3 The Origin of Birds: Current Consensus, Controversy, and the Occurrence of Feathers

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3.1 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 nineteenth century and its acceptance following the publication of Darwin’s epochal book *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, turtles 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 functionary 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 2 years after the publication of Darwin’s book (von 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

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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 1960s and 1970s, 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 scepticism (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 1980s, 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; Agnolín 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 1990s (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, 2020). 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 and 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 Agnolín et al. (2019).

3.2 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 (e.g., *Eoraptor*, *Herrerasaurus*) 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. 3.1a) and the Ceratosauria (Fig. 3.1b), 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 include 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 into three major lineages early in their evolutionary history, the Megalosauroidea (Spinosauroidea in older literature), Allosauroidea (Fig. 3.1c) and Coelurosauria, although the exact taxonomic composition of the three clades somewhat differs, especially in respect to inclusion or exclusion of basal taxa (e.g. Holtz 1998; Allain 2002; Rauhut

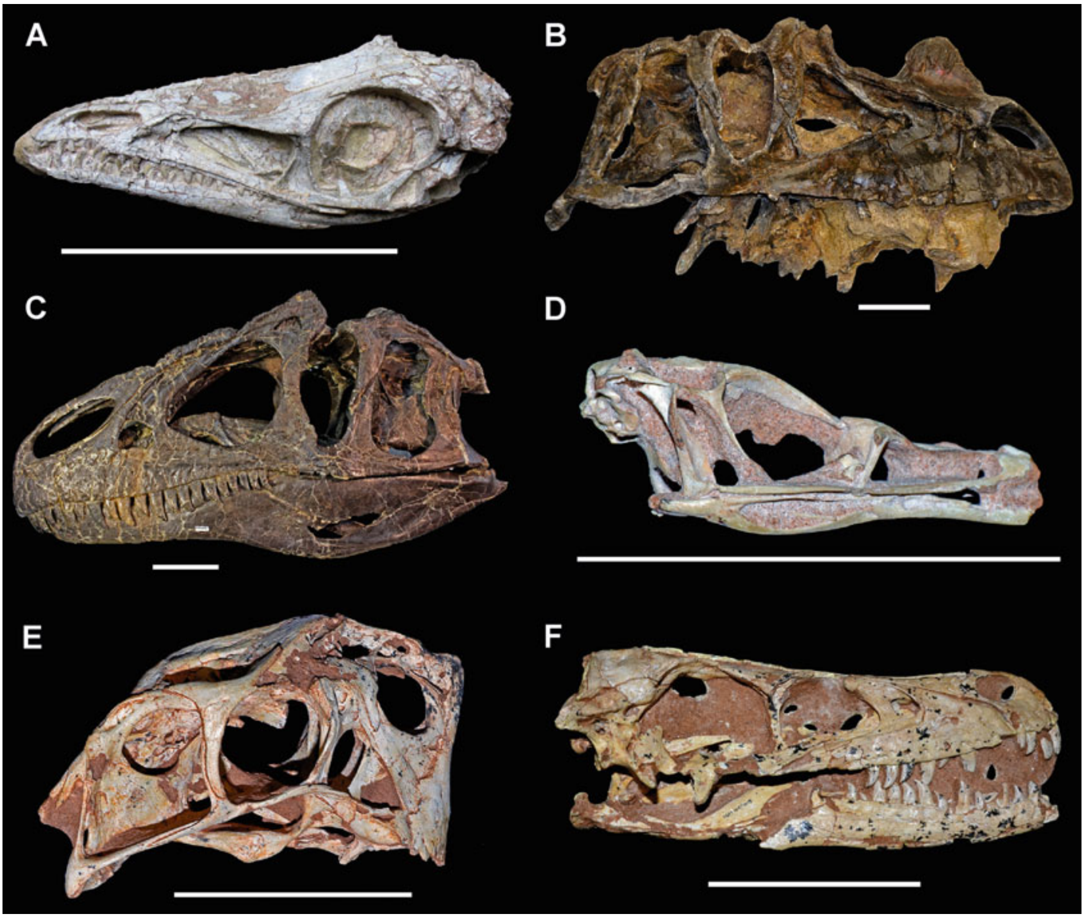

Fig. 3.1 Skulls of representatives of different theropod clades. (**a**) Coelophysid *Coelophysis bauri* (NMNH P-42200; photo courtesy Jörg Schneider) in left dorsolateral view. (**b**) Ceratosaur *Ceratosaurus nasicornis* (USNM 4735) in right lateral view. (**c**) Allosauroid *Allosaurus* sp. (MOR 693; photo courtesy Serjoscha Evers) in left lateral view. (**d**) Alvarezsauroid *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

2003; Rauhut and Xu 2005; Smith et al. 2007; Benson 2010; 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 2010; 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 and 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 and 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 and 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 most other fossil animals (e.g. Makovicky and 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, Choiniere et al. 2014; Turner et al. 2012; Agnolín and 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 20 years agree that Tyrannosauroidea are one of the most basal clades. Tyrannosauroidea 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 and Carr 2016).

Tyrannosauroidea 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 Ornithomimosauroidea do not exceed 5–6 m in length and weighed less than 600 kg (Benson et al. 2018), 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. The clade was originally coined by Gauthier (1986) to include birds (Avialae) and theropods that share characters, especially in the manus that are not present in ornithomimosaurs. 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. 3.1e and 3.2a), Troodonotidae (Fig. 3.2b), Dromaeosauridae (Fig. 3.1f), and Avialae (including modern 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 therizinosaurs), including Alvarezsauroidea (Fig. 3.1d), 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

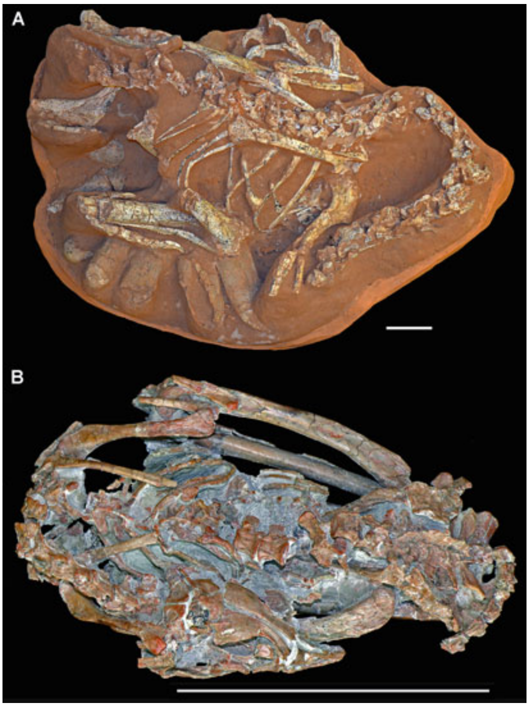

Fig. 3.2 Non-avian theropod skeletons documenting avian-like behaviour. (**a**) Postcranial skeleton of the oviraptorosaurid *Citipati osmolskae* in a brooding position on a nest of eggs (IGM 100/1004). (**b**) Troodontid *Mei long* in an avian-like sleeping position (IVPP V12733). Scale bars are 10 cm

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 and Fucheng 2005; Hu et al. 2009, 2018; Xu et al. 2009, 2011; Godefroit et al. 2013a, b; Foth and Rauhut 2017), the Alvarezsauroidea 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 Dromaeosauridea or Troodontidae (Maryańska et al. 2002). Basel members of this clade are *Archaeopteryx* and *Alcmonavis* 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 and Zhou 2017). The clade that embraces Confuciusornithidae and extant birds including all their descendants is the Pygostylia (Chiappe 2002). This clade contains two major groups, the Enantiornithes and Ornithuromorpha (Euornithes), which are summarized as Ornithothoraces (Sereno 1998; Chiappe 2002). The Enantiornithes are small-bodied, toothed Avialae, which represent 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 and 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 and Zhou 2017). The most successful group of Ornithuromorpha are the Aves (Neornithes), which represent 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).

3.3 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 and Brusatte 2011; Langer et al. 2014; Ezcurra 2017; Martínez and 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 Averostra,

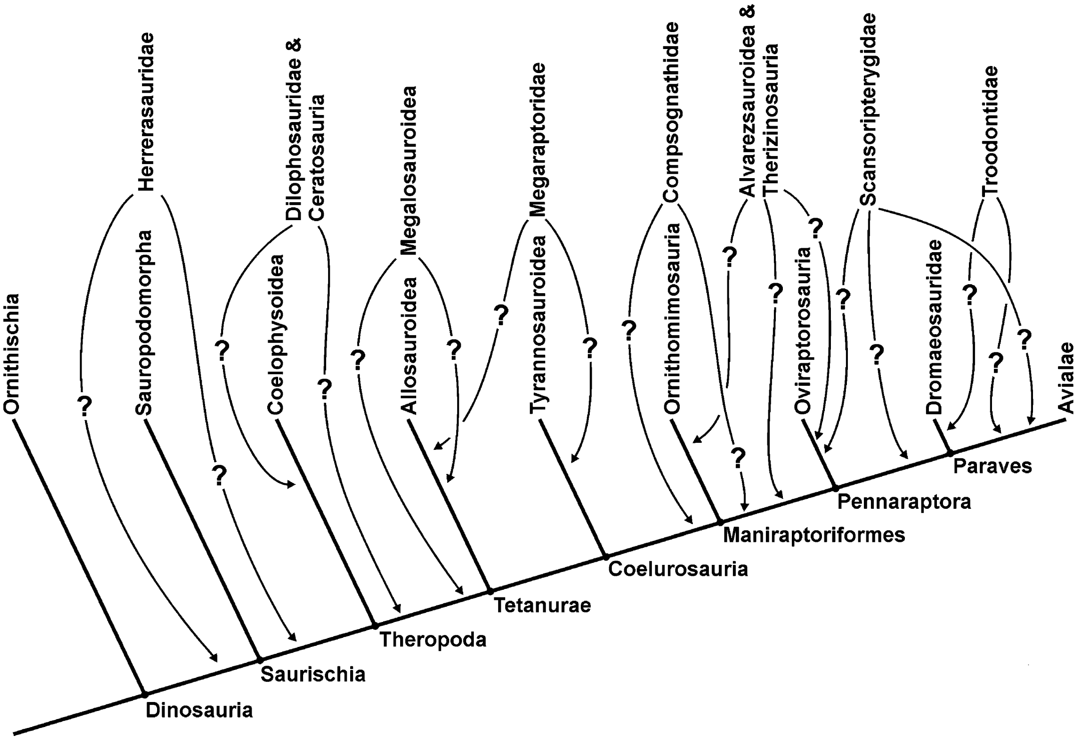

Fig. 3.3 Simplified cladogram of theropod relationships, showing common relationships between theropod dinosaurs and alternative phylogenetic positions for several problematic taxa (modified from Rauhut 2003)

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 and Currie 2000; Calvo et al. 2004), 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 (Sereno 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 and 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 juveniles (e.g. *Juravenator*: Chiappe and Göhlich 2010; *Scipionyx*: Dal Sasso and Maganuco 2011), and some of the characteristics 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. 2009, Xu et al. 2015; Choiniere et al. 2014; 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 Alvarezsauroidea. Originally thought to be basal birds (e.g. Perle et al. 1994; 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, 2014; Foth et al. 2014; Xu et al. 2018), and Sereno (1999) suggested that alvarezsauroids were the sister taxon to Ornithomimosauria. The problem with alvarezsauroids was that most first discoveries of this clade were of highly derived members that have a very aberrant morphology (e.g. Perle et al. 1994; 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, 2014; Xu et al. 2018), our understanding of alvarezsauroid 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 Therizinosauria. As with alvarezsauroids, the first discoveries of therizinosaurs were of highly derived forms (e.g. Maleev 1954; Perle 1979, 1982; Barsbold and Perle 1980), and even the placement in one of the principal clades of dinosaurs of these animals was at first unclear (see Paul 1984). Only with the discovery of more basal forms did the theropod affinities of therizinosaurs become firmly established (Russell and Dong 1993). 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. 2014; Cau 2018), although most recent analyses have favoured a more basal position of therizinosaurs, outside the Pennaraptora (Oviraptorosauria + Paraves; e.g. Senter 2007; Zanno 2010; Xu et al. 2011, 2017; Turner et al. 2012; Agnolín and Novas 2013; Brusatte et al. 2014; Foth et al. 2014; Foth and 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 Therizinosauria-Oviraptorosauria clade, an implicit weight analysis of the same data matrix found the therizinosaurs 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 membranous 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 and Novas 2013; Godefroit et al. 2013a; Foth et al. 2014; Rauhut et al. 2019), apart from other occasional 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 and 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 and Novas 2011, 2013; Cau et al. 2015, 2017; Foth and 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 and 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).

3.4 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 was 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 and Wickramasinghe 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 and 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 1990s (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 2020), and for some more basal coelurosaurian taxa, such as the compsognathid *Sinosauropteryx* (Chen et al. 1998) and the tyrannosauroid *Yutyrannus* (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 in 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 et al. (2018), in a study of probable forelimb myology of *Concavenator*, did not find any evidence for these knobs representing attachments of interosseous ligaments, as suggested by Foth et al. (2014), their significance remains controversial.

Probably the 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 in 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. 2020). 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.

3.5 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. 3.3). 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, therizinosaurs, and alvarezsauroids; Maniraptora is part of Maniraptoriformes, together with ornithomimosaurs; Maniraptoriformes is a subclade of Coelurosauria, together with Tyrannosauroidea; Coelurosauria is part of Tetanurae, together with Megalosauroidea and Allosauroidea; 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. 3.4), 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, 2020; Xu and 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, 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 and Pol 2019)—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 and 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 and Vinther 2020, and references therein), and further improvements of methods such as UV photography have great potential to provide new insights into the preservation and structure of feathers in fossil taxa.

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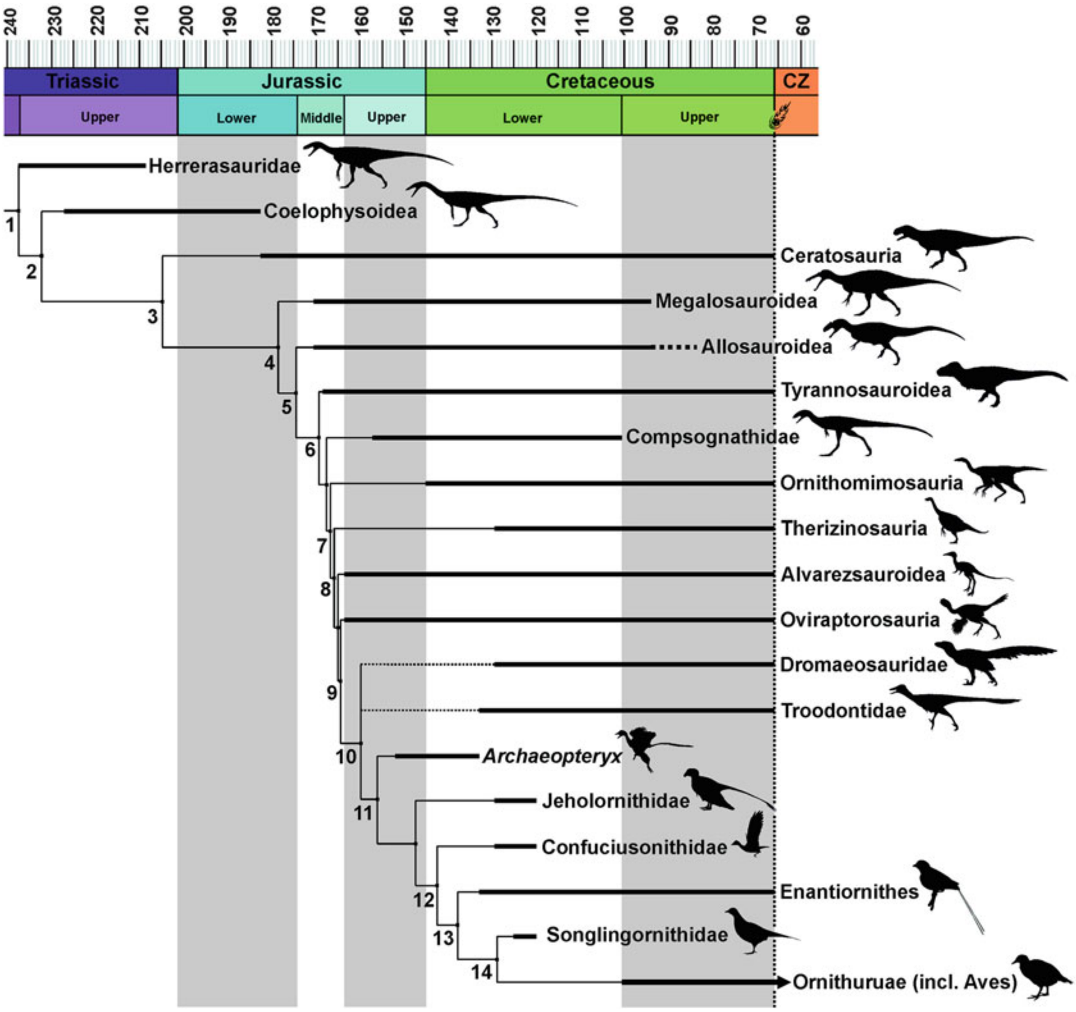

Fig. 3.4 Simplified time-calibrated theropod phylogeny showing the major events of character evolution along the theropod-bird transition. (**1**) **Theropoda**: bipedal locomotion∗, initial vertebral pneumatization and ventilatory air sacs∗, increased metabolic rate∗, thin bone walls, four-fingered hand (∗plesiomorphic characters); (**2**) **Neotheropoda**: widely arched 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, ploughshare-shaped pygostyle. All silhouettes taken from (www.phylopic.org)

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