# Chapter 11

# Dinosaurs and the Hierarchy of Life

Are birds related to dinosaurs or not? *Deinonychus* carried the question full circle. First Huxley and then Ostrom argued that small dinosaurs are closely related to birds. And the same charges of homoplasy launched at *Compsognathus* in Huxley's time were thrown at *Deinonychus* a century later. Are the resemblances of modern birds to extinct dinosaurs genealogical, or merely a coincidence - the result of convergent evolution?

As we watched the debate between Ostrom and his critics unfold, each side asserted emphatically that it was correct. But they couldn't both be right. Birds could have only one true set of relationships, one historic line of descent. The trick was to figure out how to test between the alternatives - how can we tell genealogical similarities from those that reflect homoplasy?

To answer this question, we first need to come to grips with what a dinosaur is from a modern scientific view point. What features must an animal have to be a dinosaur? While this seems like a simple question, when we arrived at Berkeley we encountered an intense debate over how to answer questions like this, that eventually grew across departmental lines to involve many of the faculty and students studying evolutionary biology across campus. The debate commanded wide attention because there was a more fundamental issue at stake that involved reconstructing the past. How can we testably reconstruct the relationships among living and extinct organisms?

## *Reconstructing Relationships: Mapping the Phylogeny of Life*

Evolutionary relationship, shared common ancestry, is what makes the various groups of living organisms distinctive and provides their biological identities today. Before there was a theory of evolution to suggest that species are in fact related, there was no reason to search for a way to map their relationships. But in the wake of Darwin's theory, many different methods have been advanced for what is known as *phylogeny reconstruction* - the mapping of evolutionary relationships.

Reconstructing and mapping ancient phylogenetic relationships has become a highly sophisticated science, because these maps can provide answers to a vast range of fundamental biological questions. Biologist now study organisms in microscopic detail as they search for information pertaining to phylogeny, using advanced technologies like high resolution X-ray CT scanners and scanning electron microscopes. Modern computers perform sophisticated image analyses, a wide array of statistical tests, a variety of phylogenetic analyses, and simulations aimed at understanding the past. Just as remote sensing technologies have revolutionized our mapping of the Earth's surface, our ability to map evolutionary relationships has made enormous strides with the advent of microprocessor computing. Thousands of biologists and paleontologists are now involved in mapping the phylogenetic relationships among the myriad branches of Life.

But even with modern technology there remain daunting obstacles. Chief among these is the fragmentary record of the past. For most living species there simply is no fossil record. Preservation is the exception to the rule - far more species have come and gone than were ever captured by the fossil record. Of those that did leave fossils, the records are at best incomplete. In general, the older the event, the less information is preserved. Even at best, fossils are mere fragments of a once living, breathing organism. How much do they really tell us about the distant past of the Mesozoic?

Several prominent biologists recently argued that fossils are in fact worthless for reconstructing ancient relationships, and that only modern species need be studied. Colin Patterson (British Museum of Natural History), a preeminent paleontologist who we met in an earlier chapter, argued that fossils had no effect whatsoever on modern conclusions about relationship[1]. After all, in living species we can directly observe molecules, soft tissues, coloration patterns, and behaviors, whereas in fossils we can only speculate about these features. Living species present so much more information that they will simply swamp any signal preserved in fossils. Coming from an enormously influential paleontologist like Patterson, this was a powerful argument. Other biologists carried the argument further, claiming that our modern capability to measure the sequences of nucleic acids in the DNA of living species means that we don't even need to keep museum specimens - a drop of fluid is all it takes to reconstruct their relationships.

But many modern species are so radically altered from the appearance of their ancestors, that little of their past is preserved. All systems, including bones, soft tissues, molecules, and behaviors can transform - none of these systems is immune to evolution. And as they change, they overwrite and gradually erase their past like a palimpsest. The problem using modern species alone becomes increasingly severe in reconstructing progressively more ancient patterns. For example, the modern amniotes - birds, crocodylians, lizards, turtles, and mammals - diverged from each other about 300 million years ago. Over that expanse of time, they evolved in such differing directions that it is difficult today to see any clues as to their relationships. Bird feathers, mammal hair, the shells of turtles, and lizard scales all seem equally different from each other. At first glance, their skeletons look equally different as well. Still, if Patterson were correct, the fossil record had no bearing on our understanding of these relationships.

Thomas Huxley had taken a different position while defending Darwinian evolution a century earlier. Arguing that the gaps separating species today were less-marked in the past, he predicted that the fossil record would provide critical intermediary stages that are clues to the evolutionary linkages between modern species. The new tools and computer programs for phylogeny reconstruction gave us a chance to test the importance of fossils, in a collaborative study with Jacques Gauthier and Arnold Kluge (University of Michigan, Ann Arbor) on amniote phylogeny[2]. A series of computer analyses that alternatively included and deleted fossils from a phylogenetic analysis of the major groups of living and extinct amniotes found that different genealogies arose when fossils were added or deleted from the analysis. Fossils unquestionably made a difference to mapping phylogeny, so the assertion that fossils were irrelevant to phylogeny reconstruction was falsified. The details of the tests were revealing. Analyzing just the most primitive amniote fossils failed to reveal very strong information on relationships among the major lineages, because those lineages had not yet become markedly differentiated. Analyzing modern species and some of their closest fossil relatives also produced poor results, because those particular fossils had already taken on most of the distinctive patterns of their living relatives. It was the intermediate fossils, which documented the history of evolutionary transformation over several hundred million years, that provided the key to understanding amniote relationships. This might seem like a case of scientists discovering the obvious, but a growing number of biologists had begun to operate under the assumption that the modern biota alone could tell the same story. Our tests showed that by looking at *both* fossils and recent species, we have the best chance of accurately reconstructing the past.

As we saw in the last chapter, a second factor that complicates phylogeny reconstruction is homoplasy, otherwise known as convergent or independent evolution. This was the basis for Harry Seeley's argument against a close relationship between birds and dinosaurs. The problem for Seeley's generation, and for John Ostrom's as well, was that there were no clear methods to determine which similarities reflect homoplasy and which reflect evidence of genealogy.

Given the complications of incompleteness and homoplasy, how do modern biologists reconstruct phylogeny? While we were students, a method called *cladistics* was developed for reconstructing or mapping phylogenetic patterns (figs. 11.01 - 11.05). Although the methods of cladistics are still evolving, there are several basic ideas that underlie most of this work. One is to assemble all the data one can possibly find with any bearing on a given problem. Like most detectives and most juries, scientists generally prefer explanations that address all the evidence, not just some of it. An explanation of relationships among modern species that rejects fossils is weak compared to one that accounts for all the information. A single explanation for *all* the data is more powerful than a series of special arguments that each address different parts of the data[3]. Underlying this idea is the same principle of parsimony - seeking the simplest explanation for all the data - that we introduced earlier.

A second basic idea in cladistics is to measure patterns of unique similarity among the intrinsic, heritable characteristics of organisms (fig. 11.02 - 11.03). Heritable features include molecular structures, DNA sequences, bone structure, muscle anatomy, coloration patterns, instinctive behaviors, and so on. Only shared heritable characteristics bear on genealogy, and only shared evolutionary novelties provide evidence of shared genealogical history. Just as children share unique resemblances to their parents, closely related species reveal their relationship in the shared possession of unique features.

To reconstruct patterns of evolutionary relationship, one of the challenges is to distinguish features that arose in a particular ancestor of interest, such as the ancestral dinosaur or the ancestral bird, from older features that had simply been inherited from even more distant ancestors in the lineage, like the ancestral reptile or the ancestral vertebrate. For instance, both birds and humans have a vertebral column, but this is not necessarily evidence of close relationship because many other organisms like lizards, salamaners, and sharks, also possess a vertebral column (fig. 11.06). The vertebral column distinguishes vertebrates as a whole from other organisms, but it provides no information on whether humans and birds are more closely related to each other, or to lizards, salamanders, sharks or some other vertebrate.

The structure of the limbs is a different story. Birds and humans both possess limbs equipped with hands and feet. Sharks and the various ‘fishes’ have fins, instead. Whereas all vertebrates possess a backbone, only some possess limbs that develop into hands and feet. From the structure of their limbs, we can distinguish members of the tetrapods lineage (fig. 11.07). Among tetrapods, we can discern smaller groups. One lineage is marked by the amniotic egg (fig. 11.08), which provides evidence that birds and humans are more closely related to each other than to salamanders or sharks (fig. 11.09). By comparing the many different features of organisms and mapping which features are found in what particular species, patterns of relationship among species emerge and the evolutionary histories of different features can be viewed in an intelligible fashion. Comparisons like this can get complicated if a lot of species and characters are analyzed, which is where the computers come in.

This brings us to a third idea behind reconstructing evolutionary relationships. Evolutionary relationships form *hierarchical* patterns, in which there are large, encompassing lineages like Vertebrata, which include smaller lineages like Tetrapoda, and which in turn includes smaller lineages like Amniota (fig. 11.10). The metaphor of a family tree is apt, because from one trunk sprout many branches, which in turn sprout twigs, and the hierarchy of relationships is obvious. To discover these hierarchies of relationships, we map patterns of characters that are hierarchical, like the pattern just noted in which all species with hands and feet have a vertebral column, but not all vertebrates have hands and feet; species with an amnion all have hands and feet, but not all tetrapods have an amniotic egg.  First the vertebral column evolved, then hands and feet, and later the amniote egg appeared in a descendant lineage.  Amniotes are members of Tetrapoda and Vertebrata, which is the more-inclusive level in the hierarchy.  There are about 40,000 living species, while Tetrapoda includes only about half of the living vertebrate species.

These ideas can be applied together to tell resemblances that are due to homoplasy from resemblances that are genuine clues to common ancestry, and this is one of the great strengths of cladistics.  Evolutionary resemblances are arrayed in a hierarchical pattern, while homoplasy is indicated by points of resemblance.  Consider insects and birds.  Both have wings, so one might argue that they are close relatives.  But when the characteristics of all of their anatomical systems are considered, the preponderance of evidence places insects deeply within the hierarchy of arthropods - the crabs, lobsters, and other organisms with jointed limbs and a rigid external skeleton.  This hierarchy is built from thousands of detailed anatomical observations, and it indicates that the insect wing evolved from non-flying arthropod ancestors.  Birds, on the other hand, lie deeply within the hierarchy of vertebrates, organisms with an internal skeleton made of bones, as we will see below.  Only the shared possession of wings tends to pull birds and insects away from their respective hierarchies and into a separate group by themselves.  But this point of resemblance between birds and insects reflects the common mechanical demands of flight, not common ancestry.

This conclusion is testable by comparing in minute anatomical detail the structures of the two wings.  If the two wings evolved from a common ancestral pattern, we might  expect some degree of resemblance to persist.  In fact, the two wings are radically different in virtually all details of anatomy and development.  A second test is to add new information to the analysis, and to recalculate the hierarchical pattern that their characters support.  For example, each new fossil discovery provides unique combinations of characteristics for the analysis and can potentially change the map of relationships.

So, if birds and dinosaurs are related, then the various characteristics of their skeletons should be arrayed into a single hierarchical pattern. If the resemblances are homoplastic, then there should be only isolated points of resemblance between the two, and we should be able to map dinosaurs and birds into separate evolutionary hierarchies. And with each new fossil discovery, we can test and re-test older conclusions.

## *Birds and Dinosaurs: One Hierarchy or Two?*

Dinosaurs and birds are undoubtedly members of many of the same levels in the hierarchy of Life. For example, both share an organization based fundamentally on cells and a reproductive mechanism that uses DNA to pass parental traits on to descendants. Both are multicellular organisms with differentiated tissues, such as muscles and nerves, and with tissues that in turn are organized into organs and organ-systems. Further, they are members of a lineage with an elongate body, a head at one end and a tail at the other, a mouth in front and an anus behind, and bilateral symmetry in which the right and left sides of the body are mirror images of each other. Dinosaurs and birds have a vertebral column, the central support of their internal skeletons, and so they lie together within the vertebrate division of the hierarchy of Life. Humans also fall within this level of the hierarchy.

But just how far into the vertebrate hierarchy do these lineages travel together? To best appreciate the controversy embroiling birds and dinosaurs, it is helpful to follow the map of relationships forward from a level that is not controversial. In order to provide an evolutionary context in which to evaluate the controversy, we will pick up the trail to birds from the beginning of vertebrate history. From there we will follow the phylogenetic map forward in time to see where these lineages split and diverge from one another onto their own evolutionary trajectories.

The first cladistic maps of vertebrate phylogeny were generated by Gareth Nelson[4] and Donn Rosen[5] (American Museum of Natural History), and their work has been extended by Colin Patternson[6], Bobb Schaeffer[7] and John Maisey[8] (American Museum of

Natural History), and many others. All agree that at the most general level, the map of vertebrate relationships is split into two major lineages which can be regarded as ‘sister lineages’ because they sprang from the same common ancestor (fig. 11.11). Each sister lineage forms a hierarchy within the more inclusive hierarchy of vertebrate relationships. These sister lineages are of unequal size today. The less-diverse of the two has been christened Petromyzontida and includes the modern parasitic lampreys. All other vertebrates are members of a lineage is known as Gnathostomata. Among their many distinctive characters, these vertebrates have jaws that are lined with teeth, improving the grasping capability of the mouth. They also have fins on either side of the body, one pair in front and one in back (fig. 11.12). Paired fins offer greater maneuverability up and down in the water column and more rapid turning than was the case in the earliest vertebrates. The oldest fossil evidence of gnathostomes indicates that the lineage extended back in time at least 500 million years. Dinosaurs, birds, and humans all have a vertebral column, jaws, and paired appendages, indicating that they belong to the gnathostome branch in the vertebrate hierarchy.

Gnathostomata includes two great sister lineages (fig. 11.11). Chondrichthyes includes the sharks and rays while its sister lineage, Osteichthyes, includes all the rest. Chondrichthians have lost virtually all of the bone in the skeleton, while in contrast Osteichthyes have increased the extent of their internal bony skeleton by adding bony ribs that articulate movably with the vertebral column, and a bony shoulder girdle that firmly anchored the front fins to the body. The ancestral osteichthyan lived in the ocean, and many of its living descendants have remained in their ancestral environment. Chief among them is the actinopterygian lineage, which contains about 18,000 species of ray-finned fishes, including all that are native to North American fresh and coastal waters. However, its sister lineage, known as Sarcopterygii, has fins that were modified in a highly characteristic fashion, paving the way toward life on land (fig. 11.13). In the front fins there appeared a single bone, corresponding to our upper arm or *humerus*, in the part of the fin closest to the body. Following the humerus are two more bones, which correspond to the *radius* and *ulna*, the two bones making up our forearms. As we saw in chapter 9, both *Deinonychus* and *Archaeopteryx* have the same bones in their skeleton. Birds, dinosaurs, and humans all inherited this pattern from the ancestral sarcopterygian.

Sarcopterygii includes two surviving sister lineages (fig. 11.11). One of these is known as Actinistia and is represented by a single species, which today lives only in deep waters around the Comoros Islands of the Indian Ocean. Its sister taxon is Choanata, which has nearly 20,000 living species. Members of Choanata are distinguished by a continuous passage from the nose through to the roof of the mouth known as the choana (fig. 11.14). There are two major living lineages of Choanata. One, named Dipnoi, includes the three living species of lungfish, which live today in freshwater streams and water holes in Africa, South America, and Australia. Its sister lineage is Tetrapoda[9], and it is to this line that birds, dinosaurs, and humans belong (fig. 11.15). Tetrapods are the vertebrates who moved onto land, transforming profoundly from the habitat and appearance of their fish-like ancestors. This momentous relocation occurred in several stages, beginning about 350 million years ago. The first tetrapods were helped along by the transformation into limbs of their more distant ancestor's two pairs of fins (fig. 11.16). The first tetrapods added a series of interlocking bones that form the wrists and ankles. Following these is a series of bones forming the hand and foot, which in turn are followed by additional rows of bones forming the fingers and toes, producing the basic pattern of bones found in the hands and feet of living tetrapods. One glance at a dinosaur skeleton confirms that dinosaurs are part of this lineage. One glance in a mirror should convince you that you are too.

Locomotion in early tetrapods was only slightly different from the motion through the water column of their fish-like ancestors. Sigmoidal side-to-side undulation of the vertebral column provided the basic thrust, as was the case in Vertebrata ancestrally, but the body was propped against the ground instead of against a water column. Even with this new ability, the earliest tetrapods probably spent most of their time in the water, feeding there and laying their eggs in the water as well. Their tails, moreover, were still designed for swimming. If we could go back in time to hunt for early tetrapods, it would take a fishing pole to catch one.

Two major tetrapod lineages survive today, namely Amphibia and Amniota. Amphibians living today include the frogs, salamanders, and caecilians. As the name of this group implies, most amphibians have ties to both the land and the water. Modern amphibians were once looked upon by naturalists as being uniformly primitive. However, in the 350 million years since branching out on their own evolutionary pathway, modern amphibians have become highly modified from the ancestral tetrapod. The skeletons of frogs are highly specialized for leaping, and salamanders are greatly altered owing in large part to the developmental retardation of certain skeletal growth patterns. Caecilians are strange, worm-like creatures whose fossil record reveals a history marked by reduction and finally total loss of the limbs.

As we have seen, Amniota, the other major lineage of tetrapods, is the lineage with the amnion. Usually the amnion is surrounded by a hard or leathery shell, like the eggs of birds or turtles. However, even human embryos grow within an amnion that develops inside the mother's womb. The evolution of the amniotic egg represented the next stage in the tetrapod transition to land by allowing the egg to be laid on land. The evolutionary histories of birds, dinosaurs, and humans lie within the phylogenetic hierarchy of Amniota.

The exact number of fingers and toes was variable in the earliest tetrapods but the number eventually stabilized at five fingers and five toes in the ancestral amniote, as it evolved greater agility and speed on land than before. The vertebral column was also strengthened to withstand the greater forces generated during locomotion on land. Whereas their fish-like relatives are more or less neutrally buoyant, in effect weightless while in the water, the terrestrial amniotes had to confront the problem of weight and gravity. In addition, the earliest amniotes have the beginnings of a sophisticated joint between the head and neck, enabling the head to bend and twist from side to side, and to take items from the ground. Fish-like vertebrates often suck food items into their mouths with a large gulp of water, but amniotes must be more agile to catch prey crawling or flying by.

The relationships among amniotes have been controversial for decades. In our years at Berkeley, Tim and Jacques Gauthier were among the first to apply cladistics to the problem of amniote phylogeny[10]. Subsequent studies confirm or map, that there are two major living lineages diverged from the ancestral amniote, namely Synapsida and Reptilia (fig. 11.15), and with this split we see the evolutionary pathways of humans diverge from that of dinosaurs and birds. Synapsida (fig. 11.17) includes humans and all other mammals, plus a host of extinct species. Up until this time, our own lineage shared more than 3 billion years of common evolutionary history with birds and dinosaurs. But about 325 million years ago, the synapsid lineage diverged onto its own trajectory, and from that time onward our own evolutionary history was distinct from that of dinosaurs and birds. In the context of Life's 4 billion years of history, we are not such distant relatives of dinosaurs after all.

Synapsid history is documented in great detail by a dense fossil record and, because it is our own history, it has been intensively explored[11]. Early synapsids were largely predatory, like their ancestors, although there were some early herbivorous experiments. Synapsids eventually evolved sophisticated means of locomotion, some being able to run, gallop, leap, climb, and even fly. In the process, the principle movement of their vertebral column transformed from the primitive side-to-side sigmoidal motion of fish-like vertebrates to a more symmetrical up-and-down movement. With symmetrical spinal movement breathing cycles became coupled to running cycles, increasing the efficiency of high-speed locomotion, a feat carried to is greatest level in modern cheetahs.

Mammals, the living synapsids, are warm-blooded and have huge brains[12], unlike all other vertebrates except birds. Richard Owen had used this resemblance as a basis for arguing that birds and mammals are closely allied. But more recent phylogenetic maps indicate that mammals are deeply internested in the hierarchy of synapsid genealogy, whereas birds and dinosaurs lie within the reptile division of the amniote hierarchy. Large brains and endothermy are points of resemblance between birds and mammals, that evolved convergently within different hierarchies of amniote phylogeny.

## *Reptilian Past*

As we shall see, there is abundant evidence, from both fossils and from all anatomical systems in living species, that birds and dinosaurs are members of the reptile lineage (fig. 11.18). Also sharing common ancestry with the ancestral reptile are living turtles, lizards, and crocodylians, plus a vast diversity of extinct species[13]. By studying living reptiles, we can reconstruct that the ancestral reptile probably had color vision and was strongly diurnal in its habits, because nearly all living reptiles are. Like our own synapsid lineage, the brain increased in relative size during the history of reptiles, although the expansion involved a different region of the brain.

A pervasive theme in reptile history involves elaboration of the jaws and feeding system. The evidence for this lies in aseries of new holes in the skull, known as *fenestrae* (fig. 11.19). The term 'fenestra' (plural = fenestrae) means 'window'. Skull fenestrae are simply openings between bones, and their evolution enabled a great expansion and strengthening of the jaw musculature. The first large fenestra appeared at the back of the skull and is known as the *posttemporal fenestra*. The first amniote already had a tiny posttemporal fenestra for the passage of a blood vessel. In Reptilia, this hole enlarged as the expanding jaw muscles invaded it (fig. 11.20).

Two lineages with living members descended from the ancestral reptile. One includes turtles or Testudines (fig. 11.18). Turtles are highly distinctive in replacing teeth, which they lack entirely, with a horny beak, and in developing a bony shell. Modern birds also have replaced teeth with a beak, and on this basis some early naturalists argued that turtles and birds are allied. But possession of a beak is virtually the only unique resemblance between birds and turtles, aside from the features that both inherited from the ancestral reptile. Both lineages have long fossil records that indicate an extensive hierarchy of separate relationships. Both primitive turtles and primitive birds like *Archaeopteryx* had teeth. When all of the fossils are mapped onto a phylogeny that includes modern species, we can see that the loss of teeth is the result of convergent evolution, rather than descent from a common toothless ancestor.

The sister group of Testudines is Sauria (fig. 11.18), which today include lizards, snakes, crocodiles, birds, and a diversity of extinct Mesozoic species. Saurians further increase the size of their jaw muscles, adding additional fenestrae in the skull. On the side of the head behind the eyes are two openings, the *supratemporal fenestra* and the *infratemporal fenestra*. Saurians also have long slender limbs, making them more agile and faster than other reptiles. Two saurian lineages have living species. These are Lepidosauria and Archosauria. Lepidosaurs include snakes and lizards[14], which are distinguished by their extensive covering of overlapping scales. Living lizards can climb, swim, and even parachute from high branches. Most lizards are predatory. In capturing insects and small vertebrates, lizards have evolved a remarkable diversity of equipment. Some, like the chameleon, have protrusable tongues to grab passing insects. Others like the Gila monster have a modified salivary gland that secretes highly toxic venom. In many snakes, the upper and lower jaws come apart at the front of the mouth, allowing them to swallow objects far larger than their head. Genealogically, snakes are simply lizards that have lost their limbs and elongated their bodies via the addition of many vertebrae to their backbones. The most primitive living snakes--pythons and their immediate relatives--still possess remnants of hind legs that afford evidence of their evolutionary descent from running lizards.

As we saw in Chapter 10, early 19th century naturalists confused dinosaurs with lizards, and the confusion sometimes persists thanks to the popular misnomers “thunder lizards” and “terrible lizards”. While indeed there are many resemblances, modern phylogenetic maps indicate these features to be inheritances from the common saurian ancestor, rather than evidence placing dinosaurs within the lizard lineage. Modern cladistics only reinforces Owen’s original insight that Dinosauria is a distinctive group. The ancestral species of Archosauria probably lived during the latest Permian, around 250 million years ago, a good 25 million years before the oldest known dinosaur.

## *Archosaurs Rule*

Since Robert Broom’s work on *Euparkeria* (fig. 11.21), naturalists have agreed that birds, crocodylians, dinosaurs, pterosaurs, and a host of other extinct reptiles descended from the early archosaurs. Archosaurs had inherited long limbs and a skull with temporal fenestration from their more distant saurian ancestors. From the ancestral reptile they inherited a posttemporal fenestra and color vision. The amniotic egg had been passed down from the ancestral amniote, and the distinctive organization of the hands and feet from the ancestral tetrapod. From the ancestral sarcopterygian, archosaurs inherited a highly stereotyped limb organization, from the ancestral osteichthyan bony ribs and a bony shoulder girdle, from the ancestral gnathostome jaws and paired appendages, a vertebral column from the ancestral vertebrate, and so on and on, back to the first single-celled Life form.

*Euparkeria* (fig. 12.06) is the closest thing we have to the actual ancestor of archosaurs. Modern phylogenetic maps now plot *Euparkeria* as the extinct sister lineage of Archosauria, together comprising the more inclusive lineage Archosauriformes (fig. 11.22). This lineage was distinguished from other saurians by even more fenestration of the skull. Two new openings were added. The *antorbital fenestra* lies in front of the eye along a greatly elongated snout, while the *mandibular fenestra*, perforates the side of the jaw below and behind the eye. Both fenestrae may have housed enlarged jaw muscles, but the antorbital fenestra may have also housed a pneumatic expansion - an air sac - expanding from the nasal passage.

The vertebral column and its primitive side-to-side sigmoidal undulation were modified in early archosaurs for a more symmetrical mode of locomotion, known as *parasagittal gait*. The vertebral column flexed in an up-and-down direction with the limbs held more vertically beneath the body. This transformation began in the ancestral archosaur, and its various descendant lineages carried the trend further to varying degrees. Early archosaurs could probably gallop at high speeds. Living crocodylians can do this while they are young, but they loose the ability as they mature. In addition to greater speed, these changes probably enabled early archosaurs to range widely in search of food and mates.

The evidence summarized so far does not indicate which particular pathway of descent from the ancestral archosaur was followed by birds. Is the road to birds via dinosaurs, or via some other archosaurian lineage? If the distinctive avian features like bipedality and flight cannot be arranged into the hierarchy of one of the known lineages, then the popular 20th century thecodont hypothesis of avian origins could well be true. However, if birds can be mapped onto one of the known archosaur pathways, then this would prove the thecodont hypothesis wrong.

One group of paleontologists, led by Alick Walker[15] (University of Newcastle-upon-Tyne) and Larry Martin[16] (University of Kansas) has maintained that birds and crocodylians are more closely related to each other than to dinosaurs or pterosaurs. They invoke the theory of homoplasy, arguing that similarities birds share with dinosaurs and pterosaurs evolved convergently. The main lines of evidence they cite are similarities between the teeth in modern crocodylians and in primitive toothed birds like *Archaeopteryx*, and in the shared presence of pneumatic cavities around the braincase.

If the teeth and braincase similarities offer valid evidence that birds evolved from crocodylians, then a complete phylogenetic map should show birds branching from within the hierarchy of crocodylian evolution. But when all the data from modern and extinct archosaurs is taken into account, this is not the case. A series of independent cladistic studies of different segments of the Crocodylian lineage, including all modern species plus a long fossil record of extinct crocodylian relatives, was recently conducted by Jim Clark (George Washington University) and Michael Benton[17] (University of Bristol), Mark Norell[18] (American Museum of Natural History), Chris Brochu[19] (University of Texas), and several other paleontologists. Molecular data on modern species, plus information on the entire skeleton in modern and fossil species was used to generate a detailed series of hierarchical maps of crocodylian relationships. None of these phylogenetic maps includes birds. While there are a few points of resemblance, when all available data are studied, the overwhelming conclusion is birds are *not* a part of the crocodylian hierarchy.

Instead of evolving flight, crocodylian history saw the elaboration of cursorial, quadrupedal locomotion styles in some descendant lineages, while others adopted an aquatic habitat to varying degrees. Modern crocodylians spend most of their lives swimming and feeding in the water. With this ecological shift, the antorbital fenestra was closed over as the skull became specialized so that only the eyes and nostrils would protrude above the water. Adult crocodilians have short legs compared to the length of their bodies, and tail-driven swimming has become their dominant mode of locomotion (fig. 12.07). As hatchlings and juveniles, crocodylians have relatively longer legs and can gallop. But as they age, the body and tail grow faster than the legs, and galloping and bipedality are sacrificed in favor of a powerful trunk and tail for swimming. Birds must lie within the hierarchy of some other archosaur lineage.

The sister lineage to crocodylians is Ornithodira (fig. 12.08). Right from the start, ornithodirans began to experiment with bipedality[20]. This is reflected in the simplification of their ankle, which forms a simple hinge joint. In early archosaurs, the bones of the ankle interlocked and moved in a series of complex rotations as the body rotated past the foot, which sprawled outwards. In early ornithodirans, the body moved over the foot, flexing the ankle in a simple hinge-like motion. In addition, the hindlimbs are elongated and are now considerably longer than the forelimbs. The neck is also longer and has become slightly S-shaped, holding the head higher than the backbone.

From the ancestral ornithodiran we can trace two descendant lineages. One of these is Pterosauria, the flying archosaurs sometimes allied to birds by early naturalists (fig. 12.09). A tiny, Late Triassic ornithodiran named *Scleromochlus* is probably the most primitive known member of the pterosaur lineage[21]. This fast-running terrestrial animal documents a pre-flight stage of its history. The oldest flying pterosaur is *Eudimorphodon* from the Late Triassic of Italy. Its forelimbs were transformed into wings, primarily through the elongation of the fourth finger, which supported a flap of skin that attached along the arm and to the side of the body. But the detail structure of the wings in pterosaurs and birds is very different. Pterosaurs went on to diversify throughout the Mesozoic. The giant pterosaur *Quetzalcoatlus* is the largest flying creature known, with a wing span of about 12 meters. But as with crocodylians, nowhere within the hierarchy of Pterosauria can we place birds. Although points of similarity like wings can be found, the similarities diminish as we compare these structures in detail. Owen, Huxley, and virtually every since has agreed that, when all available information is taken into account, flight arose independently in birds and pterosaurs.

The sister group of pterosaurs is known as Dinosauromorpha. As the name suggests, this is the evolutionary trail of dinosaurs[22]. The Middle Triassic *Lagosuchus* bears a detailed resemblance to dinosaurs in the structure of its pelvis, very long, graceful hindlimbs, and shortened forelimbs (fig. 11.22-11.23). The structural disparity between the small hands and huge feet suggests that dinosauromorphs moved almost entirely on their hindlimbs. The massive pelvis and sacrum carried more of the animal's weight than when it was evenly distributed on all fours. The head of the femur is bent inward to fit into the hip socket, and there is a small crest of bone over the top of the hip socket, enabling the knees to be carried close against the body. The tibia, fibula, and metatarsal bones are elongated, and the structure of the feet indicates that the earliest dinosauromorphs stood and walked on the balls of their feet, not flat-footed like their ancestors. Only three toes touched the ground, and three-toed trackways dating back to the Triassic document the narrow gait of dinosauromorphs. The feet struck the ground near the midline of the body. With their knees rotated in close to their flanks, and with the up-and-down flexure of their vertebral column, dinosauromorphs had a swift, bounding mode of bipedal running.

### *Dinosauria: Portrait of the Founder*

Dinosauria presents a further elaboration of several of these trends (fig.11.24). The hands of early dinosaurs were largely freed from their primitive role in locomotion and took on other functions, becoming highly distinctive in the process. The thumb could bend inwards to oppose the other fingers of the hand. This is similar, but not identical, to the situation in the human hand (fig. 11.25). In both cases, one end of the *first metacarpal bone*, a bone in the palm, is offset to permit the thumb to be pressed *against* the other fingers instead of just bending parallel to them. In humans the offset occurs at the base of the first metacarpal bone, where the first metacarpal fits against the wrist. In dinosaurs the offset occurs at the other end of the bone, where the thumb joins the palm (fig. 11.26). The primitive dinosaur thumb was less mobile than the human thumb, but their hands could nonetheless grasp objects, and among Mesozoic vertebrates this was a revolutionary innovation (fig. 11.27).

This twisting of a single bone might seem like a trifling evolutionary step, but it reflects a more complex underlying genetic change. Over much of vertebrate history, the front and hind limbs were built on similar structural plans that present almost mirror images of each other. In most vertebrate lineages, evolutionary changes affect both front and hind limbs together, not one to the exclusion of the other. The Giant Panda – a living mammal species -- presents a famous example of this phenomenon. Pandas feed exclusively on bamboo leaves, which they strip from the stalks with a unique bony strut that protrudes from one of the wrist bones near the base of the thumb. Remarkably, there is a similar, non-functioning bony protuberance on the corresponding bone of the ankle, near the base of the first toe. It is evident from this and similar examples that a genetic linkage exists between the fore- and hindlimbs. Only the bony strut in the wrist is functional, but the genetic linkage between the two limbs brought about a corresponding structural change in the ankle. In most tetrapods, this linkage usually causes heritable, evolutionary changes in one limb to be manifested in the other. In the ancestral dinosaur, this linkage was broken. Unlike the foot, the dinosaurian hand is markedly asymmetrical. The outer two fingers each lost one phalanx and the remaining parts of the digits became almost vestigial structures. In contrast, the thumb, index, and middle fingers were robustly constructed, and the strength of the hand appears to have been focused there.

With the hands and forelimbs no longer supporting the body, the hindlimb played a much greater role in locomotion. Evidence of this is found in the pelvis and sacrum of dinosaurs, which Richard Owen had found so distinctive. The *ilium*, the upper bone of the pelvis, was especially expanded and more massive (fig. 11.28). The ilium forms both the roof of the hip socket and part of the attachment to the vertebral column. The vertebrae of the sacrum, which lie between the right and left halves of the pelvis, are fused together in adult dinosaurs. In addition, the specialized ribs coming off of the sacral vertebrae are massively expanded to provide a stronger attachment to the ilium. Quite simply, the bigger pelvic frame indicates bigger pelvic musculature for a more powerful ‘motor’ to move the legs.

In addition, the hip socket, or acetabulum, provides evidence of a major reorientation in the posture and movement of the femur. In other tetrapods, the acetabulum forms a closed cup, and the femur pressed into the socket which acts as the fulcrum for the hip. In dinosaurs, the hip socket has a hole in the middle, a condition referred to as a *perforate acetabulum*. Instead of extending out to the side and pressing straight into the socket, the dinosaur femur was oriented more vertically, its head bends inward almost at a right angle and pressed against the top and back of the thickened acetabular rim. A robust *supraacetabular buttress* and *antitrochanter* arose over the perforated socket, to withstand the redirected forces of the inturned head of the femur, The shaft of the femur and the leg were held in a plane roughly parallel to the vertebral column, the *parasagittal plane*, and the knee was held close against the body. Bony bumps, or *trochanters*, on the femur expanded to provide stronger attachment points and greater leverage for the massive muscles originating on the enlarged pelvis.

Birds share all of these features of the hindlimb. Richard Owen had described the perforated acetabulum in *Archaeopteryx*, as well as the other features. The hands of *Archaeopteryx* are very different from the hands of early dinosaurs, but even so there are marked similarities, like the offset in the thumb. Birds also display many of the features that distinguish Dinosauromorpha, Ornithodira, Archosauria, Sauria, Reptilia, and so on. Hence, there appears to be a hierarchy of similarities between birds and Mesozoic dinosaurs.

The ancestral dinosaur was small compared to the “fearfully great” image conveyed in the name of the group. It probably weighed about the same as an adult human. The head was long and narrow, with a pointed snout. Its mouth extended literally from ear to ear, and its jaws were lined with sharp, serrated teeth that curved toward the back of the mouth. A deft predator, it could have hunted a wide range of prey items, from insects to animals larger than itself. It could potentially swallow items as large as its head, but this is no indication that it actually did so. The rare examples of stomach contents in early dinosaurs are of much smaller animals.

It was habitually bipedal and able to run rapidly for considerable distances in pursuit of agile, fast prey. The ancestral dinosaur had large eyes and large optic lobes in its brain for processing visual information. These provided a sophisticated sense of sight, including color perception, acute long-distance vision, and refined sensitivity to smallest movements. Its hearing was also well-developed. Because the head was held high off the ground on a long, flexible neck, these sensory receptors could be very rapidly directed and re-directed over wide fields to quickly locate and track potential prey. Sight and hearing were probably the principal sense organs, with a relatively less-developed sense of smell. The oldest unquestionable dinosaur fossils were collected in South

America, from Late Triassic rocks (approximately 230 million years old). Several different localities in Argentina and southern Brazil have produced several different species of early dinosaurs. Of these, only *Herrerasaurus* (fig. 11.24) has become reasonably well-known[23] and, owing largely to the incompleteness of the others, exact relationships among the basal species is not yet understood. In North America, rocks of nearly the same age, or perhaps only slightly younger age, have also yielded fragmentary bones of early dinosaurs. During the early 1980's we accompanied a group from Berkeley's Museum of Paleontology, collecting in the Petrified Forest National Park, discovered *Chindesaurus*, a close relative of the South American dinosaurs[24]. With this discovery, dinosaurs seemed to appear abruptly in the fossil record, already diversified into several species, and distributed to both hemispheres.

Each of these early dinosaurs has unique anatomical specializations that preclude it from direct ancestry to other dinosaurs. Because it must have taken some length of time for the specializations to evolve, and because dinosaurs have a global presence at their earliest appearance, it is likely that the species ancestral to all other dinosaurs lived a few million years earlier than the oldest known fossils, during the Middle or Early Triassic (between 235 and 245 million years ago). A few tantalizing bone fragments collected from Early Triassic rocks might represent something even closer to the ancestral dinosaur than the species named above, but more complete fossils are needed to tell whether these are truly dinosaurs. Even if unequivocal evidence is eventually traced as far back as the Early Triassic, Dinosauria, the icon for ancientness in our culture, originated only after 90% of the history of Life had already passed.

Determining *where* the ancestral dinosaur species lived is even more difficult to narrow down than *when* it lived. Throughout the Triassic, today's continents were welded together into the continuous land mass known as Pangaea. Unlike today, there was little or no land positioned at either the North or South rotational poles and there were no polar ice caps, and the continental masses that had collided to form Pangaea were positioned closer to the equator. As a result, the Triassic climate on average was probably warmer and seasonal temperature fluctuations were less extreme than today. Without either oceanic or climatic barriers, dinosaurs dispersed throughout Pangaea.

Owing both to their mobility and to the evidence of an even earlier, undiscovered history for the lineage, the fact that the oldest known dinosaur fossils come from South American doesn't necessarily mean that Dinosauria originated on that continent. The ancestral species might have lived anywhere on Pangaea during the first half of the Triassic.

### *A Single Hierarchy*

There are many differences between this picture of the ancestral dinosaur and modern birds, but because the two are separated by more than 200 million years we should expect some profound differences. More significantly, there are numerous unique and detailed similarities between birds and early dinosaurs. And, moreover, these similarities lie in an internested hierarchy of novel resemblances that link dinosaurs back in time via the ancestral archosaur to the ancestral amniote, to the ancestral tetrapod, the ancestral vertebrate, and ultimately to the ancestral cell. It is also true that points of similarity seem to link birds with other groups. But when data from the entire skeleton are examined, when fossils and modern species are examined collectively, and when the map of vertebrate phylogeny is considered as a whole, there is only one hierarchy into which birds fit. So, genealogy, not homoplasy, appears to offer the most powerful explanation of the similarities between birds and dinosaurs.

Does this necessarily mean that birds are dinosaurian descendants? The scientific world view that we encountered at Berkeley is to obsessively test conclusions. Rather than accept the easy answer, we should test the dinosaur-bird hypothesis further, by mapping the hierarchy of dinosaur evolution. If birds are really the living descendants of Mesozoic dinosaurs, we should be able to map a distinctive trail of hierarchical clues through Mesozoic fossils. We should be able to plot birds onto a specific part of the map of dinosaur phylogeny.

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Figure Captions for Chapter 11

Fig 11.01 Life is arrayed in a hierarchy, in which lineages are arranged within more inclusive lineages. At each level, there are distinguishing features. The relationships among species can be diagrammed in several ways. All three of these diagrams represent the same hierarchy of relationships, in which B and C are each other's closest relatives. Together, they form the sister lineage to D. Similarly, B-C and D together form the sister lineage to A.

File Name: 10_01.AI

Fig. 11.02 Phylogenetic maps, otherwise known as cladograms, use solid lines to represent lineages. At the lowest levels in the hierarchy of Life, these are lineages of interbreeding organisms.

File Name: 10_02.AI

Fig. 11.03 Environmental factors sometimes create reproductive barriers that split a population into separate, diverging lines of ancestry and descent. These are speciation events. On a cladogram they are represented by nodes - where two or more branches split apart.

File Name: 10_03.AI

Fig. 11.04 The relative timing of speciation events is represented vertically, from oldest to youngest branchings.

File Name: 10_04.AI

Fig. 11.05 Like geographic maps of different scales, branches on a phylogenetic map, like those labeled A - F, may consist of a single species, or thousands of related species. Branch F, for example, might represent hundreds of species that are simply depicted as a single lineage.

File Name: 10_05.AI

Fig. 11.06 Vertebrata forms a distinct lineage whose members are distinguished by their common possession of a backbone or vertebral column (blue).

File Name: 10_06.AI

Fig. 11.07 Among vertebrates, members of the tetrapod lineage are distinguished by limbs that develop into hands and feet (blue).

File Name: 10_07.AI

Fig. 11.08 Birds, mammals, lizards, crocodylians, and turtles have an egg with an amnion - a fluid filled sack in which the embryo develops. This distinctive egg distinguishes members if Amniota.

File Name: 10_08.TIF

Fig. 11.09 Amniota is a lineage contained within the more inclusive lineages Tetrapoda and Vertebrata.

File Name: 10_09.AI

Fig. 11.10 The hierarchy of vertebrate relationships can be mapped by tracing the hierarchical arrangement of shared evolutionary novelties, otherwise known as synapomorphies.

File Name: 10_10.AI

Fig. 11.11 Phylogenetic map or cladogram of vertebrate relatinships.

File Name: 10_11.AI

Fig. 11.12 Three gnathostomes, highlighting the characteristic jaws and paired appendages.

File Name: 10_12.AI

Fig. 11.13 Representative members of the sarcopterygian lineage, showing the common pattern of organization in the front limb.

File Name: 10_13.AI

Fig. 11.14 A pathway for water or air, from the naris to the choana, is diagnostic of the Choanata lineage.

File Name: 10_14.AI

Fig. 11.15 Phylogenetic map of relationships of the major lineages of Tetrapoda.

File Name: 10_15.AI

Fig. 11.16 The evolution of the tetrapod forelimb occurred in successive modifications of the fin.

File Name: 10_16.AI

Fig. 11.17  About 325 million years ago, the synapsid lineage diverged onto its own trajectory, and from that time onward our own evolutionary history was distinct from that of dinosaurs and birds.

File Name:	10_17.AI

Fig. 11.18  Phylogenetic map of major living and extinct reptile lineages.

File Name:	10_18.AI

Fig. 11.19  Fenestrae are openings in the skull of reptiles.

File Name:	10_19.AI

Fig. 11.20  The pattern of fenestrae is one of many features that offer clues about reptile relationships.

File Name:	10_20.AI

Fig. 11.21 Basic archosaur skeletal anatomy, illustrated by Euparkeria.

File Name:	10_21.AI

Fig. 11.22 Phylogenetic map of archosauriform relationships.

File Name:	10_22.AI

Fig. 11.23  The primitive dinosauromorph Lagosuchus was a facultative biped, capable of bursts of speed on its hind limbs along.

File Name:	10_23.AI

Fig. 11.24  Diagnostic regions of the dinosaur skeleton are the pelvis, hip, and hand, illustrated here by *Herrerasaurus*.  The hip modifications locked dinosaurs into a narrow gait.  The hands could grasp, much as our own hands can.

File Name:	10_24.AI

Fig. 11.25  The bones of the human hand, as they relate to the skin of the palm.

File Name:	10_25.AI

Fig. 11.26 the opposable thumb of humans is formed by a joint at the base of metacarpal I, whereas in dinosaurs the offset bending occurs at the first knuckle of the thumb.

File Name: 10_26.AI

Fig. 11.27 The hands of early dinosaurs all show the characteristic offset of the thumb.

File Name: 10_27.AI

Figure 11.28 These archosaur pelves show the primitive closed socket acetabulum, compared with the perforated acetabulum (blue) of dinosaurs.

File Name: 10_28.AI