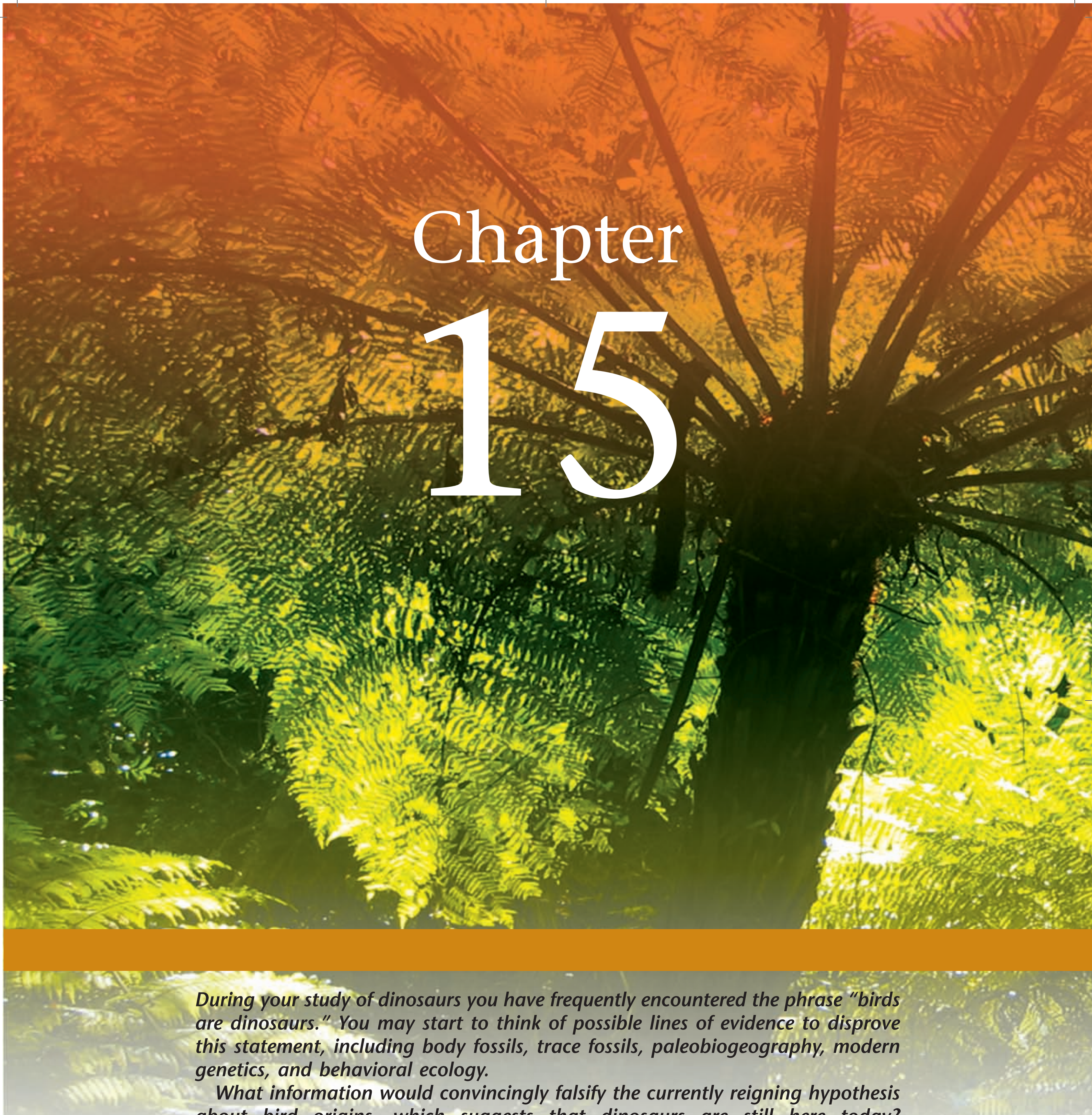
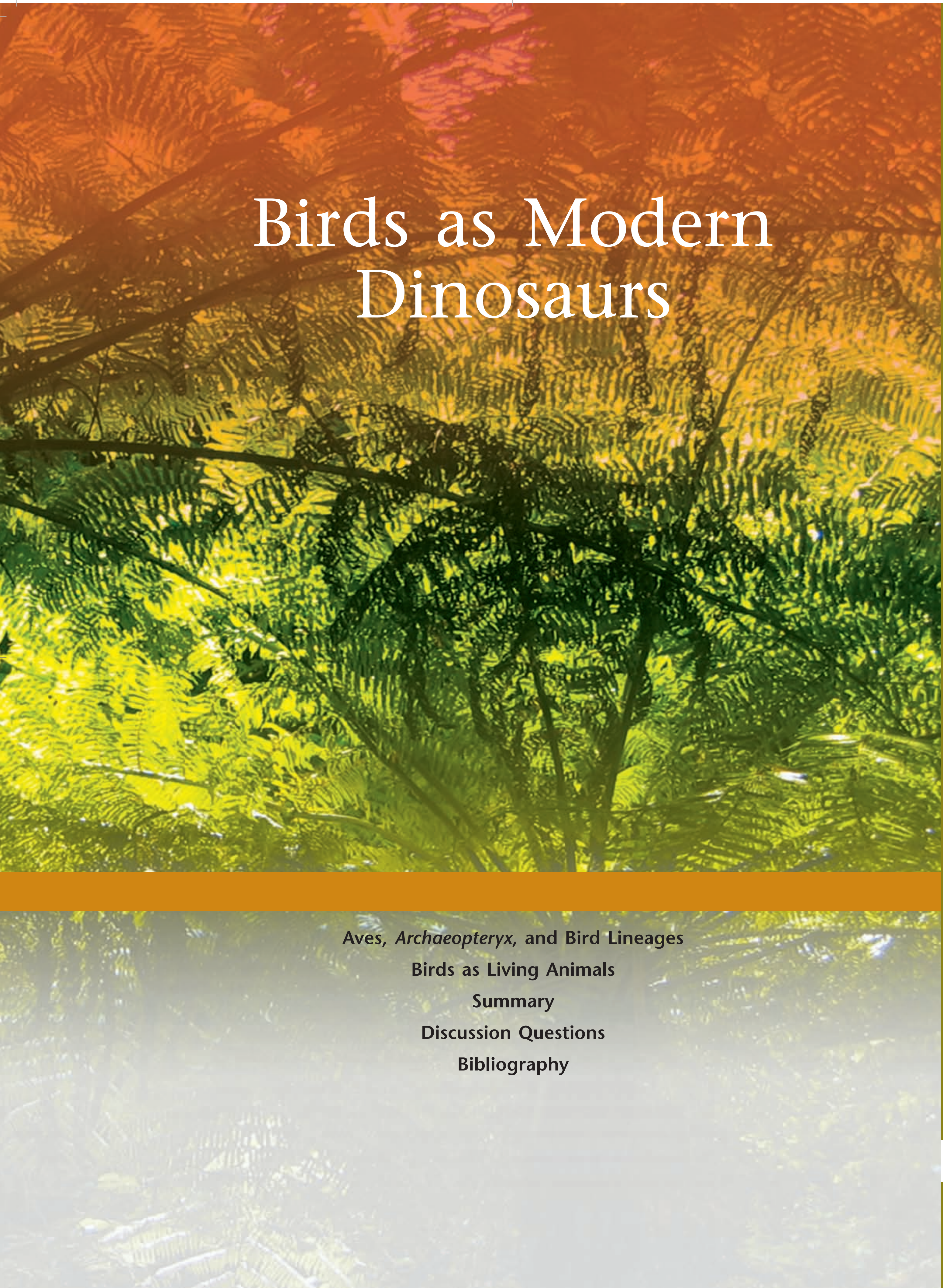
Chapter 15

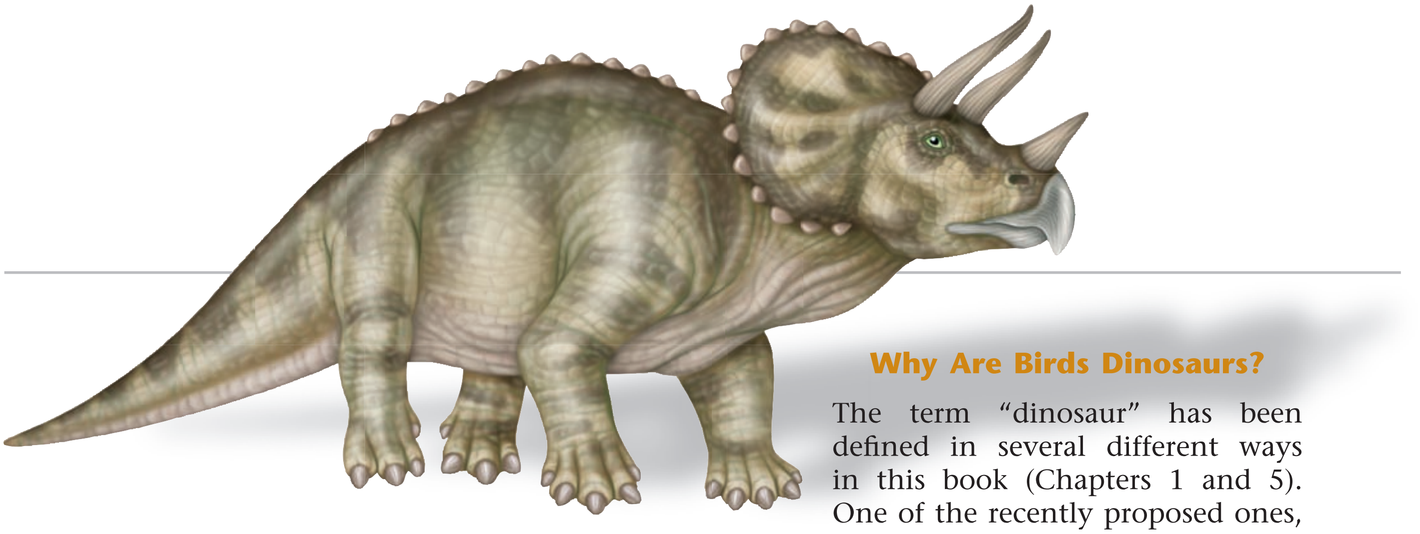


During your study of dinosaurs you have frequently encountered the phrase "birds are dinosaurs." You may start to think of possible lines of evidence to disprove this statement, including body fossils, trace fossils, paleobiogeography, modern genetics, and behavioral ecology.

What information would convincingly falsify the currently reigning hypothesis about bird origins, which suggests that dinosaurs are still here today? Conversely, what types and amounts of evidence would convince you to conditionally accept the hypothesis? How do modern birds provide clues regarding their possible dinosaurian ancestry, and what behaviors do they show that are unknown in dinosaurs?



Birds as Modern Dinosaurs



Why Are Birds Dinosaurs?

The term "dinosaur" has been defined in several different ways in this book (Chapters 1 and 5). One of the recently proposed ones, which aids in interrelating most of the preceding chapters with this one, is:

> *An animal that is a member of the group descended from the most recent common ancestor of* Triceratops *and birds.*

The reason why *Triceratops*, a ceratopsian (Chapter 13), is singled out in this definition is because it represents the most advanced ornithischian, and birds represent the most advanced saurischians. Saurischians and ornithischians are different clades of dinosaurs, but they diverged from a common ancestor. Hence, whenever their most recent common ancestor lived (probably in the Middle to Late Triassic) is also when dinosaurs as a clade began. This application of phylogenetic methods results in a geologic range of dinosaurs from Late Triassic to the present, not from the Late Triassic to the end of the Cretaceous. Consequently, dinosaurs did not become extinct – they are still here today as birds.

The purpose of this chapter is to show that dinosaurs and birds are now intertwined topics that can provide perspectives on the past, present, and future of dinosaur studies. The long history of dinosaurs is intrinsically connected to modern birds because birds are dinosaurs just as much as humans are mammals. Moreover, observations of modern birds lend insights on how their extinct non-avian cousins may have lived and especially how they behaved. Yet another consideration is how the 145-million-year evolutionary history of birds is related to subjects other than dinosaurs, such as environmental changes during the latter part of the Mesozoic Era and mass extinctions at the end of the Cretaceous (Chapter 16). Consequently, birds comprise a crucial topic within dinosaur studies, one that helps to complete a picture of the evolutionary history of dinosaurs.

Aves, *Archaeopteryx*, and Bird Lineages

Birds share a large number of synapomorphies with non-avian dinosaurs, which means that their node-based clade, Aves, is within the Dinosauria, Saurischia, Theropoda, Tetanurae, Coelurosauria, Maniraptiformes, Maniraptora, and the stem-based clade Aviale (Fig. 15.1). Aviale is defined as including all living birds and maniraptorans more related to them than the dromaeosaur *Deinonychus*, so it includes a few non-avian theropods. This means that Dromaeosauridae and Aviale are sister

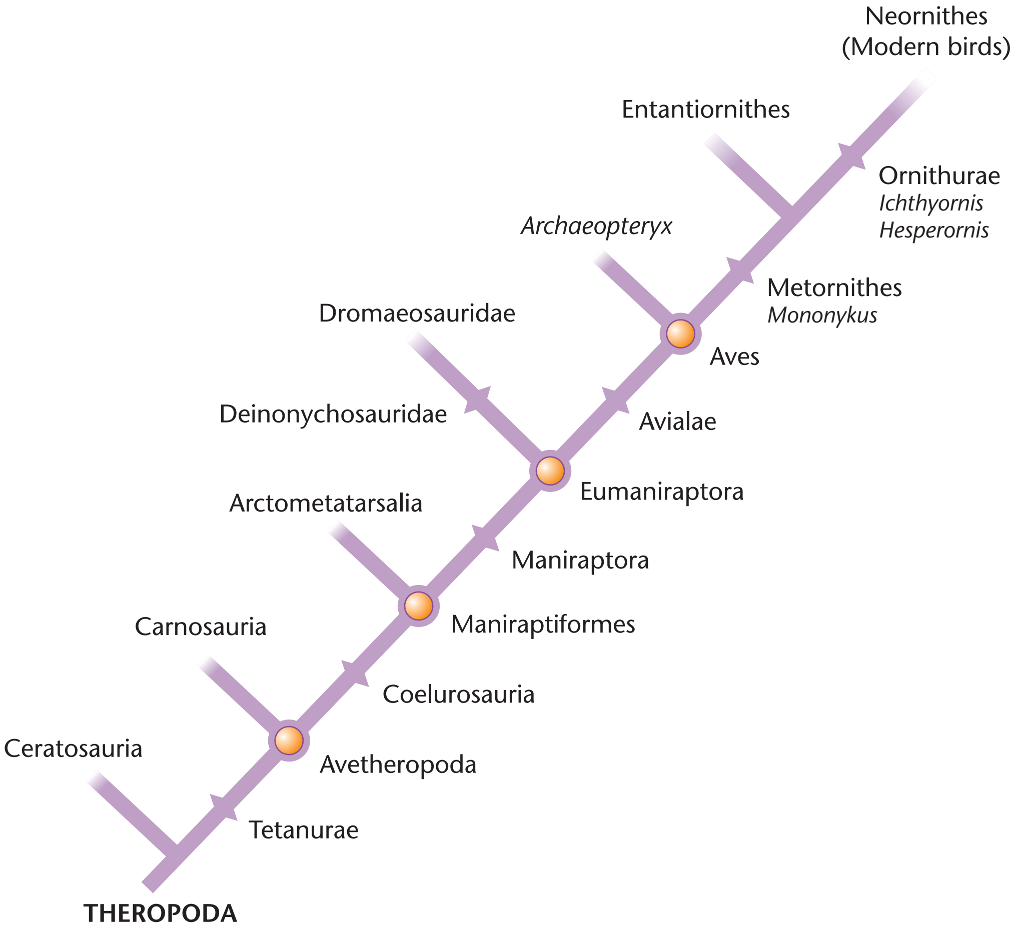


FIGURE 15.1 Cladogram showing the lineage within Theropoda leading to Aves (birds) and subsequent clades nested within Aves.

clades. More specifically, birds are defined cladistically as *Archaeopteryx lithographica* of the Late Jurassic (Chapters 3, 6, and 9) and all descendants of their most recent common ancestor. The important point about this definition is that *Archaeopteryx*, an exemplary "transitional" fossil (Chapter 6), is not considered to be the common ancestor of all birds, but rather is the most basal bird known. No other contenders for the superlative appellation of "oldest bird," also thought to have lived in the Late Jurassic, have been verified yet. However, tracks similar to those made by undoubted avians have been described from Late Triassic strata of Argentina. The large time gap between these tracks and *Archaeopteryx* suggests small non-avian theropods as the tracemakers, but research on this hypothesis was still being conducted at the time of this writing.

Characters of Aves (Fig. 15.2) include:

- Reduction of the number of caudal vertebrae to 23 or less. Their tails became shorter, which fused into a small structure called a **pygostyle** (although also present in a few non-avian dinosaurs).
- A forearm that is more than 90% of the length of the humerus and a fore limb length considerably longer (more than 120%) than that of the hind limb, which shows the tendencies of these limbs' use for flight.

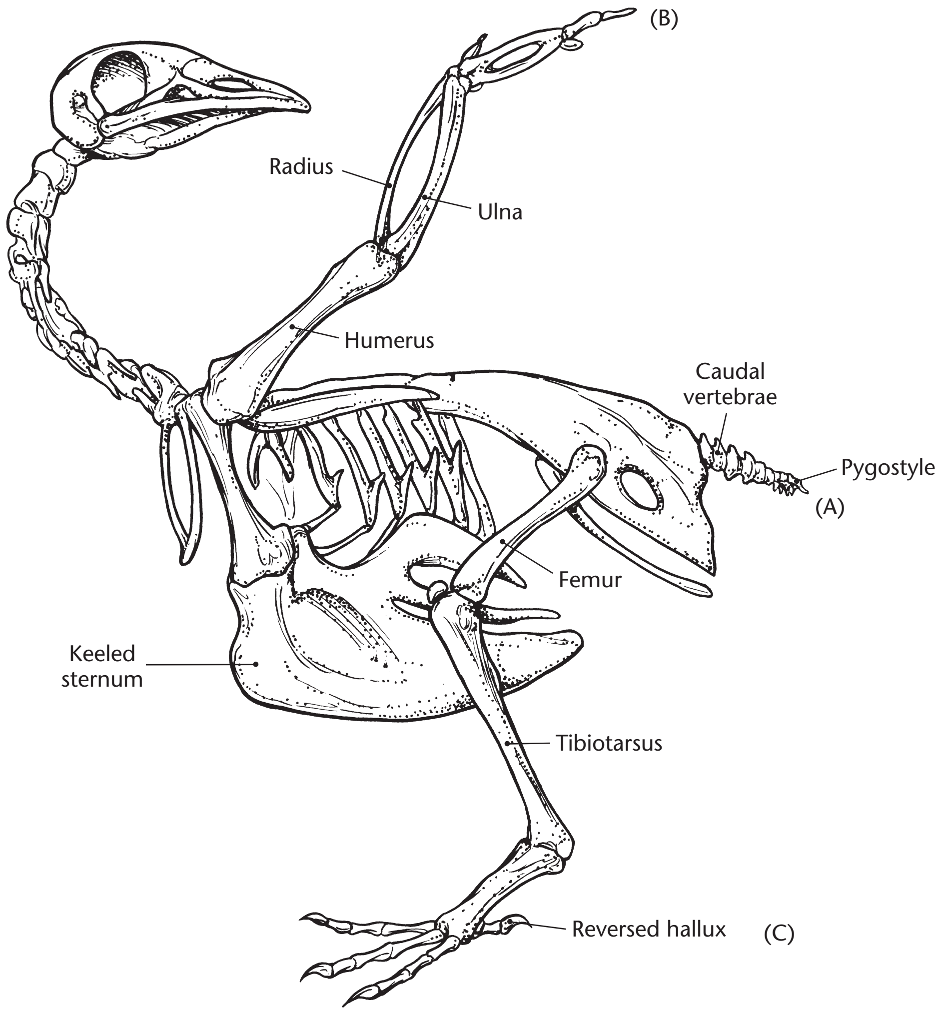


FIGURE 15.2 A few characters defining Aves (birds): (A) reduction of caudal vertebrae into a pygostyle; (B) forearm more than 90% of the length of the humerus and forelimb considerably longer (more than 120%) than the hindlimb; (C) anisodactyl foot, with a reversed hallux adapted for perching. Notice also the keeled (carinate) sternum and elongated coracoids.

- An anisodactyl foot, with three forward-pointing digits (II through to IV) and a reversed hallux (digit I) adapted for perching.

Keep in mind that these characters are added to the previously mentioned characters of the theropod ancestors of birds, which means that this condensed list does not come close to describing what is defined as a bird. For example, the possession of feathers used to be a primary criterion for identification of an animal as a bird, especially under the Linnaean classification scheme, but numerous discoveries of non-avian feathered theropods have revoked this single-character identifier. Instead, feathers can be viewed as a possible plesiomorphy in birds and the few theropods that shared a common coelurosaurian ancestry. Feathered non-avian theropods (Chapter 9) include *Beipiaosaurus*, *Caudipteryx*, *Microraptor*, *Protarchaeopteryx*, *Sinornithosaurus*, *Sinosauropteryx*, and others, all from the Early Cretaceous of China. A more inclusive trait is the possession of low-density pneumatic bones, evident

FIGURE 15.3 The Late Jurassic bird *Archaeopteryx lithographica* of the Solnhofen Limestone, Bavaria, Germany. Compare with Figure 2.4. Humboldt Museum für Naturkunde, Berlin/Peabody Museum of Natural History, Yale University.

in both theropods and birds (Chapter 9). Modern birds also have a number of air sacs throughout their bodies that help to lower their density and thus aid in flight.

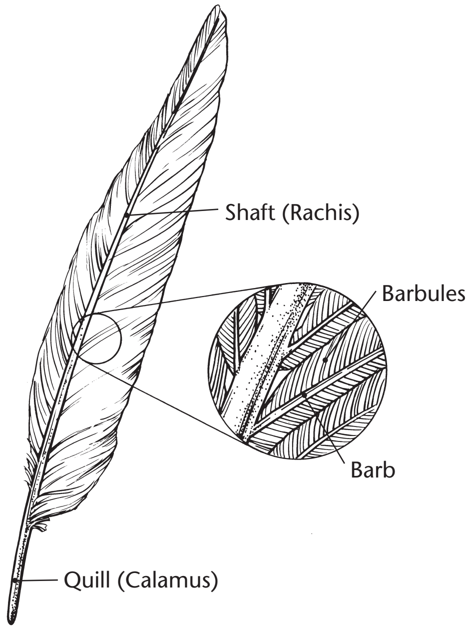
As far as *Archaeopteryx* is concerned, it was small by dinosaurian standards, especially in the Late Jurassic when it shared the landscape with massive sauropods (Chapter 10). It is about 45 cm long, probably weighed less than half of a kilogram, and is comparable to the size of a large crow (Fig. 15.3). *Archaeopteryx* shows a mix of features normally associated with non-avian theropods and birds exclusively:

- A tail composed of an intermediate number of caudal vertebrae, which makes it short for a theropod but long for a bird.
- Claws on its fore limbs identical to those of some theropods, but not seen on most birds.
- Flight feathers connected to the fore limbs identical to those seen in most birds, but not in most theropods.
- Teeth in the jaws that are atypical of most birds, but non-serrated, which is atypical for theropods.
- A furcula (“wishbone”) that represents a fusing of the clavicles, present only in a few theropods (such as some maniraptors), but in all birds.

Archaeopteryx also recently had its head examined and was found to be, for all practical purposes, “bird-brained.” This investigation used CT scans (Chapter 4) to develop a finely resolved three-dimensional picture of the braincase for one specimen of *Archaeopteryx*, and the results showed that its brain was much more akin to that of a modern bird than a reptile.

Archaeopteryx was found in a fine-grained limestone, the Solnhofen Limestone of Bavaria, Germany. This deposit probably formed in a lagoon and dates to about 152 Ma in the Late Jurassic. Seven specimens and one feather represent *Archaeopteryx*; the feather, which was found in 1860, is presumed to be from this specimen because no other feather-bearing fossils have been found in the Solnhofen. The first complete skeleton with feather impressions was found in 1861, and its discovery contributed to then-raging debates about evolutionary theory prompted by Darwin’s publication of *On the Origin of Species* in 1859 (Chapter 3). The other specimens were found at various times from 1877 to 1992. Interestingly, one of the specimens had been mislabeled in a museum collection as a pterosaur; John Ostrom realized its actual identity when he first saw it in 1970 (Chapter 3). In a similar manner, yet another specimen was discovered three years later when

FIGURE 15.4 Anatomy of a typical flight feather.



a closer examination of a skeleton initially identified as the small, Late Jurassic coelurosaur *Compsognathus* revealed that it was actually *Archaeopteryx*. Thus far, no other species of undoubted Late Jurassic birds are documented, making *Archaeopteryx* the sole known product of bird evolution in the Jurassic.

Of course, the most intriguing of the many interesting traits of *Archaeopteryx* are its feathers, which were originally recognized for their scientific significance and are still the subject of debate today. The reason for this interest is that the feathers of *Archaeopteryx* have the appearance of those seen in most modern birds. In modern birds, a feather is a keratinized integument that originates in a layer of skin below the surface of the animal; these feathers can be broadly categorized as **downy feathers** and **flight feathers** (Fig. 15.4). The primary function of downy feathers is insulation, a property exploited by humans who use these feathers as fill in winter coats and sleeping bags. In contrast, flight feathers are used mainly for aiding lift and descent by creating surfaces that move air in ways conducive to controlled flight. Some flightless birds still retain flight feathers as a primitive (but vestigial) trait, which indicates their descent from flighted ancestors.

A typical feather consists of a central, hollow **shaft** that terminates proximally into a **quill**. The shaft has **barbs** that branch from it at about 180° from one another (on opposite sides of the shaft). The barbs interlock through smaller **barbules** in a fashion similar to the teeth in a zipper. In a flight feather, the barbs collectively form a planar structure called a **vane**, creating air foils that help considerably in the aerodynamic ability of flighted birds. Downy feathers are relatively less organized, and the barbs will radiate in seemingly random directions, forming ill-defined vanes or no vanes at all.

Like any other structure, both types of feathers have more than one function. For example, bright colors and varied patterns contribute to intraspecies displays. The multiple uses of feathers can at least partially explain why flightless theropods such as *Caudipteryx* would have color banding evident in feathers that composed their tail fan. This banding is the only known direct evidence of coloration in dinosaurs. The hair-like dorsal fringe seen in *Sinosauropteryx* was probably composed of downy feathers, which were not used for flight either. This evidence suggests that the flight feathers seen in *Archaeopteryx* may have evolved for the purposes of display or insulation first, then flight later.


(A) (B)

FIGURE 15.5 *Confuciusornis sanctus*, an Early Cretaceous bird from China. (A) Fossil specimen, with carbonized margin indicating presence of feathers. (B) Reconstruction of living animal. Note the prominent digits on the wings, indicating a primitive condition. Naturhistoriches Museum Basel, Basel, Switzerland.

Compared to *Archaeopteryx*, the most primitive bird interpreted so far is *Rahonavis ostromi*, found in Upper Cretaceous rocks of Madagascar. Its unusual mixture of maniraptoran and avian traits led to some controversy over whether it actually represents a bird or not, and its geologic age (well after the Late Jurassic) contributed to this skepticism. A clade of primitive birds that comprises a sister clade to all birds other than *Archaeopteryx* and *Rahonavis* is **Confuciusornithidae**. This clade is represented by abundant specimens of its namesake, *Confuciusornis sanctus* (Fig. 15.5) as well as *Changechengornis hengdaoziensis*. As might be surmised from their names, both species are from China, and they come from the same Lower Cretaceous formation.

Judging from the numerous and varied species found so far, Aves diversified considerably throughout the Cretaceous, suggesting that their evolution was relatively rapid and their ecological niches became more specifically definable. Some forms had definitely achieved full flight and probably had arboreal lifestyles, whereas others adapted to new habitats such as semi-arid inland areas and shallow marine regions. For example, avians are likely the tracemakers of bird-like tracks in some of the oldest Cretaceous strata of Spain, and these tracks are interpreted as having been made by shorebirds. This implies that birds had already radiated to such habitats within 10 million years of *Archaeopteryx*. A few presumed dinosaur eggs and nests have also been suspected of actually belonging to avians; some Late Cretaceous eggshells closely match those known from birds. The oldest embryonic avian remains, found in Mongolia, are also Late Cretaceous and probably belong to the bird *Gobipteryx minuta*. Overall, the fossil record for birds improves dramatically in Cretaceous deposits, in comparison to their extreme rarity in Jurassic strata. Additionally, discoveries of the last 25 years in particular have added exponentially to unraveling the evolution of Cretaceous birds. At this writing, more than 50 genera of birds had been identified from Cretaceous strata, hailing from every continent, except Antarctica, and contributing to the ever more complicated cladograms which change with each new discovery (Table 15.1).

TABLE 15.1 Cretaceous birds, their approximate geologic ages, and general localities.

Genus	Age	Geographic Location
Alexornis	Late Cretaceous	Mexico
Apatornis	Late Cretaceous	Western USA
Apsaravis	Late Cretaceous	Mongolia
Avisaurus	Late Cretaceous	Western USA
Baptornis	Late Cretaceous	Western USA
Cathayornis	Early Cretaceous	China
Changchengornis	Early Cretaceous	China
Chaoyangia	Early Cretaceous	China
Confuciusornis	Early Cretaceous	China
Coniornis	Late Cretaceous	Western USA
Enaliornis	Early Cretaceous	UK
Eoalulavis	Early Cretaceous	Spain
Eocathayornis	Early Cretaceous	China
Eoenantiornis	Early Cretaceous	China
Gargantuavis	Late Cretaceous	France
Gobipterx	Late Cretaceous	Mongolia
Halomornis	Late Cretaceous	Eastern USA
Hesperornis	Late Cretaceous	Western USA
Iberomesornis	Early Cretaceous	Spain
Ichthyornis	Late Cretaceous	Western and Eastern USA
Jibenia	Early Cretaceous	China
Kizylkumavis	Late Cretaceous	Uzbekistan
Kuszholia	Late Cretaceous	Uzbekistan
Lectavis	Late Cretaceous	Argentina
Liaoningornis	Early Cretaceous	China
Nanantius	Early Cretaceous	Australia
Neuquenornis	Late Cretaceous	Argentina
Noguerornis	Early Cretaceous	Spain
Otogornis	Early Cretaceous	China
Parahesperornis	Late Cretaceous	Canada
Patagopteryx	Late Cretaceous	Argentina
Protopteyrx	Early Cretaceous	China
Rahonavis	Late Cretaceous	Madagascar
Sinornis	Early Cretaceous	China
Soroavisaurus	Early Cretaceous	Argentina

Although discussion still continues about whether Archaeopteryx was capable of self-powered flight (that is, flapping its wings instead of merely gliding), the Early Cretaceous Sinornis of China has characteristics closely associated with full flight.

One of the key features used to determine whether a bird flew is the degree of development seen in its sternum, to which the large flight muscles are attached. These sterna can be bony, cartilaginous, or completely absent; the latter two conditions are coincident with flightlessness. A bladed appearance to the middle of a sternum is a **keel** (also known as **carina**), analogous to the central ridge on the bottom of a boat. Once the keel is well-developed, the sternum is called **carinate**. *Archaeopteryx* has a mildly carinate sternum, whereas the Early Cretaceous *Sinornis* of China has a proportionally more carinate sternum. When coupled with elongated coracoids in the shoulder region (for the further attachment of flight muscles), this evidence advocates *Sinornis* as a flyer. Yet *Sinornis* and many other Cretaceous birds, such as the Early Cretaceous *Iberomesornis* of Spain, still retained teeth and other primitive traits that reflected their dinosaurian heritage.

Other Cretaceous birds varied from fully flighted to flightless varieties. For example, the very odd, wingless, cursorial *Mononykus* from the Upper Cretaceous of Mongolia was first classified as a non-avian theropod, but is now placed within Aviale and is considered more closely related to *Archaeopteryx* than to most other maniraptorans. Other flightless Late Cretaceous birds included the tern-like shorebird *Ichthyornis* and the toothed, marine diving bird *Hesperonis* (Fig. 15.6). Thus, birds certainly had taken to the air and shared flight time with pterosaurs during the Cretaceous, but they also ran in the same deserts as dromaeosaurs and swam in the same waters as plesiosaurs and other marine reptiles (Chapter 6). This expansion of habitats for birds is all the more remarkable because it happened during the last 70 million years of the Mesozoic, when most dinosaurs of the previous 90+ million years apparently spent all of their time firmly on the ground.

Of all the clades of Cretaceous birds, none of those with toothed species, such as **enantiornithines**, survived into the Tertiary Period. Although the fossil record for birds has improved considerably in recent years, inadequate information is available

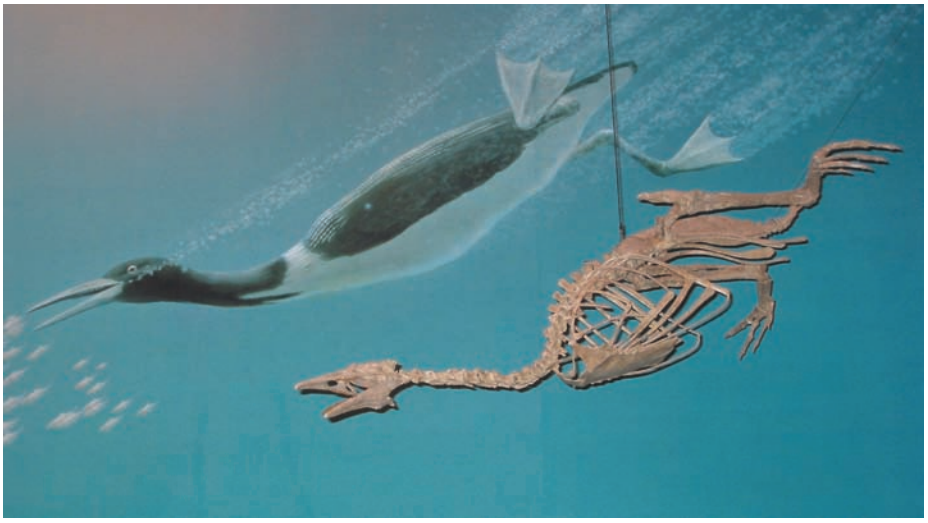


FIGURE 15.6 Skeleton of *Hesperornis regalis*, a Late Cretaceous diving bird recovered from marine deposits in Kansas, and artistic reconstruction behind it. Note the vestigial wings, indicating secondary flightlessness in a Cretaceous bird. Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma.

to figure out when declines occurred in bird populations. Nevertheless, all lineages with the exception of the **neornithines**, known generally as "modern birds," went extinct either before or at the end of the Cretaceous Period. Why only these birds and no others made it into the Tertiary is unknown. One commonality of Late Cretaceous neornithines is that most were apparently shorebirds. This habitat preference may have had a survival advantage for whatever events happened toward the end of the Cretaceous and beginning of the Tertiary Periods (Chapter 16). Alternatively, the presence of these species in the fossil record may be a result of a preservation bias in the form of the more frequent burial of nearshore species. Taphonomy is the filter through which all interpretations of the fossil record necessarily must be made (Chapter 7), and birds in particular are difficult to preserve as body fossils because of their often small, hollow bones. As a result, the fossil record for birds is not expected to be very rich, making the discoveries of recent years from the Late Cretaceous all the more remarkable.

Bird Ancestors: Theropod Hypothesis and the Origin of Avian Flight

The most widely accepted hypothesis for bird ancestry in the Mesozoic is that certain lineages of small theropods, in combination with environmental factors that affected natural selection of these theropods, resulted in the evolution of birds by the Late Jurassic. As mentioned before, the shining example used as evidence in this evolutionary scenario is *Archaeopteryx*, known as the long-presumed link between reptilian ancestors and avian descendents. A theropod ancestry of *Archaeopteryx* is interpreted on the basis of its numerous anatomical features allied with theropods (Chapter 9):

- Both upper and lower jaws bearing pointed teeth.
- Tridactyl manus with digits I through to III, digit II the longest of the three, ending in claws.
- Semilunate (half-moon shaped) carpal in the wrist.
- V-shaped furcula.
- Ankle with differentiated (unfused) metatarsals II through to IV.
- Ascending process on the astragalus.
- Tridactyl pes symmetrical around digit III, with digit I retroverted (anisodactyl) and well-developed claws on all digits.
- Saurischian pelvis with long pubis.
- Gastralia.
- Six unfused sacral vertebrae.
- Moderately long tail (about 25 caudal vertebrae), with elongate processes (zygopophyses) that interlock to stiffen it.

Modern birds form a contrast:

- No teeth.
- Forearms where the carpals, metacarpals, and phalanges fuse into a **carpometatarsus** (the distal end of a chicken wing shows this structure quite well).
- A **synsacrum**, where the pelvic bones fuse with the sacral vertebrae.
- A pygostyle (although a few non-avian maniraptorans also have this feature).
- Fusion of the metatarsals (anklebones) into a **tarsometatarsus**.

Obviously, *Archaeopteryx* is not just an ordinary bird. Its teeth, unfused bones in the forearm, manus with phalanges and claws, unfused sacrum, long tail, and unfused bones in the ankle, along with many other traits, all point to its classification as a theropod. Yet it is also a bird because of modifications to this theropod body plan that represent novel traits.

On the basis of the previously mentioned traits for *Archaeopteryx*, Aves and Deinonychosauria are hypothesized as having a common ancestor from the node-based clade Coelurosauria. Depending on how a cladogram for birds and their theropod relatives is arranged, some predatory theropods, such as the Early Cretaceous *Deinonychus*, *Dromaeosaurus*, *Utahraptor*, and Late Cretaceous *Velociraptor*, are probably part of a sister clade to birds. A possible point of confusion is that, because of this common ancestry, both deinonychosaurs and primitive birds may have been feathered. This hypothesis is supported by the discovery of one feathered deinonychosaur, the Early Cretaceous *Sinornithosaurus* of China. This circumstance does not mean that birds were the ancestors of deinonochysaurs, but rather that they descended from the same ancestor and later became contemporaries. The largest problems with the theropod–bird hypothesis do not lie in working out whether birds evolved from theropods; a detailed comparative analysis reveals that more than 100 characters are shared by coelurosaurian dinosaurs and avians. The questions that are still unanswered are when and how birds evolved from theropod ancestors.

The "when" part of the theropod–bird question is probably easier to answer in a preliminary way. The stratigraphic position of *Archaeopteryx* indicates a minimum age of Late Jurassic for the evolution of birds. This suggests that the most immediate ancestors of birds may have originated during the Middle Jurassic or the earliest part of the Late Jurassic, with divergence from a hypothetical coelurosaur (probably maniraptoran) ancestor. A few fragmentary maniraptoran remains have been found in Late Jurassic deposits of North America, indicating a maniraptoran presence on two continents at that time. However, the lack of more complete, identifiable maniraptoran specimens is particularly vexing in this respect, because a gap results in the fossil lineage of coelurosaurs to avians. Nevertheless, the characters of *Archaeopteryx* with relation to other theropods and its stratigraphic position serve as a predictor not only for where in geologic time these avian ancestors lie, but also for what they should look like.

The question of how flighted birds evolved from flightless theropods is a rather contentious debate that may not be resolved in the near future. This pessimistic assessment acknowledges that the majority of data supporting the competing hypotheses are based on inferences gained from functional morphology and biomechanical analyses. Because the morphological features that define birds are intrinsically linked to adaptations for flight, the causes for the evolution of flight in certain theropods must be considered. As a result, two main hypotheses have been proposed for the origin of bird flight:

1. the **arboreal hypothesis**; and
2. **cursorial hypothesis**.

The arboreal hypothesis, known colloquially as the "trees-down" hypothesis, states that small, feathered theropods climbed into trees, evolved into gliding forms, and eventually gave rise to forms capable of full flight. The cursorial hypothesis, also known as the "ground-up" hypothesis, postulates that small, fast-moving, bipedal theropods flapped their feathered arms while pursuing and swatting at prey such as insects, which eventually led to jumping, short flights, then full flight in later descendants. Both hypotheses presume that feathers evolved from the skins of theropods in some rudimentary state as "proto-feathers" that were not associated with flight, thus meaning that the feathers were exaptations. Exaptations are inheritable traits that were already favorably adapted for a selective pressure before it happened (Chapter 6), meaning that these proto-feathers did not evolve specifically for flight, but later helped with flying. After all, although feathers are useful for flighted birds today, they are not a prerequisite for flying ability in animals. For example, among tetrapods, pterosaurs and bats both independently developed full flying capabilities without the benefit of feathers. Consequently, theropods could have had feathers well before natural selection was applied in either an arboreal or cursorial scenario, and the feathers could have served an entirely different function.

Of these two hypotheses, the cursorial hypothesis was more popular with paleontologists until recently. It may have been more acceptable simply because it was less weak than the arboreal hypothesis. A turning point in this debate came about as a result of the recent discovery of three Early Cretaceous non-avian theropods that were apparently adapted for arboreal lifestyles. Two species, *Epidendrosaurus ninchengensis* and *Scansoriopteryx heilmanni*, are relatively small. They have an unusually long digit III on their hands, and long forearms, collectively. These traits would have served well for climbing trees. Another species, *Microraptor gui*, is also small (smaller than *Archaeopteryx*, in fact) and has feathers on all four limbs, which suggests that it was a glider. Adaptations for gliding are useless if the same animal also could not climb trees or similarly high objects, thus *Microraptor* is also assumed to have been a tree climber.

As just demonstrated, the debate over trees-down or ground-up origins for bird flight centers on functional morphology, and from such studies other apparent contradictions become apparent. For example, *Archaeopteryx* has claws on its manus that could have been used for climbing and feet that were seemingly adapted for perching. Nonetheless, its hallux is slightly too short for good perching, and it also has legs that were adapted for bipedal running. Likewise, its flight feathers are well developed, yet the bony sternum is poorly developed (in fact, only one specimen has a sternum preserved). Despite seven skeletons, some of them exquisitely preserved, and an inordinate amount of study by many careful and brilliant paleontologists over the course of 145 years, the exact details about how *Archaeopteryx* lived or got to where it was in its evolutionary history are still being debated.

Another problem with relying on functional morphology for either hypothesis is that few actual experiments or observations of modern analogues are included to test the assumptions. For example, no modern birds swat at insects or any other prey with their feathered arms for food gathering while they run, which disfavors the cursorial hypothesis. Similarly, the only modern analogue that favors the arboreal hypothesis is represented by one species of bird that has claws on its wings adapted for climbing trees, the hoatzin of South America (*Opisthocomus hoazin*). The hoatzin only has this ability in its juvenile state, as the adults have fused digits in their manus, just like any other bird.

Other independent data, such as trace fossils or facies associations, have not been integrated to any great extent into arguments for either hypothesis. For example, if theropod ancestors of birds were indeed cursorial before short flights, then preserved trackways of such behavior would help to confirm that this happened. Unfortunately, arboreal theropods would have left far fewer tracks, and scratch marks left on trees would have had low preservation potential. Another problem would be distinguishing non-avian theropod tracks from bird tracks in Jurassic rocks. So far no Jurassic bird tracks have been recognized, although the aforementioned avian-like tracks from the Late Triassic of Argentina are intriguing clues to animals that had feet similar to those of modern birds. With regard to *Archaeopteryx*, if it was at least partially ground dwelling, its short hallux means that it probably would not have left an impression of this digit. As a result, only a typical tridactyl and presumably non-avian theropod footprint would be evident.

One other piece of evidence relating to the trees-down or ground-up hypotheses is the paleoenvironmental context for *Archaeopteryx*. Its exclusive occurrence in lagoonal deposits of the Solnhofen Limestone means that it may have been flying far away from any forested areas, which would favor the cursorial hypothesis. Alternatively, all of the specimens in the Solnhofen also could have floated into the lagoon from forested areas (the "bloat-and-float" hypothesis explained in Chapter 7), which would not have negated the arboreal hypothesis. Other evidence supporting the latter scenario is the occurrence of the probable arboreal non-avian theropods, *Epidendrosaurus*, *Scansoriopteryx*, and *Microraptor*, in lake deposits, which means that they may have floated out into a water body before sinking to the bottom and becoming part of the fossil record.

The preceding discussion was presented in the context of an "either-or" argument, but in science alternative hypotheses do not have to be limited to just two. A third hypothesis, which is actually a variation of the cursorial one, is that ground running was helped along by vigorous flapping that increased theropod running speeds. Such an adaptation certainly would have aided in predator avoidance, which would have been particularly important for small theropods in the Late Jurassic. Under this hypothesis, natural selection of these flapping "pre-avian" theropods would have progressively led to full, self-powered flight. The contrast between this model and the previous cursorial model is that one would have been used for predation, whereas the other would have been used for avoiding it.

Yet another modification of the cursorial hypothesis is actually a neat synthesis of it with the arboreal hypothesis, which calls for the evolutionary development of **wing-assisted incline running**. This hypothesis differs from the others in that it has incorporated much experimental data from modern birds (partridges), rather than theorizing based on functional morphology. These experiments showed that juvenile partridges were capable of running up steep inclines, including vertical tree trunks, journeys that were made easier by an energetic flapping of their wings. This method also would have been an excellent method for predator avoidance, particularly if the predators were non-avian theropods with relatively short arms. The researcher who documented this behavior also tested the effects of feather area on incline running by trimming the feathers to half their length or cutting them off completely. Birds without feathers could not run up slopes greater than 60°, and the half-feathered individuals also were 10–20° behind the fully-feathered in climbing ability. This study thus helps to explain how a "half-wing" in a theropod would still have an evolutionary advantage over "no wing." The results also changed the perspectives of paleontologists who had not been studying extant avian dinosaurs for clues of their evolutionary history.

Although birds are theropods, the exact mechanisms responsible for the evolution of flightless theropod lineages into flighted birds are still poorly understood, although they are becoming clearer with each fossil discovery. Indeed, anatomical data derived from non-avian maniraptorans, *Archaeopteryx*, and other primitive birds have clearly demonstrated the clear progression of the fore limbs, chest, and shoulder girdles, adaptations favoring self-powered flight. For example, ratios of armspans to body lengths of the feathered non-avian theropods *Sinosauropteryx*, *Protarchaeopteryx*, and *Sinornithosaurus* show a potential progression from leapers to gliders (where wider armspans correlate with "wingspans"). Furthermore, *Archaeopteryx* may have been either a glider or used self-powered flight, but it may have been surpassed in the latter respect by the non-avian theropod *Cryptovolans*, which had a better developed keel (Chapter 9). Doubtless the steps of this evolutionary process and its contributing factors will gain even more clarity with further study and new fossil discoveries.

Bird Ancestors: "Thecodont" Hypothesis

Debates about bird ancestry included a hypothesis that birds originated from archosaur lineages separate from dinosaurs. A group of archosaurs, previously called

thecodonts, was considered as a common ancestral group to crocodilians, pterosaurs, and dinosaurs (Chapter 6). Based on cladistics, this grouping is now understood to be paraphyletic, and the recently held understanding is that Archosauria had at least two clades split from it, Crurotarsi and Ornithodira. Crurotarsans gave rise to some extinct crocodilian-like animals such as phytosaurs, as well as lineages that led to modern alligators and crocodiles. Ornithodirans gave rise to both pterosaurs and dinosaurs, both of which arrived on the Mesozoic scene by the Late Triassic.

Although these relationships seem clear now, this was not always the case. For example, under previous Linnaean classifications, thecodonts were more or less a conglomerate of crurotarsans and ornithodirans, and their evolutionary relationships were poorly understood. The first well-reasoned proposal of a thecodont origin for birds, stated in 1926 by German paleontologist Gerhard Heilmann, was based on the then-factual lack of clavicles (furcula) in theropods. In contrast, some primitive Triassic archosaurs did have clavicles. By Heilmann's logic, using a principle first articulated by Louis Dollo (Chapter 3), a structure that is lost is not re-acquired in an evolutionary lineage. This would have meant by default that non-dinosaur archosaurs were the ancestors of birds. However, when some maniraptors were later found to have furculas, the premise of Heilmann's hypothesis was negated and the theropod-origin hypothesis was correspondingly strengthened. Similarly, subsequent hypotheses of either thecodont or other archosaur ancestors have been based on only a few morphological traits shared by birds and the proposed bird ancestors. These attempts have not withstood critical scrutiny. Although the theropod–bird lineage admittedly has some gaps, a thecodont–bird lineage has chasms.

Evidence that added fuel to this still-simmering controversy was the announcement that feather-like structures were found on the dorsal surface of *Longisquama insignis*, a small Late Triassic archosaur from central Asia. The structures superficially do look like feathers in that they have central shafts with symmetrical branching forming elongated vanes, and they seem to originate from the body of the animal. *Longisquama*, which has been known to paleontologists for about 35 years, was interpreted as a gliding animal because of these unusual structures and its lightly built skeleton. However, these structures were only recently interpreted as feathers. As of this writing, the topic of whether the structures are indeed feathers, some odd type of scales, or some previously unknown structure is still unresolved. Regardless, preliminary claims of the presence of feathers on one specimen of a Late Triassic archosaur unrelated to dinosaurs do not automatically erase the enormous amount of character data that support dinosaur–bird ancestry. Feathers do not make a one-character "magic bullet" that proves a relationship of any given fossil to birds. By analogy, hair-like structures described in the wings of pterosaurs are not construed to imply that they were the ancestors of modern bats.

One consensus view is that birds represent convergent evolution from separate lineages. In this scenario, a thecodont ancestry provided bird descendants and theropod ancestry provided other bird descendants. This compromise nevertheless conjures a more complicated scenario than if birds had originated from just one lineage. It requires a sort of faith that such a unique body plan could have evolved independently from different lineages within approximately the same span of geologic time. Considering that the theropod hypothesis is backed by a robust data set and the competing ones are not, and that the coincidence of the more than 100 characters shared by theropods and birds is impossible to ignore, the most logical course is to conditionally accept the theropod hypothesis.

An interesting variation on the non-avian–avian theropod hypothesis is that some Cretaceous flightless and feathered "non-avian" theropods were actually descended from avian ancestors. As a result, the evolutionary sequence would have been:

1. non-avian flightless theropod;
2. avian flighted theropod; and
3. avian flightless theropod.

However, cladistic analyses of *Archaeopteryx* and other avians indicate that these are more derived forms than the flightless theropods conjectured as their descendants, therefore casting doubt on such an ancestor–descendant relationship. Regardless, the affirmation of this hypothesis would only modify the currently supported scenario for avian descent from non-avian theropods.

Nonetheless, a word of caution is warranted for any paleontologists who too quickly embrace a hypothesis as completely confirmed. Human prejudice can influence how evidence is viewed, fitting it to the hypothesis rather than cultivating awareness of how it may not fit. In other words, people see what they want to see. For example, a few years ago paleontologists named "*Archaeoraptor*," a new Early Cretaceous genus of dinosaur from China, on the basis of a single specimen that had a blend of half-deinonychosaur and half-avian features. This specimen was hailed as further confirming dinosaur–bird links and was given much publicity in the popular press before undergoing peer review. However, a more careful examination later revealed that it was a chimera: the posterior half of a dromaeosaur, later identified as *Microraptor*, had been pasted to the anterior half of a fossil bird, *Yanornis martini* (Chapter 9). This two-for-one specimen was not a hoax perpetrated by the paleontologists who described it, but nevertheless it was embarrassing to them and the magazine that first announced it. The lesson from this mistake is that the euphoria surrounding a potentially important fossil find is understandable, but healthy skepticism helps to prevent hasty interpretations that just happen to reaffirm a currently reigning hypothesis.

Bird Evolution in the Cenozoic

As mentioned earlier, birds had already filled numerous niches, including those in aquatic environments, by the end of the Cretaceous. Thus, the extinction of both ground-dwelling dinosaurs and aerial pterosaurs opened many more niches for birds and mammals by the early part of the Cenozoic. In spite of the extinction of all bird clades, except the neornithines, birds diversified quickly in these niches during the first 10 million years or so of the Tertiary Period. Shorebirds, similar to (and probable ancestors of) modern flamingos, herons, and ducks, were particularly common early in the Tertiary. The largest group of modern birds, the **passerines**, otherwise known as songbirds (wrens, larks, sparrows, warblers, chickadees, crows, jays, magpies, and so on), occupied most other niches available in terrestrial environments.

Passerines comprise about 60% of all known species of modern birds, numbering nearly 6000 species. Their evolution was most likely dependent on their vocalizations, which are key novelties linked to their reproductive cycles. The sounds of lambeosaurines from the Late Cretaceous can be reasonably inferred on the basis of their huge nasal chambers (Chapter 11), but fossil passerines of the past 20 million years, with their tiny and delicate bones, are not amenable to a similar analysis. Because their vocalizations did not fossilize, passerines are poor subjects for cladistic analyses, demonstrating in this instance that cladistics is only one tool available to a paleontologist, not a panacea. The diversification of passerines not only changed the sound of terrestrial ecosystems, but also affected the biogeographic dispersal of flowering plants, as many of these birds ate fruit and had other interactions with flowering trees and shrubs.

Although fore-limb adaptations to flight comprise a hallmark of birds, some lineages show the evolution of secondary flightlessness during the early part of the Tertiary Period. This situation means that the inheritance of a lack of flying

FIGURE 15.7 Track of greater rhea (*Rhea americana*), a large ratite native to Patagonia, Argentina. Notice its close anatomical resemblance to Mesozoic theropod tracks depicted and described in previous chapters, with prominent digits II–IV, phalangeal pads, and well-developed claws.

ability recurred like so: flightless non-avian theropod → flighted bird → flightless bird. Modern birds can be broadly divided into **carinates** (flighted birds) and **ratites** (flightless birds), although exceptions to this dualistic classification are posed by a few species of flightless carinates. Among these birds are penguins, which probably evolved from flighted diving birds and now essentially "fly" through a liquid medium (using the same flapping motion) instead of the air.

Ratites, which include ostriches, emus, rheas, kiwis, and cassowaries, are of the most interest to dinosaur paleontologists because they are biomechanical and possible behavioral analogues to some flightless theropods of the Mesozoic. In fact, numerous studies of rhea and emu tracks have been used as modern analogues to Mesozoic theropod tracks (Fig. 15.7). A Tertiary ratite that might have been as terrifying as some Cretaceous dromaeosaurs to the mammals of its time was *Diatryma*, described by Edward Cope in 1876 (Fig. 15.8). *Diatryma* was a 2-meter tall bird that towered over most mammals about 50 million years ago. It probably weighed more than 150 kg and had a large head and beak adapted for meat eating. However, *Diatryma* was surpassed in mass by a bird that only recently went extinct, the herbivorous elephantbird (*Aepyornis maximus*). At nearly 3-meters tall and weighing 400 kg, the elephantbird was larger than any deinonychosaur, with the exception of *Utahraptor* (Chapter 9). It died out only about 1000 years ago, and its decline coincided with the arrival of humans in its habitats on Madagascar about 2000 years ago. Other ratites that went extinct within recent memory were the moas (e.g., *Dinornis*) of New Zealand (Fig. 15.9). *Dinornis maximus* was the tallest bird known (one specimen was 3.7 meters tall), and weighed more than 200 kg. However, other species of moas varied in size and most were considerably smaller. These ratites were probable victims of overhunting and habitat alteration by humans, and the last

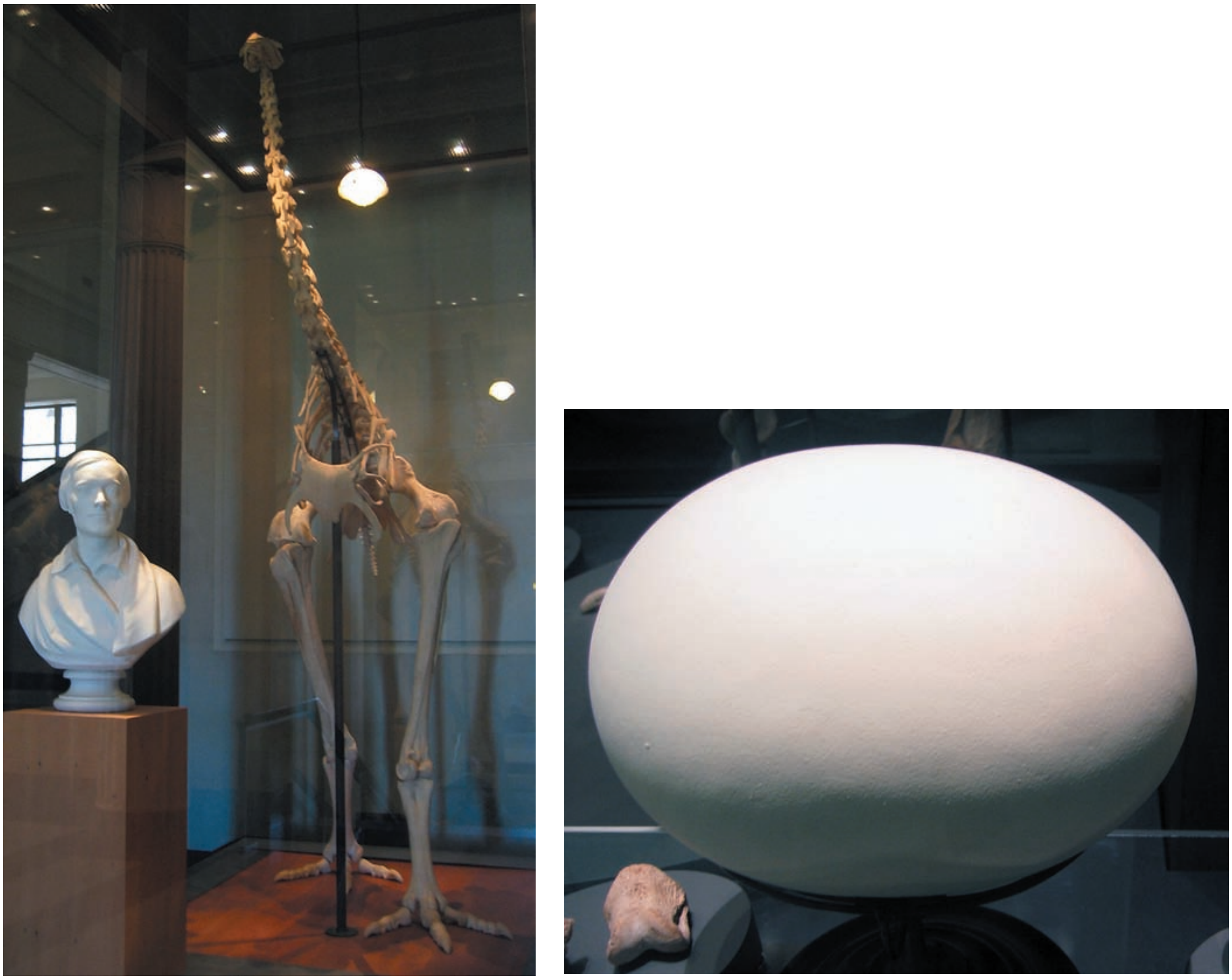
FIGURE 15.8 Skeleton of the frightening Tertiary ratite *Diatryma* of North America. Be aware of its anatomical similarity to theropod skeletons from Chapter 9. Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma.

possible moa sighting was in 1947. Other modern ratites and many carinates similarly have been decreasing at rapid rates as a result of overhunting and human alterations of habitats, signaling the beginnings of a possible mass extinction for birds well into the Cenozoic (Chapter 16).

Carinates are by far the more diverse of the two groups and include the aforementioned passerines, but also (in general, and not cladistic categories):

1 waterbirds – albatrosses, boobies, cormorants, frigatebirds, gannets, grebes, loons, pelicans, petrels, and shearwaters;
2 wading birds – bitterns, cranes, egrets, herons, ibises, spoonbills, storks;
3 shorebirds – avocets, gulls, mudhens, oystercatchers, plovers, rails, sandpipers, stilts, and terns;
4 gamebirds – grouse, quails, and turkeys;
5 raptors – falcons, hawks, eagles, and owls, to name a few.

The preceding list is not meant to be memorized, but to impress that the variability of birds is almost taken for granted unless one starts to name all of them. This modern assortment put together with the Cenozoic fossil record of birds collectively point toward a post-Cretaceous success of birds that calls into question the popular appellation of the Cenozoic as the "Age of Mammals." In terms of shear numbers of species and individuals, it more arguably is the "Age of Birds."



(A)

(B)

FIGURE 15.9 *Dinornis*, a recently extinct genus of moas, which were a group of ratites native to New Zealand. (A) Skeleton of adult *Diornis maximus*; bust of Sir Richard Owen (Chapter 3) for scale. (B) Egg of *D. giganteus*, with a calculated volume of about four liters (!). Auckland Museum, Auckland, New Zealand.

Birds as Living Animals

Not surprisingly, bird reproduction is very similar to what has been interpreted for theropod dinosaurs, but other dinosaur clades may have shared behavioral traits with birds too.

Reproduction

Displays and courting behavior are common aspects of mating for birds, as well as auditory wooing through the use of songs. Displays can be made through colorful or prominent plumage (e.g., peacocks) as well as sometimes-complicated dances or songs performed for the benefit of receptive females, showing some parallels to some modern primates. Related to such pre-mating behaviors are territorial displays, where male birds will make aggressive movements or sounds that clearly communicate "stay away" to rivals. Interestingly, these behaviors rarely lead to actual fights between rival males, which have been conjectured for ceratopsians and pachycephalosaurs (Chapter 13).

Birds show a myriad of mating behaviors. Although they are often admired as paragons of "family values" because of the large number of species that have monogamous pair bonding, a significant number of species also slip in the occasional bird on the side. In such instances, bird pairs may be classified as **socially monogamous**, meaning that they help one another to raise their young, or **genetically monogamous**, where they are the only genetic parents of the young. Observations of bird behavior in recent years now suggest that the latter is actually rare, although most birds remain socially monogamous. Accordingly, many bird pairs will raise young that are not a result of their mating. In cases of nest parasitism (discussed in Chapter 8), some young that are raised may not even belong to the same species.

Nest building, now attributed to an ornithopod, *Maiasaura*, a few non-avian theropods such as *Troodon* and *Oviraptor* (Chapter 9), and at least one species of titanosaurid sauropod (Chapter 10), is common in modern birds, although not ubiquitous. Some birds do not nest at all, but lay their eggs on bare ground or rock. Similarly, a few bird nests consist of the barest scrape of a ground surface. However, others are among the most elaborate of any tetrapod-made structures, consisting of finely woven grasses or sticks, or borings made into hard soils augmented by vegetative material (Fig. 15.10A–C). Nests can be solitary or closely spaced in nesting colonies, the latter of which has been proposed for *Maiasaura*. Nesting colonies sometimes show regular spacing between individual nests, indicative of space requirements needed by parents for raising their respective broods (Fig. 15.10D).

Growth

Avian growth rates are often rapid, which is consistent with their endothermic physiology (Chapter 8). However, different groups of birds differ considerably in whether their young are born atricial or precocial, a consideration discussed for juvenile dinosaurs (Chapters 9 and 10). Most passerines, raptors, and herons have altricial juveniles, which means that they require much parental maintenance, including brooding that conserves body heat. In some instances, juveniles may stay in close proximity to their nests, even as they approach adult size (Fig. 15.11). On the other hand, most shorebirds and "game birds" (turkeys, grouse, quail) have precocial young that are active and somewhat self-sufficient soon after hatching. The latter situation enables parents to divide duties in raising the young, whereas the former almost necessitates that both parents are constantly around while their young develop.

Regardless of whether a species of bird is altricial or precocial in its juvenile stage, they all reach breeding age within a relatively short period of time compared to average lifespan, some as early as one year after hatching. Again, this is indicative of rapid growth rates relative to many mammals, and similar growth rates have been calculated for what are presumed as precocial juvenile theropods (Chapters 8 and 9). After they reach breeding age, most birds cease or otherwise slow their growth. The majority of bird species live less than 30 years (and some considerably less than that), but a few species of parrots can live more than 50 years in captivity.

Locomotion

The various ways that birds move are incredibly varied, going far beyond descriptions of merely "flying." Although most species of modern birds are indeed capable of

(A)

(B)

FIGURE 15.10 Variety of nests constructed and used by modern birds. (A) Ground scrape with a clutch of eggs on a sandy beach made by American oystercatcher (*Haematopus palliatus*), Georgia, USA. (B) Large and elaborate stick nest of osprey (*Pandion haliaetus*), Florida, USA. (C) Hole nest (burrow) in semi-consolidated sand with vegetation stuffed inside, made by kotare (kingfisher: *Halcyon santus*), North Island, New Zealand. (D) Nesting colony of takapu (Australasian gannet: *Morus serrator*) showing regularly spaced nest mounds formed by guano, North Island, New Zealand.

(C)

(D)

FIGURE 15.10 Continued

extended self-powered flight, they range from completely flightless (cursorial) to the fastest animals on Earth, once airborne (e.g., peregrine falcons, *Falco peregrinus*). As mentioned earlier, most flightless birds fit into a category of ratites, although a few flightless passerines evolved via the geographic isolation of New Zealand and other remote islands. Moreover, a few flighted birds also are maneuverable on the ground and can easily outrun their prey or predators. Other non-cursorial or non-aerial variations on locomotion include:

1 swimming on the surfaces of water bodies;
2 swimming under water surfaces;
3 diving;
4 burrowing; and
5 climbing.

FIGURE 15.11 Altricial juveniles of magnificent frigatebirds (*Fregata magnificens*), which have 1.7–2.4 m wingspans as adults but are completely dependent on their parents for the first year of life, despite approaching their sizes. Notice their eerie resemblance to non-avian theropods, downy feathers and all. San Salvador, Bahamas.

Because of this range of movements, birds can soar high above the Earth's surface (as much as 6000 m), dive as deep as 500 m, or live in nearly every other terrestrial and aquatic environment. This diversity of lifestyles far exceeds those known for non-avian dinosaurs, although avians had the advantage of more time to evolve them.

Perhaps the most noteworthy aspect of avian locomotion is how it is used for **migrations**, and in this respect birds are the most impressive of all tetrapods. A migration is the movement of birds between where they spend their winters and where they breed, hence these movements are seasonal and annual. Because reproduction often requires much caloric energy for mating, the development of eggs, and raising of young, birds will migrate away from their winter habitat to a place that has more calories and other nutrients available (Chapter 8), as well as adequate nesting habitats. Some of these migrations cover tens of thousands of kilometers, and even flightless birds, such as penguins, are known to migrate (via swimming, not waddling) hundreds of kilometers. Similar seasonal and annual migrations have been postulated for some dinosaurs that show large latitudinal variations, such as some hadrosaurids (Chapter 11), and some dinosaurs were clearly adapted for high-latitude (polar) environments as well (Chapter 8).

Feeding

Birds show a wide range of feeding strategies, from herbivorous (seeds, leaves, or fruits) to insectivorous to carnivorous, the latter manifested as either predation or scavenging. Darwin's original observations of finches in the Galapagos Islands noted

FIGURE 15.12 Wood-boring activities of birds related to nesting and feeding. (A) Hole nest in tree trunk made by pileated woodpecker (*Dryocopus pileatus*); Idaho, USA. (B) Oak acorns (*Quercus* sp.) wedged in holes made by acorn woodpecker (*Melanerpes formicivorus*) in trunk of ponderosa pine (*Pinus ponderosa*); California, USA.

how beak shapes for otherwise very similar species varied considerably in accordance with adaptations for food acquisition, for example, seed-crushing versus fruit eating versus insect nabbing. Not all birds are restricted to just one source of food, and some species switch from herbivory to insectivory to carnivory according to their needs. Even hummingbirds, which were always thought of as nectar eaters, prey upon and eat insects to supplement their diets. Other insectivorous birds, such as woodpeckers, have special adaptations to their bills and skulls for rapid hammering into wood in search of wood-boring insects, but they also can construct hole nests in tree trunks (Fig. 15.12A). A few shorebirds have long bills (partially to compensate for proportionally long legs) that are well suited for probing deeply into beach sands for crustaceans and molluscans. Of course, sharp beaks and talons associated with strong, grasping feet and rapid or near-silent flight, present in raptors and owls, are easily associated with predatory behaviors. However, one of the fiercest of predatory birds is the flightless cassowary (*Casuarius casuarius*) of northern Australia, which has been known to kill people with its vicious kicks. A similar kicking behavior has been conjectured for a few deinonychosaurs, which had large, sickle-like claws on digit II (Chapter 9).

Besides such obvious morphological adaptations, a few birds are the only tetrapods other than primates known to use tools for feeding. For example, some species of herons will hold feathers or similar lures in their beaks above a water surface to attract fish; nuthatches will use pieces of bark to force open bark on a tree trunk to acquire insects; and crows probe for insects using sticks or leaves. Some species of birds also show a feeding behavior markedly different from the vast majority of reptiles: **caching**, which is the storing of food for later consumption. One of the best examples of this type of behavior is in the acorn woodpecker (*Melanerpes formicivorus*), which drills holes into bark of trees and then tightly wedges acorns into these holes. Entire trees then become "grocery stores" for woodpeckers to visit later (Fig. 15.12B). Both tool use and caching are unknown in Mesozoic dinosaurs, and the evidence for such behavior is expected to be scanty, based on current analogues.

A noteworthy aspect of the interrelationships of bird feeding and flowering plants is their well-documented interdependence. Numerous flowering plants are dependent on birds for cross-pollination and seed dispersal, and likewise many birds are dependent on flowering plants for food and nesting materials. Indeed, some paleontologists have hypothesized that the near coincidence of the oldest flowering plants (Early Cretaceous) and oldest birds (Late Jurassic) in the geologic record possibly indicates a cause-and-effect relationship. Whether birds or pollinating insects played a role in the development of flowering plants is unknown, but the clear interconnections between birds, flowers, and fruits today argue for similar relationships in the geologic past.

Social Life

Modern birds are represented by nearly 10,000 species, hence their social lives are difficult to classify. The broadest categories that can be made for them are:

1. male–female pairs (discussed earlier); and
2. flocks.

Some male–female pairs rarely gather with others of their species; such spatial separation is probably related to male territoriality, food resource allocations, or other habitat requirements. Of course, any given flock of birds may be composed of a large number of male–female pairs, which increases the likelihood of gene mixing between pairs. The advantages of large flocks are numerous:

1. a collective protection of young ("strength in numbers");
2. finding food is easier with more eyes looking for it;
3. predators are more easily avoided for the same reasons as in (2); and
4. navigation during migrations.

Regardless of whether social behavior is limited to a few individuals or thousands in a breeding colony, much of it is facilitated by verbal and non-verbal communications. Non-verbal forms of communication include feather displays (plumage) and body movements; some of the latter consist of elaborate dances that either entice or intimidate. Verbal communications in birds are among the most complex of all tetrapods, but fall into two general categories, **calls** and **songs**. Calls are typically innate (not learned) and consist of brief vocalizations that express alarm, scold a predator or other intruder, signal other birds in a flock to stay together, or simply identify an individual so that another of its species knows its position. For example, blue jays will make sharp, loud calls that increase in number and tempo when a predator is in the vicinity of a nest. Geese will honk while in flight so that they can maintain their group formations. Crows will call to one another as a sort of linked chain as a flock moves over its territory. On the other hand, songs, which are normally learned, are often very complicated and can consist of numerous variations on a main theme. Songs are used for wooing or territorialism, and some birds even accomplish both tasks with the same song. The distinctiveness of most bird songs, particularly for passerines, enables carefully listening humans to distinguish species on the basis of sound alone. However, a few species of birds have song catalogues of thousands (e.g., brown thrashers), and others are excellent mimics of a large number of songs of other species (e.g., mockingbirds), which indicate a greater functionality to songs than mere flirting or fighting.

Male–female pairs are postulated for non-avian dinosaurs in some instances and are especially appealing hypotheses in cases where slightly different-sized and dual, parallel trackways might occur (Chapter 14). Flocking behavior, or at least the formation of large socially interacting groups of non-avian dinosaurs, is suggested by some ornithopod and sauropod nesting grounds, as well as monospecific bone beds of theropods, ornithopods, and ceratopsians (Chapters 9, 11, and 13). Vocalizations were likely in at least a few species of ornithopods, especially hadrosaurids with elaborate sinuses capable of directing air to make sounds (Chapter 11). Whether Mesozoic landscapes and seascapes were filled with the intermingled calls and songs of non-avian and avian dinosaurs is unknown.

Health

Although most bird species are very healthy, a few individuals suffer from ectoparasites and diseases (Chapter 7). Diseases in particular, whether fungal, bacterial, or viral, can spread quickly in some bird species because of close proximities of large numbers of individuals in flocks, exacerbated by the rapid movement of flighted birds. Avian diseases are receiving more attention in recent years because a few birds are recognized carriers of some diseases that also affect humans, such as salmonella and West Nile virus. Salmonella is contracted by contact or consumption of uncooked chicken eggs or chicken flesh. West Nile virus is transmitted through both mosquitoes and birds, causing a multiplicative effect that creates higher risk than if only one of these animals carried it.

Although most birds that reach adulthood seem outwardly healthy, injuries are common in those birds that spend a great deal of time on land or in the water. Cursorial birds might develop noticeable limps from skeletal or muscular maladies, which could have been caused by overuse or any number of other stresses. Missing feet or legs are a problem for waterbirds that rest on ocean surfaces, where their dangling feet tempt sharks and other predators (Fig. 15.13).

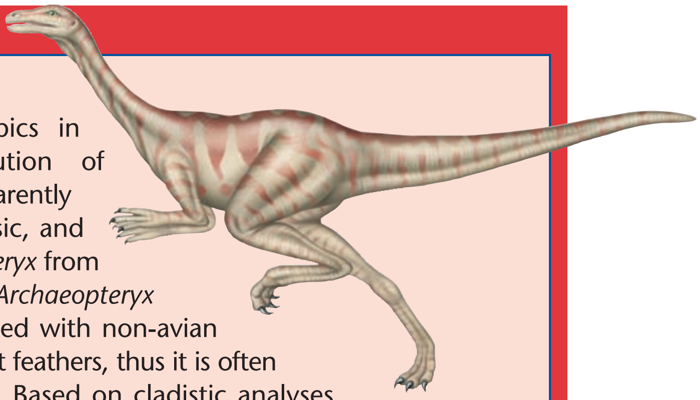
Injuries and deaths of birds from predation in terrestrial environments, although commonplace, are increased dramatically by habitat alterations that take away normal roosting spots or vegetative cover needed by birds to avoid detection. Such problems are compounded by the introduction of non-native predators that break the rules of the "Red Queen" (Chapter 6). In other words, these predators are from an evolutionary track in which their prey animals did not develop defenses against them. House cats in urbanized areas exemplify how habitat fragmentation and non-native predators combine to decimate songbird populations in North America; cats in the USA are estimated to kill hundreds of millions of birds each year. Migratory birds in particular are vulnerable to such risks, especially for ground-nesting species that subsequently experience increased juvenile mortality. Non-native organisms introduced to an environment, which have a disproportionately deleterious impact on native organisms, are termed **invasive species**. Invasive species, when co-occurring

FIGURE 15.13 Evidence of unsuccessful predation of a modern avian dinosaur: a footless laughing gull (*Larus altricilla*) on a beach in Georgia, USA. This observation was confirmed by examination of its trackways, which showed well-defined right-foot tracks alternating with impressions made by the metatarsal nub of the left leg.

with habitat alterations, have resulted in some species of birds becoming endangered or extinct.

The paleopathology of non-avian dinosaurs, covered previously (Chapter 7), indicates these animals certainly had some health problems, suffered injuries, or were subjected to predation. However, no evidence has been presented to suggest that habitat alterations combined with the introduction of invasive species accelerated dinosaur extinctions at any time. The latter factor is largely the product of human activities, although birds themselves are capable of transporting organisms long distances in short periods of time. Nevertheless, a large amount of information, multi-faceted and integrated, now adds up to a powerful argument that the end-Cretaceous extinction of non-avian dinosaurs was related to a sudden, catastrophic change in habitats. This mass extinction ensured the proliferation of birds in the Cenozoic, but it still inspires much curiosity: why did some dinosaurs make it past the Cretaceous, but others (including some avians), did not? This point of inquiry is the subject of the next and last chapter (Chapter 16).

SUMMARY

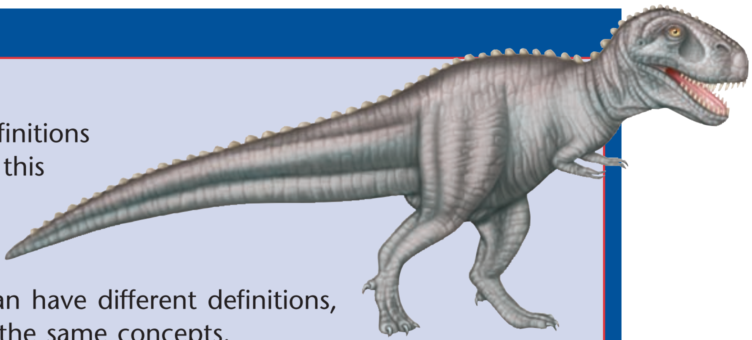


One of the most discussed topics in dinosaur studies is the evolution of dinosaurs into birds. Avians apparently began in the Middle to Late Jurassic, and the oldest known bird is *Archaeopteryx* from the Late Jurassic of Germany. *Archaeopteryx* shows a blend of features associated with non-avian theropods and birds, including flight feathers, thus it is often identified as a "transitional" fossil. Based on cladistic analyses of character traits, the most probable ancestor to *Archaeopteryx* was a maniraptoran, and deinonychosaurs comprise a sister clade to *Archaeopteryx* and other birds. Birds diversified considerably during the Cretaceous Period; more than 50 species are known from that period. Cretaceous bird evolution resulted in an impressive expansion of habitats, but most of their clades were extinct by the end of the Cretaceous. Subsequent diversification of birds has led to their inhabiting nearly all near-surface terrestrial and aquatic environments. Cenozoic birds can be broadly categorized as ratites ("flightless") and carinates ("flighted"), with ratites representing modern analogues to non-avian theropod dinosaurs. Modern birds are represented by more than 10,000 species, although a significant number of these have become extinct in the past several hundred years as a result of human overhunting and habitat alterations.

Two current hypotheses for the development of full flight in birds are the cursorial ("ground up") and arboreal ("trees down") hypotheses, with some variations on those themes. Although each hypothesis has its merits, they are largely based on functional morphology of non-avian and avian theropods. Recent insights into this realm, as well as experiments with living birds, have now generated variations of these hypotheses that could combine elements of each.

Birds are extremely diverse in their reproduction, growth, feeding, locomotion, social lives, and health, and in some instances their behaviors overlap with hypothesized dinosaur behaviors. Birds thus provide models of comparison for paleontologists interested in these facets of dinosaur behavior. Recent bird extinctions are largely the result of human-caused factors, such as habitat alterations that prevent adequate cover, food, and nesting material for birds, as well as invasive species of predators that decimate bird populations. Of these factors, habitat alterations have the most applicability to understanding non-avian dinosaur extinctions.

DISCUSSION QUESTIONS



1. What were the three definitions given for "dinosaur" in this book in Chapters 1, 5, and 15? How are they different or similar? Explain how this word can have different definitions, yet they still can convey the same concepts.
2. Review the characteristics of theropods, especially the lineage leading to maniraptorans, covered in Chapter 9, and compare them to what is described for *Archaeopteryx* in this chapter. How many matches did you find? What contrary evidence, if any, would sway you from accepting the hypothesis that birds originated from theropods?
3. Feathers in birds today have different (but often overlapping) purposes, such as insulation, display, and flight. In the case of flightless coelurosaurs, such as *Caudipteryx*, which of these functions was most likely and why?
4. Why is it that a bird has a saurischian hip (and is a saurischian), yet ornithischians are called the "bird-hipped" dinosaurs?
5. Look at Table 15.1 and eliminate all genera from China. What percentage of change happens to the number of genera? Also, considering that the oldest known bird is *Archaeopteryx* from Germany, what hypotheses could explain avian dispersal and diversifications without the Chinese finds?
6. Some carinates developed flightlessness in ecosystems that lacked appreciable numbers of mammals. What evolutionary factors may have resulted in the selection of reduced wings, which brought these birds back to a state similar to those of their theropod ancestors?
7. You are doing fieldwork in the southwestern USA on an excavation of Upper Triassic rocks when you discover what seems to be a bird skeleton. Which hypothesis of bird origins, theropod or "thecodont", would your discovery support and why? Would it necessarily only support one of the hypotheses? What supplementary evidence would support or disprove your initial identification of the skeleton as avian?
8. Which of the hypotheses for bird flight seem most plausible to you, based on the evidence presented here, and why? What body fossil or trace fossil evidence would be needed to support or disprove the hypothesis you currently favor?
9. Given the bird nests shown in Figure 15.10, arrange them in order of "most likely" to "least likely" to be preserved in the fossil record. What factors are involved in their preservation? How could some unusual conditions result in your changing this ranking?
10. If all birds went extinct tomorrow, how would the world be different? What ecosystems might be affected the most and in what ways? (Hint: Think of bird interactions with both insects and plants.)

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