Chapter 14, The Mistaken Extinction, by Lowell Dingus and Timothy Rowe, New York, W. H. Freeman, 1998.

Chapter 14

The Road to Jurassic Park

As graduate students, it seemed that *Archaeopteryx* was the sole source of information about early bird evolution. Our textbooks said little about other Mesozoic birds because there wasn't much known about them. Avian history was a dark and murky for a span of 85 million years following *Archaeopteryx*, and not until the beginning of the Tertiary did the trail of fossils leading toward today's birds resume.

Suddenly, an explosion of new discoveries has illuminated the darkness. In the last fifteen years, new Mesozoic birds have been collected in many parts of the world. South America, Spain, and Asia, are producing a wealth of new Cretaceous fossils, including complete skeletons of mature birds, entire nests of eggs, embryonic skeletons, and as we saw in the last chapter there are new fossils preserving feathers. With every professional paleontological meeting, it seems, someone announces a new Mesozoic bird. Others bring pictures or specimens representing new species, but show them only to a privileged few. Thanks to the press, the new discoveries are feeding rumors and excitement on a global scale, as the growing league of bird-watchers race to add one of the rarest species to their "life list"--a Mesozoic bird.

Through the blinding flash of new discoveries, the Mesozoic roots of bird evolution are dimly coming in to focus, and what was *terra incognita* in our student days is now crossed by a several major highways (fig. 14.01). But some highly contentious issues remain, and very different visions of early avian history are pictured by different paleontologists. The new phylogenetic maps are like a *Consumer Reports* study on the paleobiology of birds and other Mesozoic dinosaurs. By matching the timing and sequence of evolutionary events, these maps can test evolutionary cause and effect. By plotting living birds on the same map with their extinct relatives, new insights into the genetics, embryology, physiology, and behavior of both living and extinct species are emerging. For example, the phylogenetic maps offer insights into whether dinosaurs were warm-blooded and whether DNA fragments recovered from Cretaceous fossils belonged to dinosaurs. Could Michael Crichton's *Jurassic Park* be more than a fantasy? As we will see, some popular ideas about dinosaurs are endorsed by phylogenetic mapping, while others earn much lower *Consumer* ratings.

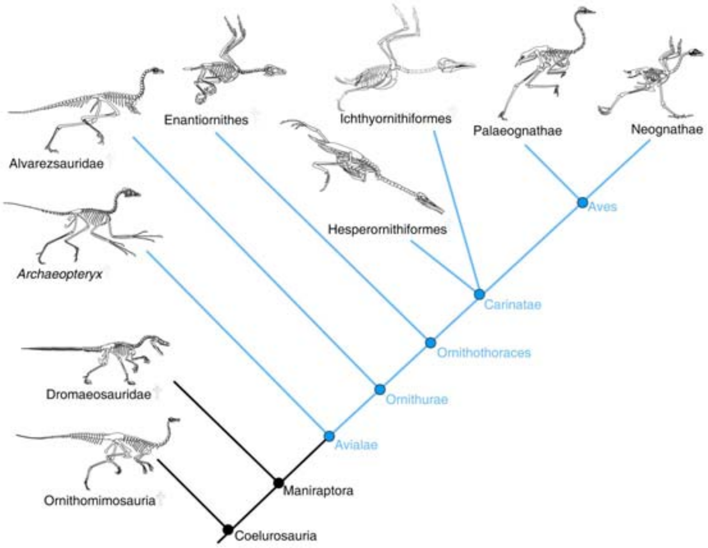

Figure 14.01 Phylogenetic map showing the relationships among the basal bird lineages (in blue).

Evolution and Development

Domestic chicks, quail, and a few other birds have been revealing biological laboratory animals for more than a century (fig. 14.02). A great deal is now known about their genetic makeup, including how some of their genes direct embryological development and growth[1]. We even know how to experimentally manipulate and alter growth patterns of embryos in the laboratory. But without a phylogenetic map, most scientists who have done this work did not realize that they were working with dinosaurs, or that their research on avian biology might unlock ancient mysteries.

Knowledge of modern genetics and embryology increased as we entered the information age. The genome is a little like a computer's hard drive. Not all its programs are used at once, and some may lie dormant for long periods. There may even be old files and outdated software that are no longer used. But with a mistaken command, older programs can still be activated, often harmlessly but occasionally with unfortunate consequences. Genomes also preserve remnants of ancient developmental programs. In a few cases, embryologists have discovered ways to turn them back on. We will probably never be able to resurrect extinct species in the laboratory as in Michael Crichton's science fiction fantasy *Jurassic Park*. But using embryological techniques to activate a bird's "genetic memory", scientists have induced modern species to re-grow some ancient structures.

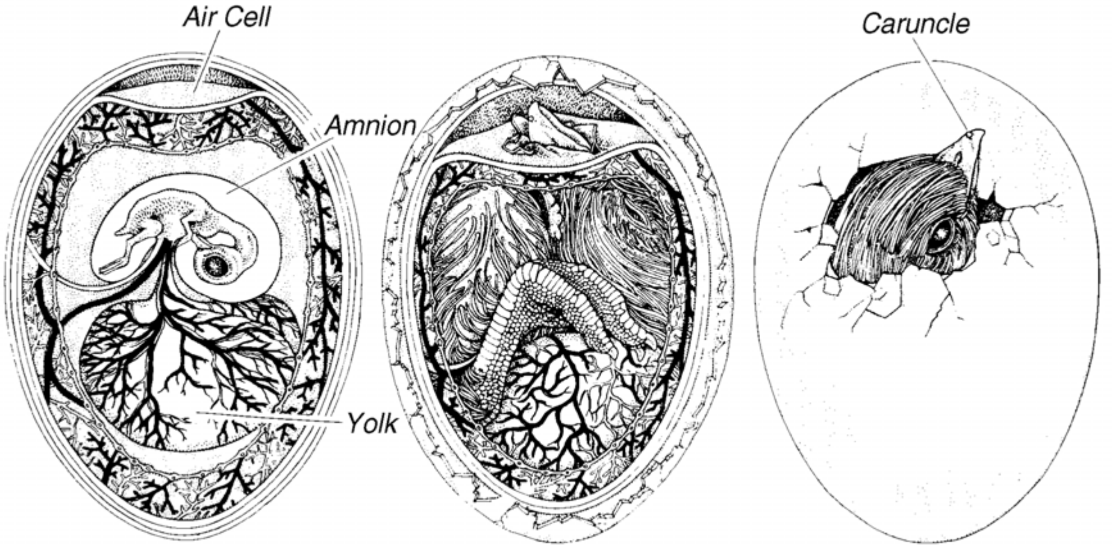

Figure 14.02 In a number of regions of the skeleton, rearrangements of bones occur during development that recapitulate similar evolutionary rearrangements in early theropod history. If birds are not descendants of Mesozoic theropods, why does their development history reflect so much of early theropod history? (from: H. Rahn, A.Ar, and C. V Paganelli. How birds breath. Scientific American, 1979).

As old programs are triggered, either in nature or the lab, we sometimes get a glimpse of the past, when 'throwbacks' to more primitive structures, known as *atavisms*¸ develop. Atavistic structures are surprising because they otherwise appear only in distantly related and more primitive species. For example, young ducks, geese, swans, and ostrich have a claw on one of the fingers. These usually disappears as the bird's mature plumage develops, but occasionally claws on the wings persist into adulthood. To pre-evolutionary biologists, birds with claws were difficult to explain. To evolutionists, however, these structures record history by reflecting the reptilian ancestry of birds.

The most significant embryological ties to the past are parallel transformation sequences that can be observed in both the developmental and evolutionary histories of an organism. Evolutionary transformations documented in the fossil record are often mirrored or *recapitulated* in the embryonic tissues of a developing embryo.

Consider the distinctive avian foot (figs. 14.03 - 14.04). As we saw in the last chapter, a lot of subtle evolutionary changes occurred as the distinctive feet and legs of living birds evolved from more primitive dinosaurs. The ancestral dinosaur had a foot with five toes. Each toe was supported by its own metatarsal bone (the metatarsals are the main girders of the foot), which was connected to the tarsal bones that form the hinge-like ankle joint (fig. 14.03). In the theropod lineage, metatarsal I (above our “big toe”) is shortened. The first toe remained functional, but no longer was it connected directly to the ankle bones. At the same time, digit V (our “little toe”) became reduced, losing all its phalanges so that only a thin metatarsal splint attached to the ankle. In avialians, digit I rotated around to the back of the foot, affording a crude grasping capability. The remaining large metatarsal bones (II, III, IV) began to fuse to each other and to some of the ankle bones, forming a single compound bone called the *tarsometatarsus*. The tarsometatarsus is made up of several bones that historically were separate and independent. Still later, digit V disappeared altogether, leaving three toes directed forward (digits II, III, and IV) and one directed backwards (digit I) as in modern birds.

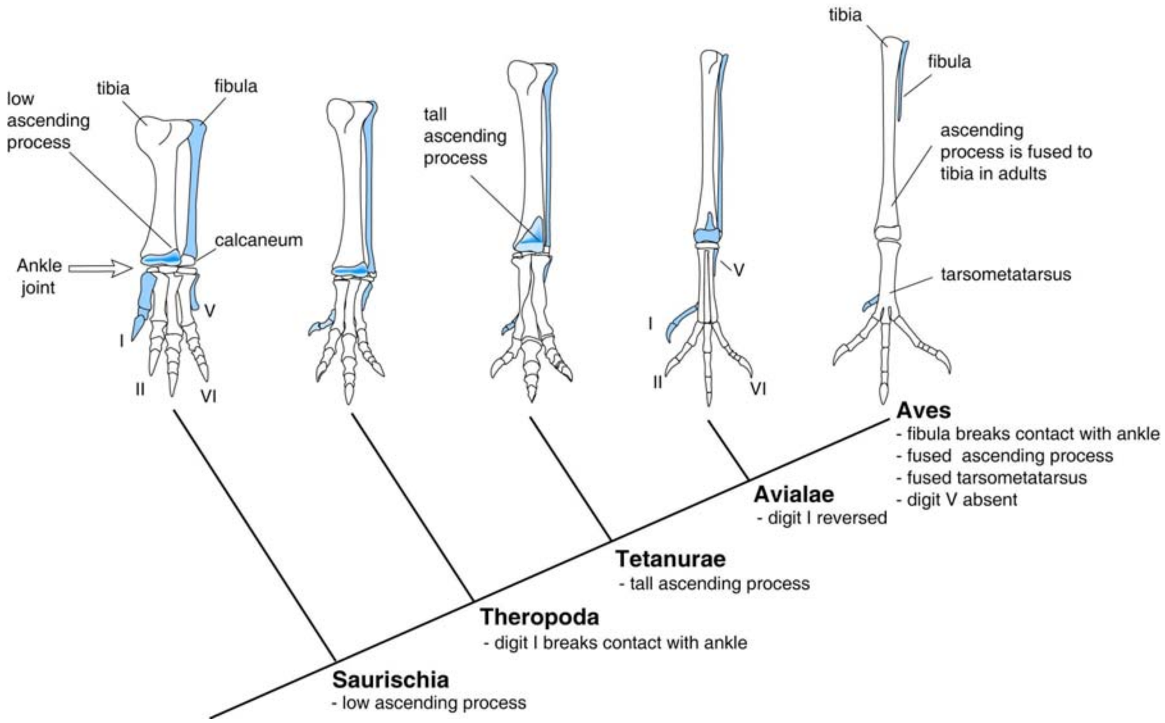

Figure 14.03 During theropod evolution, the first toe, the fifth toe, the ascending process, and the fibula were all rearranged.

Comparable changes occur early during the development or *ontogeny* in most birds (fig. 14.04). These changes generally mirror the same sequence documented in evolutionary history, although the transformations take place in embryonic tissues like cartilage rather than bone. While still inside the egg, evidence of five toes is visible as the hindlimb starts to grow. The cartilaginous beginnings of five metatarsal bones arise, all in contact with the developing ankle cartilages, in the same configuration found in dinosaurs ancestrally. But soon, digit I separates from the ankle and slides down the side of metatarsal II, later rotating around back to afford a grasping capacity. The growing cartilages for the remaining three metatarsals (II, III, IV) eventually coalesce as they turn to bone, to form the compound tarsometatarsus. The tiny remnant of metatarsal V eventually disappears so that no trace of a fifth digit is seen in adults. In all of these changes, the developing embryo repeats or *recapitulates* the same changes that occurred during the evolutionary history of its ancestors. In the avian foot, ontogeny recapitulates phylogeny. If adult birds have only four toes, why do their embryos begin development with five?

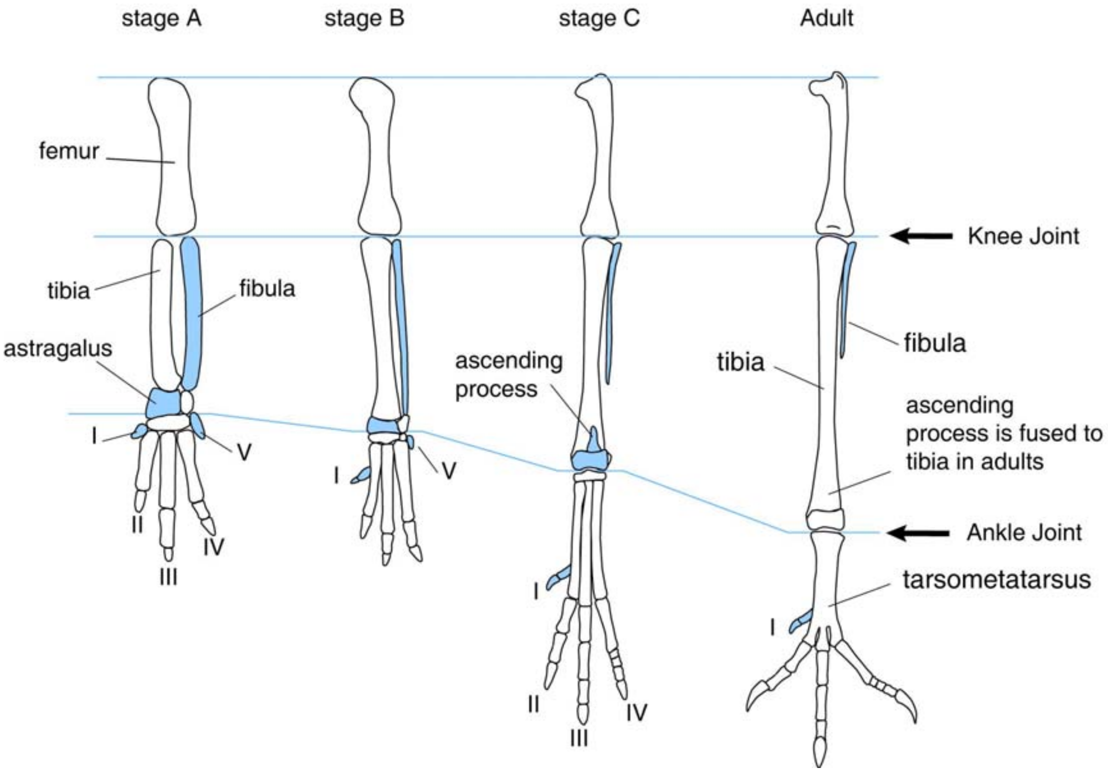

Figure 14.04 During bird development, the bones of the foot undergo rearrangements that are similar to those occurring in theropod evolution (see fig. 14.03).

To pre-evolutionists, this was difficult to explain. But to evolutionists, these recapitulated sequences in bird development development are historic relics that express ancient genetic programs[2]. Birds have five toes at the start of their lives because their ancestors did. Darwin was the first to make sense of recapitulations and atavisms[3]. He explained in the *Origin of Species* that genealogical relationship is the fundamental source of biological similarity among different organisms, regardless of whether that similarity was expressed between adults or between an adult and an embryo. Atavisms and recapitulations are to embryology what fossils are to paleontology.

The discovery of a recapitulation is what led to the discovery of a close genealogical tie between birds and extinct dinosaurs. Carl Gegenbaur--a great 19th century evolutionary morphologist and embryologist--became an ardent evolutionist as soon as he read Darwin's *Origin of Species*. Gegenbaur was the first to study both the early development of the ankle in a modern bird and the ankle bones of the Jurassic theropod *Compsognathus*[4]. During growth, the "solid" foot of adult birds begins with all the parts that remained separate through out life in *Compsognathus.* Among reptiles, only *Compsognathus* exhibited this pattern, hence dinosaurs were the closest reptilian cousins of birds. As we saw in Chapter 10, Thomas Huxley extended Gegnbaur's embryological observations to the entire hindlimb, and became the most vocal advocate for the bird-dinosaur connection of the 19th century. So, with the importance of comparing patterns of ontogeny and phylogeny in mind, we now return to our tour of dinosaur phylogeny, rejoining our evolutionary map at the beginnings of birds.

Ever Since the Jurassic

More than a century after its discovery, our most direct evidence for the origin of birds still comes from *Archaeopteryx,* the oldest flying bird from the Late Jurassic Solnhofen limestones. A consensus has emerged that *Archaeopteryx* was probably a good runner and an adequate flapping flyer[5]. But it probably could not flap over long distances, nor could it glide especially well. The hand and wrist bones were unfused, and the shoulder bones retained a number of primitive features suggesting only limited flight capability. These differences also imply that the arms of *Archaeopteryx* may not have been used exclusively for flapping flight. Just how the astounding flight capabilities of modern birds evolved from such a primitive ancestor was as murky as the fossil record of birds. But the new Mesozoic discoveries preserve transitional stages, so we can now map the evolution of modern flight capabilities, step by step, through the Mesozoic.

Only one other extinct bird has been reported from Jurassic rocks, a toothless bird named *Confuciusornis,* recently described by Larry Martin (University of Kansas)[6] and colleagues Zhongue Zhou ands Lian-Hai Hou (Chinese Academy of Sciences). They took the presence of a Jurassic toothless bird as evidence that the bird-dinosaur hypothesis was wrong. They argued that its occurrence indicated that bird origins must predate *Archaeopteryx* by millions of years. Still more anomalous is that the alleged primitive dinosaurian cousins of birds -- the dromaeosuars like *Deinonychus* -- are known only from younger rocks. If birds descended from dinosaurs, they argued, the sequence of fossils was wrong. But more recent workers studying the age of the Chinese fossils report that the rocks are of Early Cretaceous age, some 20 million years younger than previously thought[7], so the toothless bird is younger than its more primitive toothed cousin. In addition, a fossil from the Late Jurassic of Colorado reported by Jim Jenson (University of Utah) and Kevin Padian in 1989 documents that non-flying maniraptorans do occur in the Jurassic[8], so the problem that confronted Ostrom, that *Deinonychus* is younger than *Archaeopteryx*, is largely solved - maniraptorans occur in time exactly where Jacques Gauthier's map predicted that they would be found.

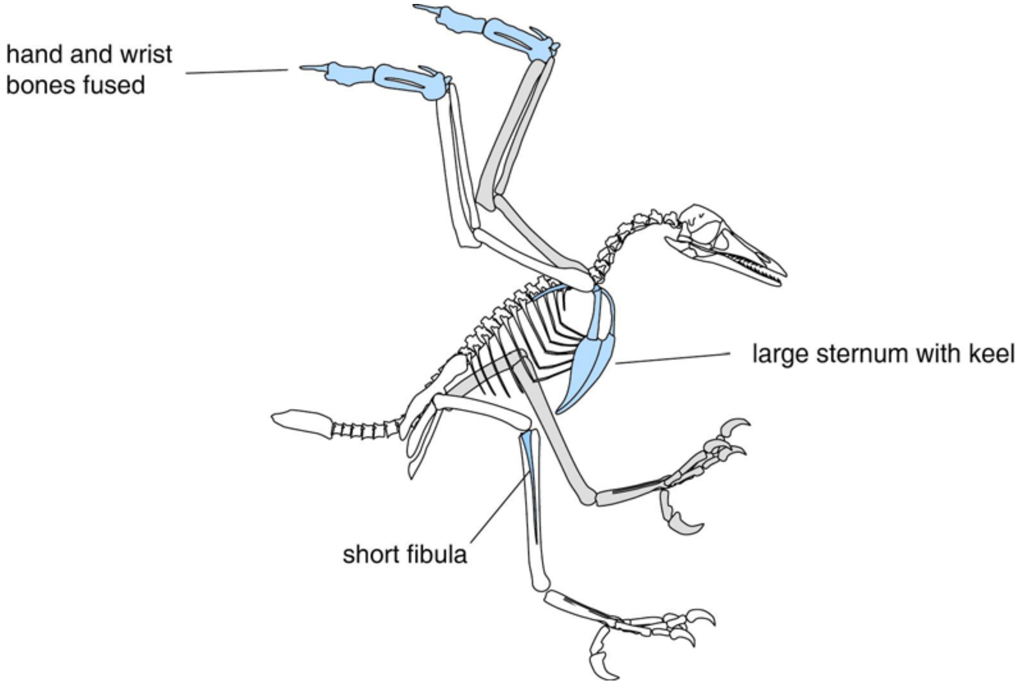

Figure 14.05 Ornithurine birds are distinguished from other theropods by many features of the hand, breast-bone, and leg.

Ornithurae: Powered Flight

Just as the discovery of small, bird-like dinosaurs closed the gap between *Archaeopteryx* and more typical Mesozoic theropods, new discoveries of Cretaceous bird fossils are beginning to close the gap between *Archaeopteryx* and modern birds. The lineage christened Ornithurae by Jacques Gauthier[9] - in reference to the bird-like tail that marks the lineage - includes all birds more closely related to living species than to *Archaeopteryx*. In the last decade, three species of Early Cretaceous Ornithurine birds have been discovered, including *Ambiortus* from Mongolia, and *Chaoyangia* and *Gansus* from China[10]. Dr. Luis Chiappe of the American Museum of Natural History is leading the effort to map these new discoveries on the phylogeny of dinosaurs.

The skeleton of ornithurine birds (fig. 14.05) implies distinctly more powerful and possibly more sustained flight than in *Archaeopteryx*. The breastbone or sternum is a large, shield-like bone at the front of the chest. The sternum in other tetrapods is rather inconspicuous, but it is the largest bone in the skeleton in most ornithurines. A high central keel is also present. If you have ever carved a turkey or chicken for dinner, you have encountered its central ridge of bone between the wings, where the white meat of the powerful breast muscles attach. The keel adds broad, strong attachment surface for the massive flight muscles, which generate the power stroke that keeps the bird airborne

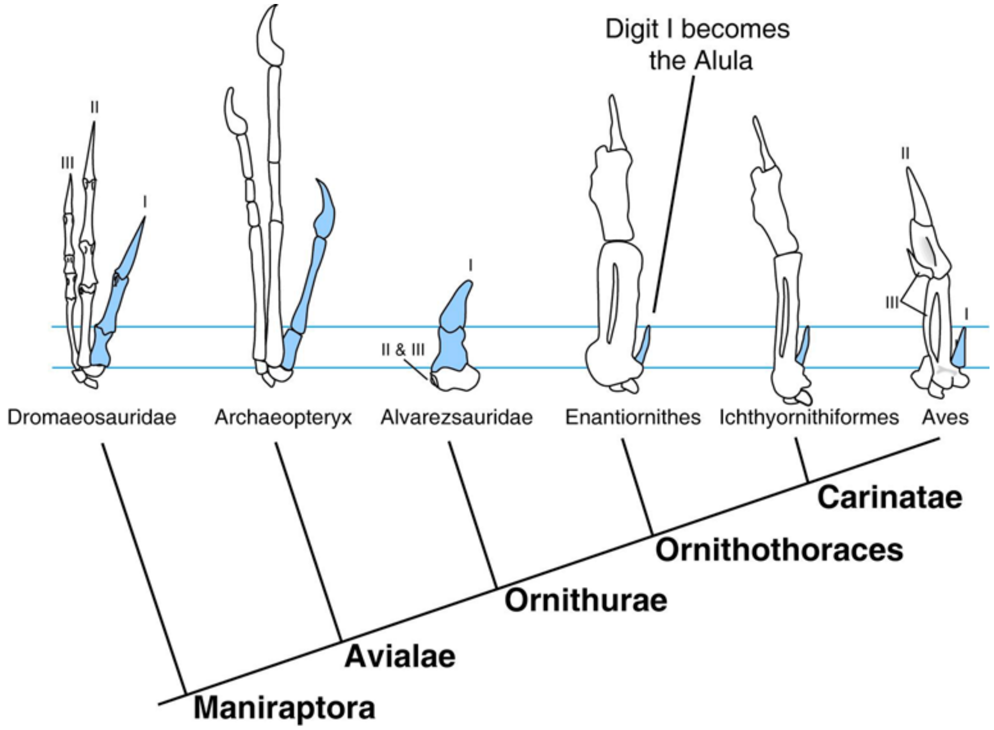

Figure 14.06 In ornithurine birds, many of the bones of the hand became fused together to form a solid structure.

A complementary change occurs in some bones of the wrist and hand, which fuse into a rigid skeleton for supporting the primary flight feathers of the wing (fig. 14.06). The ornithurine hand is a solid structure built from historically separate elements. In bird embryos, they form as separate elements that fuse soon after hatching--another recapitulation.

In mutant strains of the domestic chicken, these elements of the hand and wrist never fuse, suspending development at a stage resembling the ancestral structure. These mutations are usually tied to recessive genes[11], which cause lethal complications soon after hatching. But in normal ornithurines, most of the separate bones of the wrist and hand fuse together, forming a strong hand for flapping. These natural mutants suggest that a simple genetic mechanism may have triggered the complex evolutionary change that occurred in the ancestral ornithurine.

A third distinctive ornithurine feature is found in the arrangement of shin bones. In most tetrapods, the tibia and fibula extend from the knee to the ankle. This is also the condition seen in young ornithurine embryos, like the chicken. Subsequently, however, the tibia grows at an accelerated rate, consuming nearly all the nutrients available for generating that part of the limb skeleton. The fibula becomes a mere a thin splint of bone below the knee in adults, leaving only the massive tibia to support the body between the knee and ankle. The "handle" of the drumstick is formed by the tibia, while the fibula is buried in the meat of the leg.

In a famous laboratory experiment, the fibula of a chick was induced to grow all the way down to the ankle, producing a leg with the primitive configuration of bones found in the distant ancestors of birds[12]. To accomplish this, a thin plate of mica was placed between the developing tibia and fibula at a very early stage, equally partitioning the available nutrients. Both grew to the same length, reaching the ankle. Some of the ankle and foot bones even remained separate, similar to the ancestral condition. The leg did not look exactly like that of *Compsognathus* or *Velociraptor*, but the resemblance in the distribution of parts was still striking[13]. This experimental simulation of a more primitive structure may reflect the operation of a simple evolutionary mechanism.

Mononykus Shakes the Tree

A bizarre new Mesozoic path on the ornithurine map was recently discovered in the Gobi desert by Perle Altangerel from the Mongolian Academy of Sciences and Mark Norell, Luis Chiappe, and James Clark from American Museum of Natural History[14]. Several specimens of a turkey-sized bird named *Mononykus olecranus* provided the first evidence that a highly aberrant, flightless lineage of birds evolved during the Cretaceous (fig. 14.07). *Mononykus* was startling because its forelimbs are profoundly shortened, and there is only one massive finger in its hand. The arms of *Mononykus* seem more suited to digging than flight. Whatever it was doing with its arms, *Mononykus* could certainly not fly.

So weird is this little creature that its identification as a bird prompted a storm of criticism from a host of paleontologists[15]. While acknowledging that the hip and shortened fibula were bird-like, Zhang Zhou argued that theses are convergent similarities, reflecting its bipedal way of life rather than its ancestry[16]. If this rings like *dé ja vu*, it is because Harry Seeley launched the same criticism at Thomas Huxley a century ago, to attack the hypothesis that birds are closely related to dinosaurs. But like Seeley, the critics have no alternative genealogical hypothesis. If *Mononykus* is not a bird, then where does it fit? Why does it have a keeled sternum, like other ornithurines? Why does *Mononykus* have fused wrist bones, a bony sternum, and a pelvis with a back-turned pubis, like other mainraptors? Why does *Mononykus* have a shortened tooth row, a stiff tail, and a tall ascending process in the ankle, like other tetanurines? Why is its skeleton hollow with a foot is equipped with a first toe set far below the ankle joint, like other theropods?

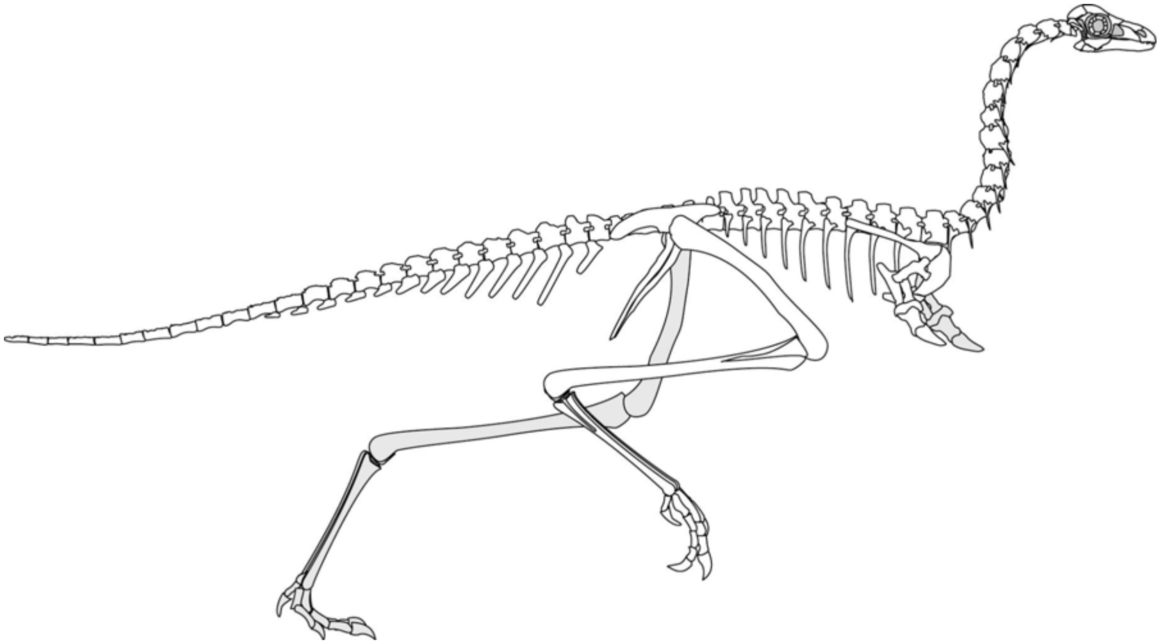

Figure 14.07 *Mononykus* represents Alvarezsauridae, a weird lineage of flightless bird from the Late Cretaceous.

The weird, dwarfed forelimbs of Mononykus are the source of controversy, because they seem so un-birdlike. However, other theropod lineages have become flightless as they evolved dwarfed forelimbs. Tyrannosaurids are the most famous extinct theropods with dwarfed forelimbs, and *Carnotaurus,* a recently discovered basal theropod from Argentina, also had dwarfed forelimbs (fig 14.08). But dwarfed forelimbs also characterize a diversity of Recent birds, including some rails, penguin, kiwi, ostrich, emu, and rhea, as well as the extinct Cretaceous foot-propelled diver named *Hesperornis*, a more recently extinguished lineage of flightless ducks from Hawaii called moa-nalos, and other flightless fossil birds of the Cenozoic. Moreover, the arms, wrists and hands in flightless birds differ in the shape and function of the bones. Convergent evolution produces structures that function similarly but differ radically in anatomical details. So, everyone agrees that forelimb dwarfism must have evolved several times within birds and their extinct theropod relatives. The alternative would be to argue that tyrannosaurids, penguins, and flightless ducks are each other's closest relatives, and no one has ever suggested this.

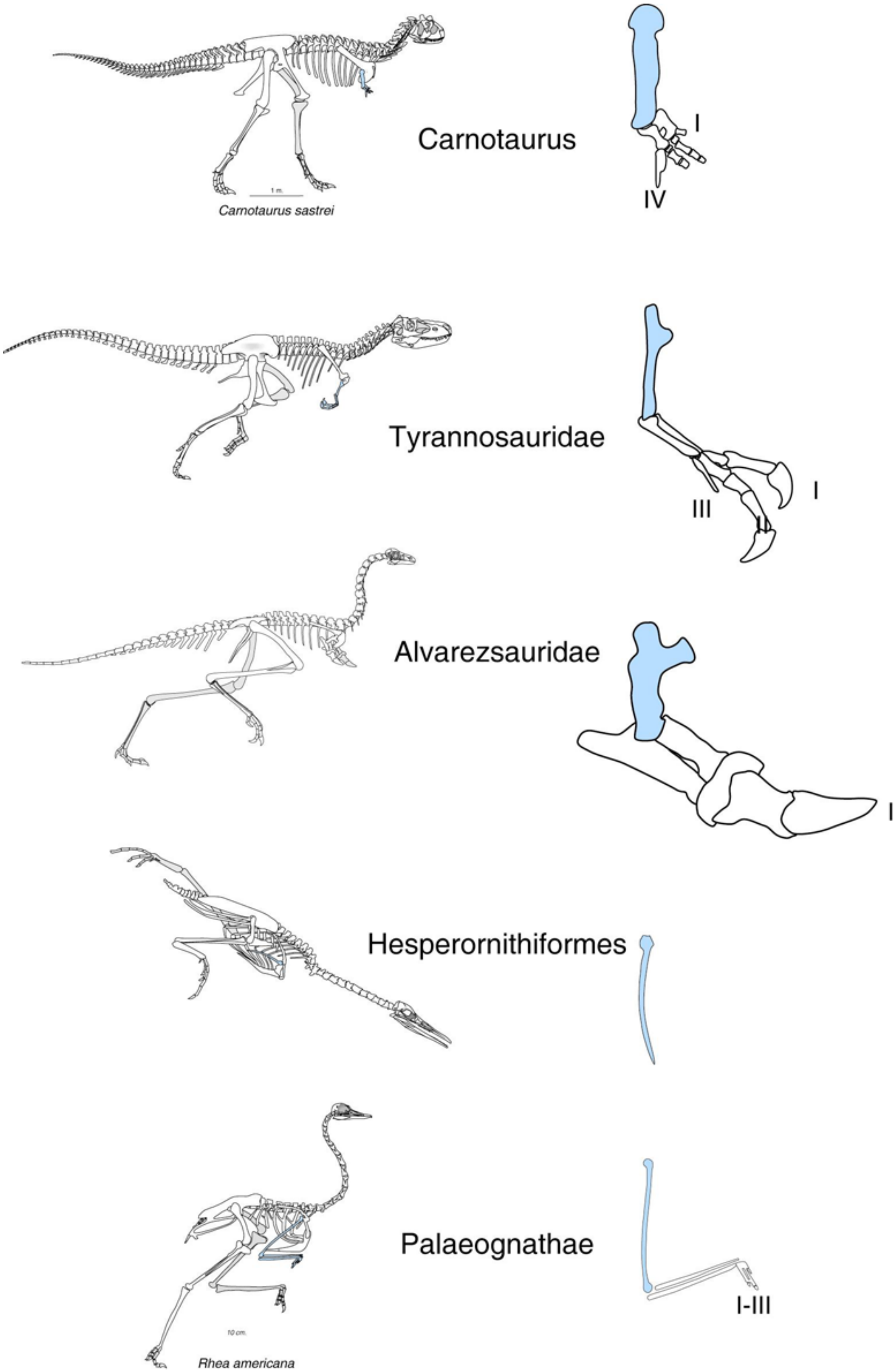

Figure 14.08 Many theropods besides *Mononykus* have independently evolved dwarfed forelimbs. A very simple genetic mechanism may have controlled these seemingly complex evolutionary changes.

Embryologists discovered long ago that ‘dwarfing’ of the forelimb is not a terribly complicated phenomenon. A diversity of natural mutations produce limb dwarfing, and others have been experimentally induced in the laboratory. Several drugs induce limb dwarfing, including thalidomide, which was inadvertently and tragically discovered to dwarf the limbs in humans whose mothers took it during pregnancy. Invariably, these drugs must be applied at a specific time during development to have this effect. Natural forelimb dwarfing and complete winglessness have also been studied closely[17]. Naturally occurring genetic mutants have been bred in the lab to create pure strains whose members carry the mutant gene. One such strain of laboratory chickens displays the *lethal wingless syndrome*, which is tied to a simple recessive gene. The shoulder bones develop normally, but the wings are either reduced to small nubs or completely absent. The legs are less severely affected, with only minor malformations in the foot. There are other complications of this syndrome, and the chicks die soon after hatching. Thus, one specific gene can’t be generally responsible for forelimb dwarfing in theropods. Nonetheless, it shows how a simple genetic mechanisms might have induced forelimb dwarfing several times over the course of theropod evolution.

Two flightless birds similar to *Mononykus* were recently discovered in the Late Cretaceous of Argentina. The first, named *Alvarezsaurus*, was originally interpreted as a non-avialian theropod. But further study of its skeleton and the discovery of *Mononykus* have established that *Alvarezsaurus* and *Mononykus* are close relatives[18]. The second was recently announced by Fernando Novas (Argentine Museum of Natural Sciences), who named it *Patagonykus*[19]. These three taxa mark a lineage – Alvarezsauridae – that was widely distributed by the end of the Mesozoic.

Ornithothoraces: Into the Trees

The lineage known as Ornithothoraces includes all birds that are closer to modern birds than to Alvarezsauridae. Here, we see an important step toward the evolution of flight capabilities in modern flapping birds. Early members are small and are distinguished from their more primitive relatives by skeletal modifications that suggest enhanced flight maneuverability[20]. Specifically, they had the ability to fly slowly without stalling. This is critical for navigating through complex three-dimensional spaces, like flying through branches to land and perch.

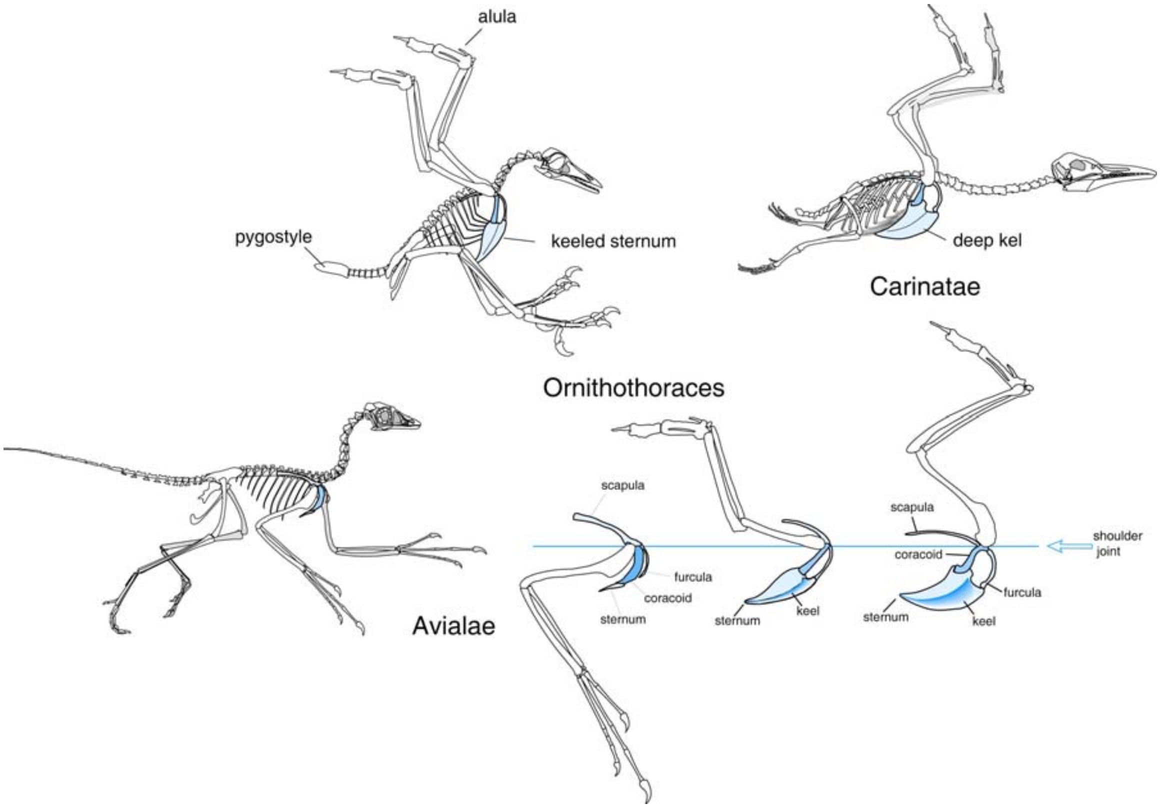

Figure 14.09 A series of changes affected to the sternum and coracoid bone in ornithothoracine and carinate birds, in association with more maneuverable and powerful flight.

One shoulder bone, called the *coracoid*, transforms into a robust strut that displaces the shoulder joint upward, away from the sternum (fig. 14.09). This increased the leverage of the flight muscles generating the power stroke, principally the *pectoralis muscle*. It also created a pulley system for a muscle anchored to the sternum that raises the wing in flight--the *supracoracoideus muscle*. These enhancements probably locked the arm into functioning exclusively for flight.

A recent discovery in Early Cretaceous rocks of Spain by José Sanz and his colleagues shows that the wings of ornithothoracian birds are equipped with the bastard wing or *alula*[21]. The bastard wing is formed by a feather that grows from the tip of the tiny thumb, and it creates a wing-slot along the leading edge (fig 14.10). By extending the thumb, the slot can be opened to help prevent turbulent flow that causes stalling. The alula and its wing-slot were critical features in the evolution of low-speed, maneuverable flight.

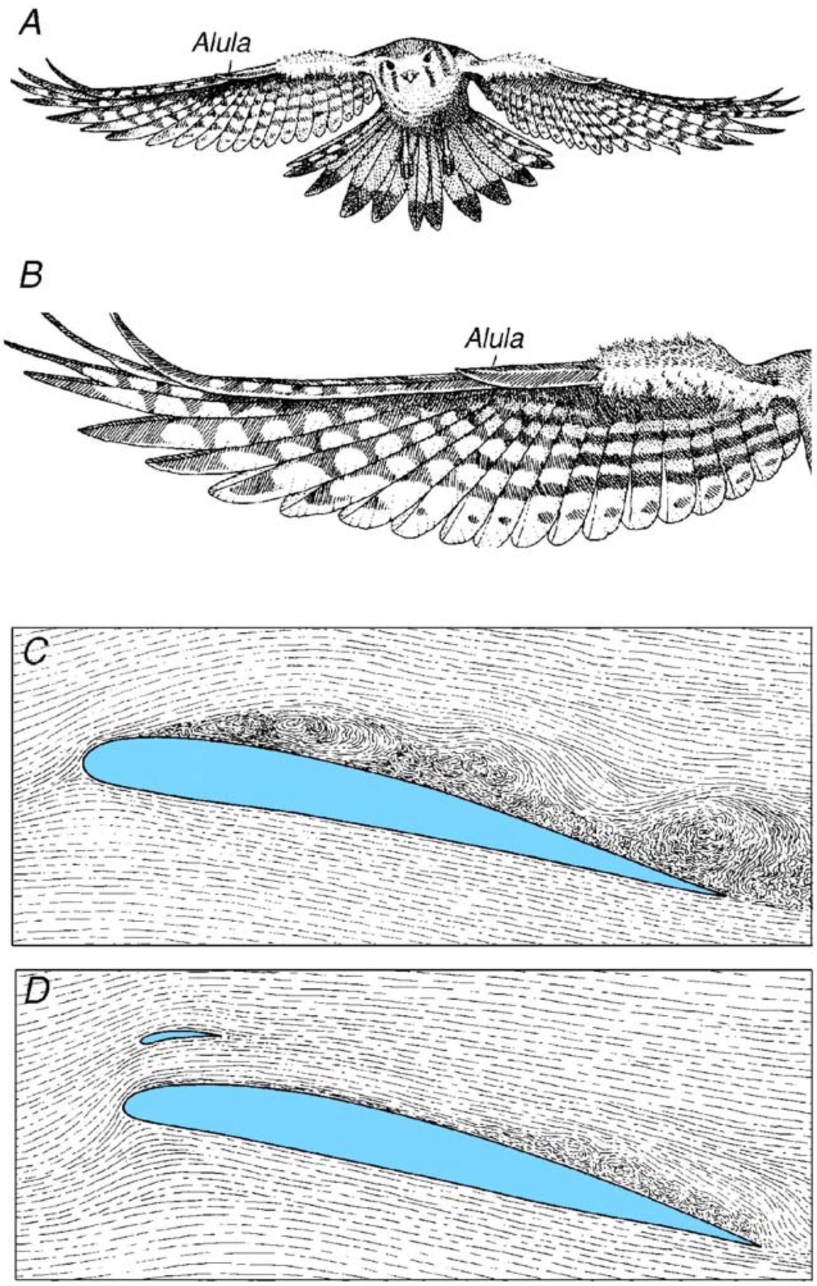

Figure 14.10 The alula is a feather extending from digit I in ornithothoracine birds, like this falcon (a - b). Cross-sections through two wings in slow flight demonstrate (c) turbulence above the wing that can cause stalling, and the effects of the alula (d) which enhances slow-speed flight. (from: T. A. McMahon and J. T. Bonner, 1983. On size and Life. Scientific American books, Inc.).

Finally, the vertebrae in the rear half of the tail fused during early development to form the *pygostyle*, the solid bony structure that supports the tail feathers. As noted earlier, Richard Owen first observed that the *pygostyle* begins development as a series of separate elements, which correspond to the individual tail vertebrae in *Archaeopteryx*. The separate elements consolidate early in development to produce the pygostyle, recapitulating the evolutionary sequence from separate to fused tail vertebrae. Consequently, the bony tail of adult ornithothoracian birds is much shorter and has fewer parts than in *Archaeopteryx* (fig. 14.11).

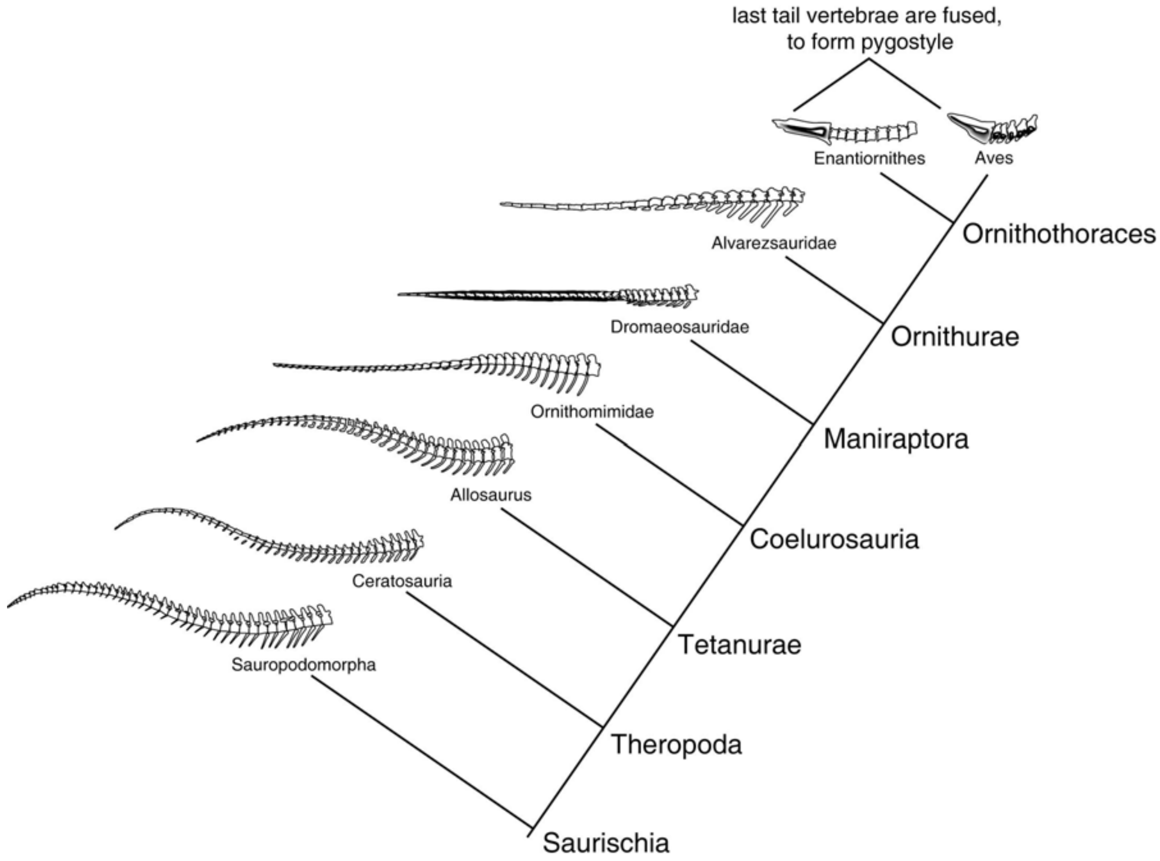

Figure 14.11 The vertebrae forming the end of the tail in ornithothoracine birds became fused together to form the pygostyle

The pygostyle enables the tail feathers to move rapidly over broad arcs. The tail feathers can be fanned and rapidly reoriented both vertically and horizontally during flight to control lift and direction precisely. Overall, early ornithothoracians were generally more powerful and maneuverable flappers than *Archaeopteryx,* more capable of the complex navigation required to fly among the branches and land in the trees.

The pygostyle also marks the beginning of a subtle shift in the way birds walked. In *Archaeopteryx* and more primitive bipedal dinosaurs, the long bony tail anchored massive muscles that pulled the thigh backwards. This retraction of the limb at the hip provided the power stroke for walking and running, much as it does in crocodiles and lizards. But with the reduced ornithothoracine tail, the muscles that retract the thigh were also reduced. These muscles are still present in modern birds, but are tiny in comparison to those of crocodiles. Therefore, the range of movement in the bird hip is limited, and the thigh rotates across a somewhat smaller arc than in more primitive theropods. To compensate, greater movement takes place at the knee, which in ornithothoracines is flexed and extended over a greater arc.

Ornithothoracian birds also have a simplified foot. The fifth metatarsal disappears and with it go all vestiges of the fifth toe. As noted earlier, this transformation is recapitulated in bird development, where a thin split is briefly present, only to disappear before hatching.

The oldest ornithothoracine is probably *Noguerornis*, which was discovered in the 1980’s in Early Cretaceous deposits of northern Spain that are slightly younger than the Solnhofen limestone[22]. *Noguerornis* was a finch-sized bird with large wing surfaces that possibly enabled the powerful bounding type of flight typical sparrows and finches. A slightly younger but more complete ornithothoracian from Spain is *Iberomesornis*[23]. About the same size as *Noguerornis*, it has slightly longer arms and a perching foot that may signal the origin of arboreality in birds. Several other basal members of ornithothoracians known from Early Cretaceous rocks of China and Mongolia offer evidence that a global diversification of flapping birds was under way by that time[24]

Enantiornithes

Entirely unknown twenty years ago, the enantiornithine lineage is now known to have been diverse and widespread in the Cretaceous[25]. Representative fossils were actually collected over a century ago, but they were misidentified as non-avian dinosaurs or as members of modern bird lineages. Enantiornithines have been recovered primarily from terrestrial deposits, suggesting that the lineage radiated widely across the continents, but they never evolved into shorebirds or seabirds. Enantiornithines are found in the Early Cretaceous of China and Spain, as well as Late Cretaceous deposits in North America, South America and Australia. Over the course of its 70-million year history, the lineage diversified into species with many different sizes and shapes. Early enantiornithines were small, sparrow-sized birds that were strong flyers (fig. 14.12). By the end of the Cretaceous there were turkey-sized forms with wing-spans of more than three feet, stilt-legged waders, and powerful runners.

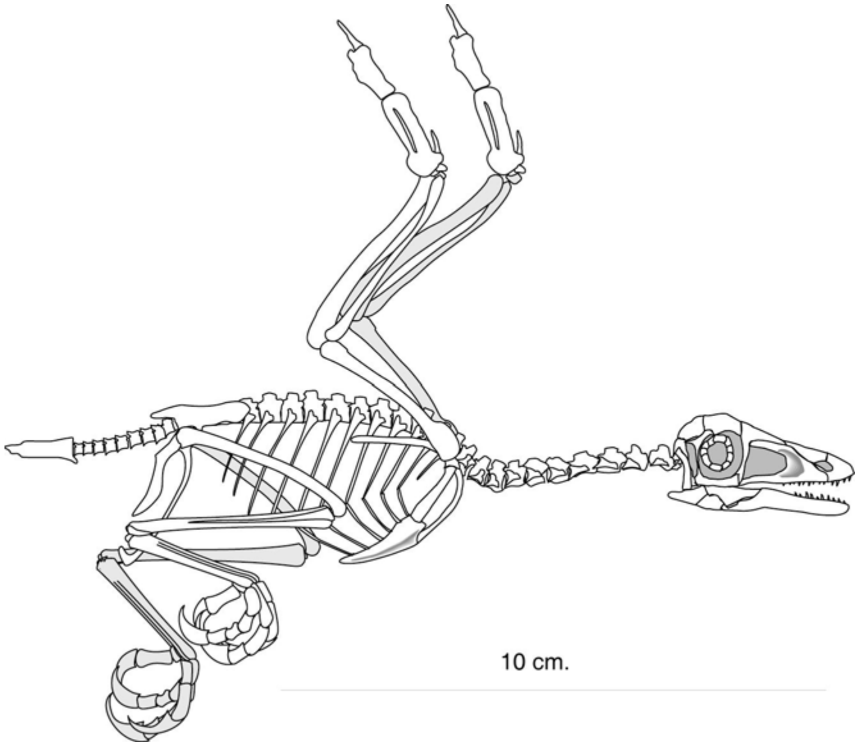

Figure 14.12 Enantiornithine birds were unknown two decades ago, but they are now represented by a diversity of Cretaceous species. This skeleton is a composite, based on several recent discoveries of incomplete skeletons.

Enantiornithes are sometimes referred to as “opposite birds” because their feet grow in an opposite pattern from other birds. Alan Feduccia (University of North Carolina) and several colleagues argue that Enantiornithes, plus *Archaeopteryx* and *Confuciusornis* comprise a lineage named “Sauriurae,” that is the sister lineage to all other birds[26]. They claim that fusion among the foot bones begins near the ankle and proceeds downward. In other birds fusion begins in the middle of the foot and grows in both directions. But these are points of resemblance, because as we have seen, apart from being members of the Avialae lineage, *Archaeopteryx* and enantiornithines lie within different hierarchies. Based on its position on the phylogenetic map, fusion in the foot bones characterizes all ornithothoracine birds and that variations on the pattern of fusion evolved within the group. There is no evidence to suggest that "Sauriurae" is a natural group, so it cannot be plotted on the evolutionary map of early birds.

A flightless lineage of extinct ornithothoracine birds that can be mapped is *Patagopteryx,* from Patagonia. This chicken-sized bird lived during the Late Cretaceous and was probably a good runner, like its more primitive dinosaurian relatives. The pelvis has lost the pubic boot so distinctive of its more primitive tetanurine relatives. Therefore, *Patagopteryx* may be a step closer to modern birds than the enantiornithines[27].

In contrast to what we were taught as grad students, a rich diversity of birds shared the landscape with their more famous Cretaceous relatives such as *Deinonychus*, *Velociraptor*, and *Tyrannosaurus*. But like them, alvarezsaurids, enantiornithines and *Patagopteryx* all became extinct at or near the end of the Cretaceous.

Carinates: air and water

Carinate birds are advanced in the structure of their skulls and flight apparatus. The respiratory passages through the snout, in front of the eyes, may have housed large structures known as *turbinates*. We will discuss these interesting structures later, when we investigate the issue of warm-bloodedness in dinosaurs. The sternum of carinates has a greatly deepened keel, indicating another step in the evolution of powerful flight muscles. The trunk is also short and stout compared with more primitive dinosaurs, with less than twelve vertebrae between the base of the neck and the pelvis. This short stout trunk enhances powered flight by providing a rigid armature for attaching larger flight muscles and absorbing greater forces during landing (fig. 14.13).

Several carinate lineages are known from fossils found predominantly in marine rocks. They represent the first aquatic invasion by dinosaurs. Many later lineages evolved a lifestyle tied to the oceans, but based on our present evolutionary map, they did so independently from terrestrial ancestors. One marine lineage, called Ichthyornithiformes, includes a Cretaceous seabird named *Ichthyornis* and a few related forms (fig. 14.13). *Ichthyornis* was a powerful flyer, like modern pelicans or frigate birds, but it was not a close relative of either[28].

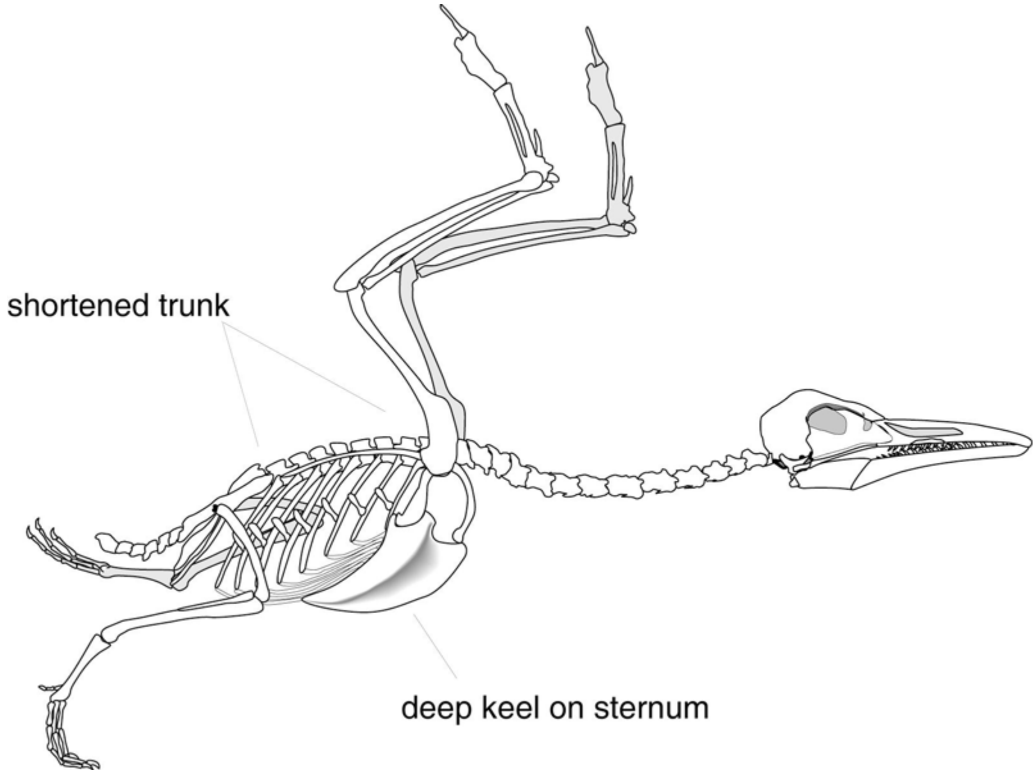

Figure 14.13 Several of the most characteristic features of carinate birdss are the shortened trunk and a deep keel on the breastbone. Pictured here is *Ichthyornis*, the most completely known member of Ichthyornithiformes, a lineage of Cretaceous seabirds. Even this species is poorly known and this drawing is a composite, made from several incomplete specimens.

A better known Cretaceous seabird lineage is Hesperornithiformes, found in Asia, Europe, and North America (fig. 14.14). These distinctive birds were entirely flightless, with dwarfed forelimbs formed only by a splint-like humerus. The rest of the wing was lost. *Hesperornis* and its close relatives were foot-propelled diving birds[29]. The pelvis is elongated and the feet were located at the back of the body, like modern penguins and loons. They probably used their feet for propulsion under water while swimming across the surface. These birds foraged for food along the coastlines of the shallow seaways that crossed North American and Asian continents during much of the Cretaceous, living on fish and other marine organisms. They must have been very ungainly on land and, apart from nesting, spent most of their lives in the water.

The oldest carinate is probably *Ambiortus* from the Early Cretaceous of Mongolia[30]. Known only from fragmentary fossils, *Ambiortus* was a terrestrial bird, like most of the lineage. The fossil records of both Ichthyornithiformes and Hesperornithiformes begin in the Early Cretaceous and disappear about five million years before the end of the Cretaceous.

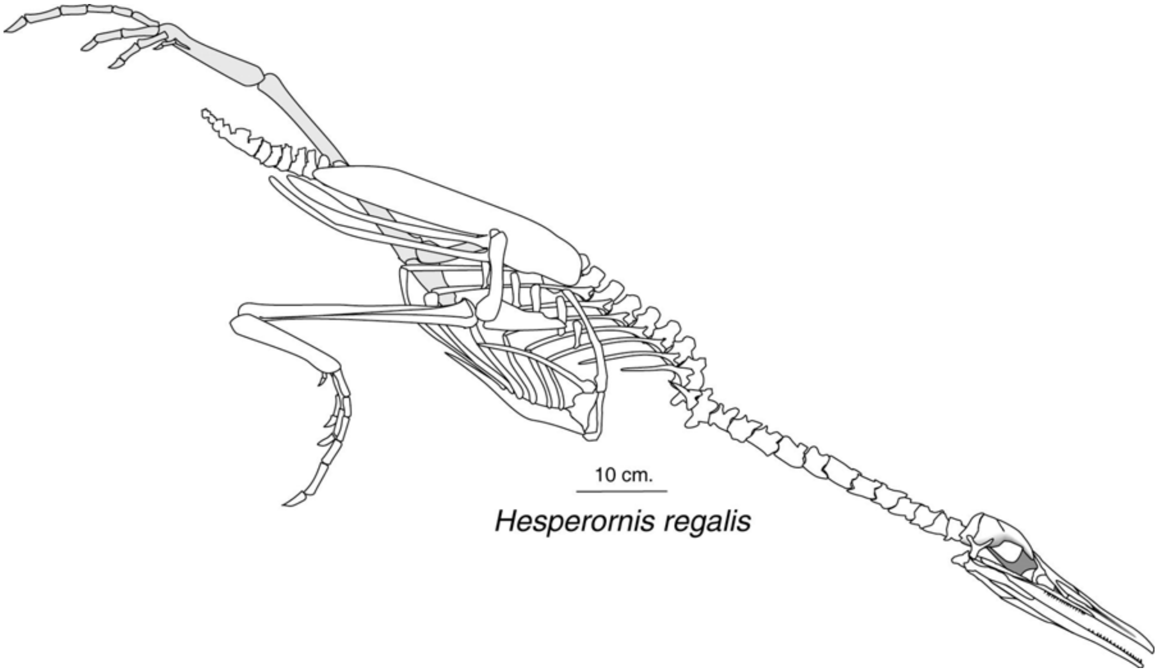

Figure 14.14 Hesperornithiformes is a lineage of Cretaceous diving birds that went extinct about 5 million years before the end of the Cretaceous.

Rare as hen's teeth

Aves is the lineage that includes the common ancestor all living bird species, and all its descendants[31]. At the height of its diversity, a few thousand years ago, Aves included more than 12,000 and perhaps as many as 20,000 species of birds. A distinctive characteristic of Aves is the complete loss of teeth (fig. 14.15). Modern birds even lose the egg tooth, which evolved at the same time as the amniotic egg, to help the embryo break out of its shell. Although many people refer to an "egg tooth" in modern birds, the structure in question is really the *caruncle,* a horny spike that grows at the tip of the beak (fig. 14.02). The true egg tooth is a real tooth, with layers of dentine and enamel, like other teeth. Even this tooth is absent in birds, and no natural atavisms--birds with teeth--have ever been observed.

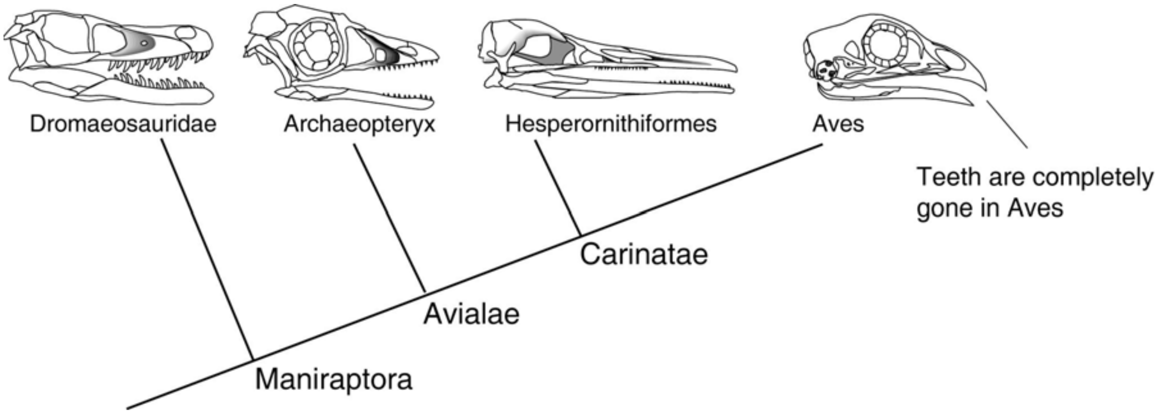

Figure 14.15 One of the most characteristic features of Aves is the complete loss of teeth.

Replacing the teeth is horny beak or bill. As the hands and arms of birds became increasingly modified and committed to flight, they lost the grasping ability of earlier theropods for capturing food and manipulating objects.   This is where the strong toothless beak comes in. The upper bill became movably hinged to the skull in front of the eyes, and a series of levers coupled its movement to that of the lower jaw. As the lower jaw dropped, the upper beak raised. This provided unparalleled versatility, and a vast diversity of specializations evolved from this basic mechanism through subsequent modification in the beaks and the leveling system between them. Modern birds tear flesh, build nests, drink nectar, and perform many other functions with their beaks.

In birds, teeth may be gone but they are not forgotten. In a laboratory experiment, embryologists induced embryonic tissues around the mouth of an unhatched chick to differentiate into tooth buds--the first stage of tooth development)[32]. Thus, the genetic program for growing teeth has been conserved in birds, but a regulatory gene has switched off the program or blocked it in some other way. As the genetic control for development is mapped in greater detail, we may see embryologists re-engineer teeth in some modern birds.

In addition, there is a greatly enlarged brain in Aves compared to those of other theropods (fig. 14.16). This potentially fascinating distinction is as yet largely unstudied, but the structures responsible for integrating sensory and motor information are clearly enlarged. More volume means more neurons, and more neurons provide greater computing power for gathering, filtering, and coordinating sensory information. Greater computing power also enhances the integration of muscular actions and responses to environmental stimuli.

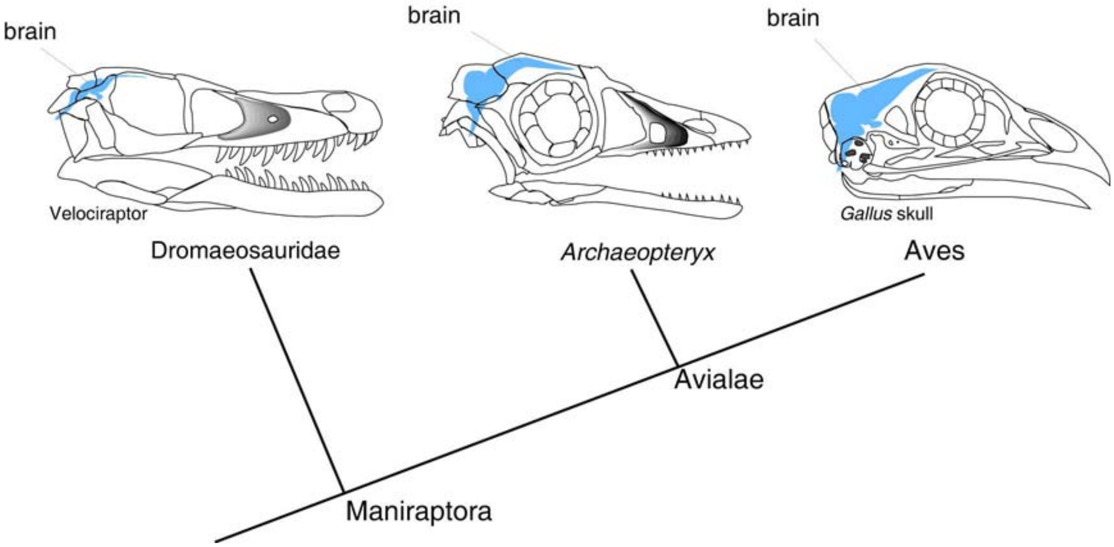

Figure 14.16 Living birds have a larger brain than their relatives among extinct theropods.

Warmer Blood

A war erupted in the early 1970's over whether dinosaurs were warm-blooded. By the time we reached graduate school, the media and scientific press had escalated the issue to global proportions. After a quarter century of debate, where does the scientific community stand today?

First, we should look a closer look at the problem. Today, only mammals and birds are warm-blooded. This means that they maintain a constant body temperature, that it is a comparatively high temperature, and that they do this via the metabolic generation of heat by metabolic activities of the cells. Warm-blooded animals are technically known as *endotherms*. They have an increased capacity for longer periods of high activity, greater independence from ambient environmental temperatures, and this has helped endotherms to colonize all parts of the globe. The alternative physiological condition, from which mammals and bird physiology evolved, is known as *ectothermy*. In ectotherms, body temperature varies more directly with the ambient environmental conditions. It may be higher or lower than in a given endotherm, depending largely on environmental conditions. Bursts of high activity can not be sustained, and environmental conditions tend to be more limiting for ectotherms.

For all its seeming advantages, endothermy comes at a high cost. Even with layers of insulation like feathers in birds and hair in mammals, heat is continually being lost to the environment. To keep their bodies at a constant temperature, the metabolic ‘engines’ of endotherms burn about five to ten times the amount of oxygen as do ectotherms of comparable size. So, endotherms usually require constant supplies of food, water, and oxygen to sustain themselves. The question of our generation was: were dinosaurs endothermic like mammals and birds, or ectothermic like other reptiles?

In one sense, the question of whether dinosaurs evolved endothermy can be decisively answered from our map of dinosaur phylogeny. Birds, living dinosaurs, are unquestionably warm-blooded. So, some dinosaurs--in fact most dinosaurs--are warm-blooded. But such an answer still begs the question of *when* in dinosaurian history endothermy arose. Were all dinosaurs endothermic, or only birds, or some combination in between? Did endothermy evolve in gradual steps or suddenly in one step.

The charge in this paleontological debate was led by Bob Bakker, who provocatively claimed that *all* dinosaurs are endothermic[33]. Like Richard Owen, Bakker was influenced by anatomical clues for an upright posture, such as the in-turned femoral head. But Bakker went beyond Owen’s conclusions and argued that upright posture *demanded* endothermic physiology in *all* dinosaurs. Bakker argued that advanced metabolic machinery was required because he thought that muscular activity is what held the limbs against the body. But by measuring the metabolic costs of locomotion in living reptiles, mammals, and birds, experimental physiologists found that simply having an upright posture did not require an elevated metabolic rate. The cost of standing, in terms of the amount of oxygen consumes, was hardly different in a mammal or a lizard[34]. Moreover, modern crocodylians are capable of spectacular bursts of activity by pulling their hindlimbs into an erect position when doing the “high walk”--a fast walk that is almost a run. They just can’t do this for long periods because their muscles quickly fatigue from the build-up of lactic acid. So, upright posture doesn’t necessarily indicate endothermy.

Bakker's also argued that relative abundances of fossil carnivores and herbivores can be used to infer physiology, but this has been a limb few other paleontologists are willing to crawl out on. Few are willing to accept that the fossil record, so dependent on water and containing such huge gaps, preserves the actual abundance of different kinds of dinosaurs in living communities, or that census numbers of fossils necessarily bear on the physiology of the population. As we saw in Chapters 7 and 8, completeness of the stratigraphic record is quite variable and in many locations probably preserves little of an ancient community's structure. Our sample size of fossils and extinct communities is so small that few scientists accept the relative abundance of fossils as a very sound datum.

Additional arguments have been advanced by different researchers in support of endothermy in all dinosaurs[35]. Speeds inferred from Mesozoic trackways are alleged to indicate that dinosaurs moved at higher than average velocities, which in turn was alleged to signal higher metabolic levels. But most trackways are of dinosaurs walking a slow speeds and only a few short trackways preserve any evidence of higher speeds - for whichever dinosaur it was that left them. The geochemistry of fossil bones was also presented as support for warm-bloodedness[36]. However, so little is known about the geochemical effects of being buried, and so few dinosaur fossils have been studied in this way, that few scientists trust the results. For a time, scientists argued that the biogeography of Mesozoic dinosaurs and their global distribution suggests that non-avian dinosaurs are ectotherms. As we saw earlier, the discovery of a rich fauna of dinosaur from Alaska's north slope, which was inside the Arctic Circle even in the Cretaceous, indicating that the biogeographic pattern is more complicated than previously thought.

More recently, two independent lines of skeletal evidence have been presented as evidence of endothermy in at least some Mesozoic dinosaurs. Both suggest that the ancestral carinate was physiologically closer to modern birds in the way it breathed and the way it grew, implying elevated metabolic levels. This connection was discovered by John Ruben (Oregon State University), who argued that to sustain high levels of activity for prolonged periods, endotherms need a constant high supply of oxygen[37]. Birds and mammals have a supercharged heart and lung system, that pump more blood and more air than in their cold-blooded relatives. Birds are even aided by the blind air sacs and pneumatic cavities that branch throughout their bodies and even invade their bones.

Modern birds can deliver high quantities of oxygen to the muscles even during extreme exercise, by breathing faster to pass more air across their respiratory membranes. Birds deliver about fifteen times more oxygen to their muscles than ectothermic reptiles, whereas mammals deliver six- to ten-times that amount. The increased oxygen supply enables the cells to metabolize *aerobically*, in contrast to the *anaerobic* metabolism of cold-blooded vertebrates. This cleaner metabolic engine permits long, sustained periods of high activity without the debilitating build up of lactic acid. Modern birds could not sustain long flights without having this aerobic metabolism sustained by their powerful heart-lung system.

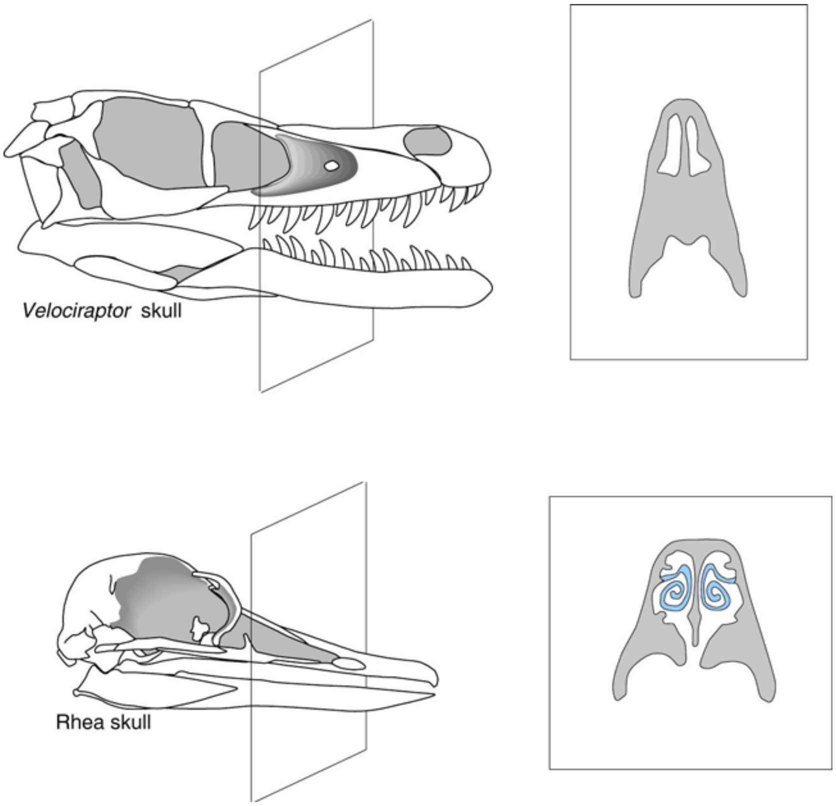

Figure 14.17 In non-carinate dinosaurs like *Velociraptor*, the respiratory passageways are simple tubes. In carinates the passageway is filled with scroll-like turbinate bones, which capture water from exhaled air, to help prevent dessication during breathing.

Rubin suggests that a series of scrolled bones or cartilages called *respiratory turbinates* (fig. 14.17), which lie inside the nasal chamber along the respiratory passage in birds and mammals, is correlated to endothermy. He argues that small, warm, fast-breathing bird or mammal can potentially loose a lot of water vapor very quickly. As cool air enters the lungs, it becomes warmed and saturated with condensing water vapor. Without a mechanism to retain body moisture while exhaling, dehydration would severely restrict the scope of activity unless an unlimited supply of water were available. Birds and mammals circumvent this limit through the respiratory membrane that covers the elaborate turbinates. Living carinates all have respiratory turbinates. *Hesperornis* may have as well, judging from the shape of the nasal chamber in front of its eyes. However, turbinates are easily lost during decay and burial, and so far, despite claims to the contrary, they have not been verified in any Mesozoic dinosaur. On the mammal side of the amniote tree, moreover, there is evidence from CT scanning of Mesozoic fossils that the turbinates arose in several steps, so the picture may not be so clear as Rubin's argument suggests.

More bony clues pointing to endothermy have been suggested by the microscopic patterns in of bone growth, which may indicate whether a bone underwent continuous, uninterrupted growth, or if there were periods in which growth stopped. This line of evidence was first championed in the 1970's by Armand de Ricqlès (University of Paris), and Anusuya Chinsamy (South African Museum) has recently carried the technique further[38]. Both have studied modern birds along with Mesozoic dinosaur specimens. Bones of enantiornithes and more distant relatives grew discontinuously, with long dormant periods that produced growth lines visible in cross-sections of the bones[39]. Similar growth lines are found in modern ectothermic reptiles -- crocodylians, lizards, and turtles -- in which there is seasonal growth. But in carinates, they report no growth lines. Chinsamy and colleagues argue that an elevated metabolic rate and warmer body may have insulated carinates from seasonal temperature fluctuations that can affect the physiology and growth in ectotherms. So far, not many species of either living or extinct dinosaurs have been studied, so these conclusions await further testing.

Ancient DNA

In Michael Crichton's fantasy *Jurassic Park* DNA was recovered from the stomachs of Cretaceous mosquitoes that were trapped in amber shortly after sucking dinosaur blood for their last supper. A recent claim by Scott Woodward (Brigham Young University) and colleagues, that fragments of DNA molecules had been extracted directly from Cretaceous dinosaur bones[40], seemed to put us on the scientific road to *Jurassic Park*. A modern technique called polymerase chain reaction (PCR) enables biologists to clone extremely tiny mounts of DNA into samples large enough that researchers can measure the characteristic sequences of nucleic acids. With a genetic blueprint for an extinct dinosaur, could we implant this DNA into a living egg and clone a Mesozoic beast?

Using PCR, Woodward and colleagues measured several short DNA sequences. But when compared to modern reptiles, the sequences showed no special similarity to any. Blaire Hedges (University of Pennsylvania) and Mary Schweitzer (University of Montana) later demonstrated that the DNA sequences are probably human -- an artifact of human contamiantion[41]. More importantly, Hendrik Poinar (University of Munich) and his colleagues reported evidence that DNA quickly decays, in a processes known as *racemization*[42]. Over a scale of hundreds to thousands of years, DNA is relatively stable. But on a scale of millions of years, racemization leads to severe deterioration of original structure. Apart from environments like amber, which embalm and preserves the soft tissues, it is looking unlikely that we will ever obtain DNA from Mesozoic dinosaurs.

Even if we could somehow recover Mesozoic dinosaur from amber, we would need not just DNA fragments but a complete, intact genome. Building a living sauropod or ceratopsian from fossil DNA fragments would be like trying to build and launch the space shuttle using something as fragmentary as the Dead Sea scrolls for an instruction manual. A second problem is that complex feedback mechanisms exist between the DNA in different genes nearby, as well as with various parts of the host cells and surrounding tissues. Only through this feedback can the right switches be thrown at the right time to produce a functioning, viable living organism. With out the proper and specific feedback from the egg containing the cloned DNA, there is little hope that development will proceed very far before something goes wrong and the embryo dies.

So, even though we are a long way from cloning extinct dinosaurs using Mesozoic DNA, a door to the genetic past may stand slightly ajar thanks to embryology of their modern descendants. But regulating the growth of a bird embryo is an enormously complex process that presents science with a vast, unexplored terrain. Much of the ancient genetic history of birds is probably erased, and the scientific road to *Jurassic Park* now appears infinitely long.

References for Chapter 14

1) Starck, J. M., 1993. Evolution of Avian Ontogenies. Current Ornithology, 10:275-366.

2) Hall, B. K. 1992. Evolutionary Developmental Biology. London, New York, Yokyo, Chapman and Hall.

3) Darwin, C. 1859. On the Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life. John Murray, London.

4) Gegenbaur, C. 1863, Vergleichendend-anatomische Bemerkungen über das Fussskelet der Vögel. Archive für Anatomie, Physiologie und Wissenschaftliche Medicin:450-472.

5) Padian, K. 1996. Early bird in slow motion. Nature 382: 400-401; Ruben, J. 1001. Reptilian physiology and the flight capacity of *Archaeopteryx*. Evolution 45: 1-17.

6) Hou, L., Z. Zhou, L. D. Martin, A. Feduccia, 1995. The oldest beaked bird is from the "Jurassic" of China. Nature, 377: 616-618; Feduccia, A., 1996. The Origin and Evolution of Birds. New Haven, Yale University Press.; Hou, L., L. D. Martin, Z. Zhou, A. Feduccia, Early adaptive radiation of birds: evidence from fossils from northeastern China. Science, 274: 1164-1167.

7) Chiappe, L., 1995. The first 85 million years of Avian Evolution. Nature, 378: 349-355.

8) Jensen, J., and K. Padian 1989. [get title] Journal of Paleontology

9) Gauthier, J. A. 1986. Saurischian monophyly and the origin of birds Pp. 1-47 In: Their Origin of Birds and the Evolution of flight, K. Padian (ed.), Memoir 8, California Academy of Sciences.

10) Chiappe, L., 1995. The first 85 million years of Avian Evolution. Nature, 378: 349-355.

11) Gruneberg, H. 1963. The Pathology of Development; a study of inherited skeletal disorders in animals. New York, John Wiley & Sons, Inc.

12) Hampé, A. 1959. Contribution a l'etude du development et dela regulation des deficiences et des excedents dans lat patte de l'embryon de poulet. Archs. Anat. Microsc. Morph. Exp. 48:345-478

13) Müller, G. B., 1989. Ancestral patterns in bird limb development: a new look at Hampé's experiment. Journal of Evolutionary Biology, 1:31-47.

14) Altangerel, P., M. A., Norell, L. M. Chiappe, J. M. Clark, 1993. Flightless bird from the Cretaceous of Mongolia. Nature 362: 623-626; Altangerel, L. M. Chiappe, B. Rinchen,, J. M. Clark, and M. A., Norell, 1994. Skeletal morphology of *Mononykus olecranus* (Theropoda: Avialae) from the Late Cretaceous of Mongolia. American Museum Novitates 3105: 1-29.

15) Patterson, C., 1993. Bird or dinosaur? Nature 365: 21-22; Wellnhofer, P. 1995. New data on the origin and early evolution of birds. C. R. Acad. Sci. Paris, 319, Series II, 299-308.

16) Zhou, Z. 1995. Is *Mononykus* a bird? The Auk 112, 958-963.

17) Gruneberg, H. 1963. The Pathology of Development; a study of inherited skeletal disorders in animals. New York, John Wiley & Sons, Inc.

18) Novas, F. 1996. Alvarezsauridae, Cretaceous basal birds from Patagonia and Mongolia; Pp. 675-702 in F. E. Novas and R. E. Molnar (eds.) proceeding of the Gondwanan Dinosaur Symposium. Memoirs of the Queensland Museum, 39.

19) Novas, F. 1997. Anatomy of *Patagonykus puerti* (Theropoda, Avialae, Alvarezsauridae), from the Late Cretaceous of Patagonia. Journal of Vertebrate Paleontology 17:137-166.

20) Padian, K. 1996. Early bird in slow motion. Nature 382: 400-401; Ruben, J. 1001. Reptilian physiology and the flight capacity of *Archaeopteryx*. Evolution 45: 1-17.

21) Sanz, J., L. M. Chiappe, B. P. Pérez-Moreno, A. D. Buscaloni, J. J. Moratalla, F. Ortega, and F. J. Poyato-Ariza, 1996. An Early Cretaceous bird from Spain and its implications for the evolution of flight. Nature 382: 442-4455;

22) Chiappe, L., 1995. The first 85 million years of Avian Evolution. Nature, 378: 349-355.

23) Sanz, J. L., and J. F. Bonaparte, and A. Lacasa, 1988. Unusual Early Cretaceous birds in Spain. Nature, 331: 433-435; Chiappe, L., 1995. The first 85 million years of Avian Evolution. Nature, 378: 349-355.

24) Kurochkin, E. V. 1995. The assemblage of Cretaceous birds in Asia. Pp. 203-208 *in* Sixth symposium on Mesozoic Terrestrial Ecosystems and Biota, A. L. Sun (ed.) Beijing, China Ocean Press.

25) Chiappe, L., 1995. The first 85 million years of Avian Evolution. Nature, 378: 349-355.

26) Feduccia, A., 1996. The Origin and Evolution of Birds. New Haven, Yale University Press.; Hou, L., L. D. Martin, Z. Zhou, A. Feduccia, Early adaptive radiation of birds: evidence from fossils from northeastern China. Science, 274: 1164-1167.

27) Chiappe, L., 1995. The first 85 million years of Avian Evolution. Nature, 378: 349-355.

28) Chiappe, L., 1995. The first 85 million years of Avian Evolution. Nature, 378: 349-355.

29) Chiappe, L., 1995. The first 85 million years of Avian Evolution. Nature, 378: 349-355..

30) Kurochkin, E. V. 1995. The assemblage of Cretaceous birds in Asia. Pp. 203-208 *in* Sixth symposium on Mesozoic Terrestrial Ecosystems and Biota, A. L. Sun (ed.) Beijing, China Ocean Press; Chiappe, L., 1995. The first 85 million years of Avian Evolution. Nature, 378: 349-355.

31) We follow the nomenclature of Gauthier (1986), who was the first to define the meaning of the name Aves to refer to the last common ancestor of modern avian species and all its descendants. Other authors commonly apply this name as a substitute for Ornithurae.

32) Kollar, E. J., and C. Fisher 1980. Tooth induction in chick epithelium; expression of quiescent genes for enamel synthesis. Science, 207:993-995.

33) Bakker, R. T. 1968. The superiority of dinosaurs. Discovery 3:11-22; Bakker, R. T. 1975 The Dinosaur rennaissance, Scientific American 232: 58-78; Bakker, R. T. 1986. The Dinosaur Heresies. New York, William Morrow.

34) Bennett, A. F., and B. Dalzell, 1973. Dinosaur physiology: a critique. Evolution 27:170-174; Bennett, A., and J. Ruben 1979. Endothermy and activity in vertebrates. Science 206:649-654; Farlow, J. O., P. Dodson, and A. Chinsamy 1995. Dinosaur biology. Annual Review of Ecology and Systematics 26:445-471.

35) Farlow, J. O., P. Dodson, and A. Chinsamy 1995. Dinosaur biology. Annual Review of Ecology and Systematics 26:445-471.

36) Barrick, R. E., and W. J. Showers, 1994. Thermophysiology of *Tyrannosaurus rex*: evidence from oxygen isotopes. Science 265: 222-224.

37) Ruben, J. 1995. The evolution of endothermy in mammals, birds, and their ancestors. Journal of Experimental biology. Fishman, J. 1995. Were dinos cold-blooded after all? The nose knows. Science 270:735-736.

38) Chinsamy, A., and P. Dodson, 1995. Inside a dinosaur bone. American Scientist,83:174-180; Farlow, J. O., P. Dodson, and A. Chinsamy 1995. Dinosaur biology. Annual Review of Ecology and Systematics 26:445-471.

39) Chinsamy, A, L. M. Chiappe, and P. Dodson, 1995. Mesozoic avian bone microstructure: physiological implications. Paleobiology 21: 561-574.

40) Woodward, S. R. et al. 1994. DNA sequence from Cretaceous period bone fragments. Science 266:1229-1232.

41) Hedges, S. B., and M. H. Schweitzer 19995. Detecting dinosaur DNA. Science 268:1191.

42) Poinar, H. N. et al 1996. Amino acid racemization and the preservation of ancient DNA. Science 272: 864-866.

Figure 14.01 Phylogenetic map showing the relationships among the basal bird lineages (in blue).

Figure 14.02 In a number of regions of the skeleton, rearrangements of bones occur during development that recapitulate similar evolutionary rearrangements in early theropod history. If birds are not descendants of Mesozoic theropods, why does their development history reflect so much of early theropod history? (from: H. Rahn, A.Ar, and C. V Paganelli. How birds breath. Scientific American, 1979).

Figure 14.03 During theropod evolution, the first toe, the fifth toe, the ascending process, and the fibula were all rearranged.

Figure 14.04 During bird development, the bones of the foot undergo rearrangements that are similar to those occurring in theropod evolution (see fig. 14.03).

Figure 14.05 Ornithurine birds are distinguished from other theropods by many features of the hand, breast-bone, and leg.

Figure 14.06 In ornithurine birds, many of the bones of the hand became fused together to form a solid structure.

Figure 14.07 *Mononykus* represents Alvarezsauridae, a weird lineage of flightless bird from the Late Cretaceous.

Figure 14.08 Many theropods besides *Mononykus* have independently evolved dwarfed forelimbs. A very simple genetic mechanism may have controlled these seemingly complex evolutionary changes.

Figure 14.09 A series of changes affected to the sternum and coracoid bone in ornithothoracine and carinate birds, in association with more maneuverable and powerful flight.

Figure 14.10   The alula is a feather extending from digit I in ornithothoracine birds, like this falcon (a - b). Cross-sections through two wings in slow flight demonstrate (c) turbulence above the wing that can cause stalling, and the effects of the alula (d) which enhances slow-speed flight. (from: T. A. McMahon and J. T. Bonner, 1983. On size and Life. Scientific American books, Inc.).

Figure 14.11 The vertebrae forming the end of the tail in ornithothoracine birds became fused together to form the pygostyle

Figure 14.12 Enantiornithine birds were unknown two decades ago, but they are now represented by a diversity of Cretaceous species. This skeleton is a composite, based on several recent discoveries of incomplete skeletons.

Figure 14.13 Several of the most characteristic features of carinate birdss are the shortened trunk and a deep keel on the breastbone. Pictured here is *Ichthyornis*, the most completely known member of Ichthyornithiformes, a lineage of Cretaceous seabirds. Even this species is poorly known and this drawing is a composite, made from several incomplete specimens.

Figure 14.14 Hesperornithiformes is a lineage of Cretaceous diving birds that went extinct about 5 million years before the end of the Cretaceous.

Figure 14.15 One of the most characteristic features of Aves is the complete loss of teeth.

Figure 14.16 Living birds have a larger brain than their relatives among extinct theropods.

Figure 14.17 In non-carinate dinosaurs like *Velociraptor*, the respiratory passageways are simple tubes. In carinates the passageway is filled with scroll-like turbinate bones, which capture water from exhaled air, to help prevent dessication during breathing.