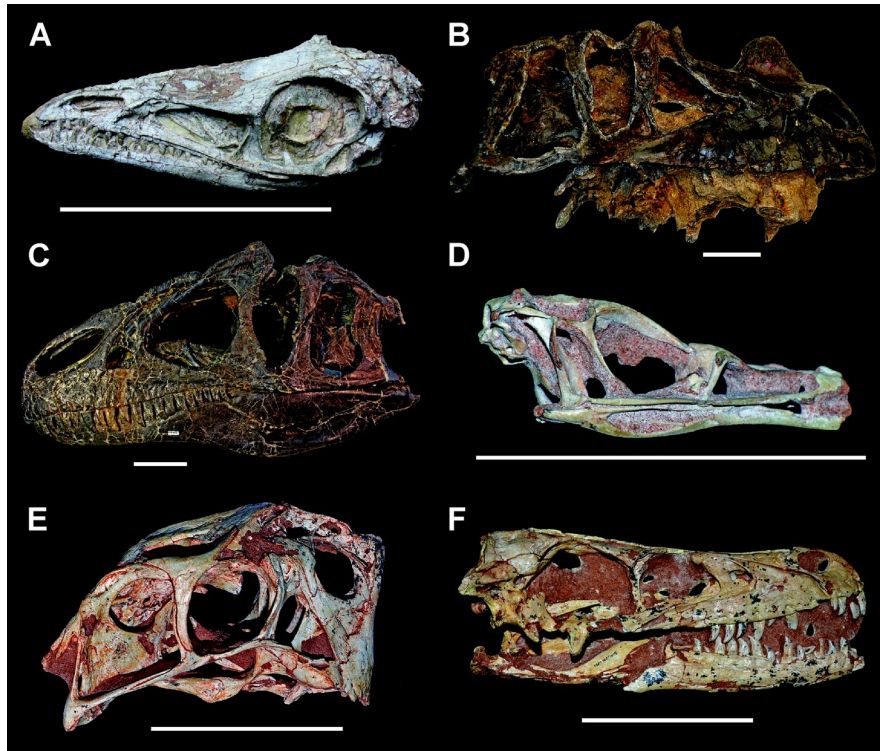


Fig. X-1. Skulls of representatives of different theropod clades. A Coelophysid *Coelophysis bauri* (NMNH P-42200; photo courtesy Jörg Schneider) in left dorsolateral view. B Ceratosaur *Ceratosaurus nasicornis* (USNM 4735) in right lateral view. C Allosauroid *Allosaurus* sp. (MOR 693; photo courtesy Serjoscha Evers) in left lateral view. D Alvarezsaurid *Shuvuuia deserti* (IGM 100/1001) in right lateral view. E Oviraptorosaurid *Citipati osmolskae* (IGM 100/978) in right lateral view. F Dromaeosaurid *Tsaagan mangas* (IGM 100/1015) in right lateral view. All scale bars are 10 cm.

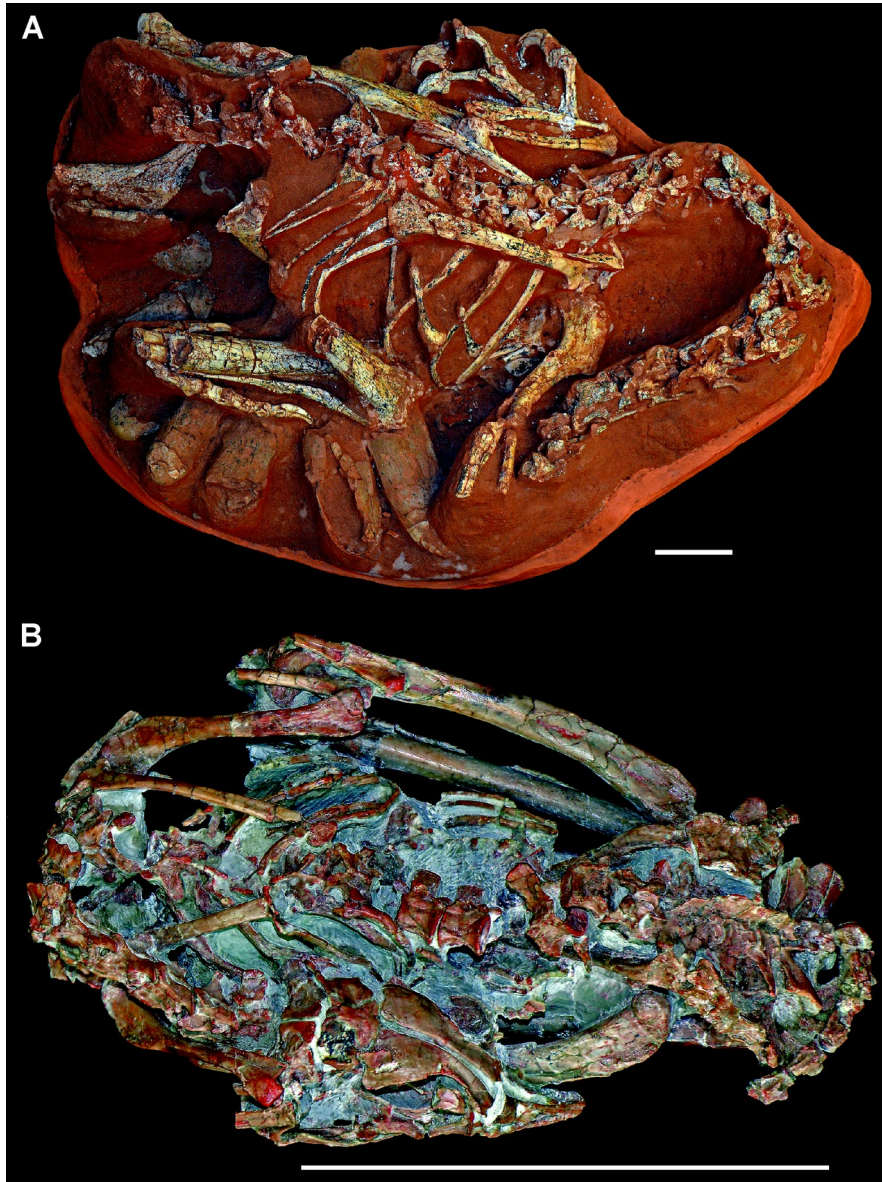


Fig. X-2. Non-avian theropod skeletons documenting avian-like behaviour. A Postcranial skeleton of the oviraptorosaurid *Citipati osmolskae* in a brooding position on a nest of eggs (IGM 100/1004). B Troodontid *Mei long* in an avian-like sleeping position (IVPP V12733). Scale bars are 10 cm.

furcula; 3) Averostra: extended vertebral pneumatization; 4) Tetanurae/Orionides: three-fingered hand with initial lateral folding mechanism; 5) Avetheropoda; 6) Coelurosauria; 7) Maniraptoriformes; 8) Maniraptora: semilunate carpal with partial lateral folding mechanism; 9) Pennaraptora: cerebral expansion, costosternal ventilator pump, V-shaped furcula, initial forelimb-flapping capabilities, increased manual lateral folding mechanism, two-layered eggshells, brooding behaviour; 10) Paraves/Eumaniraptora: extreme miniaturization, elaborated visual cortex, forelimb elongation and thickening, asymmetric egg shape, egg shells with low porosity and without ornamentation, potential third (external) layer in eggshell; 11) Avialae: aerial locomotion, asymmetric pennaceous feathers, lateral facing glenoid, forelimb elongation and thickening with increased flapping capabilities, shortened bony tail; 12) Pygostylia: crop, dorsolateral facing glenoid, strut-like coracoid, U-shaped furcula, fused sternum, rod-like pygostyle, posterior pubis orientation, one active ovary and oviduct; 13) Ornithothoraces: alula wing feather, sternal keel, synsacrum with 8 or more vertebrae; 14) Euornithes/Ornithuromorpha: kinetic skull, full forelimb-flapping capabilities and manual lateral folding mechanism, fused carpometacarpus, fusion of pelvic bones, metatarsal fully fused, increased egg size, plowshaped pygostyle. All silhouettes taken from (www.phylopic.org).