Chapter 12, The Mistaken Extinction, by Lowell Dingus and Timothy Rowe, New York, W. H. Freeman, 1998.

Chapter 12

The Evolutionary Map for Dinosaurs

Many different groups of dinosaurs have been implicated in avian origins. In fact, so many different branches on the dinosaur tree have names with the root ‘ornitho-‘, meaning bird-like, that they are hard to keep straight. But even granting that *some* dinosaurs show similarities, many others look nothing like birds. It is difficult to recognize *any* special resemblances between *Triceratops* and a bird, for example. Even though we have traced a hierarchy of relationship linking birds and dinosaurs this far, some paleontologists challenge that comparing birds to dinosaurs as a whole presents only the confusing mosaic of resemblances expected of convergent or homoplastic evolution.

Another challenge of a sort comes from Late Triassic rocks in Texas, where a small animal named *Protoavis* - the primordial bird - was unearthed by a researcher in Lubbock. *Protoavis* is said to be a long lost ancestor of birds that links their pathway of evolution to dinosaurs, but not via *Archaeopteryx*, nor through dinosaurs like Huxley’s *Compsognathus* or Ostrom’s *Deinonychus*. The discovery of *Protoavis* resurrected the theory of homoplasy, but with a different twist. Birds may be descended from dinosaurs after all, but not from any of the usual suspects.

Once again we meet with allegations that can’t all be true, so how can we test between them? If birds have rightfully inherited the "family" name Dinosauria, they will all lie along a single branch in the hierarchy of dinosaur relationships. If not, we will find only conflicting points of similarity, randomly adorning different evolutionary pathways. We can test between these alternatives by following an evolutionary map for dinosaurs, starting with the ancestral dinosaur species, and tracing all its descendant lineages to their natural ends. All we need is a map.

At about the time we arrived at Berkeley as new graduate students, Kevin Padian arrived as a new assistant professor of paleontology. Padian had studied pterosaur evolution at Yale under John Ostrom’s supervision, during the height of the battle over *Deinonychus*. And Padian brought the excitement of bird origins to Berkeley, where he served as dissertation supervisor for Jacques Gauthier, as well as for one of us. Gauthier’s dissertation included a cladistic analysis of the relationships among dinosaurs, using the methods described in an earlier chapter[1]. When he published this work in 1986 it created a new round of controversy on bird origins because it was the first attempt at a strictly hierarchical map of dinosaur genealogy, and it supported a dinosaurian ancestry for birds.

A decade later, Gauthier carried the debate back to Yale University, filling the professorship vacated by John Ostrom's retirement. To read the newspapers, you might think that that decade, which saw dozens of new fossil discoveries and refinements in mapping technique, only stoked the flames of controversy over dinosaur relationships. Some paleontologists challenge Gauthier's work, pointing to the persistence of controversy as an indication that cladistics simply doesn't work, and journalists are quick to publish these allegations. But others argue that today's cladistic map of dinosaur relationships is basically accurate and in need only of minor polishing.

So, while no one today doubts that areas on the map of dinosaur genealogy are controversial and in need of further work, are these just refinements of a fundamentally sound cladistic structure, or should we dump the last decade of work and start over?

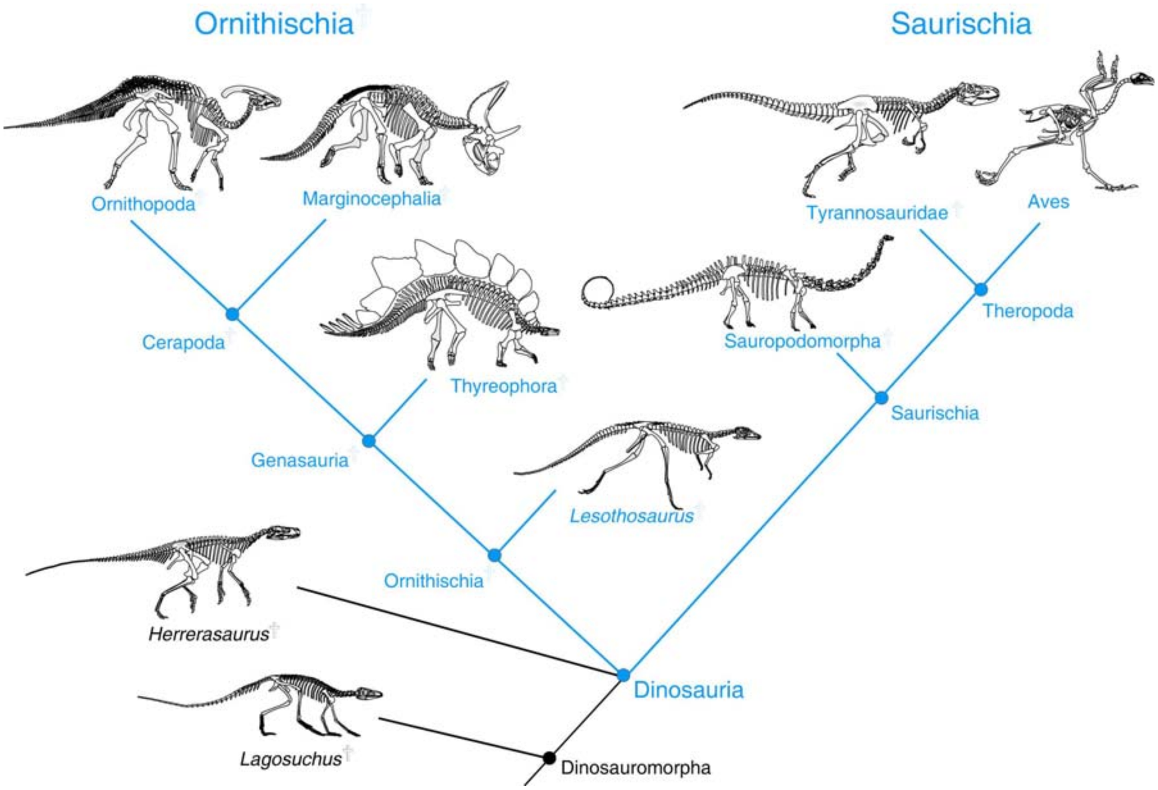

Figure 12.01 Phylogenetic map or cladogram showing the relationships of the major lineages of dinosaurs (in blue). Crosses indicate extinct lineages.

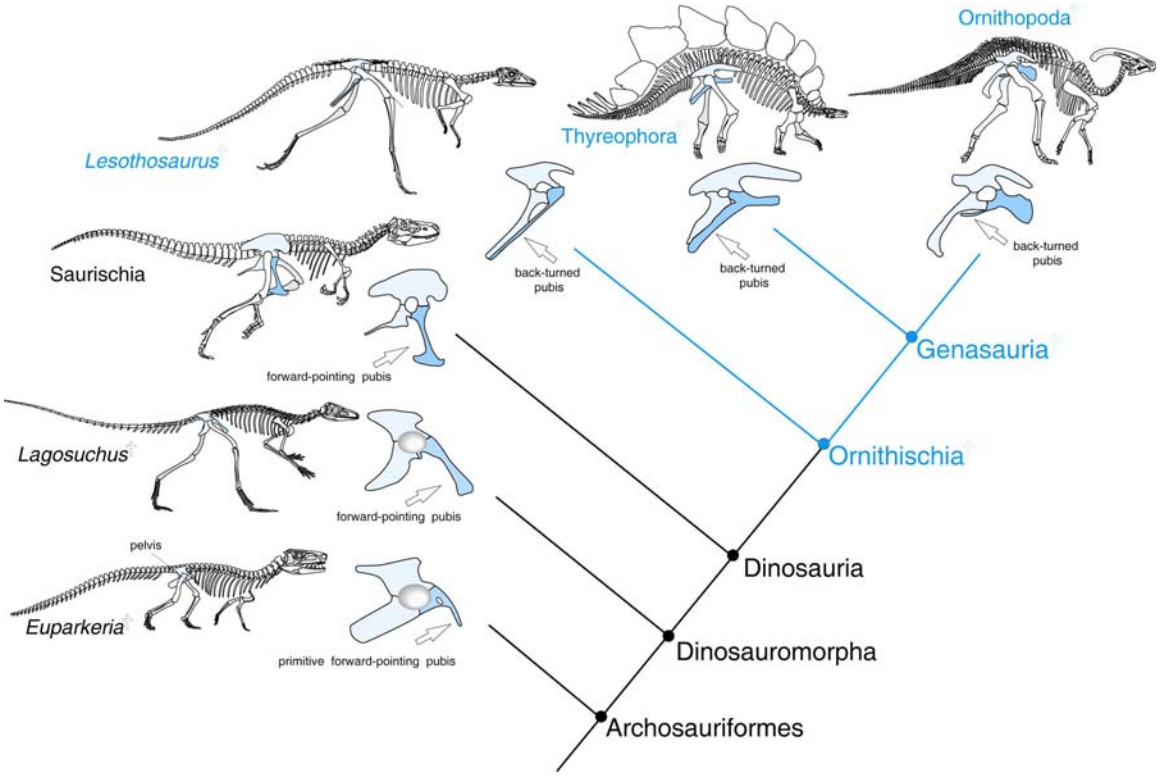

Figure 12.02 Ornithischian dinosaurs have a distinctive pelvis (light blue), in which the front bone, known as the pubis (dark blue) is turned backwards, making room for the long digestive tract that it takes to digest a diet of bulk vegetation. Crosses indicate extinct lineages.

Mapping Dinosaur History

By the end of the 19th century, there was general agreement that the dinosaurs known to Richard Owen all belonged to two grand sister lineages (fig. 12.01) known as Ornithischia, the bird-hipped dinosaurs, and Saurischia, the lizard-hipped dinosaurs[2]. As we will see, both names are more fanciful than accurately descriptive of the lineages they represent. Nevertheless, Gauthier's cladistic analyses and all subsequent analyses confirm this basic division of dinosaurs, and even modern critics of the bird-dinosaur hypothesis agree. Ornithischians and saurischians are both recognized as dinosaurs because they have a thumb that can grasp, along with the fully perforated acetabulum and sharply in-turned femoral head indicative of upright, parasagittal gait. All dinosaurs discovered subsequently are members of one or the other of these two distinctive sister lineages.

Despite the unanimity on these two major features of dinosaur history, there are some controversial points near the beginning of the dinosaur map. In particular, the position of *Herrerasaurus*, who we met in the last chapter, is a little uncertain. Recent analyses disagree on whether *Herrerasaurus* is the first cousin of Dinosauria, a basal member of Saurischia, or a member of one of the lineages within Saurischia. If the former position holds true, *Herrerasaurus* would be a member of the larger group Dinosauromorpha, but it would not be a proper dinosaur, because it did not share the common ancestor unique to ornithischians and saurischians. But the position of this one species has little bearing on the distinctiveness of Ornithischia and Saurischia, each of which has its own unique features. The question now is whether one of these two great dinosaurian sister lineages gave rise to birds.

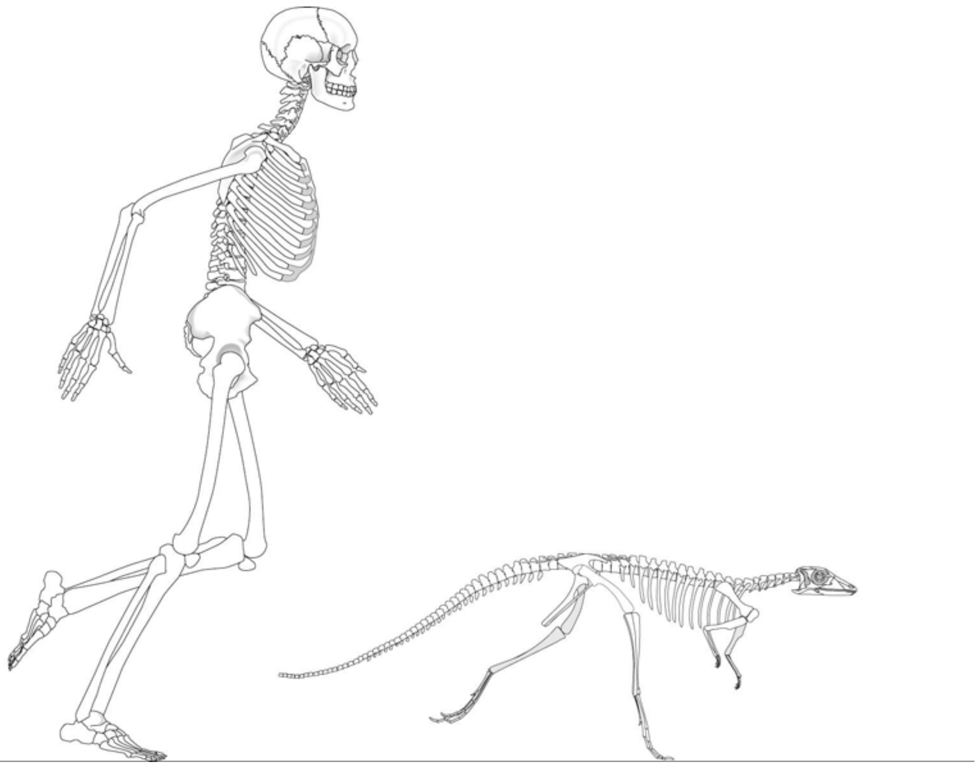

Figure 12.03 The oldest ornithischians were all relatively small. Shown here is the Early Jurassic *Lesothosaurus*, compared to a modern 6-foot tall human for scale.

With such a suggestive name, Ornithischia might seem the place to start in seraching for avian ancestry. The name ‘ornithischian’ refers to a bird-like ischium -- a bone of the pelvis. However, it is a different pelvic bone, the pubis, not the ischium, that is bird-like in being back-turned (12.02). Despite the misnomer, we can still ask whether the pubis is a mere point of resemblance or if it marks a longer trail to birds. The oldest ornithischians are from Late Triassic deposits in Argentina, and they are known from slightly younger deposits in North America and South Africa. Early ornithischians[3] were similar to other early dinosaurs in being small bipeds (fig. 12.03), but several unique features mark their lineage, which mostly reflect a shift in diet. Ornithischian teeth and jaws are designed for tearing and grinding plants, and the ribs and pelvis housed an enlarged digestive tract. A new bone, the *predentary*, forms the front of the ornithischian lower jaw (fig. 12.04). In all but the oldest ornithischians, the front-most teeth are gone and a horny beak rimmed the front of the mouth. In all but one of the very earliest ornithisichians, the teeth are set in from the margins of the mouth, where they were probably covered by fleshy cheeks that assisted chewing.

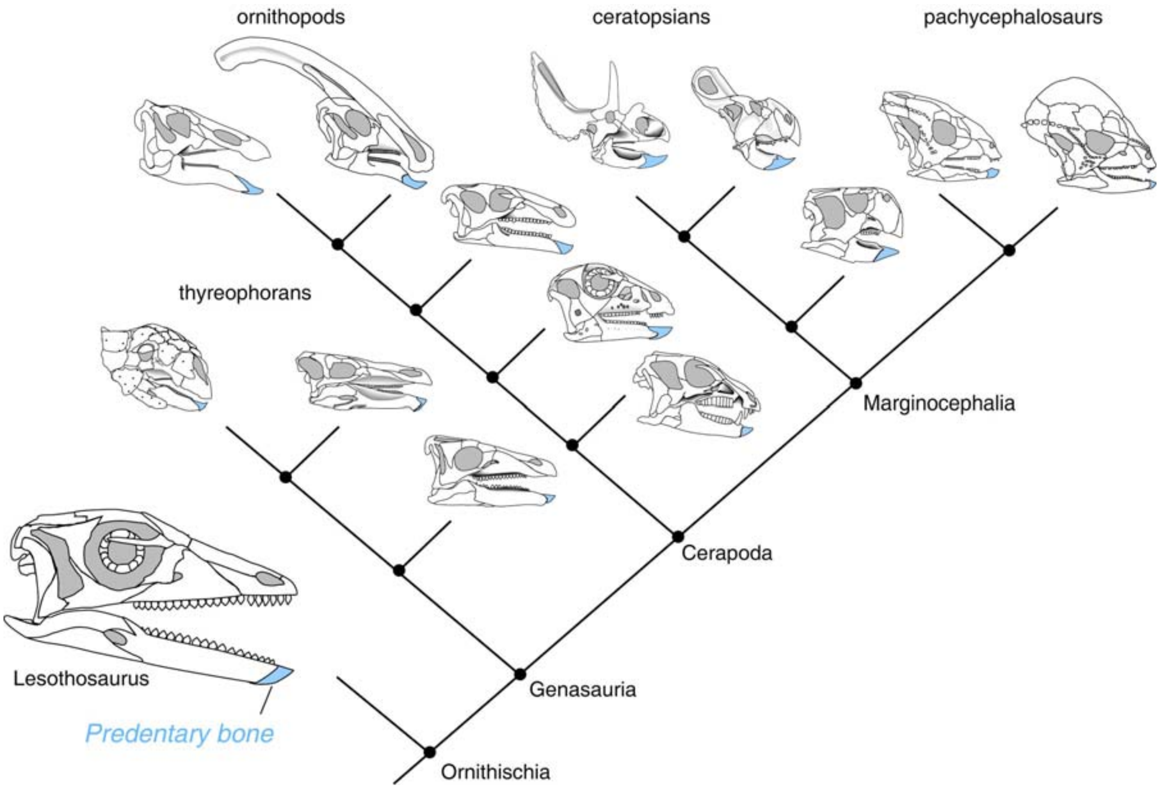

Figure 12.04 The predentary bone (in blue), a unique feature of ornithischians, contributed to their ability to crop and strip vegetation. The predentary bone is present in all known members of the lineage.

Abdominal expansion is indicated by the characteristic modifications of the pubis (fig. 12.01). In most other reptiles the pubis points down and forwards, but in ornithischians it is rotated backwards, making room for a longer intestinal track to digest the relatively insoluble cellulose of plant cells. One last modification is a network of *ossified tendons* along the backbone. Normally, tendons are strong, flexible, rope-like fibers that attach the fleshy body of a muscle to a bone. In ornithischians, bone formed within some of the tendons along the back, forming a mesh that permitted some up-and-down flexing and extension of the vertebral column, but it prevented any adverse rotation. Perhaps this increased rigidity of the vertebral column offered a sturdier framework from which to suspend their enlarged gut.

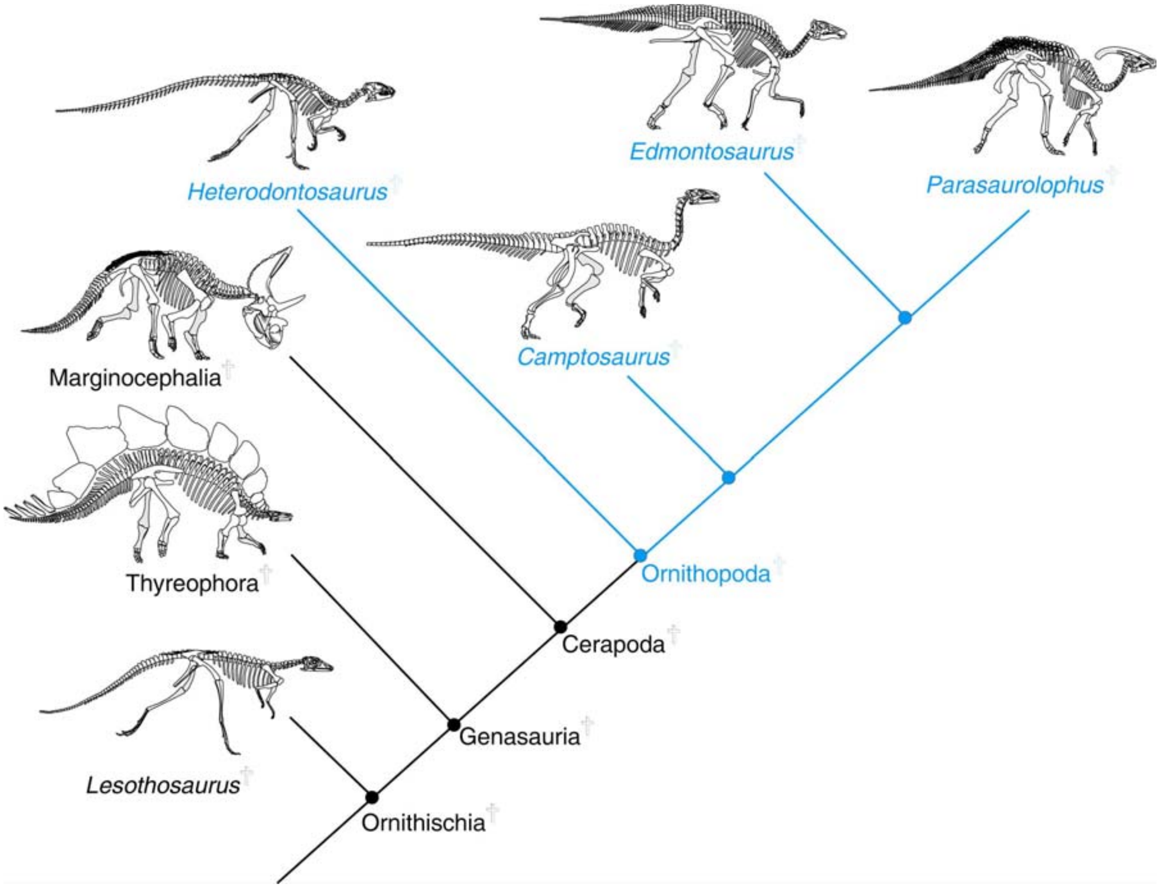

Figure 12.05 Phylogenetic map or cladogram showing the relationships among representative ornithopods (in blue). All lineages depicted on this map are extinct (indicated by crosses).

Ornithischia is a diverse lineage and within it are several different evolutionary paths. The ornithischian lineage with the longest fossil record is Ornithopoda (fig. 12.05). This name means bird-like foot, in reference to the three-toed ornithopod foot. The lineage was so christened by Yale’s preeminent dinosaur specialist of the 19th century, O. C. Marsh, at a time in which only a small number of dinosaur fossils were known. More recent discoveries indicate that virtually all early dinosauromorphs left 3-

toed tracks, so the namesake feature that caught Marsh's attention is more widely spread that he knew when he coined the name.

Ornithopod history[4] has been mapped in detail by David Weishampel (Johns Hopkins University), David Norman (University of Cambridge), John Horner (Montana State University), Paul Sereno (University of Chicago), and their colleagues. Ornithopods probably existed in greater numbers and are more abundantly fossilized than any other dinosaur. By their first appearance in the Early Jurassic, ornithopods had already dispersed around the world. Early members were small, about three to six feet in length. They were distinguished by unique dental modifications which, in some of the more derived members of the lineage, produced a great increase in the grinding capability of the teeth. This was accomplished by increasing the numbers of teeth and the rate at which they were replaced throughout life. Some later ornithopods had as many as 1000 teeth in the mouth. There was also an evolutionary increase in body size. Some of the Cretaceous forms reached nearly 40 feet in length, and adults weighed several tons. Richard Owen's *Iguanodon*, which lived during the Early Cretaceous, is one of the more derived, large-bodied ornithopods. The name for Dinosauria might have been very different had Owen first studied the comparatively tiny Early Jurassic ornithopods. Apart from the resemblances found in dinosaurs ancestrally plus the back-turned pubis, birds and ornithopods bear no special similarities. Recent mapping efforts have found only points of resemblance between the two, and the giant ornithopods only become more different from birds with time. Despite their enticing name, ornithopod dinosaurs are not the ancestors of birds, and available evidence indicates that the lineage went extinct in the terminal Cretaceous event.

The sister lineage of Ornithopoda is Marginocephalia (fig. 12.06), the 'margin-headed' ornithischians[5], who had weird skull modifications that make them highly distinctive. Various segments of their history have been mapped by Paul Sereno, Peter Dodson (University of Pennsylvania), Catherine Forster (Cornell University), Tom Lehman (Texas Tech University) and a host of associates. The two major lineages of marginocephalians are Ceratopsia and Pachycephalosauria. Some authors derive the latter

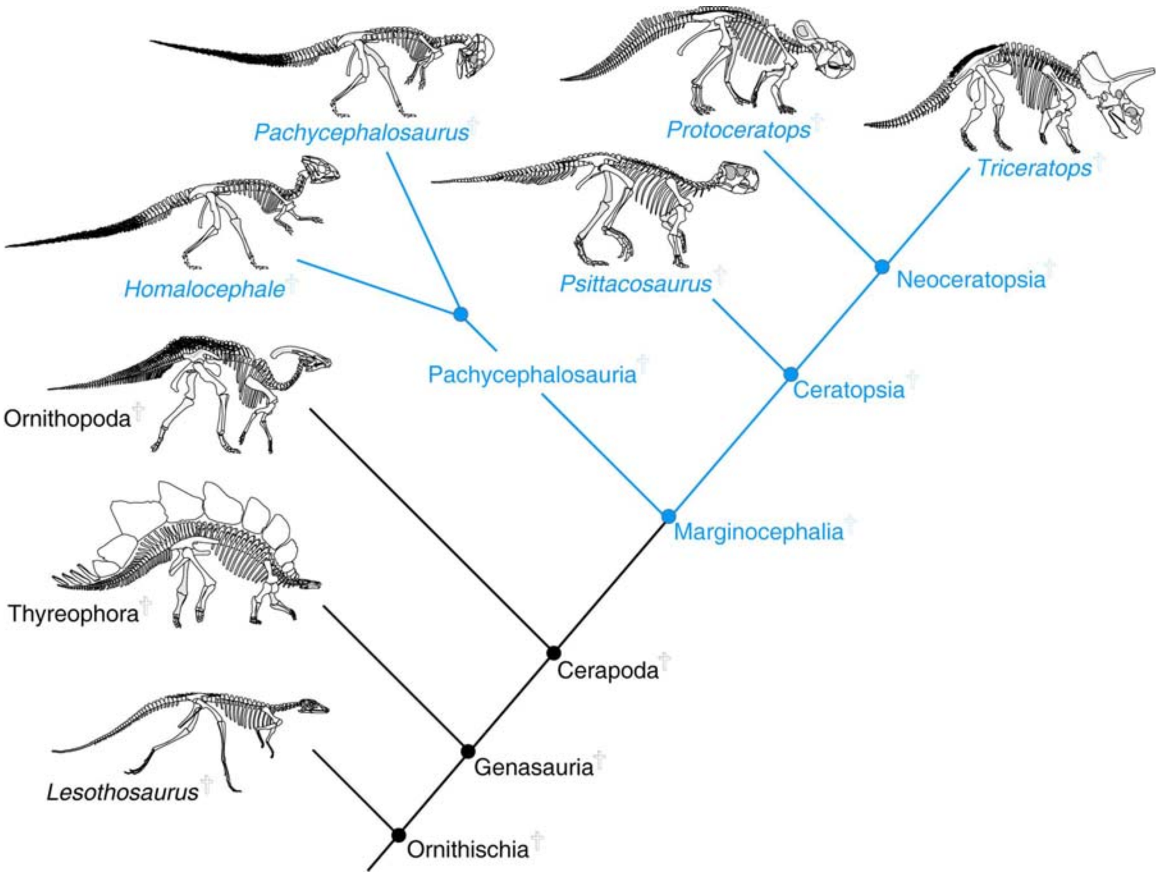

Figure 12.06 Phylogenetic map or cladogram showing the relationships among representative marginocephalians (in blue). All lineages depicted on this map are extinct (indicated by crosses).

directly from ornithopods, but this point of disagreement doesn't affect our search for the ancestry of birds. Pachycephalosaurs, the 'thick-headed' ornithischians evolved high domes of thickened bones over the top of the brain. The name is not particualry descriptive of early flat-headed forms, but it is apt for later members of the lineage. So extreme is their head thickening that, when pachycephalosaurs were first discovered, paleontologists thought them to be pathological. Others considered them to be dinosaur 'knee-caps'. As more complete specimens were recovered, it was clear that these bony domes were parts of the skull, and mechanical analyses suggest that pachycephalosaurs used their heads as battering rams. Comparable head-butting and flank-butting behavior occurs in modern musk ox, mountain sheep, and goats, usually in battles with members of their own species over territory and mates.

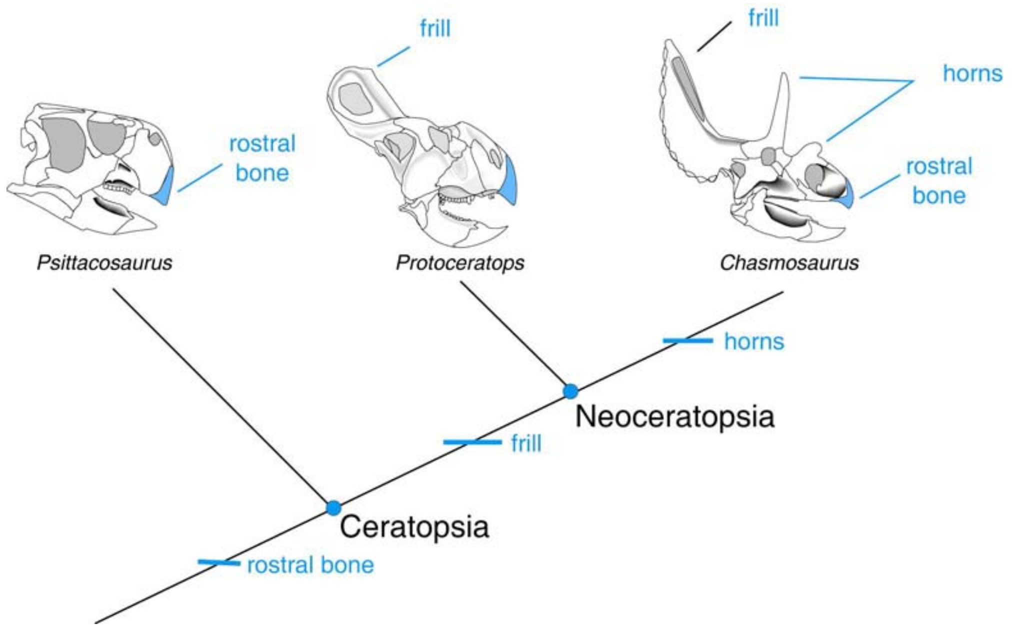

Figure 12.07 The ceratopsian lineage is distinctive in having a rostral bone that created a sharp beak. Later in ceratopsian history the frill arose, and still later horns appeared. All three of these animals is a ceratopsian, but the name is accurately descriptive of only one.

The other marginocephalian lineage is Ceratopsia--the horned ornithischians[6]. When first discovered in the 19th century, the only known skulls possessed horns. Since then, there have been numerous ceratopsian species discovered that lack horns and are primitive in other respects, so this is another name that is misleading. One distinctive feature of the lineage is the rostral bone (fig. 12.07), a unique structure that forms the upper part of the beak above the predentary bone. Even the primitive horn-less ceratopsians have a rostral bone, indicating that the acquisition of a powerful beak preceded the evolution of frills and horns. Early ceratopsians were relatively small, like the early ornithopods and pachycephalosaurs. When running at high speeds they were bipedal, but at lower speeds they probably moved on all fours. Later ceratopsians were rhino-sized animals that reverted habitually to quadrupedal locomotion. With increased size, the shelf at the back of the head also expanded into a fan-shaped sheet of bone protruding up and backwards from the head, reaching more than four feet long in some species. Variable patterns of horns and projections from the cheek region appeared, and the edges of the frill became elaborately ornamented in some species as well. Marginocephalian history led to a terrific diversity of form, but most of this was in a different direction from the evolutionary pathway taken by birds. Marginocephalians survived until the very end of the Cretaceous, but all available evidence indicates that they were extinct when the Tertiary dawned.

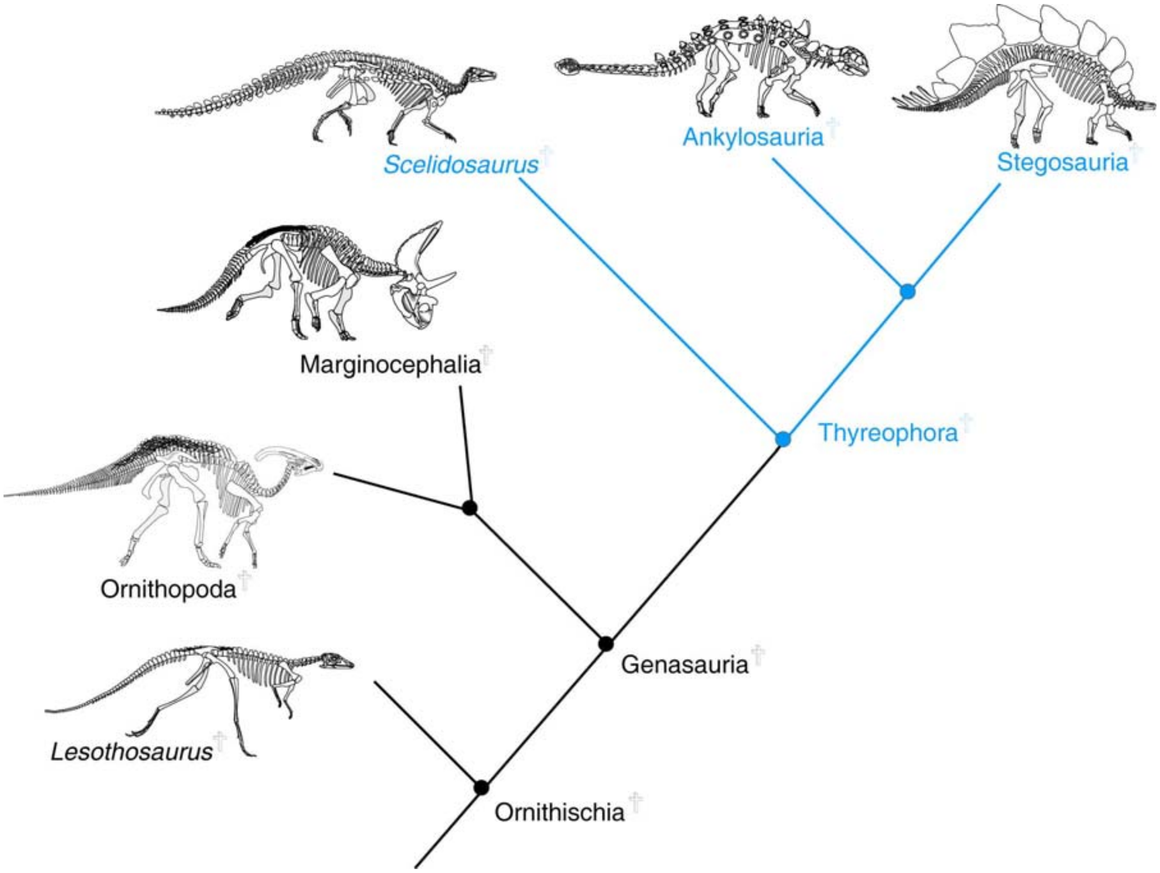

Figure 12.08 Phylogenetic map or cladogram showing the relationships among representative thyreophorans (in blue). All lineages depicted on this map are extinct (indicated by crosses).

The third major lineage of ornithischian dinosaurs is Thyreophora (fig. 12.08), whose name means ‘shield-bearers’ in reference to their body armor (fig. 12.09). There are several thyreophoran lineages[7], the most distinctive of which are the ankylosaurs and stegosaurs, whose histories have been studied by Peter Galton (University of Bridgeport) and Walter Coombs (Western new England College), Teresa Maryanska (Polish Academy of Sciences), and others. The thyreophoran fossil record extends back to the Early Jurassic, where its early members were small, like other early dinosaurs. They possessed an armor shield of bony scutes which floated in the skin along the back and sides of the body. Descendant lineages like the ankylosaurs became fully armored and were completely covered with a patchwork of bony scutes. Ankylosaurs were most common in the Late Jurassic and Early Cretaceous, and they were squat, lumbering quadrupeds that approached two tons in weight. Stegosaurs, the plated dinosaurs, have a distinctive paired row of plate-like scutes along either side of the backbone, from the head to the tip of the tail. In some cases, an additional row or two of smaller scutes lies on either side of these, and tail scutes may form spikes of varying lengths. Despite the diversity, nowhere in the thyreophoran lineage is there evidence of a close relationship to birds. The last thyreophorans died out in the terminal Cretaceous event along with the other surviving members of the ornithischian lineage.

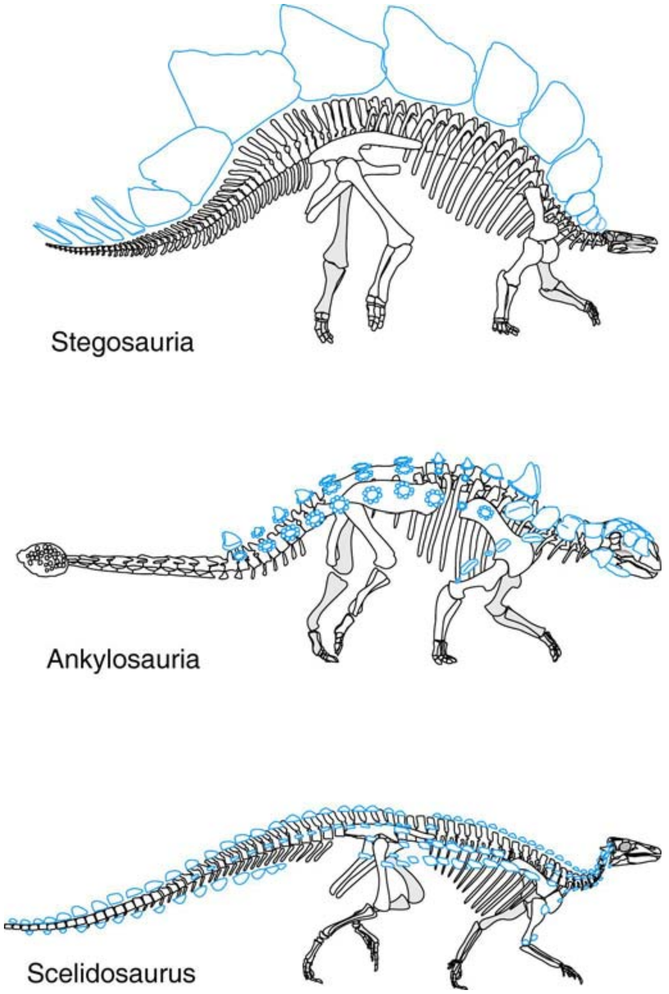

Figure 12.09 All thyreophorans had body armor in the form of scutes (blue) that floated in the skin. Each descendant lineage had its own distinctive scute pattern.

So, although ornithischians inherited from the ancestral dinosaur a number of unique similarities with birds, beyond these we find only points of resemblance, like the back-turned pubis, that might link them to birds. Moreover, there is no evidence to suggest that birds ever possessed a predentary bone or ossified tendons, nor do any known features place birds within the hierarchies of Ornithopoda, Thyreophora, or Marginocephalia. If birds descended from the ancestral dinosaur, it was not via the ornithischian branch of the family tree. Ornithischia became extinct in the terminal Cretaceous event.

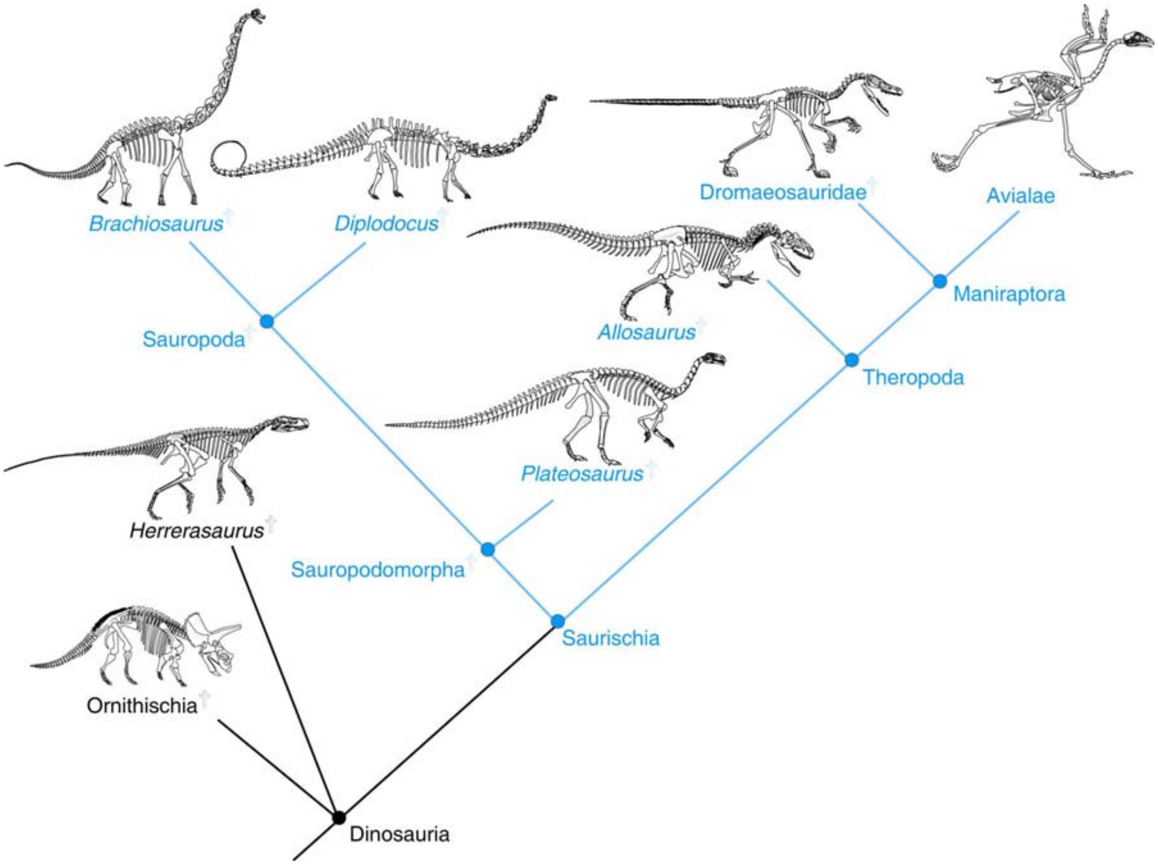

Figure 12.10 Phylogenetic map or cladogram showing the relationships among representative saurischian dinosaurs (in blue). Extinct lineages are indicated by crosses.

Saurischians

If Thomas Huxley was right that the evolutionary road to birds runs through dinosaurs, then it must lead into saurischian (fig. 12.10), rather than ornithischian dinosaurs. This became one of the central questions that Jacques Gauthier asked in his cladistic dinosaur- mapping expedition[8]. Does Saurischia, as commonly constituted by 20th century paleontologists, include all descendants of the ancestral saurischian? In other words, are birds the descendants of saurischian dinosaurs and if so, which saurischians are the closest relatives of birds?

One distinctive features shared by all members of the saurischian lineage is a very long neck (fig. 12.11), in which each vertebrae is elongated, and in some cases additional vertebrate are added to the neck from the rib cage. The ribs on the neck vertebrae are also lengthened, each extending backwards along several vertebrae. This combination of long vertebrae and long overlapping cervical ribs enabled the neck to move smoothly and function as an integrated unit. Saurischians also have a distinctive hand. The second or index finger is the longest, instead of the third finger as was the case in dinosaurs ancestrally (fig. 12.12), and the thumb was equipped with a large, recurved claw. While the long neck is obviously bird-like, a powerful grasping hand seems unexpected in the ancestor of a delicate bird. But the hand in the early saurischians resembles birds in its axis of symmetry -- the second finger is the longest, with shorter digits arrayed on either side. In most other reptiles the axis of hand symmetry runs through either the third or fourth finger.

The earliest saurischian fossils come from Late Triassic deposits of Africa, South America, Europe, and North America. The largest Triassic saurischians were about fifteen feet in length and weighed perhaps 200 pounds, but most were much smaller. Like other early dinosaurs, all Triassic saurischians were bipedal. Two different saurischian lineages, Sauropodomorpha and Theropoda, have been mapped and virtually all saurischians belong to one or the other. These too have unfortunate names if we look at their strict translations. The sauropodomorphs would have ‘lizard-like’ feet and theropods would have ‘mammal-like’ feet, if their names were accurately descriptive, but neither name is.

Over most of their history, sauropodomorphs[9] were herbivorous. Their teeth were blunt and spatula-shaped, few in number, and unable to chew vegetation. Instead, they cropped and stripped foliage from stems, which was swallowed for processing in a muscular gizzard whose presence is indicated by clusters of large smooth stones found in the ribcages of well-preserved specimens. An overwhelming theme in sauropodomorph history is size. During the Jurassic, they became the largest land animals ever, reverting to quadrupedality, and evolving unbelievably long necks and tails in the process. One of the most distinctive features of all sauropodomorphs is that they have tiny heads in comparison to other dinosaurs. In later, more derived members of the group, the head seems ridiculously small compared to the immense body. Giants like *Supersaurus* may have reached 130 feet (40 meters) in length. A single neck vertebra of *Ultrasaurus* is over three feet long[10], and there were perhaps as many as 17 of individual vertebrae in the neck, though not all vertebrae were equally long. The limbs were columnar and elephantine in proportion, to support a bulk estimated in the very largest species to approach 100 tons. This is nearly 10 times the weight of an adult male African elephant. Despite the name of this lineage, in most of its members the bones of the toes and feet were reduced to stubs, and it must have seemed that their bodies were set upon four great posts instead of arms and legs. What could be less birdlike? Several species survived in the southern-most parts of North America and in South America until the end of the Cretaceous, but none crossed the K-T boundary alive.

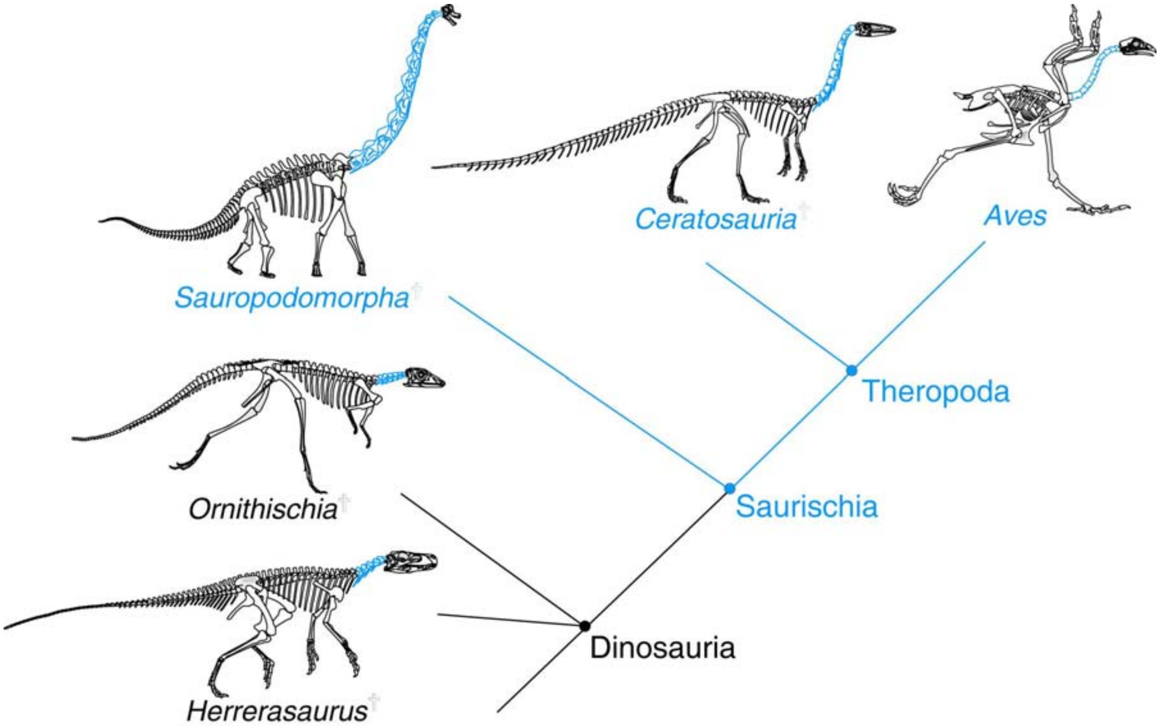

Figure 12.11 Saurischians are distinguished by a long neck, compared to other members of Dinosauria. Extinct lineages are indicated by crosses.

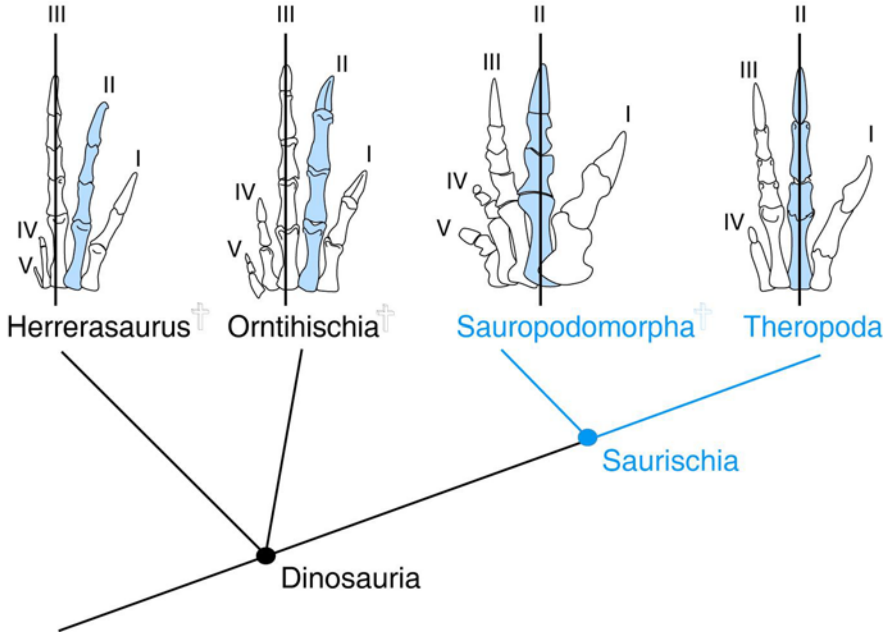

Figure 12.12 Compared to other dinosaurs, saurischians have a distinctive hand, in which digit II is longest. The longest finger defines the axis of symmetry of the hand, on either side of which are shorter digits. Extinct lineages are indicated by crosses.

Theropods

This leaves us with one last dinosaur lineage - known as Theropoda (fig. 12.13). Most of the unique features of basal theropods are associated with a predatory life-style and they further enhanced an inherited body plan already well equipped for this task. Added to the ancestral armament of sharp teeth and claws, theropods have a *kinetic* or flexible lower jaw, in which a mobile joint between the bones of the lower jaw enabled it to bend downward and outward. Some paleontologists argue that this was for swallowing prey items larger than their own heads, while others contend that it was a buffer of flexibility in dealing with struggling prey, preventing the slender jaw bones from snapping. Also distinctive is the attachment of the head to the neck, in which a large, ball-shaped *occipital condyle* (fig. 12.14) at the back of the skull fits into a deep socket formed by the first two neck vertebrae. This bony joint supported wide motion of the head, with a stable, strong connection to the neck. Placing the eyes, ears, and nose in a skull that can be rapidly directed from right to left, up or down, amplifies the ability to extract precise spatial information from light, sound, and smell. The long, mobile neck inherited from saurischian ancestors amplified head mobility even further.

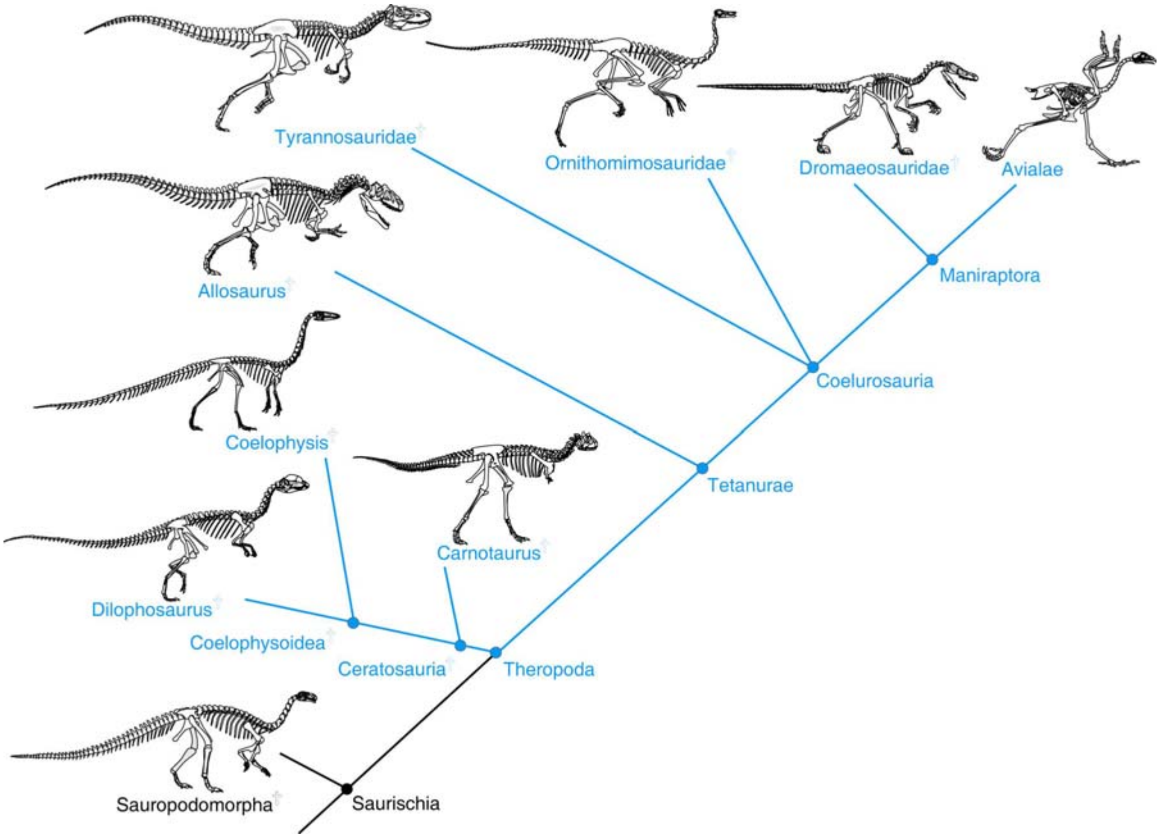

Figure 12.13 Phylogenetic map or cladogram showing the relationships among representative theropod dinosaurs (in blue). Extinct lineages are indicated by crosses.

Early theropods[11] also have hands designed for snagging and raking flesh. The second and third fingers were elongated, and the mobile thumb worked with them in concert. Each of the three grasping fingers was tipped by a strongly curved raptorial claw equipped at its base with a large tubercle that increased the leverage of the muscles in the forearm as they closed the fingers around an object. The fourth finger was reduced and fifth finger was lost altogether in all adult theropods but *Eoraptor*[12]. Throughout their history, theropods have been obligate bipeds, with a pelvis and hindlimb modified to withstand the entire burden of swift, forceful running. Although the ancestral dinosaurs was probably an habitual biped, theropods carry this trend to a far greater degree than other dinosaurs. Additional vertebrae are incorporated into the sacrum for a stout attachment between the backbone and pelvis, and the pelvis itself was enlarged to support greater thigh muscles. This also happens in some of the giant sauropodomorphs and ornithischians, but even small theropods have a stronger pelvis. In the foot, the first or 'big' toe became reduced and separated from the bones forming the ankle joint. On the outside of the foot, the fifth digit is reduced to a vestigial, non-functional splint of bone.

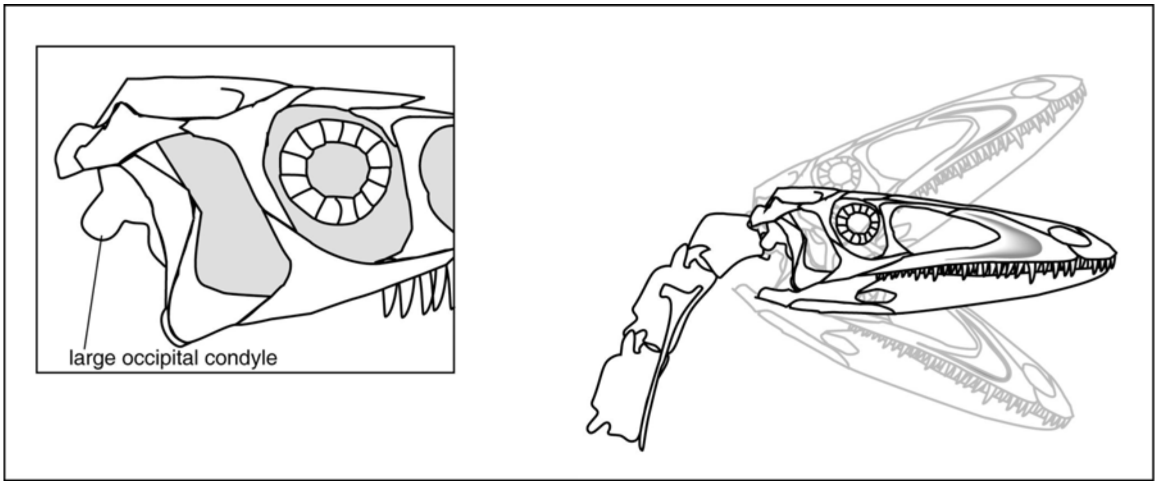

Figure 12.14 Theropods are distinctive in having a joint between the head and neck that gives the head great mobility.

Many of these characters are bird-like. For example, all birds have a highly mobile joint between the head and a long neck, and many have jaws with kinetic joints. Even small birds have a massive pelvis and sacrum. Unlike early theropods, in the foot of adult birds, the fifth toe is entirely absent. However, all five digits are present in bird embryos, and all five lie in contact with the developing ankle joint. As development proceeds, the first digit breaks away from the ankle and slides down the side of the foot, before twisting around the back. As this happens, digit V is gradually lost and adult birds wind up with only four toes. The development or *ontogeny* of bird embryos recapitulates an ancient evolutionary pattern. As we will describe in a later chapter, nowhere else among reptiles do these two patterns of ontogeny and phylogeny in the bones of the foot coincide in precisely this way.

A last distinctive theropod character is the one discovered by John Hunter in his brutal experiment on the arm of a crow. Theropod bones are thin-walled, tubular, hollow structures. Like the frame of a bicycle, the tubular construction provides both lightness and a high bending strength to withstand the high levels of force generated in fast locomotion. Hunter discovered that the avian skeleton is hollow and Owen cited the hollow skeleton of *Archaeopteryx* as evidence that it is a bird[13]. Paleontologists commonly claim that the hollow skeleton evolved as an adaptation to lighten the skeleton for flight. However, all theropods, even *Tyrannosaurus rex,* has hollow bones, but no believes that it could fly. The hollow skeleton obviously serves the function of flight, but it would be nearly 100 million years before descendant theropods recruited the tubular skeleton for this new mode of locomotion.

Figure 12.15 The coelophysis quarry at ghost Ranch, new Mexico, when it was re-opened in 1981. The large white plaster-jacketed block at the left end of the quarry contained dozens of skeletons (photo by T. Rowe)

Critics of a bird-theropod connection correctly point out that pterosaurs and some small mammals also have hollow skeletons, and that a tubular skeleton must have evolved convergently several times[14]. They argue that convergent features offer no insight into the relationship between birds and theropods. As we have already seen, this similarity between birds, pterosaurs and mammals constitutes a mere point of resemblance, rather than a mappable hierarchy that includes birds. However, in the case of theropods, there are many additional special similarities to birds. By following the trail of anatomical clues, we can test whether hollow bones offer evidence of common ancestry for birds and theropods, as we trace the map of theropod genealogy to its natural conclusion.

The fossil record of theropods is not very good, probably because of their hollow skeletons rarely withstand the dynamics of sedimentation and burial. Most known theropod skeletons are incompletely preserved, and gaps spanning tens of millions of years still punctuate our knowledge of theropod history. This is the same general problem that faced Darwin and Huxley, although in their time the gaps were more on the scale of 100 million year intervals. So, while many problems in our map of theropod history remain, today's resolution is far better than a century ago.

By the Late Triassic, two theropod lineages had arisen, namely Ceratosauria and Tetanurae. Ceratosaurs, which were first mapped and named by Gauthier[15], are the best known Triassic and Early Jurassic theropods, having a global distribution at their earliest appearance in the fossil record[16]. Possibly the richest dinosaur locality ever discovered is the *Coelophysis* bone bed at Ghost Ranch, New Mexico (fig. 12.15). There, dozens, perhaps even hundreds, of *Coelophysis* individuals, including juveniles and adults, were buried together *en mass* in a Triassic grave[17]. The Late Jurassic *Ceratosaurus nasicornis* is the last known member of the lineage in North America, but more recent discoveries in South America, Madagascar in India may indicate that Ceratosauria had a Gondwanan distribution in the Cretaceous.

Currently, there are only about a dozen or so species of ceratosaurs, but they document a 170-million-year history, from the Triassic into the Late Cretaceous, so our record of this lineage is highly incomplete. In several skeletal features, a few of the smaller ceratosaurs show additional similarities to birds, including fusions between bones in the feet, and further strengthening of the pelvis and sacrum. But there are other theropods that share even greater degrees of resemblance to birds, and the available evidence indicates that ceratosaurs disappeared from the northern hemisphere before the Cretaceous began, and from the southern hemishpere at its end.

Stiff- tailed Tetanurines

The trail of clues to avian ancestry leads into the tetanurine, or stiff-tailed theropods, that make up the sister lineage to ceratosaurs[18]. There is much yet to be discovered about their early history, which probably extended into the Triassic, judging from the antiquity of their sister lineage. But the oldest informative tetanurine fossils currently known are from the Late Jurassic, almost 100 million years after the lineage most likely originated. Tetanurines are more bird-like than other theropods in virtually all parts of their skeleton. Breathtaking new specimens from China may even offer evidence linking the origin of feathers, or at least ‘proto-feathers’, to an early evolutionary stage in tetanurine history.

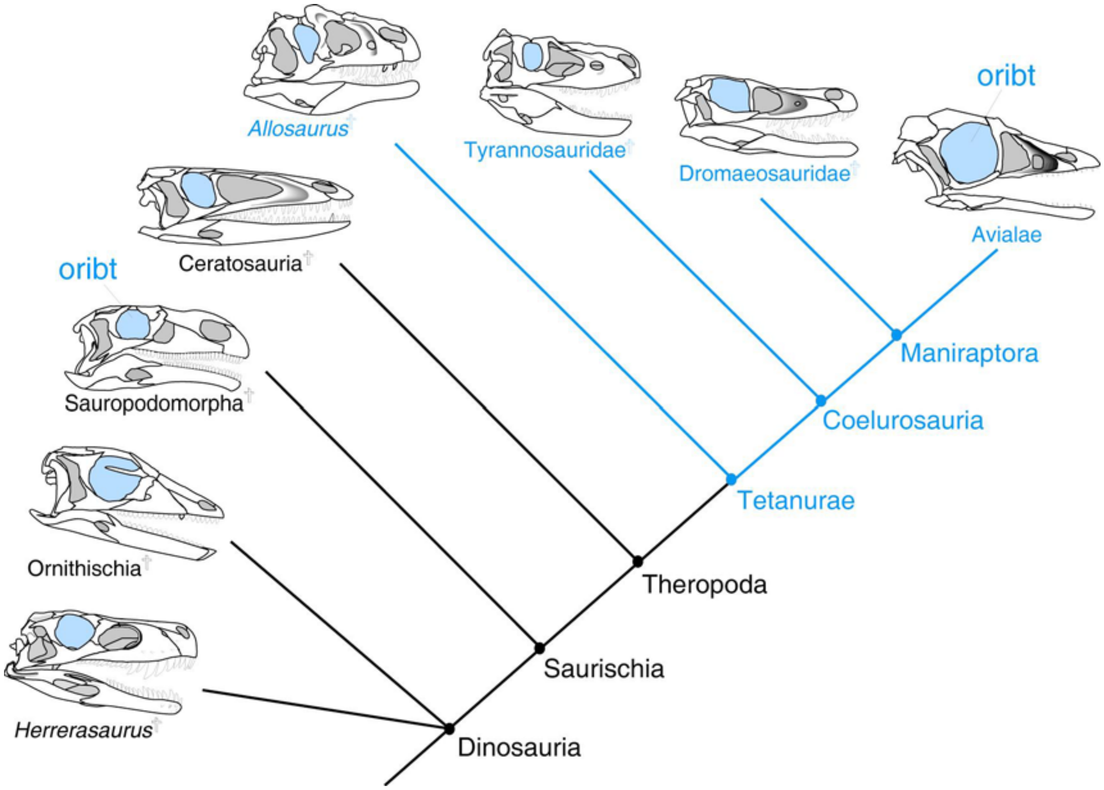

Figure 12.16 In tetanurine dinosaurs, the teeth lie entirely in front of the orbit (in blue), which held the eyeball. This began a trend in which the tooth row was successively shortened, from back to front, as the teeth were reduced in size.

The tetanurine snout was more delicately built than other theropods. The teeth, if present at all, lie entirely in front of the eye (12.16). Over much of their history, there was a gradual loss from the back of the jaws to the front, and several lineages evidently lost their teeth independently. The tetanurine forelimb took on a striking of resemblance to birds. The wishbone or *furcula* appeared early in the history of this lineage, along with more powerful arms and hands (12.17). The wishbone occurs today only in birds, prompting some biologists to argue that it is an adaptation for flight. But many non-flying Mesozoic tetanurine dinosaurs have a wishbone, so it would appear that the furcula was only secondarily co-opted into taking a role in flight. The wishbone extends between the two shoulder joints and the breastbone or *sternum*, and when the wishbone appeared, the sternum became a rigid, bony structure to anchor large pectoral muscles. The arms and hands were also longer, the hand now consisting of only three adult fingers. Together, these changes enormously enhanced the reach and power of the forelimb.

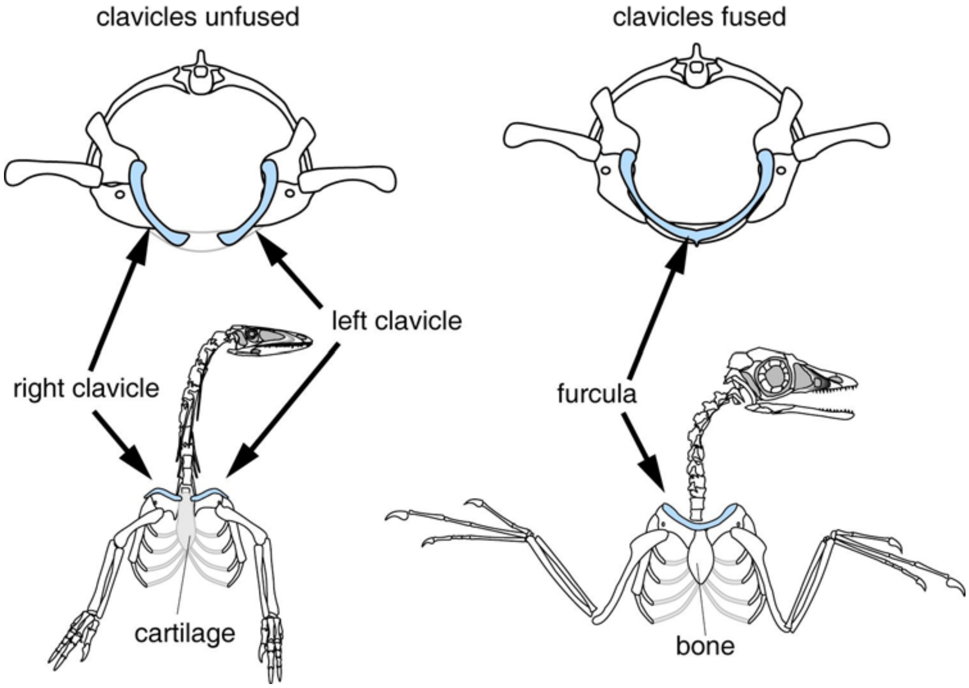

Figure 12.17 The collar bones or clavicles became fused together in tetanurines, forming the wishbone, or furcula. Although often tied to flight, the furcula is present in dinosaurs like *Allosaurus*, which no one has claimed could fly.

More subtle resemblances to birds are found in this lineage as well. For example, in the ankle, a tall sheet of bone laps up onto the front of the *tibia* or shin bone (12.18). This *ascending process* is an easy feature to spot on the drumstick of a young bird, and you can generally find it on the legs of chickens or turkeys that you eat, right about where you hold the drumstick when taking a bite out of it. In more mature birds, the ascending process usually becomes fused indistinguishably to the tibia, and this may function to solidify the bones above the ankle joint. Only birds and extinct tetanurine dinosaurs possess this ascending process, whatever its function.

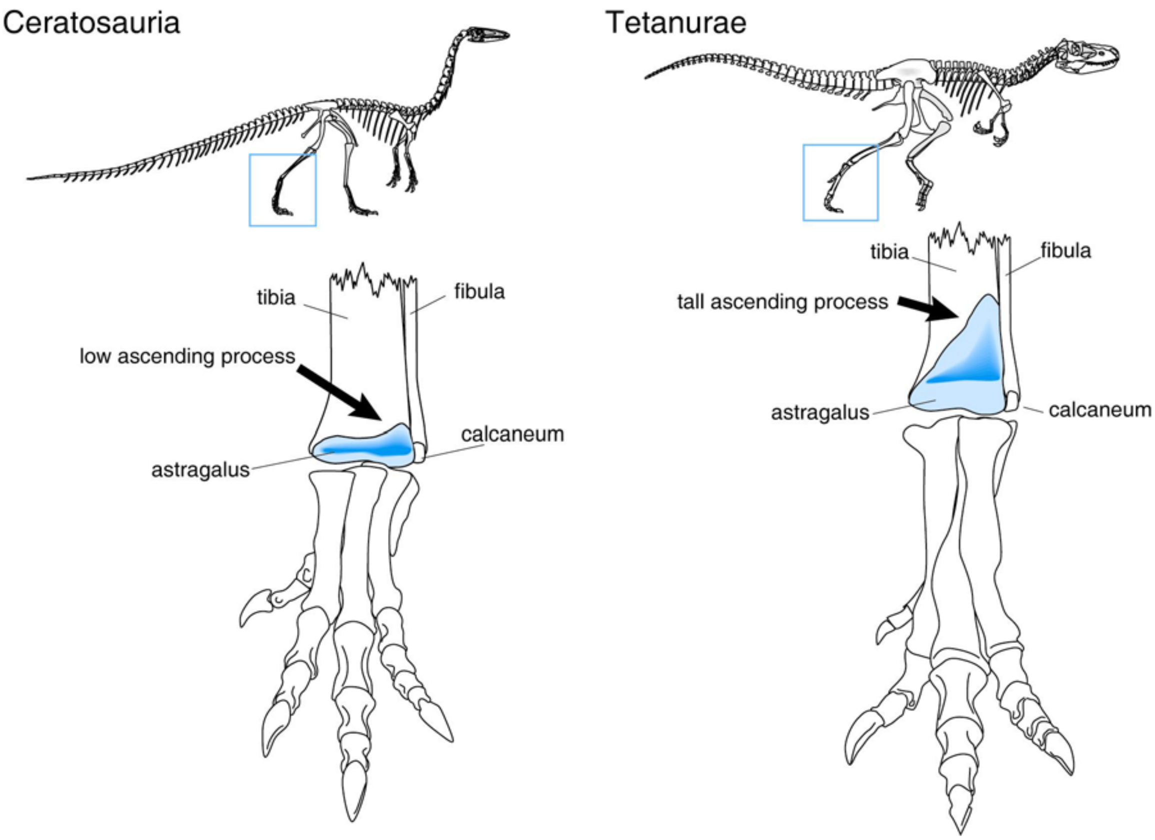

Figure 12.18 Tetanurine dinosaurs are distinctive in having a sheet of bone extending from the ankle joint upwards over the shin bone. This sheet is known as the ascending process, and it is still visible in the drumstick of young birds as a sheet of cartilage.

Lastly, the entire rear half of the tetanurine tail has become stiffened, in a highly distinctive fashion that earned the line its name. Tails are not often completely preserved in Mesozoic theropods. But when they are, the rear is stiffened, forming a ramrod-straight structure, with a mobile base. Even in post mortem rigor mortis, where the neck becomes arched backwards by the stiffening muscles, the end of the tail is straight. The death postures of the exquisite Solnhofen limestone specimens of *Compsognathus* and *Archaeopteryx* show that the tail was rigid. The stiff tetanurine tail probably served to enhance dynamic stabilization during fast locomotion.

Owen's *Megalosaurus* and Huxley's *Compsognathus* are among the basal members of Tetanurae, and for many years not a whole lot more was known of the early history of the line. But spectacular recent discoveries are rapidly filling out our knowledge of this history and they indicate an unsuspected diversification of tetanurines in the Jurassic and Cretaceous. From 1986 - 1990, Philip Curry (Tyrell Museum, Drumheller) directed a joint Sino-Canadian expedition into the People's Republic of China whose specific focus was the dinosaur faunas of central Asia. These were extremely successful expeditions and they recovered several new theropods from Jurassic and Cretaceous rocks. Among these were *Monolophosaurus*, a large crested theropod from the Middle Jurassic of Xinjiang, China[19], and *Sinraptor*[20], which are both probably allied to *Allosaurus* or to Owen's *Megalosaurus*.

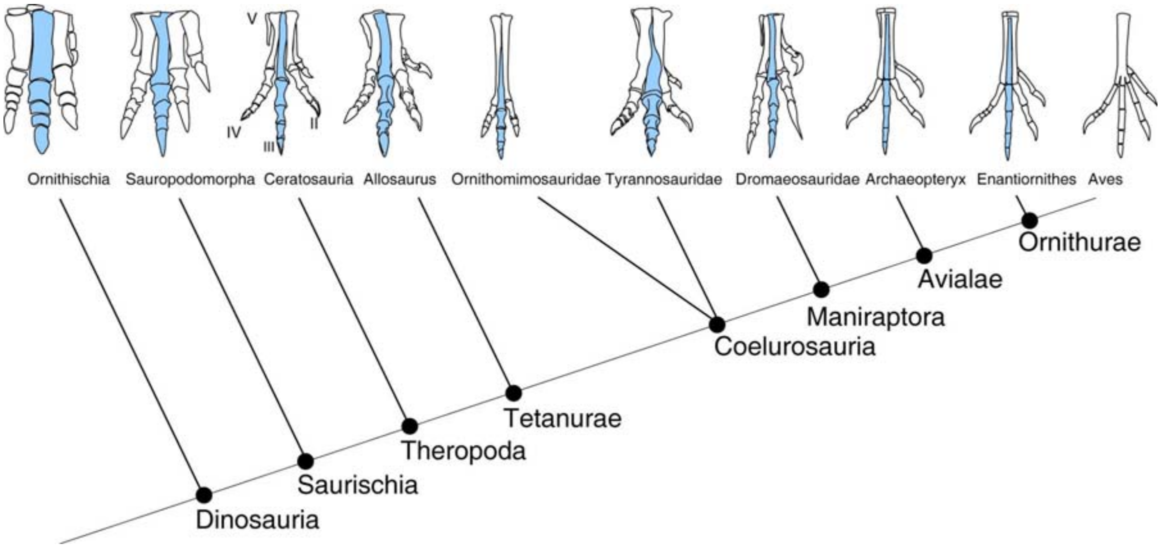

Figure 12.19 In coelurosaurian theropods, the middle bone of the foot, metatarsal III (blue), is pinched between the others, as the foot bones were more tightly packed together to make a stronger foot.

In 1995, Rudolfo Coria and Leonardo Saigado announced the discovery of a gigantic theropod exceeding even the size of *Tyrannosaurus rex*, exceeding 40 feet in length and approaching 8 tons. *Giganotosaurus*[21] was found in Late Cretaceous sediments, but its skeletal structure indicates that it was part of a lineage that had diverged from the others very early in tetanurine history. In 1996, Paul Sereno (University of Chicago) and a group of his associates announced the discovery of excellent new specimens of *Afrovenator* and *Charcharodontosaurus*[22]. *Charcharodontosaurus* also rivaled *Tyrannosaurus* in size. This third giant thropod was mapped along with *Allosaurus*, Curry's *Sinraptor*, and *Giganotosaurus*, into a lineage christened Allosauroidea. These are exciting discoveries of an unsuspected diversity of

Mesozoic theropods, but everyone agrees that the new discoveries represent an extinct side branches of tetanurines, not the ancestors of birds.

A breaking discovery at the time of writing, this one from Early Cretaceous rocks in the Liaonang province of northeastern China, may provide evidence of the first feathers in what is unequivocally a non-flying, basal tetanurine dinosaur. Like the Solnhofen deposits, the beds that yielded this specimen have turned up a bonanza of fossils with some soft tissues preserved. One specimen being displayed in the media has a fringe of feather-like structures along its back bone. Could these be protofeathers? The bird-dinosaur hypothesis predicts that structures intermediate between scales and feathers might be found in a non-flying theropod. As with the discovery of *Archaeopteryx*, the pace of publicity has outstripped the pace of scientific evaluation and publication.

Among tetanurines, we can follow the trail of anatomical clues into Coelurosauria[23], a lineage distinguished by some rather subtle characteristics. For example, in the foot, the middle bone becomes pinched, as all three of the metatarsal bones are more tightly packed to produce a stronger foot (12.19). Descendants of the ancestral coelurosaur form a cluster of evolutionary paths that lead to tyrannosaurids, ornithomimosaurs, oviraptorids, maniraptorans, therizinosauroids, and several others. Here again the exact relationships are a little unclear, largely because we have not had time to digest and map abundant new information. But there has been time for researchers to appreciate that each line has features that distinguish them from other tetanurines like *Allosaurus*.

The first lineage to consider is the great Tyrannosauridae -- *Tyrannosaurus rex* and its closest relatives -- which probably also approached 8 tons. Tyrannosaurids are paradoxical in their behavior, as well as in their exact placement on the map of theropod relationships. Although they evolved to huge size, their forelimbs became dwarfed to the point that we can only speculate as to their function. Because tyrannosaurids have long, slender, bird-like feet, along with other resemblances in the pelvis and neck, they may be closer to birds than any of the lineages describes so far. This is a case where gaps in the fossil record make the precise relationships of these huge modified tetanurines uncertain. But this point of uncertainty is unimportant from the standpoint of bird origins. No one doubts that the tyrannosaurid lineage died out at the end of the Cretaceous.

The modern ostrich came to mind when O. C. Marsh described the first ornithomimosaur - the bird-mimic saurian. These tetanurine theropods were lightly built, with long cursorial hindlimbs and very long arms with slender hands. Most distinctive is the loss of teeth, and the mouth is instead bordered by a bird-like beak. However, the oldest and most primitive ornithomimosaur, *Harpymimus*[24], retained some teeth, documenting a transitional stage in this evolutionary loss that was independent of that in birds. The ornithomimosaur brain is very large and bird-like. In fact, it very nearly reaches the relative size of the brain in modern flightless birds, such as the ostrich and emu. The eyes of ornithomimosaurs were also huge, suggesting a further improvement in visual acuity. Primitive members of the lineage were medium-sized theropods, about 10 feet in length, but some later species range up to 20 feet long and were 6 feet tall at the hip. The largest is *Deinocheirus mirificus*, known only from its arms, but these are seven feet in length! Ornithomimosaurs are indeed very birdlike, but other theropods show even more unique similarities, and current evidences indicates that the lineage died out at the end of the Cretaceous.

The oviraptor lineage[25] would surely win the contest for the dinosaur with the weirdest head. A dozen and a half species are known from the Late Cretaceous of the Asia. They are small, sleek cursorial bipeds, that ranged up to perhaps 15 feet in length. They were also toothless, like ornithomimosaurs, but their shortened jaws and beak were much more powerful, similar to the beaks of modern parrots. The skull is shortened and very deep. Bizarre crests and pneumatized outgrowths of the head are highly distinctive of the lineage. Owing to their highly unusual skulls and jaws, we can only speculate upon their exact diet. None has been preserved with gastroliths, and it is hard to picture them digesting foliage. But if oviraptorids were herbivorous, as has been claimed, they must have eaten seeds and fruits more than leaves. Their hands and feet, which have the usual theropod armament of recurved claws, suggest that oviraptorids were predatory.

The name Oviraptor means ‘egg stealer’. But a recent discovery of associated oviraptorid embryos and adults revealed that this was the most misleading name for any dinosaur lineage. During the Central Asiatic Expeditions in the 1920’s by the American Museum of Natural History, an adult *Oviraptor* was found preserved near nests that contained dinosaur eggs presumed to belong to *Protoceratops*. The discovery suggested that *Oviraptor* was preying upon the *Protoceratops* eggs, hence the name ‘egg stealer’. In 1993 American Museum paleontologists discovered nests containing the eggs and embryos of *Oviraptor*[26]. As it turns out, most of the eggs once thought to belong to *Protoceratops* are actually eggs of *Oviraptor*.

At one of these sites, a skeleton of *Oviraptor* was preserved actually sitting on a nest of eggs in a brooding posture exactly like that of many modern birds[27]. There is no evidence of post mortem transport, making it improbable that some other factor could account for the life-like association of the adult on the nest. The eggs are arranged neatly and systematically, implying that the eggs were manipulated and positioned by the parents into a specific configuration as is typical of most modern birds. This specimen provides the first direct evidence of the history of parental brooding so characteristic of modern birds. Paleontologists are now asking whether this discovery bears on another question. Modern birds sit on their eggs to keep the nest warm. What was *Oviraptor* doing on its nest if it couldn’t generate its own body heat? No doubt this specimen will be closely studied by everyone evaluating evidence for warm-bloodedness in extinct dinosaurs.

So, ornithomimosaurs and oviraptorids and possibly several other coelurosaur lineages bear special resemblances to birds, and the trail to birds is growing much warmer. But there is still one more lineage to consider that is even more bird-like.

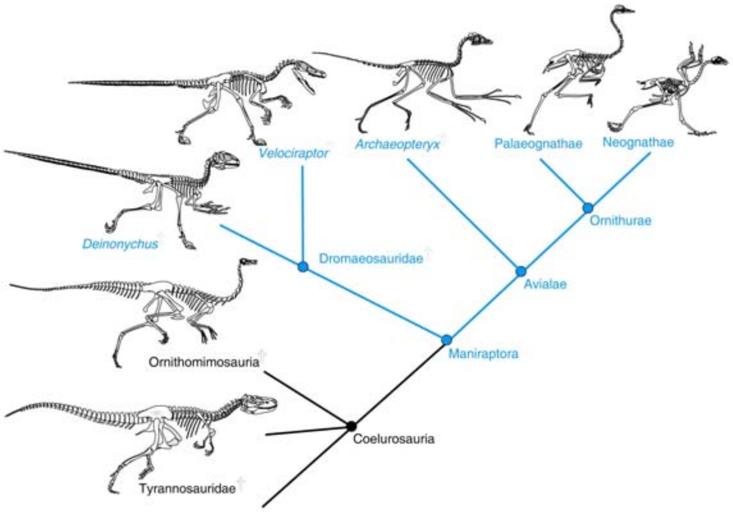

Figure 12.20 Phylogenetic map or cladogram showing the relationships among representative maniraptoran dinosaurs (in blue). The palaeognath and neognath lineages comprise the two major sister lineages of living birds. Extinct lineages are indicated by crosses.

Maniraptorans

The somewhat different evolutionary paths traced by John Ostrom and Jacques Gauthier met in maniraptoran theropod dinosaurs (fig. 12.20). Gauthier's expedition to map saurischian phylogeny uncovered abundant new anatomical evidence supporting Ostrom's claim that *Deinonychus* and *Archaeopteryx* are indeed closely related. Owing to the weight of this evidence, Gauthier coined the name Maniraptora -- the raptorial-handed dinosaurs -- for the evolutionary path that includes Dromaeosauridae and its sister lineage Avialae[28]. The most famous members of the dromaeosaur lineage are *Deinonychus* and *Velociraptor*. Avialae, named by Gauthier for the winged theropods, is the lineage that includes *Archaeopteryx* plus modern birds and everything else descended from their last common ancestor. On the cladistic map, *Deinonychus* and birds are members of sister lineages.

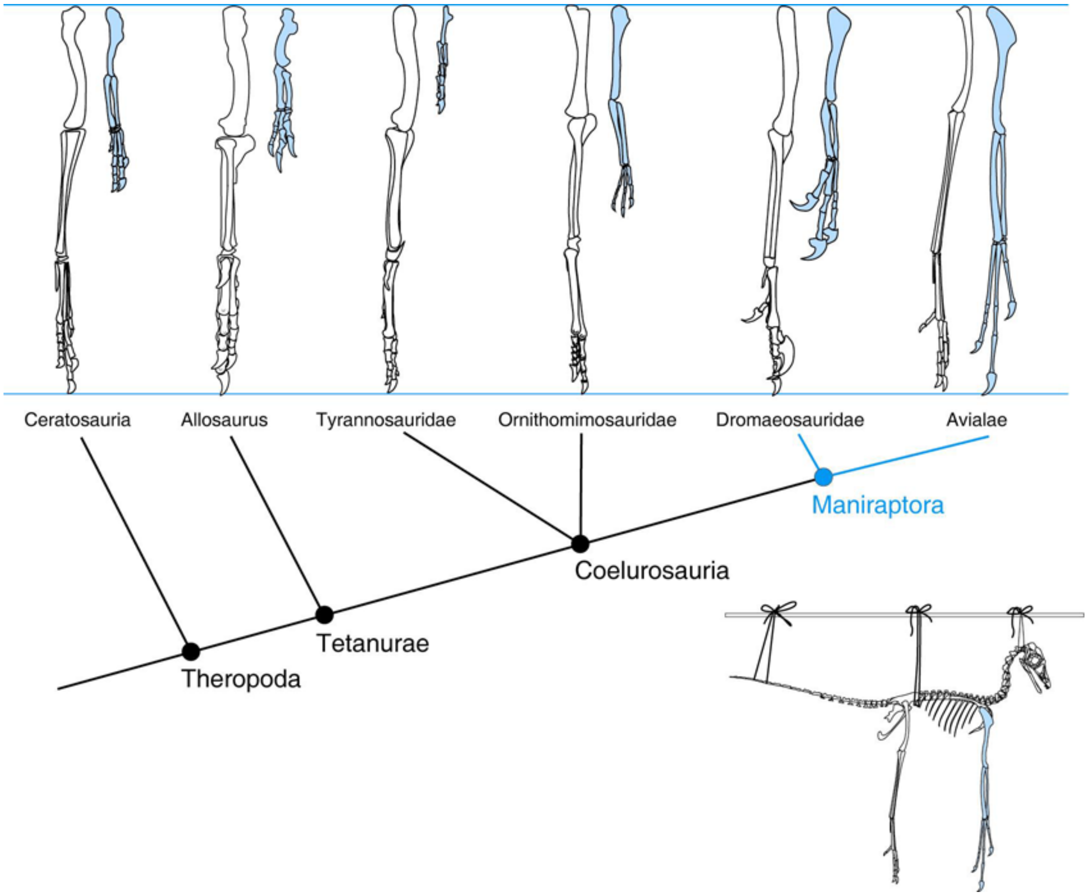

Figure 12.21 Maniraptoran dinosaurs are distinguished by longer arms than in other theropods. Their arms are ¾ the length of the hindlimbs, or greater. The dromaeosaur illustrated above is *Velociraptor* and the avialian is *Archaeopteryx.*

The maniraptoran lineage is distinguished from other tetanurines by its skull, arms, and tail. The skull was simplified through the loss of a bone called the *prefrontal*, which was previously situated above and in front of the eyeball, along the rim of the eye socket. This seemingly obscure anatomical detail is significant because it may signal the presence of a large *salt gland* or *nasal gland* above the eyeball. This structure is unique to birds among living species. It helps maintain a balanced concentration of blood salts, preventing dehydration and death from a prolonged or extreme imbalance. In tetrapods, the kidneys also play a big role in this. The kidneys of warm-blooded mammals and birds are enhanced, probably to compensate for rapid salt buildups driven by their higher body temperature and faster moisture loss. In mammals, sweat glands help the kidneys excrete excess salts. But in birds, there are no sweat glands. Instead, the kidneys are augmented by a salt gland, which removes and excretes salt from the blood in very high concentrations. The salt gland permits many birds to live in the arid deserts of the American Southwest and Mexico, where they survive dehydration without developing poisonous levels of blood salts. Marine birds survive by drinking sea water because they are able to excrete excess salt through the nasal gland. It is this gland that enables birds to exploit many of the diverse habitats that they occupy today. The subtle loss of the prefrontal bone in maniraptorans may signal an important evolutionary step in avian physiology.

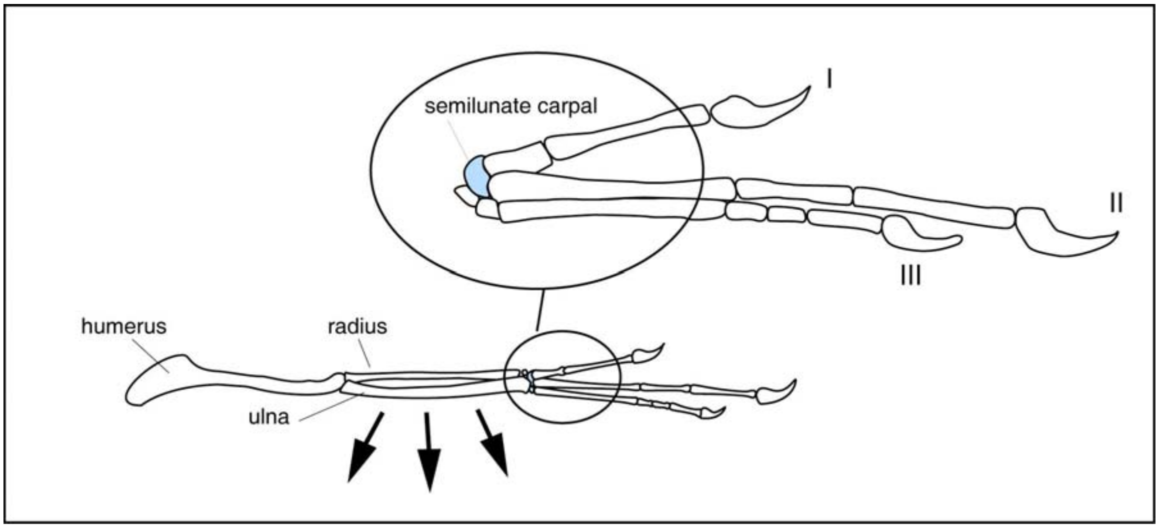

Figure 12.22 The forearm in maniraptorans is distinctive in having a bowed ulna and a wrist with the semilunate carpal. Together with the wishbone and hollow bones inherited from more primitive theropods, maniraptorans had virtually all the major components for flight.

No one would suggest that maniraptors like *Velociraptor* and *Deinonychus* could fly. Yet these dinosaurs had most of the skeletal modifications that later proved essential for flight in modern birds[29]. Their arms are even more elongated, to roughly 3/4 the length of the hindlimb (fig. 12.21). The hands are extremely long and slender. The short thumb reflects an extensive grasping capacity, and the tips of all three fingers are armed with trenchant, recurved claws--an elaboration of the pattern found in the ancestral theropods. The muscles operating the maniraptoran forelimbs originated from a powerfully built shoulder girdle. Although a bony sternum and wishbone arose in the ancestral tetanurine, they are noticeably stronger whenever they have been preserved in basal maniraptorans. This strong armature enhances power both when the hands reach out to grab prey and when they pull the quarry back toward the mouth.

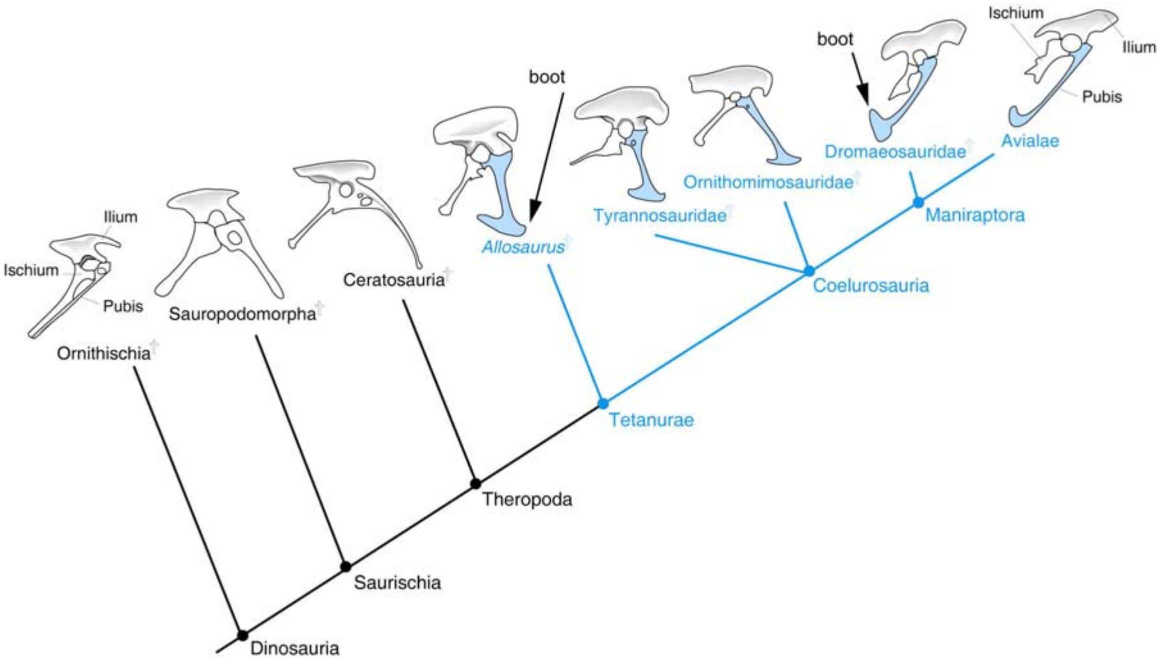

Figure 12.23 Another distinctive feature of maniraptorans is that the pubis (blue)is backturned, superficially like the condition in ornithischians. However the maniraptoram pubis is derived from a more general tetanurine (blue) pattern in which there is an expansion known as the pubic boot at the end.

More subtle clues to the relationship between dromaeosaurs and birds are visible in the forelimbs. The *ulna* and *third metacarpal* bones are bowed, instead of being straight (fig. 12.22). More importantly, there is a distinctive bone in the wrist, the *semilunate carpal*. This half-moon shaped bone lies at the base of the thumb and index finger. The same structure is present during early development in modern birds, it fuses to the adjacent bones of the hand in adults. In living birds, the semilunate carpal is important in directing movement of the hand in a fan shaped motion during the wing's flight stroke. In basal maniraptorans it may have helped snap the hands forward to quickly grab fleeing prey. The joint surfaces and muscle scars on the bones suggest that basal maniraptorans may have been able to fold their hands against the body much like modern birds while resting. For John Ostrom, this bone was one of the keys to allying *Deinonychus* and *Archaeopteryx*. For Gauthier, it was another element in the hierarchy of features linking birds and all theropods.

The pelvis and tail also exhibit subtle evidence for close relationship. The pubis has rotated backwards (fig. 12.23), superficially like its orientation in ornithischian dinosaurs. In the tail, the transition point between mobile vertebrae at its base and stiff vertebrae at is end lies near the pelvis. Almost the entire tail was stiff, and much of the musculature that once attached to the tail has shifted to the pelvis. Taken together, these features indicate a more forward center of gravity in maniraptorans. Birds carried this trend further by suspending the center of gravity between the wings during flight.

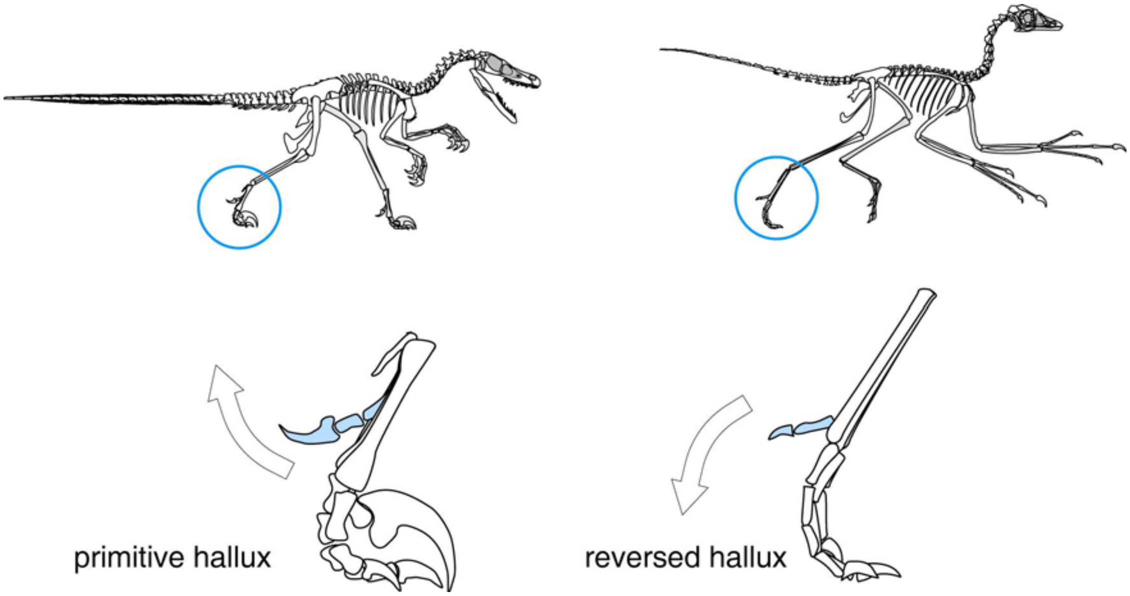

Figure 12.24 In avialians, the big toe or hallux is reversed, affording a grasping capability not found in other theropods.

In Avialae, we reach the point on the map representing the last common ancestor shared by *Archaeopteryx* and living birds[30]. As we have seen, the Solnhofen specimens of *Archaeopteryx* preserve long flight feathers, extending backwards from the hand and arm to produce the airfoil wing that enabled flight. The snout is slender and pointed, and the teeth are reduced in size and number, foreshadowing the origin of the avian beak. There is also an enlarged brain--one of the most characteristic features of birds among modern tetrapods. The arms and hands are nearly half again as long as they are in dromaeosaurs, to support of their new mode of locomotion. Corresponding modifications in the hindlimb produce a more solid structure with fewer separate elements that can withstand the forces generated in landing, as the bones of the ankle and foot begin to fuse into a solid structure. In addition, the big toe or *hallux* has moves onto the back of the foot, affording a degree of grasping capability (fig. 12.24). The tail is also shortened to no more than 23 separate vertebrae. Thanks to these and other characters, for the last century almost everyone has agreed with Richard Owen that *Archaeopteryx* is a bird.

Protoavis - Triassic Bird?

A challenge to the idea that birds are avialian, maniraptoran, tetanurine theropod dinosaurs came from Dr. Sankar Chatterjee of Texas Tech University, with the discovery of a fossil for which he coined the named *Protoavis texensis*[31]. It was collected from Late Triassic rocks, predating *Archaeopteryx* by 75 million years, and pushing the origin of birds to the earliest stages of dinosaur evolution. Chatterjee maintains that *Protoavis* is on the direct path from dinosaurs to birds, and that *Archaeopteryx* and the other theropods described above represent an unrelated side path on the map of avian evolution. The scientific community has been skeptical of Chatterjee's proposal because many of the bones from the skull are flattened and difficult or impossible to interpret. Moreover, there is reason to suspect that *Protoavis* represent a death assemblage of different animals instead of associated parts of a single kind of animal. The hind limb has a primitive unfused ankle and foot, lacking a tall ascending process, and it may belong to a ceratosaur or something closer to *Herrerasaurus*. It is doubtful that the elements comprising the hand are from the same creature, if in fact they are hand bones. Only Chatterjee and Larry Martin (University of Kansas) have defended this view; everyone else wants to see more complete specimens and more data before they consider abandoning the cladistic map that summarizes so much actual data.

The Origin of Flight

One of the points made clear by Gauthier and Padian in collaborative work at Berkeley is the importance of not confusing the problem of the origin of birds with the problem of the origin of flight. Even though we may never know exactly what stages the ancestors of birds passed through as they evolved flight, we can still read from the evolutionary map compiled by Gauthier and his successors, that the preponderance of evidence favors the hypothesis that birds are the descendants of extinct Mesozoic theropod dinosaurs. So, given that birds are, in a genealogical sense, dinosaurs, it would appear that powered flight arose in a lineage that descended from a bipedal, cursorial, fast running theropod dinosaurs, smaller in size but much like *Velociraptor* or *Deinonychus* in general design. Our map suggests that flight evolved from the ground up, but exactly how this happened is another question altogether.

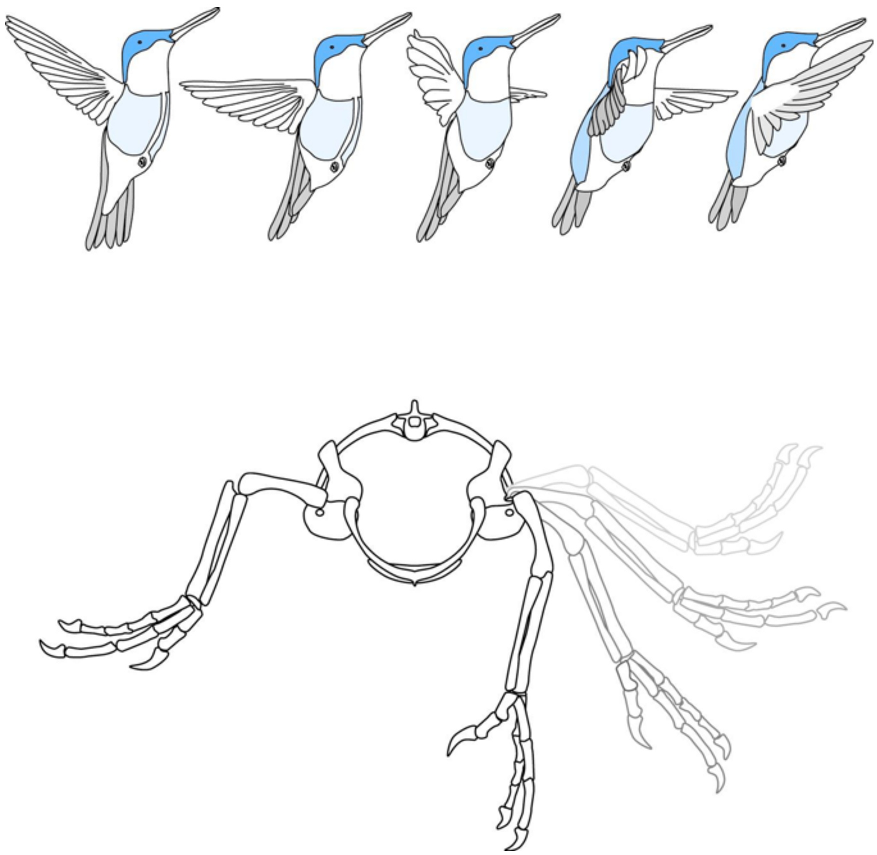

Figure 12.25 The flight stroke of birds, looked at from the side in a hummingbird, is very much like the raptorial, prey-grabbing motion of the arms in more primitive maniraptorans, viewed here from above.

Intuitively, it has always seemed more likely that flight evolved through a gliding stage, and John Ostrom faced severe criticism with his ground-up argument on that basis. A question that Ostrom had been forced asked is, “how could the beginnings of the flight stroke arise in a cursorial animal?” Birds seem to move their wings in a unique way to achieve lift - how did this evolve? Although it is a difficult question, Ostrom found a plausible answer in the diet of early theropods. Their armament of trenchant claws and sharp teeth points to a predatory existence. The powerful architecture of the forelimb and hands suggests that the arms were snapped forward to grab at a potential prey item or to smother an insect[32]. And this motion is very much like the motion of the flight stroke (fig. 12.25).

There is now a growing body of experimental information that clarifies how birds use their wings during flight[33]. To generate lift, the forelimbs are thrown forward and somewhat downward. Adding to this argument is independent evidence based on the physics of aerodynamics. Several researchers recently demonstrated that even small increases in the surface area of the hands can generate significant levels of lift, provided that the surface is shaped like an airfoil. The long hands of early maniraptorans and avialians could provide lift, if the hands were being accelerated forward. This is not to say that early maniraptorans were able to fly, but that they may have used the aerodynamic properties of their hands for balance and maneuverability while chasing prey or escaping over broken ground. Many living birds can run very fast and are highly maneuverable even when running across uneven surfaces. Running birds can use their wings to help maintain balance, and young birds even flap their wings to gain greater speeds while running. Even though the forelimb is committed to flight in most adult birds, it can still aid terrestrial locomotion at points in their lifetimes. Differences between the situation in birds and Mesozoic dinosaurs have also come to light, and it is clear that the flight stroke is considerably modified over the likely movements of non-flying dinosaurs. But, this at least shows the plausibility of the argument that flight evolved from the ground up.

With a more rigorous, hierarchical map of dinosaur genealogy, Gauthier and Padian were able to highlight the sequence of changes documented in theropod history to show that the ground-up theory was in fact plausible[34]. As we have just seen, over theropod history there was a series of changes in which the arms became successively longer and more powerful, and the shoulder girdle was heavily reinforced. All of these changes are consistent with both a predatory existence and the earliest stages of the evolution of flight. Once there was reason to suspect that the true historic pathway of avian descent was from ground up, the ecology and physics behind such a transition were not so hard to understand. After all, this is the same strategy that human invention has taken in the creation of flying machines.

Not surprisingly, another argument about the origin of flight is emerging that represents a consensus of the trees-down and ground-up hypotheses. This argument recognizes the long temporal gap that separates the Late Jurassic *Archaeopteryx* and the various Cretaceous dromaeosaurs. If our map of theropod history is correct, then the histories of both lineages must have extended to a common ancestor that lived in or before the mid-Jurassic. It is possible that from a cursorial dinosaurian ancestor, the predecessors of avialians became arboreal - small tree-climbing maniraptoran dinosaurs - and that the transition to powered flight actually did take place in the trees. While there is no direct evidence of such intermediate tree-climbing maniraptorans, some paleontologists argue that the claws of *Archaeopteryx* were designed for climbing, implying a non-preserved tree climbing phase in their history. More obviously needs be learned to understand the whole process that occurred as flight evolved in extinct theropods.

Down the Road

Whereas points of resemblance might be found between birds and pterosaurs, or birds and ornithischians, or birds and ceratosaurs, we have now mapped the position of birds within a single hierarchy relationships. Although it really begins at the origin of Life, in the last two chapters we have traced the hierarchy of avian relationships from the origin of Vertebrata, through the emergence of vertebrates onto the land, and onto the dinosaurian pathway of reptilian evolution. Cladistic techniques enable mapping of the most characteristic features of birds backwards in time, matching each feature back to the particular ancestor in which it arose. Ironically, Gauthier mapped many of the characters that Richard Owen had used to verify the avian affinities of *Archaeopteryx*, like a wishbone and a hollow skeleton, to positions in the hierarchy of evolutionary relationships among extinct theropod dinosaurs.

Paleontologists following Gauthier’s trail have unearthed additional evidence that birds are avialian, maniraptoran, tetanurine, theropod, saurischian, dinosaurs. From the ancestral dinosaur, birds (fig. 12.26) inherited an in-turned femoral head and a perforate acetabulum, and from the ancestral saurischian a long neck and a hand in which second finger is the longest. To the ancestral theropod, birds owe their hollow bones and a flexible joint between the neck and head. The wishbone, a three-fingered adult hand, and the ascending process of the ankle can be traced back to the ancestor of tetanurines. The ancestral maniraptoran added still longer arms with a semilumate carpal in the wrist.

And the ancestral avialian added still longer arms, flight feathers, and the ability to fly. From today's perspective, Huxley and Ostrom were right - the evolutionary road to birds passes through dinosaurs.

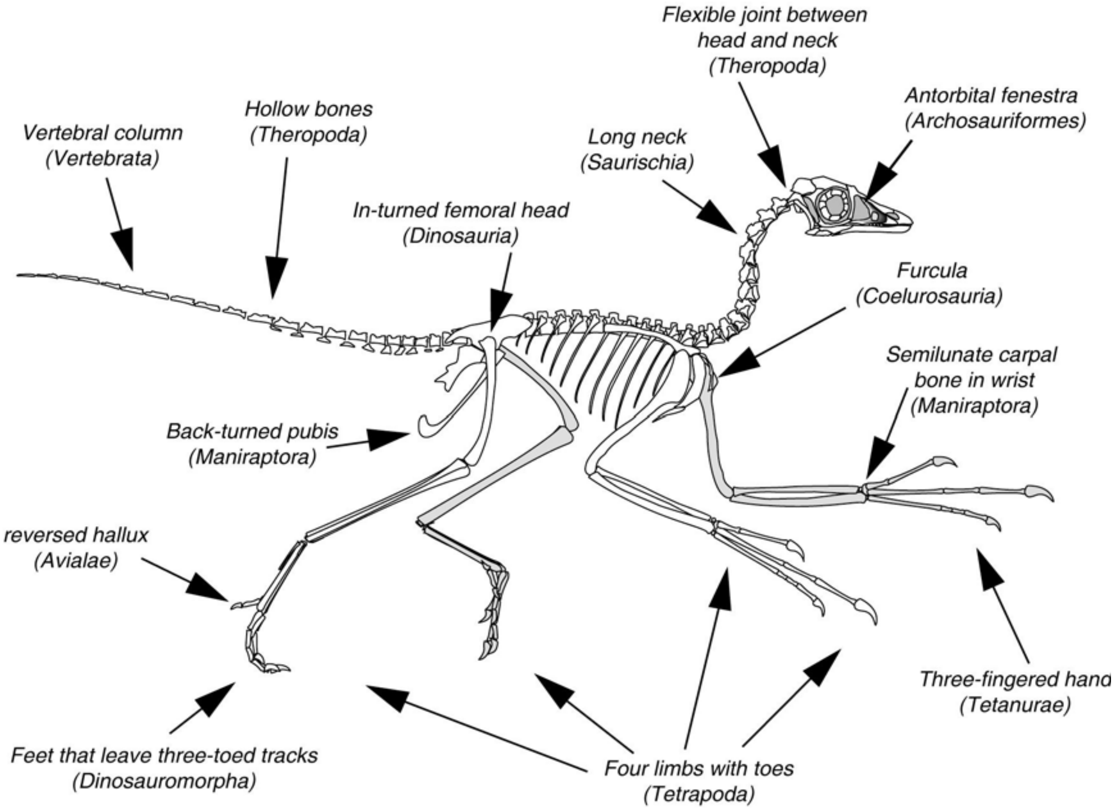

Figure 12.26 The various features of birds, illustrated here by Archaeopteryx, can be traced to historic times of origin. For example, from the ancestral vertebrate birds inherited a vertebral column; from the ancestral tetrapod four limbs with wrists/ankles, and fingers/toes; feet that leave three-toed trackways from the ancestral dinosauromorph; an in-turned femoral head from the ancestral dinosaur; a long neck from the ancetral saurischian, a flexible jointe between the head and neck from the ancestral theropod, and so on.

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