

Chapter 2

The Origins of the Bird Brain: Multiple Pulses of Cerebral Expansion in Evolution

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Abstract Birds demonstrate extraordinary cognitive and emotional capabilities. The majority of these performances are most likely supported by their developed cerebrum. Birds, as well as mammals, have a much larger cerebrum compared to reptiles, given a similar body size. Since the common ancestral reptiles of birds and mammals had a relatively small brain according to paleobiological evidence, birds and mammals must have evolved to expand their brains independently after they diverged into different lineages. In the lineage leading to modern birds, brain expansion occurred multiple times, possibly in response to different selective pressures. This chapter includes focused discussions on three major pulses regarding brain evolution of the bird lineage. In each discussion, possible important selection factors to trigger the brain expansion are proposed. First, a discussion is on the emergence of amniotes (the common ancestor of reptiles, birds, and mammals) in the Paleozoic Era. Adaptation to terrestrial habitats and increased parental investment might play essential roles in brain expansion. Second, a discussion focuses on how theropod dinosaurs in the bird stem lineage evolved their brains in the Mesozoic Era. In the bird stem lineage, predatory behavior and body miniaturization were probably associated with the development of the brain. Finally, we discuss the evolutionary process of cerebrum expansion in modern birds during the Cenozoic Era. Acquisition of powered flight and endothermic metabolism are proposed as the main contributing factors of cerebral expansion in modern birds.

Keywords Amniotes • Reptiles • Dinosaurs • Cognition • Flight • Metabolism
Endothermy

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2.1 Introduction

Mental capacities of nonhuman animals have fascinated us since the beginning of time. We know and hear many intriguing reports and anecdotes about surprisingly high “intelligence” and rich “emotion” of animals. Some stories are rather products of imagination due to our anthropomorphic bias. However, rigorous scientific research has also proven that various kinds of “intelligence” and “emotion” truly exist in nonhuman animals (Shettleworth 2012; Wasserman and Zentall 2006). Among different “smart” animals, birds have been one of the most popular subjects of extensive studies (Ackerman 2016; Marzluff and Angell 2013; Heinrich 2009). Just like mammals, birds have shown superb abilities in parental care, communication, long-term memory, associative learning, observational learning, concept formation, and toolmaking and use. Some researchers even suggest that birds demonstrate theory of mind (Emery and Clayton 2004, 2005) and support or console each other (Fraser and Bugnyar 2010, 2012). Based on these lines of evidence, the similarities of mental capacities between some avian species and primates have been pointed out (Emery and Clayton 2004; Güntürkün and Bugnyar 2016; Navarrete et al. 2016).

These abilities in birds, as well as in mammals, are substantially associated with their enlarged and differentiated brains, the cerebrum in particular (Cross et al. 2013; Shanahan et al. 2013). Both birds and mammals have much larger brain as a whole, the cerebrum specifically, compared to any other vertebrates (Northcutt 1981). Relative to similar-sized reptiles and fishes, the brain size difference is at least a factor of 10. As discussed extensively in other chapters in this volume, there are significant differences in the cerebral organization between birds and mammals. The avian brain lacks a laminated cortex, which plays essential roles in perception, cognition, and motor control in the mammalian brain and is highly expanded especially in the primate brain. Despite the lack of a laminated cortex, the fact that birds have the capability of accomplishing similar cognitive feats suggests that the enlarged cerebrum of birds and mammals has, to some degree, equivalent functions. In contrast to the cerebrum expansion, the brainstem is relatively conserved in terms of size, structure, and function among birds, mammals, and reptiles, although its role in cognitive and affective functions should not be underestimated.

When and why did the avian cerebrum become enlarged? For the last 300 million years, the cerebrum expansion occurred at least three times in the lineage leading to modern birds. First, it occurred when the common ancestors of all amniotes (reptiles, birds, and mammals) emerged during the Carboniferous Period in the Paleozoic Era over 300 million years ago (MYA). Almost immediately, lineages of reptiles and mammals were diverged from the ancestral amniotes. About 200 MYA, the lineage of stem birds was then separated from the non-avian reptilian group. The second cerebral expansion occurred during the transition from theropod dinosaurs to ancestral birds in the Mesozoic Era. Many Mesozoic birds became extinct with other dinosaurs by 66 MYA, and direct ancestors of modern bird species appeared

and flourished in the Cenozoic Era. The third and most extensive expansion of the cerebrum occurred then. In this chapter, we will discuss these three events of cerebrum expansion—ancestral amniotes, dinosaurs, and modern birds—to understand the origin of avian brain capacity.

2.2 From Water to Land: Emergence of Amniotes

2.2.1 Timeline

Reptiles, birds, and mammals are together categorized in a group called amniotes because only amniotes have an amnion, an extraembryonic membrane. The amniotic membrane protects embryos in a stable fluid environment within a shell, enabling them to survive on a dry land. Anamniotes, such as fishes and amphibians, lay eggs in the water and have an aquatic larval stage, while amniotes no longer need to stay close to a body of water. The first amniotes evolved from ancestral amphibians over 300 MYA during the Carboniferous Period in the Paleozoic Era (Fig. 2.1). The emergence of amniotes is probably one of the most seminal events in vertebrate evolution. This is the beginning of the diverse and successful terrestrial

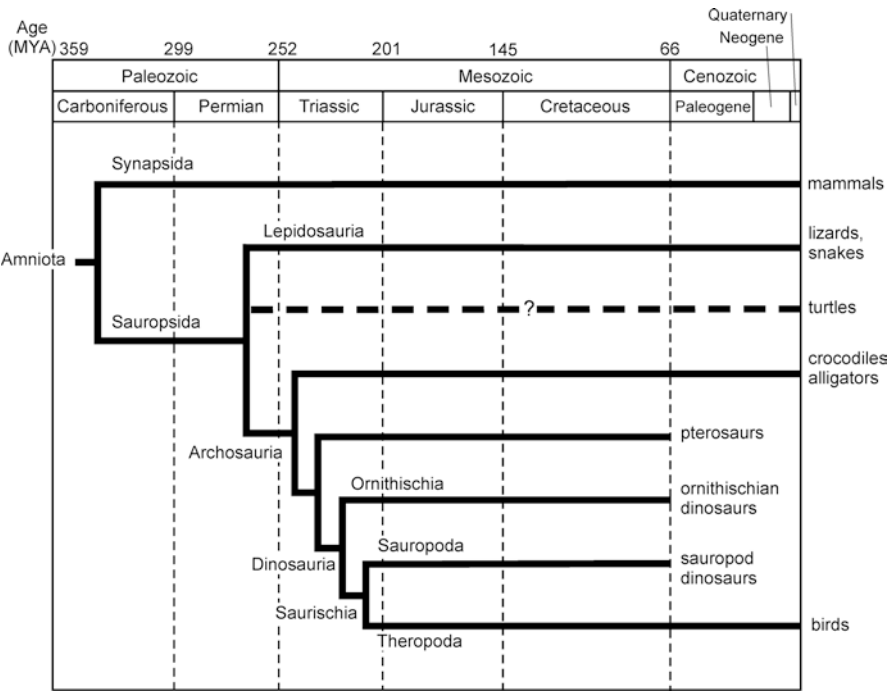


Fig. 2.1 Timeline of amniote evolution. Phylogeny based on Carroll (1988)

animals that ultimately lived in a wide variety of physical and biological niches. Almost immediately after the first amniotes appeared, the lineage was divided into sauropsids (“lizard faces” including anapsids and diapsids) and theropsids (“beast faces,” also called synapsids). Sauropsids ultimately led to diverse groups of reptiles and birds. The lineage of theropsids eventually gave rise to mammals in the Late Triassic (235–201 MYA).

2.2.2 *Early Amniotes*

What did the early amniotes look like? *Diadectes*, which had some characteristics of both reptiles and amphibians, were terrestrial animals during the Early Permian (290–272 MYA) (Carroll 1988). They had a proportionally large skull and a barrel-shaped body of 1.5–3 m long, unlike relatively small extant amphibians. Their dental features suggest that they were probably herbivores.

Truly indisputable amniotes include *Hylonomus* and *Paleothyris* during the Late Carboniferous (Carroll 1988). Unlike large Permian amphibians, they were lizard-like creatures of a small body (about 20 cm), slender limbs, and sharp teeth. They probably possessed developed stretch receptors in the muscle for improved musculoskeletal coordination, as do extant lizards. Based on these physical characteristics, we can assume that these animals were most likely agile hunters and fed on insects (e.g., spiders, dragonflies) and small animals (e.g., amphibians) on land.

2.2.3 *Brain Development*

To study the brains of extinct animals is a challenge. Detailed neuroanatomical analysis is impossible. Soft tissues like brains are rarely fossilized. However, cranial endocasts can be generated from fossil braincases. By examining endocasts, the general size, shape, and surface morphology of the brain can be postulated. Endocasts may be formed naturally through fossilization. They can also be produced artificially by filling a molding material into the endocranium. While traditional molding has a risk of harming the fossils, recent advances in imaging technology allow researchers to digitally generate virtual endocasts using high-resolution computed tomography techniques. Although endocasts are quite informative, they need to be evaluated with caution. The braincase holds not only the brain itself but also cerebrospinal fluid (CSF) surrounding the brain. The CSF can take up a significant portion of the cranial volume, and thus endocasts may not represent the exact shape and surface characteristics of the brain. In addition, the brain size itself does not indicate the number of neurons and the complexity of connections. A recent study showed

that the forebrains of large-brained parrots and corvids have a higher density of neurons than the primate brains of the same size (Olkowicz et al. 2016). Thus, the capacity of neural computation per unit mass may be different even if the brain sizes are comparable.

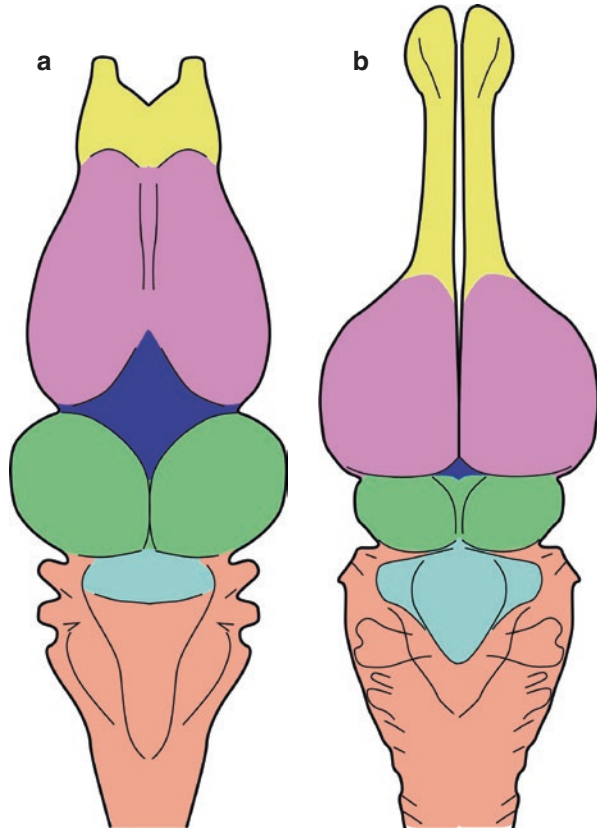
The general organization of vertebrate brains is essentially the same among all living species. Based on endocasts, this seems plesiomorphic for extinct vertebrates as well. Vertebrate brains include three major subdivisions along the rostral-caudal axis: forebrain (or prosencephalon), midbrain (or mesencephalon), and hindbrain (or rhombencephalon) (Butler and Hodos 1996). The forebrain consists of the cerebrum and thalamus, which are closely interconnected and often serve functions in synchrony. As a result, their development is highly correlated to each other. At the most rostral part of the cerebrum, olfactory bulbs are visibly large in many vertebrates. The midbrain includes the optic tectum (superior colliculus in mammals), torus semicircularis (inferior colliculus in mammals), and tegmentum. The optic tectum is particularly well-developed and elaborated in amniotes. The caudal-most region, hindbrain, includes the pons, medulla oblongata, and cerebellum. The midbrain and hindbrain are together categorized as the brainstem.

The innovation of extraembryonic membranes, especially the amnion, led to dramatic changes in the brains of amniotes (e.g., *Hylonomus* and *Paleothyris*) from those of Permian amphibians (e.g., *Diadectes*). Amniote brains, the forebrain in particular, are larger than anamniote brains given comparable body sizes (Jerison 1973; Northcutt 1981).

According to the endocast of *Diadectes*, they had a relatively small, narrow, and elongated brain (Hopson and Gans 1979). Such characteristics suggest that the brain of *Diadectes* was probably similar to that of living amphibians. In general, amphibians have a rather diminutive cylindrical brain, which includes relatively large olfactory bulbs, small cerebral hemispheres which are in contact with optic lobes, and a small cerebellum. The relative volumes of their entire brain, as well as the forebrain, are similar to those of bony fishes of similar body size (Jerison 1973; Northcutt 1981).

No data are currently available about the brains of *Hylonomus* and *Paleothyris*. However, it is reasonable to assume that their brains were more similar to lizards (reptiles) than amphibians in order to carry out their active locomotion for insectivorous diets (Fig. 2.2). If so, their brains, forebrains in particular, were enlarged and developed to some degree, compared to *Diadectes*. Forebrains of living reptiles are generally about one to two times larger than amphibians of similar body sizes (Northcutt 1981). As discussed in a chapter by Jarvis in this book, this enlargement may be due to an expansion of the cerebrum, a pallial region called the dorsal ventricular ridge (DVR) in particular (Jarvis et al. 2005; Reiner et al. 2004). Directly caudal to the cerebral hemispheres, reptiles have optic lobes, which are in turn adjacent to an expanded cerebellum.

Fig. 2.2 The top views of brains of a living amphibian (**a**, frog) and reptile (**b**, alligator). Each color represents a different brain subdivisions: olfactory bulbs (yellow), cerebrum (magenta), thalamus (dark blue), optic lobe (green), cerebellum (light blue), and brainstem (orange). Brains are not scaled to size



2.2.4 Selective Factors

2.2.4.1 Terrestrial Habitat

One important consequence of the emergence of embryonic membranes is that amniotes evolved to truly and freely explore the terrestrial environment. The amniote brains must now have a different neural system to obtain sensory signals that transmitted through the surrounding air, instead of fluid. Compared to the aquatic habitat, a new motor system also became necessary to control different kinds of movements on land. Because early amniotes (e.g., *Hylonomus* and *Paleothyris*) were capable of agile locomotion, it is likely that brain areas for motor systems needed to be developed and enlarged. For example, similar to the reptilian brain, the early amniote brain probably had more developed and differentiated basal ganglia (subpallium) in the cerebrum, compared to those of amphibians.

The basal ganglia are known to play a major role in motor control in all vertebrates (Reiner et al. 1998). They receive dopaminergic projections from the mid-brain tegmentum and influence motor functions through outputs to the tectum and/

or the pallium in the cerebrum. In living amphibians, both the basal ganglia and midbrain dopaminergic areas are relatively small and not clearly differentiated. The amphibian tectum is the primary output for motor control, while projections to the pallial regions are limited. In contrast, the reptilian (as well as avian and mammalian) basal ganglia are highly enlarged and differentiated into striatal and pallidal regions. Similarly, the midbrain dopaminergic cell populations include the substantia nigra and ventral tegmental area. As for the output of the basal ganglia, the amniote basal ganglia send projections to both the tectum and pallium to control movements.

2.2.4.2 Parental Investment

Ancestral amphibians, just like their extant counterparts, had external fertilization, laid numerous eggs in the water while newly emerged amniotes fertilized internally, and laid fewer eggs (or kept them within the body). As a result, amniotes had increased parental investment compared to anamniotes. Parental investment can be defined as any investment (e.g., time and energy) by the parent for the survival and reproductive success of offspring (Trivers 1972). Such significant changes in parental investment were associated with various social aspects of sexual selection, including male-male competition and mate choice. In extant amniotes, these complex social behaviors often necessitate the development of the forebrain (a pallial region in particular) to process species-specific sensory signals, make appropriate choices and decisions, and control complex social behaviors. While the pallium in all tetrapods receives projections from thalamic sensory nuclei to execute such functions, projections are more extensive in amniotes than anamniotes, and both the pallium and thalamus of amniotes are much more enlarged and elaborate (Butler and Hodos 1996). We can assume that early amniotes had a larger and more developed pallial region than anamniotes to deal with these biological problems.

2.3 From Large to Small: Dinosaurs in the Bird Stem Lineage

2.3.1 Timeline

During the Mesozoic Era (about 252 to 66 MYA), sauropsids were greatly proliferated (“the Age of Reptiles”). Sauropsids diverged into archosaurs (“ruling lizards”) and lepidosaurs (“scaly lizards”) by the Early Triassic Period. The former led to crocodiles, dinosaurs, pterosaurs, and birds, while the latter led to lizards and snakes. Dinosaurs (“terrible lizards”) were one of the most successful vertebrates over 150 million years in the Mesozoic Era. They appeared in the Late Triassic (about 225 MYA) and then became dominant in the terrestrial, aquatic, and aerial

niches of the Jurassic Period. Huxley (1868) first proposed and later Ostrom (1973) reinforced the hypothesis that the stem lineage of birds appeared from a group of theropod dinosaurs. Although the issue has been debated extensively, most of paleontologists support this hypothesis today. By the end of the Cretaceous (about 66 MYA), all the dinosaurs except the lineage to modern birds rather abruptly disappeared.

2.3.2 Dinosaurs in the Bird Stem Lineage

Dinosaurs are categorized into two groups: saurischians (“lizard-hipped”) and ornithischians (“bird-hipped”) based on pelvic structure. Interestingly, birds were originated from a “lizard-hipped” branch of dinosaurs, rather than “bird-hipped” ornithischian dinosaurs. Saurischians further include carnivorous theropods (“beast-footed”) and herbivorous sauropods (“lizard-footed”). The earliest birds were considered to be derived from bipedal theropods during the Jurassic Period. The exact evolutionary steps from theropods to modern birds are not completely understood and continuously revised due to new findings. Here, five major clades of the bird stem lineage—Tetanurae, Coelurosauria, Maniraptora, Paraves, and Avialae—are discussed. The relationships of these clades are shown in Fig. 2.3.

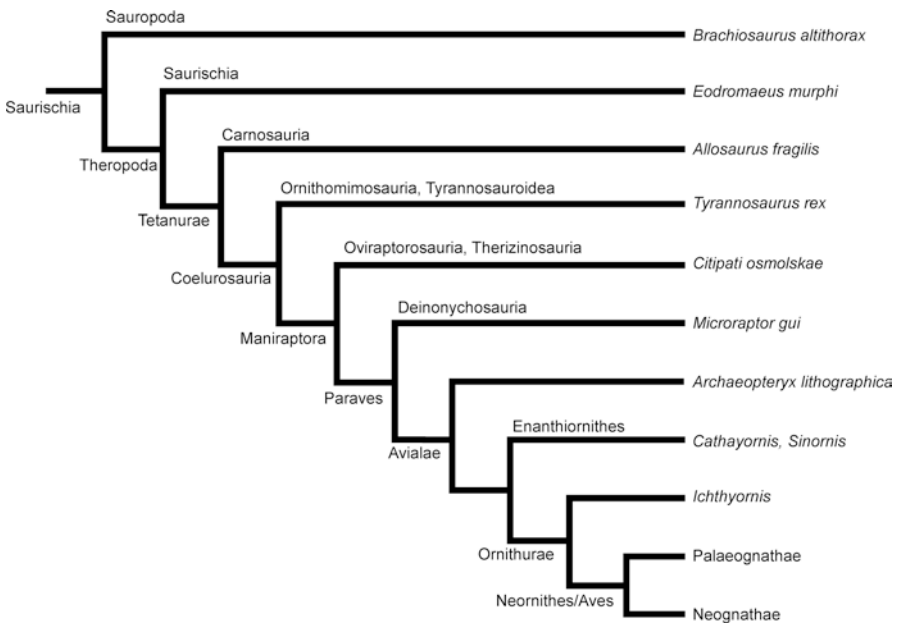


Fig. 2.3 Phylogeny of theropods, focusing on the bird stem lineage. Phylogeny based on Gauthier and de Queiroz (2001) and Turner et al. (2012)

Tetanurae (“stiff tails”): Dinosaurs in this large theropod group are diverse in terms of size and appeared during the Early or Middle Jurassic Period. It includes two subgroups—Carnosauria and Coelurosauria—primarily based on size and proportion differences. In general, coelurosaurs are smaller than carnosaurs, which include large *Allosaurus fragilis* (about 8.5 m long, Glut 1997) and *Carcharodontosaurus saharicus* (over 12 m long, Sereno et al. 1996). However, enormous tyrannosaurids (e.g., *Tyrannosaurus rex*, about 12 m long, Hutchinson et al. 2011) belong to Coelurosauria.

Coelurosauria (“hollow-tailed lizards”): This clade consists of all theropods more closely related to birds than to carnosaurs. These relatively small theropods are recognized from the Late Jurassic and Early Cretaceous. Many feathered dinosaurs have been discovered in China from the Middle-Upper Jurassic and Lower Cretaceous. Most of these feathered dinosaurs turn out to be coelurosaurs (Xu and Guo 2009; Xu et al. 2012). The major coelurosaurian groups include Maniraptora, Ornithomimidae, and Tyrannosauridae.

Maniraptora (“hand snatchers”): All dinosaurs closer to birds than to ornithomimids are members of this group. It contains the subgroups Paraves, Oviraptorosauria, and Therizinosauria. Fossil records of maniraptorans appeared during the Jurassic Period. They show skeletal characteristics, which were essential steps for the evolution of gliding and/or powered flight. For example, maniraptorans are the only dinosaurs that have elongated forearms (which become wings in birds) and a sternum (where flight muscles attach, but see Zheng et al. 2014).

Paraves (“near bird”): This group includes all dinosaurs more closely related to birds than to oviraptorosaurs. It has two major subgroups: Avialae and Deinonychosauria. The latter further includes the dromaeosaurids (e.g., *Microraptor gui*, *Deinonychus antirrhopus*) and troodontids (e.g., *Zanabazar junior*). Although the origin and evolution of avian flight is still in debate, at least some paravians were experimenting with flight—parachuting, gliding, and/or hopping from tree to tree. For example, *Microraptor gui*, a basal dromaeosaurid dinosaur found in China, had four wings located on both the forelimb and hind limb (Xu et al. 2003). Using these developed wings, they should have been able to glide. However, powered flight probably did not start till the clade of Avialae.

Avialae (“bird wing”): All dinosaurs closer to birds than to *Deinonychus* are members of this group. Gauthier and de Queiroz (2001) used this term to include all flying [winged] dinosaurs. This group includes Ornithurae (including Aves), Enantiornithes, as well as the famous *Archaeopteryx lithographica*, the exact position of which is still uncertain. *Archaeopteryx* lived in the Late Jurassic (about 150 MYA). The first specimen was discovered in 1861 in Southern Germany, just a few years after the publication of Darwin’s *On the Origin of Species*. It is small in body size (up to 50 cm long, 0.8–1 kg body weight) and has both dinosaur-like characteristics (e.g., a jaw with sharp teeth, claws, and a bony tail) and birdlike features (e.g., broad feathered wings) (Callaway 2014). Since the early 1990s, new specimens showing dinosaur-bird transition have been discovered in China. They include other feathered dinosaurs, such as *Anchiornis huxleyi* (160 MYA) and *Aurornis xui* (160 MYA). A recent phylogenetic analysis suggests that *Aurornis xui*, but not *Archaeopteryx*, is the basal-most avialan (Godefroit et al. 2013).

2.3.3 Brain Development

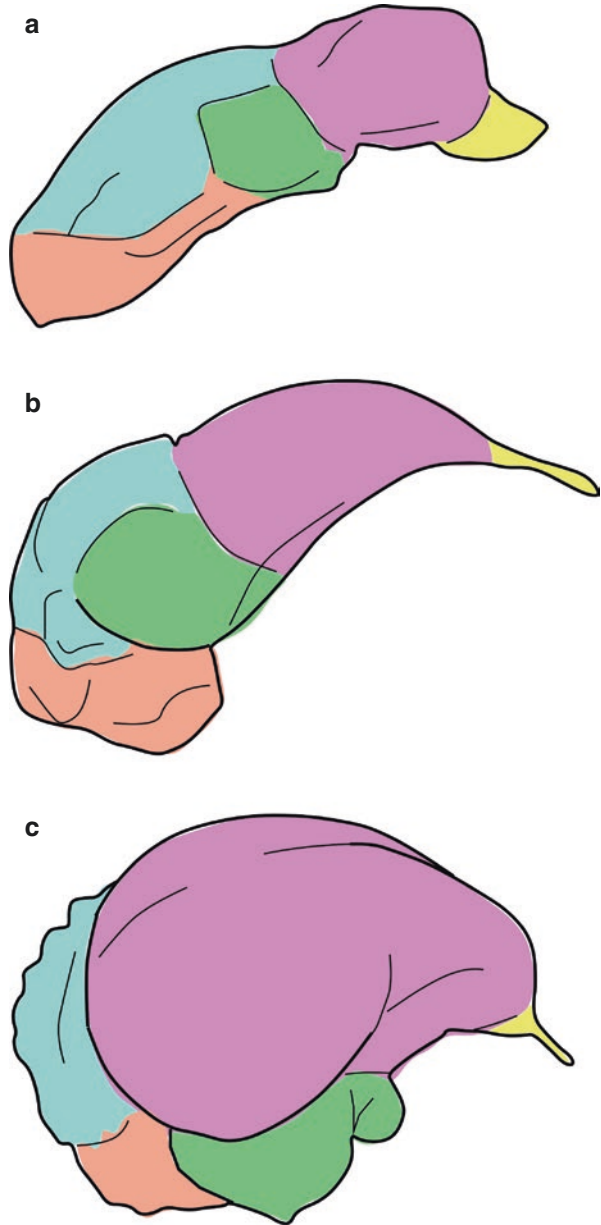
Fossil endocasts suggest that the brains of non-avian theropod dinosaurs are not much different from those of living reptiles in terms of relative size and overall shape (Hopson and Gans 1979; Hopson 1977; Jerison 1969, 1973). Due to scarce fossil records in the bird stem lineage, little is known about the transition process from diminutive theropod brains to highly developed avian brains. However, new fossil findings of maniraptorans from China have started to shed an insight into this issue. These data show that maniraptoran brains (e.g., *Archaeopteryx*) are volumetrically situated intermediately between early theropods and modern birds (Balanoff et al. 2013).

Recent studies suggest that the cerebral expansion in the bird stem lineage occurred at least three times and started early in theropod history—probably after the divergence of coelurosaurs in the Middle Jurassic Period about 180–160 MYA (Balanoff et al. 2013; Larsson et al. 2000). Endocasts of the coelurosaur *Tyrannosaurus* show overall cerebral features that are different from those of two carnosaur species (*Carcharodontosaurus* and *Allosaurus*). For example, the dorsal roof of the cerebrum is positioned higher than the cerebellum in carnosaurs, while the cerebellum of *Tyrannosaurus* has moved to a more elevated position (Larsson et al. 2000). This coelurosaur characteristic of an elevated cerebellum is also observed in *Archaeopteryx* as well as in modern birds. In terms of endocast volumes, *Tyrannosaurus* is about 50% larger for total brain volume and 100% larger for cerebrum volume than *Carcharodontosaurus*. The expansion of the total brain volume of *Tyrannosaurus* is probably due to a larger proportion of the cerebrum (32.6%) compared to that in *Carcharodontosaurus* (24%).

The next development and enlargement of brains probably occurred in the Late Jurassic about 150 MYA after maniraptorans appeared. The brain volume of avialan *Archaeopteryx* is approximately three times larger than those of reptiles of comparable size (Alonso et al. 2004). Compared to reptiles and ancestral theropods, the brain of *Archaeopteryx* shows some characteristics shared by modern birds (Fig. 2.4), such as reduced olfactory bulbs, expanded cerebral hemispheres, a large cerebellum directly caudal to the cerebrum, and a midbrain (including optic lobes) displaced lateroventrally. The cerebral surface has a slight sign of a longitudinal indentation (vallecula), implying that it has a brain region called the Wulst (Balanoff et al. 2013). However, the brain of *Archaeopteryx* is not an avian brain. If the body mass is about the same, modern birds have much larger brains than *Archaeopteryx*.

Examinations of endocasts of other maniraptorans suggest that the cranial expansion was not unique in *Archaeopteryx*, but probably a generalized phenomenon in maniraptorans (Balanoff et al. 2013). For example, endocast images of oviraptorosaur *Citipati osmolskae* (Fig. 2.4) and an unnamed troodontid show the avian characteristics mentioned above, such as reduced olfactory bulbs, expanded cerebral hemispheres, a large cerebellum directly caudal to the cerebrum, and optic lobes displaced lateroventrally. Volumetric analyses show that the total brain and cerebrum volumes relative to body size were similar among all maniraptorans including *Archaeopteryx* (Balanoff et al. 2013).

Fig. 2.4 Postulated brain organization based on endocasts (adapted from Balanoff et al. 2013 with permission). (a) *Citipati osmolskae* (an oviraptorosaur from the Late Cretaceous), (b) *Archaeopteryx lithographica*, and (c) *Melanerpes aurifrons* (woodpecker). Each color represents a different brain subdivisions: olfactory bulbs (yellow), cerebrum (magenta), optic lobe (green), cerebellum (light blue), and brainstem (orange). Endocasts are not scaled to size



Furthermore, the data suggest that at least some members of Paraves have brains that are somehow different from those of other maniraptorans. A principal component analysis was conducted to study the effects of different brain structures (olfactory bulbs, cerebrum, optic lobes, cerebellum, and brainstem) relative to total brain volumes (Balanoff et al. 2013). The results showed a clear volumetric separation between Paraves and Oviraptorosauria. The difference is largely defined by the cerebral expansion in Paraves.

2.3.4 Selective Factors

2.3.4.1 Predatory Behavior

An early brain expansion was observed in Coelurosauria compared to Carnosauria (Larsson et al. 2000). One possible factor for the brain expansion might be related to differences in active predatory behavior in coelurosaurs. Although both coelurosaurs and carnosaurs are carnivorous, the former tend to be smaller than the latter. Compared to carnosaurs, coelurosaurs also have relatively small skulls and longer forelimbs (Carroll 1988). Such physical characteristics suggest that coelurosaurs were more vigilant and agile hunters than carnosaurs and that they needed a developed sensory (visual in particular) system to detect prey, as well as an efficient motor system to control swift activity. The midbrain contains the optic tectum that has a precise visual map of the surrounding environment (Butler and Hodos 1996) and the acoustic tectum (torus semicircularis). The midbrain also sends descending projections to motor areas in the brainstem and spinal cord in living amniotes. It is reasonable to assume that these predators have a developed midbrain system, as well as the cerebellum, to react swiftly to external stimuli and generate quick movements.

2.3.4.2 Body Miniaturization

Subsequently, multiple stages of brain expansion occurred in the bird stem lineage. Another important factor that made continued effects on this lineage is sustained miniaturization of the body size. By analyzing extensive fossil databases, researchers showed that such miniaturization occurred specifically in the bird stem lineage, but not in non-avian dinosaur lineages (Lee et al. 2014b). The ancestral tetanuran is approximately 163 kg about 198 MYA, followed by coelurosaurs (27 kg, 173 MYA), maniraptorans (10 kg, 170 MYA), paravians (3 kg, 167.5 MYA), and avialans (0.8 kg, 163 MYA). Thus, along 50 million years, dinosaurs in the lineage leading to avialans shrunk from an average of 163 kg to just 0.8 kg. These changes are depicted in Fig. 2.5.

As a result of miniaturization, stem birds could evolve to obtain physiological and anatomical changes. These smaller animals had higher metabolic rates, feather elaborations, increased aerial ability, reduced snouts, developed beaks, and enlarged eyes and brains (Lee et al. 2014b). The critical selective pressures for miniaturization are not known. However, arboreal lifestyle might be one important driver (Benton 2014). Living in trees requires smaller bodies, along with sharper claws and keener vision, in addition to elongated forearms for wings.

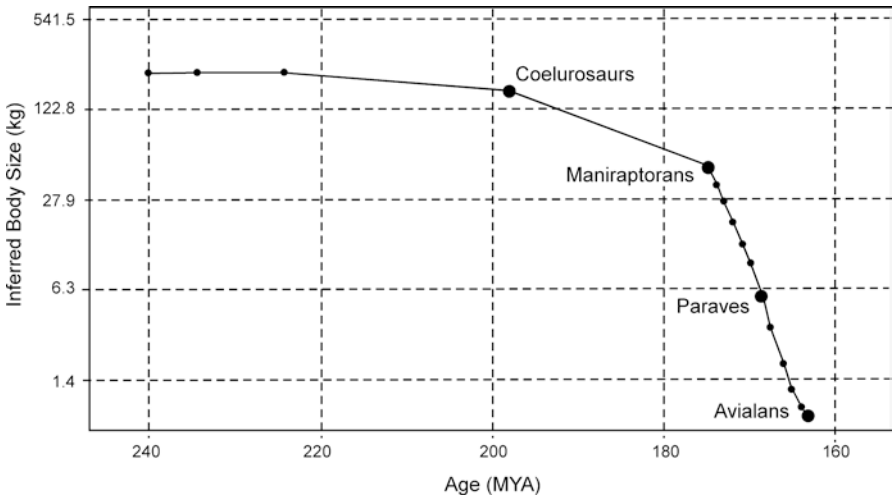


Fig. 2.5 Body miniaturization along the bird stem lineage (adapted from Lee et al. 2014b with permission). Circles represent nodes (“ancestors”) along the bird stem lineage. Large circles represent nodes discussed in this chapter

2.4 From Cold to Warm: Flying Birds

2.4.1 Timeline

Modern birds emerged from a subgroup of Avialae called *Ornithurae* (“bird tails”), which includes all decedents of the common ancestor of modern birds as well as extinct toothed birds, such as *Ichthyornis* and *Hesperornithes*. Both *Ichthyornis* and *Hesperornithes* lived in the Cretaceous Period (Clarke 2004). *Ichthyornis* resembles modern flying seabirds, such as gulls, with a developed wings and a large sternum. *Hesperornithes* is a group of flightless, but strong, swimming waterbirds. The crown group—the most recent common ancestor of all living birds and all of its descendants—is categorized in the clade *Neornithes* (“new birds”) or *Aves* (sensu Gauthier and de Queiroz 2001). The oldest fossil definitively placed in *Neornithes* was *Vegavis iaai*, a member of the duck lineage (Clarke et al. 2005). This bird lived in the Late Cretaceous (about 67 MYA) in Antarctica, suggesting that living bird lineages coexisted with other avialans before the Cretaceous/Paleogene (K-Pg) boundary about 66 MYA.

2.4.2 *Diversification of Modern Birds*

Modern birds are the most successful tetrapods in terms of the number of species. According to the International Ornithological Congress World Bird List (v6.2), there are 10,637 extant avian species, 40 orders, 239 families, and 2289 genera (Gill and Donsker 2016). The timing of this great diversification is still in debate. Some molecular studies indicate a gradual radiation during the Cretaceous Period (Haddrath and Baker 2012; Jetz et al. 2012; Lee et al. 2014a). On the other hand, fossil records of Neornithes from the Cretaceous Period are quite limited (Clarke et al. 2005), suggesting that modern birds underwent extraordinary “big bang” diversification for a short period of time after the mass extinction event (Ericson et al. 2006; Feduccia 1995; Jarvis et al. 2014). A recent extensive whole-genome analyses also support the “big bang” hypothesis that a rapid diversification occurred within a short period of time during the K-Pg transition (36 lineages within 10–15 million years) (Jarvis et al. 2014). If this is the case, modern birds, together with placental mammals (O’Leary et al. 2013), diversified rapidly in the ecological niches where their potential predators and rivals (e.g., non-avian dinosaurs, pterosaurs, and other avialans) no longer existed.

Based on comparative anatomy, they are divided into two subgroups, Palaeognathae (“old jaw”) and Neognathae (“new jaw”) (Livezey and Zusi 2007). Palaeognathae include flightless ratites, such as Struthioniformes (ostriches), Rheiformes (rheas), Casuariiformes (emus), and Apterygiformes (kiwis). Neognathae consists of Galloanserae (Galliformes, e.g., chickens, turkey; Anseriformes, e.g., ducks, geese) and Neoaves (all other diverse birds). Neoaves further include Columbiformes (pigeons), Passeriformes (songbirds, corvids), Psittaciformes (parrots), Falconiformes (falcons), Strigiformes (owls), Accipitriformes (eagles, hawks), Charadriiformes (gulls, shorebirds), and Apodiformes (hummingbirds).

2.4.3 *Brain Development*

The brain of modern birds has some fundamental characteristics that were shared with other Mesozoic avialans based on information from endocast data. The avian brain has relatively small olfactory bulbs, large cerebral hemispheres, lateroventrally displaced optic lobes, and an enlarged cerebellum. However, endocasts also clearly show that modern birds evolved to have much larger brains than other avialans (Alonso et al. 2004; Balanoff et al. 2013). For example, when total endocranial volume relative to body mass is compared, birds with the same size have 1/3 to 5 times larger brains than the brain of *Archaeopteryx* (Alonso et al. 2004). In particular, the enlargement of the cerebrum is clearly obvious in modern birds compared to that of *Archaeopteryx*. The extensive cerebral expansion causes a further displacement of optic lobes ventrally to the point that the midbrain beneath the cerebrum is only partially visible from the dorsal viewpoint.

From the endocast information, it is difficult to pinpoint the exact cerebral region that expanded in birds. However, it is most likely that two pallial areas, DVR (Jarvis's chapter) and Wulst, expanded the most in modern birds (Shimizu 2001). When the cerebra of extant birds and reptiles are compared, these two regions are highly developed and enlarged in birds compared to that of reptiles. Other cerebral substructures, such as the basal ganglia (including striatum and pallidum), appear to be similar volumetrically between reptiles and birds. Either the Wulst or DVR is not a unitary entity with a single function. Both structures are critically involved in diverse functions associated with sensory, cognitive, motor, and limbic systems (Shimizu and Watanabe 2012).

The extant avian cerebellum is an extremely differentiated and efficient machine consisting of numerous neurons. It has a number of parallel grooves (folia, lobules) on the cortical surface, a characteristic which is also found in mammals, as well as some elasmobranchs and fishes, but not reptiles. These grooves are fissures of the cerebellar cortex, in which layers of numerous neurons are efficiently folded like an accordion. The cerebellum of *Archaeopteryx* appears to be well-developed in terms of size (Alonso et al. 2004; Balanoff et al. 2013). However, the interpretation was challenged because at least a portion of the "cerebellum" might be a torus semicircularis, making the "true" cerebellum much smaller (Kurochkin et al. 2007). Furthermore, no detailed information is available about the surface morphology of the *Archaeopteryx* cerebellum. From endocast data, it is unclear whether non-avian maniraptorans had folia or lobules in the cerebellum. Since cerebella of extant reptiles are lissencephalic, it is possible that *Archaeopteryx* did not have an avian-like elaborated cerebellum. Thus, even if endocasts suggest that the general size and shape of the cerebellum are comparable, the cerebellum of *Archaeopteryx* or any other non-avian maniraptorans might not have the same computational capacity as that of modern birds.

2.4.4 *Selective Factors*

2.4.4.1 **Flight**

Of over 10,000 species of Neornithes, most birds fly, while about 60 living species do not (Roots 2006). Powered flight is definitely a signature behavior of modern birds. The exact origin of volant avians has been a contentious issue among paleobiologists for decades. Some non-avian maniraptorans in the Mesozoic Era had feathered wings, with which they were also probably able to leap, glide, parachute, and/or flap for powered flight. Two main hypotheses about the origin of flight have been proposed—ground-up and tree-down. The former hypothesis proposes that small-bodied terrestrial avian ancestors obtained feathers for thermal insulation or sexual display, but not for locomotion. Then the flight stroke evolved for fast ground-running activity. The latter hypothesis argues that avian ancestors lived in an arboreal environment. They climbed up trees using claws and then parachuted or

glided between trees using feathered wings. *Archaeopteryx* probably flew, but whether or not they had the capability of powered flight has been debated. For example, a relatively developed cerebellum of *Archaeopteryx* suggests that their neural system is equipped for flight (Balanoff et al. 2013, but see a discussion above). However, they also had a rather flat sternum lacking a well-developed keel. Modern flying birds have sterna with the keel, to which breast muscles (pectoralis and sternocoracoideus) necessary for powerful strokes attach.

Regardless of the exact beginning of the avian powered flight, it is clear that powered flight became ubiquitous among Neornithes in the Cenozoic. In order to have the capability of powered flight, the avian brain needed to undergo radical changes in the neural system—the visuomotor system in particular. While there were major neural changes for the coordination of muscles related to flying locomotion, the most important change involved all systems adapting to high speeds of flight behavior. Birds are the fastest animals in the animal kingdom. Falcons can fly at a speed of over 100 km/h and dive about 400 km/h (Tucker 1998; Tucker et al. 1998). With such a high speed, humans have only blurry views, while birds can detect and analyze their surroundings instantly and maneuver themselves precisely to avoid collisions. Furthermore, flying adds the vertical dimension of the environment which birds must also process. These biological problems forced the bird brain to expand such neural areas for processing abundant visual input efficiently, while controlling or correcting motor activities instantly.

In all amniotes, visual information is sent from the retina to both the midbrain (optic tectum) and thalamus (lateral geniculate nucleus) (Shimizu and Watanabe 2012). Each area further sends projections eventually to the DVR via the tectofugal pathway and the Wulst via the thalamofugal pathway. In birds, the optic tectum is an extremely developed and differentiated structure, containing at least 15 layers of diverse neurons. Similarly, the subsequent cerebral targets, the DVR and the Wulst, are also large developed structures, which in turn send projections directly and indirectly to enlarged motor areas in the brainstem and cerebellum. It is likely that these areas—the optic tectum, lateral geniculate nucleus, DVR, Wulst, and visuomotor areas in the brainstem—evolved to meet the demands associated with becoming animals with powered flight.

2.4.4.2 Endothermy

Today, birds and mammals are only homeothermic endotherms that can internally regulate and maintain their body temperature. In endotherms, the primary source of the heat is a high resting metabolic rate, which is supported by aerobic metabolism. In contrast, reptiles are ectothermic animals that regulate their body temperature using external heat sources, the sun in particular. Since skeletal evidence suggests that the common ancestral amniotes of the avian and mammalian lineages were almost definitely ectothermic, endothermy must have evolved independently in the therapsid-mammalian lineage and the theropod-bird lineage.

When and how endothermy in these lineages evolved is not fully understood. Paleobiological evidence suggests that metabolic changes did not occur suddenly in the lineages of birds and mammals. Rather, the resting metabolic rate and body temperature had increased gradually throughout their stem lineages (Lovegrove 2016). However, in the case of birds, it is most likely that true homeothermic endothermy was acquired only by Cretaceous Ornithurae (Hillenius and Ruben 2004). Strong evidence of, or the lack of, endothermy can be physically observed in the design of the nasal cavity in fossils. Based on the design of the nasal cavity, we can speculate whether or not extinct animals had nasal respiratory turbinates, or conchae, which are curled bony protrusions from the walls of the nasal cavity into the breathing passage. Respiratory turbinates are essential for animals with a high resting metabolic rate (i.e., living birds and mammals) in order to recover a significant portion of water and heat (Fig. 2.6). However, ectothermic animals, such as reptiles, do not need or possess such a mechanism. Fossil analyses suggest that

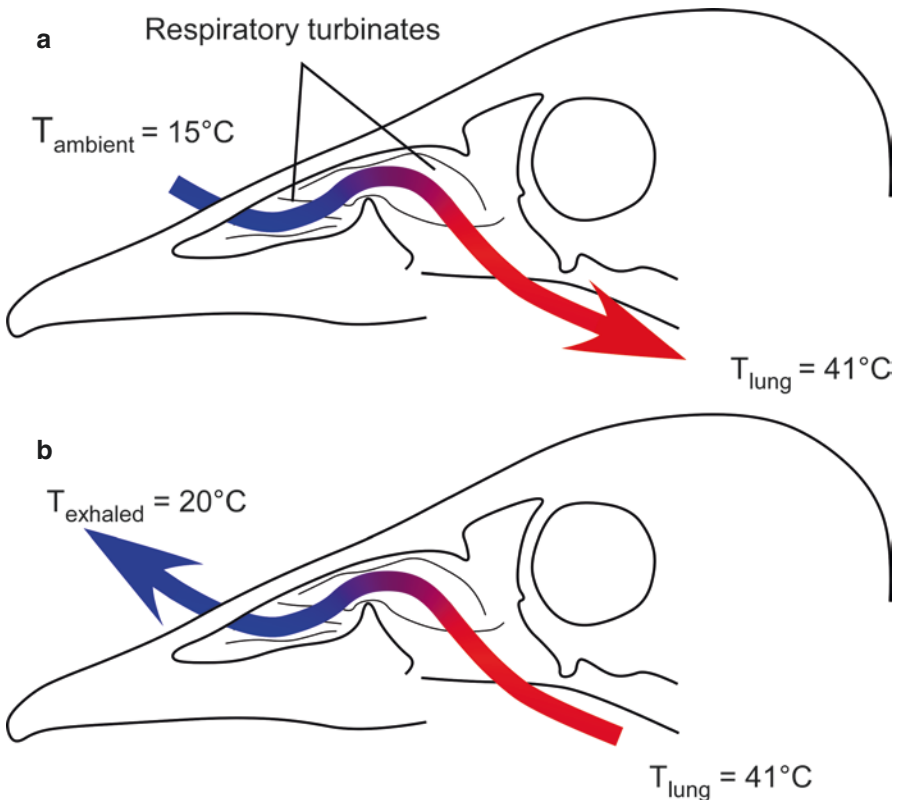


Fig. 2.6 Respiratory turbinates in birds (adapted from Hillenius and Ruben 2004 with permission). When birds inhale (**a**), air passing through the respiratory turbinates is heated and humidified. When birds exhale (**b**), air is cooled down and dehumidified through the respiratory turbinates

theropod dinosaurs, as well as other avialans (e.g., *Archaeopteryx* and Enantiornithes, Martin and Zhou (1997), did not have any indication of the mechanism, while Ornithurae in the Early to Late Cretaceous probably had ones. These observations are consistent with the hypothesis that endothermy probably evolved with modern birds and their immediate ancestors.

The major reason that only ornithurine birds acquired endothermy might be related to their ability of powered flight although there are other relevant abiotic and biotic factors, such as ambient temperature, humidity, CO₂ level, body size, and musculature type. Bennett and Ruben (1979) argue that the evolution of a higher metabolic rate and endothermy are accidental secondary events, preceded by an enhanced aerobic capacity for prolonged locomotor activity. In the case of birds, long-distance powered flight is the sustained performance requiring aerobic metabolism. The capacity for long-distance activity was probably required to compete against rivals in order to increase territory/home range size for resources. In contrast, ectotherms rely on anaerobic metabolism for bursts of intense movements, but such behavior cannot last long due to fatigue associated with the accumulation of lactic acid and the depletion of stored fuel. Once endothermy was obtained, it perhaps enabled birds to have stamina and time necessary to perform behaviors above and beyond long-distance powered flight. These behaviors include sophisticated courtships to attract potential mates, parental care for offspring, patrolling of extensive territories, and other complex behaviors that can be categorized as cognition. Selection of these complex behaviors might result in the cerebrum expansion, especially the DVR and Wulst, which may play important roles in such higher cognitive capacities (Shimizu and Watanabe 2012).

In order to clarify the relationship between the endothermy and cerebral development, it would be useful if we had a detailed information about the metabolism of Pterosauria (“wing lizards”). Although their exact flight capabilities are also still controversial, skeletal features suggest that most pterosaurs could sustain powered flapping flight (Witton 2013). Pterosaurs lived from the Late Triassic to the end of the Cretaceous Period (228 to 66 million years ago). Since pterosaurs and dinosaurs belong to two different clades in archosaurs, pterosaurs evolved volancy independently from the stem bird lineage. In terms of brain development, the two most notable characteristics of the pterosaur brain are its large semicircular canals in the inner ear and the cerebellum, follicular lobes in particular. Both structures are essential for maintaining equilibrium and controlling vestibular coordination associated with aerial movements. However, the brain volume of pterosaurs is intermediate between reptiles and birds (Witmer et al. 2003). Importantly, the cerebrum development is not impressive compared to that of modern birds. Whether pterosaurs are endothermic or ectothermic is not yet resolved (Clarke and Portner 2010). If there is a relationship between endothermy and cerebral expansion, the hypothesis predicts that they had a high metabolic rate and body temperature, but did not reach the level of endothermy as in modern birds.

Finally, the importance of homeothermic endothermy as a necessary step for the cerebrum expansion may be the case for mammals as well. In mammals, the evolution of large and complex brains occurred in three major pulses (Rowe et al. 2011),

which may roughly correspond to the evolutionary processes of endothermy in the avian lineage (Lovegrove 2016). According to the examination of nasal respiratory turbinates in synapsids that gave rise to mammals, endothermy was attained relatively early in the lineage even before the earliest eutherian mammals emerged about 160 MYA from the Jurassic of China (Hillenius and Ruben 2004; Luo et al. 2011). In the lineage of synapsids, terrestrial cursoriality might have been the sustained performance requiring aerobic metabolism. Such activities are further associated with olfaction and brain areas for olfaction, such as olfactory bulbs and piriform cortex. Further analysis is warranted to clarify the relationship between the evolution of endothermy and cerebral expansion in mammals.

2.5 Concluding Remarks

In the bird lineage, expansions of the brain have occurred multiple times during the last 300 million years. As seen in Fig. 2.7, discussions in this chapter focused on three possible pulses—at the emergence of amniotes in the Paleozoic, during the therapsid evolution in the Mesozoic, and the most extensive cerebral expansion in the crown birds in the Cenozoic. Thus, it is most likely that truly impressive cognitive and emotional capabilities of birds flourished only after the K-Pg boundary. We discussed several critical selective factors at each pulse of expansion, including terrestrial habitats, parental investment, predatory behaviors, body miniaturization, and increased metabolic rate. The most critical factor for the enlarged cerebrum of

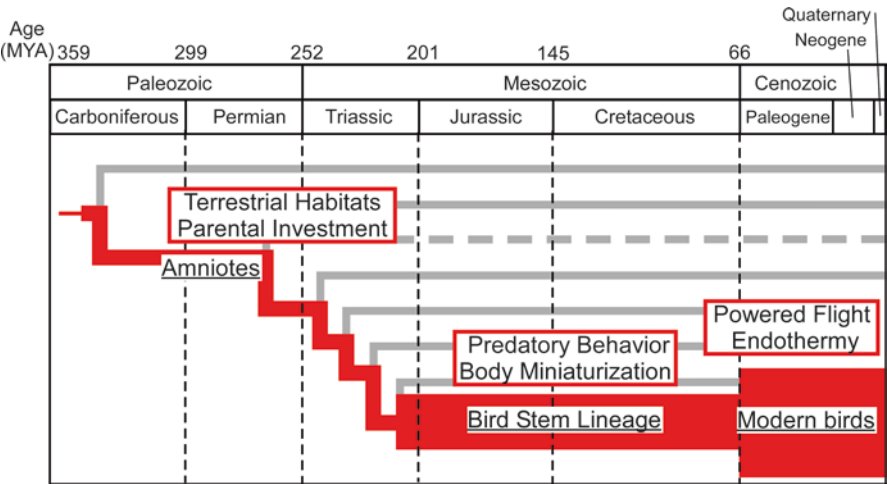


Fig. 2.7 Three pulses of the cerebral expansion along the lineage leading to modern birds. The expansion occurred multiple times—at the emergence of amniotes in the Paleozoic, during the therapsid evolution in the Mesozoic, and the flourishing of modern birds in the Cenozoic. The thickness of the red line schematically represents the degree of cerebral expansion

modern birds might have been the evolution of homeothermic endothermy 66 MYA in order to support long-distance flight. Endurance based on endothermy in turn enabled birds to spend more time and energy to conduct various complex behaviors, which required to develop and enlarge the cerebrum. Without endothermic metabolism, birds might have had a brain like Mesozoic avialans or pterosaurs—having developed visual, vestibular, and motor systems, but a relatively small cerebrum. A large cerebrum is a brain structure for animals that can afford a long duration of sustained activity owing to endothermy. In this respect, the evolution of cognition and emotion in modern birds can be regarded as a fortuitous result of long-range powered flight.

Acknowledgments The authors thank Tadd B. Patton, Michel A. Hofman, Douglas G. Barron, and Lynn B. Martin for critically reading the manuscript and providing helpful suggestions.

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Evolution of the Brain, Cognition, and Emotion in
Vertebrates

Watanabe, S.; Hofman, M.A.; Shimizu, T. (Eds.)

2017, X, 299 p. 76 illus., 25 illus. in color., Hardcover

ISBN: 978-4-431-56557-4