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Chapter 10
Dinosaurs Challenge Evolution

Enter Sir Richard Owen

More than 150 years ago, the great British naturalist Richard Owen (fig. 10.1) ignited the controversy that *Deinonychus* would eventually inflame. The word "dinosaur" was first uttered by Owen in a lecture delivered at Plymouth, England in July of 1841. He had coined the name in a report on giant fossil reptiles that were discovered in England earlier in the century. The root, *Deinos*, is usually translated as "terrible" but in his report, published in 1842, Owen chose the words "fearfully great"[1]. To Owen, dinosaurs were the fearfully great saurian reptiles, known only from fossil skeletons of huge extinct animals, unlike anything alive today.

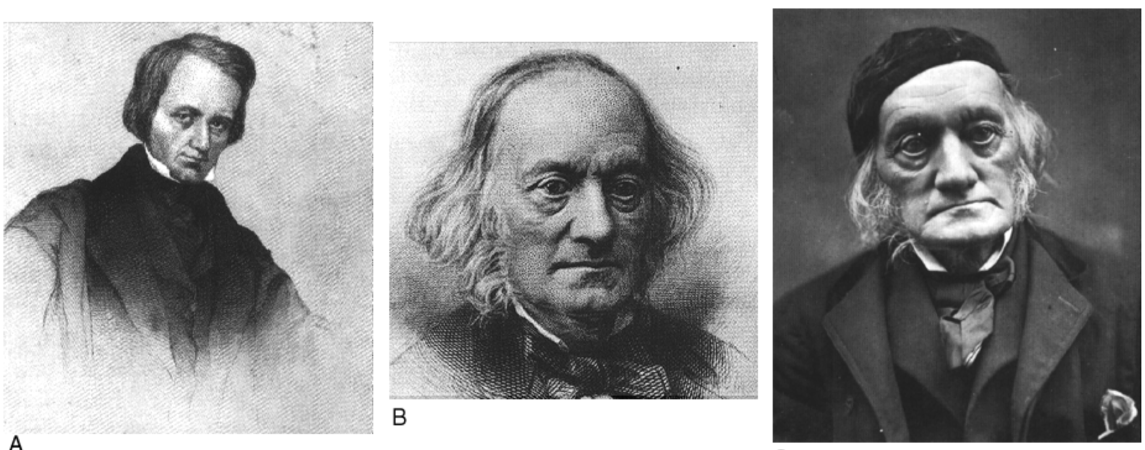

Figure 10.1. Richard Owen as, A) a young man at about the time he named Dinosauria, B) in middle age, near the time he described *Archaeopteryx*, and C) in old age. A) from: Desmond, A., and J. Moore, 1991, Darwin - the life of a tormented evolutionist, Warner books; (b) from: Norman, D., 1985. The Illustrated Encyclopedia of Dinosaurs, Crescent Books; (c) from: Desmond, A., 1982, Archetypes and Ancestors. Blond and Briggs, London.

Dinosaur bones were discovered long before Owen first spoke their name, but no one understood what they represented. The first scientific report on a dinosaur bone belonging was printed in 1677 by Rev. Robert Plot in his work, *The Natural History of Oxfordshire*. This broken end of a thigh bone, came to Plot's attention during his research. It was nearly 60 cm in circumference--greater than the same bone in an elephant (fig.10.2). We now suspect that it belonged to *Megalosaurus bucklandii*, a carnivorous dinosaur now known from Oxfordshire. But Plot concluded that it "must have been a real Bone, now petrified" and that it resembled "exactly the figure of the lowermost part of the Thigh-Bone of a Man, or at least of some other Animal..."[2] Plot did not believe it belonged to a horse, an ox, or even an elephant, but rather to a giant man, evidently relying on biblical accounts of "giants in the earth."

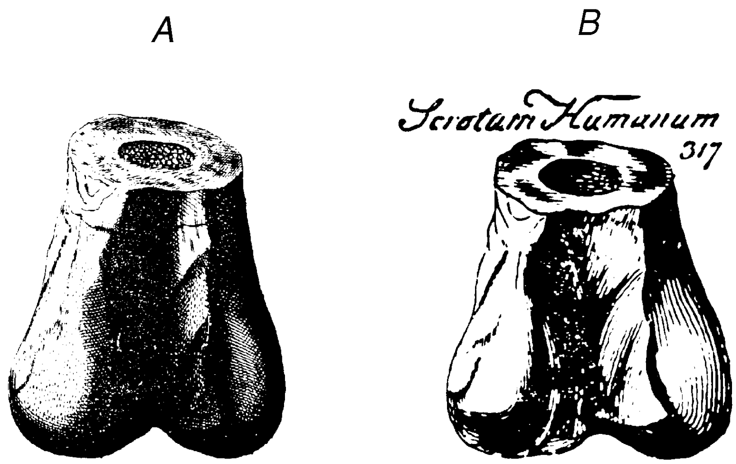

Figure 10.2. A) Robert Plott's figure (1677) of what was probably the first dinosaur bone known to science. B) Richard Brooke's figure (1763) of the same bone, now christened with the first proper Linnaean name for a dinosaur. (from: Halstead, L. B., and Sarjeant, W. A. S., 1993, Scrotum humanum Brookes - the earliest name for a dinosaur? Modern Geology 18:221-224.).

In 1763, Robert Brooke published an even more amazing interpretation of the same specimen. In his *Natural History of Waters, Earths, Stones, Fossils and Minerals, With their Virtues, Properties and Medicinal Uses: To which is added, The method in which LINNAEUS has treated these subjects*, Brooke labeled Plot's original illustration *Scrotum humanum*[3]. This ribald name might have been forgotten were it not for Carolus Linnaeus. This great Swedish botanist established a system of taxonomic classification and nomenclature that was already in widespread use in 1763. The Linnaean system uses a binomial or two-names to describe species, for example, our name *Homo sapiens*.

To correct previous errors and to accommodate reinterpretations, taxonomic names are constantly changing and evolving. Linnaeus set out rules governing the coining and use of taxonomic names, and a commission of scientists now oversees amendments to the Linnaean rules. The rule of priority states that when one species (or specimen) has been given different names (usually by different naturalists) the valid name will be the first given. Brooke's ignominious name for Plot's specimen used a proper Linnaean binomial, the first such name ever applied to a dinosaur bone and, under the Linnaean Rules, the proper name for what we now call *Megalosaurus*.

It is perhaps fortunate, then, that Plot's specimen has been lost, so it is impossible to confirm that it belongs to what we call *Megalosaurus*. Citing technicalities of the Rules, two paleontologists[4] formally recommended abandoning Brooke's terminology. The Linnaean Commission agreed, laying to rest this false-start to the scientific study of dinosaurs.

The early 19th century saw the beginnings of our modern understanding of dinosaurs. Numerous discoveries of dinosaur bones were made in Britain, and they provoked more insightful interpretations. In 1824, British naturalist William Buckland described a broken jaw with a single, recurved, serrated tooth of *Megalosaurus* also from Oxfordshire (fig.10.3). Buckland's interpretation is evident from his title "Notice on the

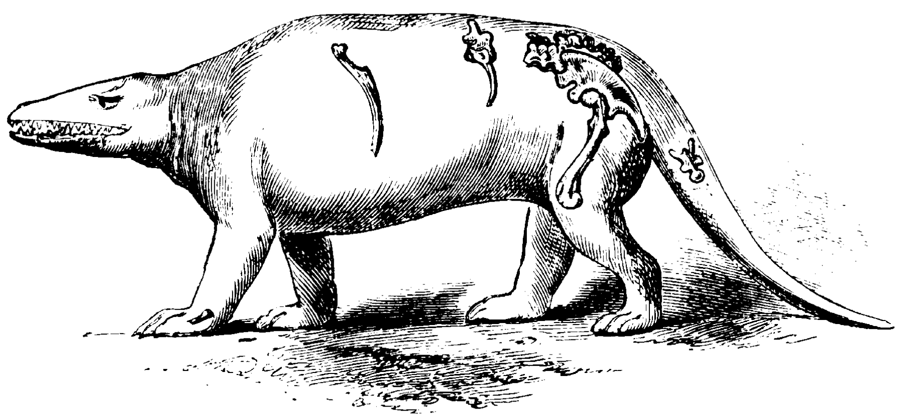

Figure 10.3. *Megalosaurus*, as restored by Richard Owen in 1854 (from: Owen, R., 1854, Geology and Inhabitants of the Ancient World. London).

Megalosaurus or great Fossil Lizard of Stonesfield"[5]. Apart from size Buckland found nothing remarkable about *Megalosaurus*. The next year Gideon Mantell, a British physician and naturalist, described *Iguanodon*[6]-- now recognized as a giant herbivorous dinosaur. Mantell thought that *Iguana*-tooth, as its name translates, was a giant lizard resembling today's green *Iguana*. In 1833, Mantell described a second dinosaur, *Hylaeosaurus armatus*, an armored herbivore, which he thought to be another extinct lizard. Early 19th century collections made by the British Geological Survey contain additional dinosaur specimens that went unrecognized until seen through Owen's eyes.

Buckland and Mantell came a lot closer than Plot, but as Owen showed, they still missed the mark[1].

Not Giant Lizards?

When he first recognized dinosaurs, Owen observed that *Megalosaurus, Iguanodon,* and *Hylaeosaurus*, shared distinctive anatomical features, so they could be grouped together using the Linnaean system. In addition to their huge size were several characters involving the hip. The thigh bone of dinosaurs has a head that bends at an angle of about 90 degrees (fig. 10.4), permitting it to fit into the hip socket or

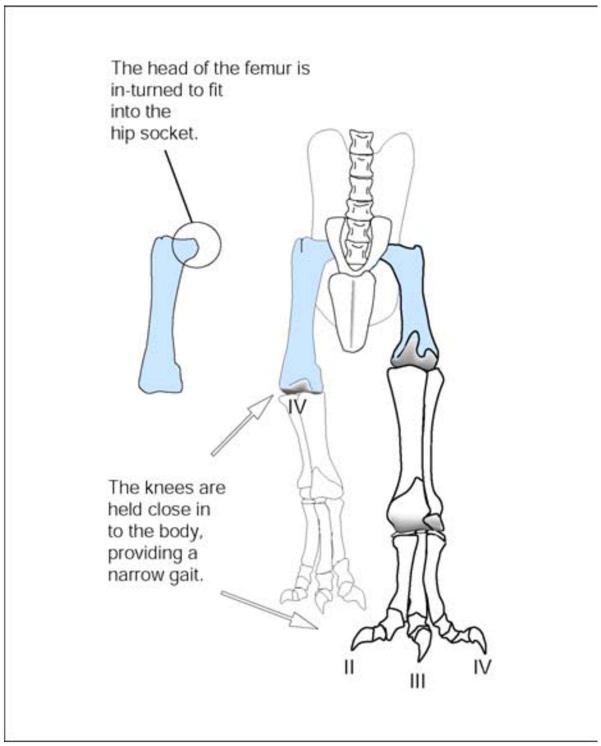

Figure 10.4. The head of the femur is in-turned to fit into the hip socket, giving dinosaurs a narrow gait, with the knees held closely in to the body.

acetabulum. Consequently, the femur is held vertically along side the body, and the hip socket has a hole where, in other reptiles, it is solid. Also, the entire pelvis, which attaches to the backbone at the *sacrum*, is elongated and reinforced to withstand great forces. So, the knees of dinosaurs are turned forward and held against the body, and the head of the thigh bone presses upward against the top of the hip socket. Dinosaurs had a narrow gait, their feet striking the ground beneath the body instead of sprawling out to the side as in lizards. Mesozoic trackways confirm this (fig. 10.5).

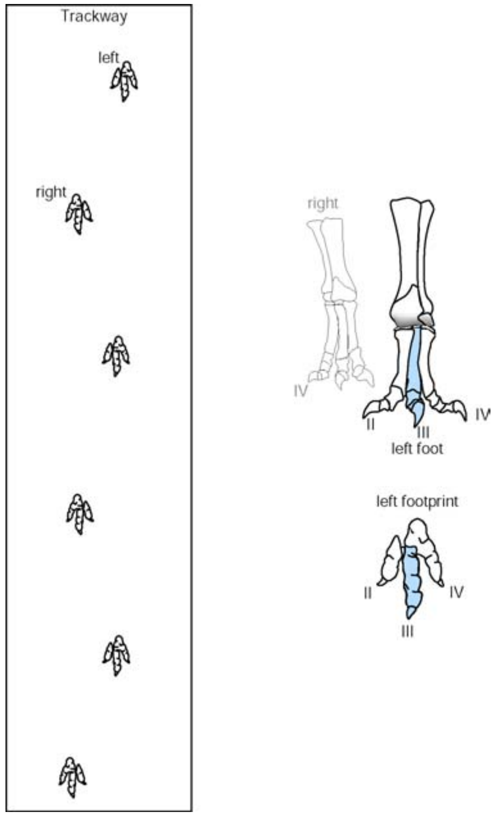

Figure 10.5. The feet of early dinosaurs left narrow three-toed trackways, indicating that the limbs were held close to the sides.

Owen pointed out that dinosaurs more closely approach the limb structure found in mammals than in other reptiles. This was a striking observation because mammals were then viewed as representing a higher level of creation than reptiles, yet here were reptiles that approached that high plane. Moreover, these long-extinct reptiles appeared far more advanced than any living reptiles. Weighing this evidence, Owen wrote, "The combination of such characters, some, as the sacral ones, altogether peculiar among reptiles, other borrowed, as it were, from groups now distinct from each other, and all manifested by creatures far surpassing in sized the largest of existing reptiles, will, it is presumed, be deemed sufficient ground for establishing a distinct tribe or sub-order of Saurian Reptiles, for which I would propose the name of *Dinosauria*."[1]

Major parts of the dinosaur skeleton remained unknown to Owen in 1841. Consequently, his reconstructions of the entire animals were based on some guesswork that later proved false. Owen knew nothing of the dinosaur hand and at first reconstructed them walking on all fours like giant bears. Nearly two decades later more complete skeletons were discovered, indicating that *Iguanodon*, *Megalosaurus*, and many other dinosaurs habitually walked on their hind limbs alone. But despite incomplete evidence, Owen drew remarkable insights about dinosaurs right from the start. On the last page of his 1842 manuscript, he wrote, "The Dinosaurs, having the same thoracic structure as the Crocodiles, may be concluded to have possessed a four-chambered heart; and, from their superior adaptation to terrestrial life, to have enjoyed the function of such a highly-organized centre of circulation in a degree more nearly approaching that which now characterizes the warm-blooded Vertebrata."[1] To Owen, these skeletons were not merely giant lizards. They bore distinctive anatomical resemblances to modern warm-blooded mammals and birds.

Dinosaurs and Evolution

Owen's remarkable conception of dinosaurs alone might have insured the group's popularity. But another thrust of his 1842 report insured that dinosaurs would always remain at the forefront of scientific thought. Owen tied dinosaurs to the theory of evolution.

By the 1840's, the scientific community was reacting to the influential work of James Hutton, George Cuvier, and Charles Lyell, as their logic and observations transformed geology into a testable science. In addition, naturalists had already been discussing various theories of evolution or transmutation of species for several decades. Darwin's grandfather Erasmus had written a book on the subject and several theories had been advanced by the great French biologists Geoffroy St Hilaire and Jean Baptiste Lamarck (fig.10.6). Darwin's ideas were as yet only sketches in one of his notebooks and remained unpublished.

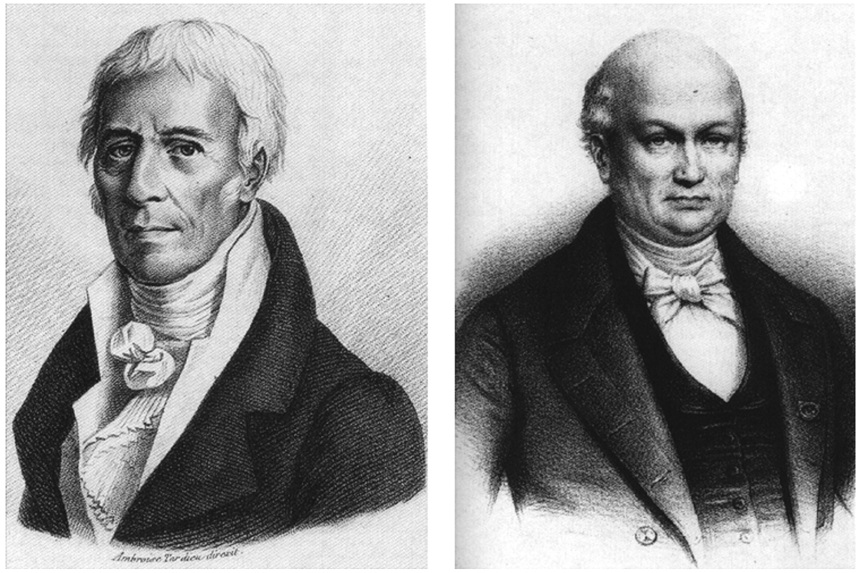

Figure 10.6. Jean-Baptist Lamarck (left) and his compatriot Etienne Geoffroy Saint-Hilaire (right) both formulated early ideas about evolution that Richard Owen used dinosaurs to refute. (from: Desmond, A., 1989, The Politics of Evolution. University of Chicago Press, Chicago, figures 2.3, 7.2).

Like Darwin's, early theories of evolution tried to explain a variety of patterns in Nature. One compelling pattern was the orderly succession of groups in the fossil record. As we saw earlier, George Cuvier interpreted the succession of fossils in rocks around Paris as evidence of successive catastrophes. By Owen's time much of Britain had been geologically mapped by Hutton and his successors. Knowing the stratigraphic sequence of rock layers, geologists could determine which of two fossils is younger and which is older. And there was a consistent pattern. The oldest vertebrate fossils, from the stratigraphically lowest rocks, mostly Paleozoic in age, were fishes. Only in younger Mesozoic rocks did the first land-dwelling tetrapods appear, and mammals and birds were confined to still younger Cenozoic rocks. Early evolutionary theorists attempted to account for this orderly succession by invoking a process of progress. Evolution proceeded as a progressive ascent on the "scale of nature". Later organisms exhibited what were deemed to be evolutionary "improvements" over earlier organisms. Owen's first study on dinosaurs would refute this view.

Owen observed that "many races of extinct reptiles have succeeded each other as inhabitants of the portion of the earth now forming Great Britain; their abundant remains, through strata of immense thickness, show that they have existed in great numbers, and probably for many successive generations." He then asked, "To what natural or secondary cause...can the successive genera and species of Reptiles be attributed? Does the hypothesis of transmutation of species, by a march of development occasioning a progressive ascent in the organic scale, afford any explanation of these surprising phenomena? Do the speculations of Maillet, Lamarck and Geoffroy derive any support or meet with additional disproof from the facts already determined in the reptilian department of Palaeontology?"[1]

Ideas about progressive evolution were rejected by later scientists because they made testable predictions about the distribution of organisms in time and space that were refuted by observations of Nature. In this way, Owen used dinosaurs to test and reject the hypothesis. Progressive evolution predicted that modern reptiles should be more advanced than their extinct counterparts. However, Owen observed that "The period when the class of Reptiles flourished under the widest modifications, in the greatest number and the highest grade of organization, is past; and, since the extinction of the Dinosaurian order, it has been declining. The Reptilia are now in great part superseded by higher classes: Pterodactyles have given way to birds; Megalosaurs and Iguanodons to carnivorous and herbivorous mammalia; but the sudden extinction of the one, and the abrupt appearance of the other, are alike inexplicable on any known natural causes or analogies."[1] If evolution occurred at all, it was not via the march of progress envisioned by Owen's French colleagues.

Owen was right, but history has treated him harshly because he advocated a view with even less merit than progressive evolution. His 1842 report concluded that "The evidence..., permits of no other conclusion than that the different species of Reptiles were suddenly introduced upon the earth's surface, although it demonstrates a certain systematic regularity in the order of their appearance... Thus, though a general progression may be discerned, the interruptions and faults, to use a geological phrase, negative the notion that the progression has been the result of self-developing energies adequate to a transmutation of specific characters; but on the contrary, support the conclusion that the modifications of osteological structure which characterize the extinct Reptiles, were impressed upon them at their creation, and have been neither derived from improvement of a lower, nor lost by progressive development into a higher type."[1] And with that, Owen's life-long campaign against evolutionists began.

Darwinian Evolution

Darwin's theory of evolution basically states that descent with modification is the process that has yielded today's diverse biota. All species, however divergent, are related, more or less closely, to each other through a long chain of ancestors and descendants. Speciation, the process of diversification, is influenced by a variety of mechanisms.

The principle mechanism of evolutionary change, according to Darwin (fig. 10.7), is natural selection that results from a struggle for survival faced by all organisms.

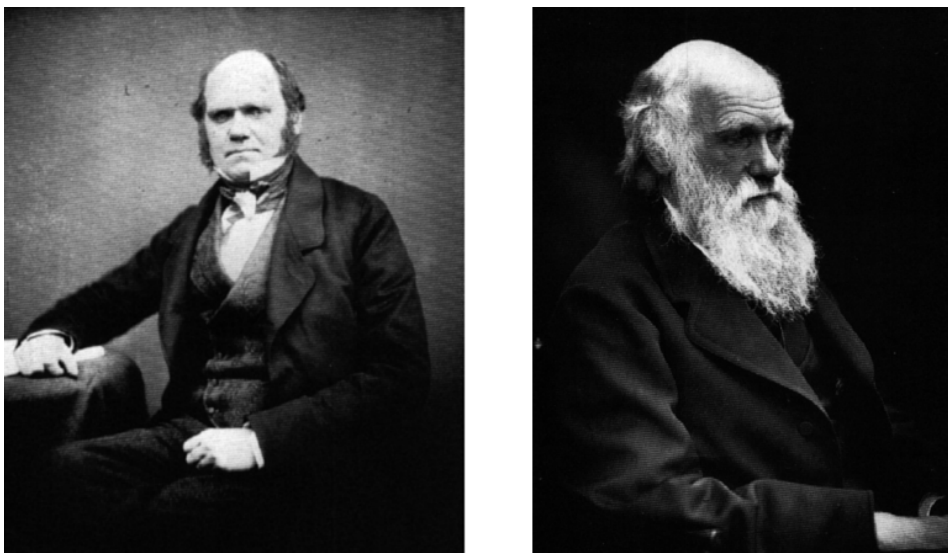

Figure 10.7. Charles Darwin in 1854 (left), at the time he began full-time research on species, and 20 years later (right). (from: Desmond, A., and J. Moore, 1991, Darwin - the life of a tormented evolutionist. Warner Books, fig. 51).

He described it this way:

> "A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one

individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase in food, and no prudential restraint from marriage. Although some species may be now increasing, more or less rapidly, in numbers, all cannot do so, for the world would not hold them."[7]

A pool of natural variation is present among individuals in any population or species, and natural selection favors traits in the pool that enhance the survival of some individuals over others. Over the vastness of geological time, survival of the fittest leads to gradual change of characteristics from one generation to the next, so descendants differ markedly from their distant ancestors. In a similar way, humans have artificially selected the traits of domestic animals and crops possessing desirable traits, whereas individuals lacking those traits are prevented from breeding. So, domestic organisms are quite different from their closest wild relatives. With sufficient time, natural selection may produce new races and species or lead to extinction:

"As man can...and... has produced a great result by his methodical and unconscious means of selection, what may not nature effect? ... natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the long lapses of ages, and then so imperfect is our view into long lost geological ages, that we only see that the forms of life are now different from what they formerly were."[7]

Darwin's theory of natural selection is often thought to be synonymous with his theory of evolution, but they are really two distinct theories. The theory of evolution relates the process of descent to the pattern of diversity that exists today. Darwin's theory of evolution differs from other theories by saying that descent leads only to divergence, and not necessarily to progress. Both progressive and degenerative changes could occur, depending on whatever particular mechanism of change was operating on a particular lineage. Descendants will simply be different from their ancestors to greater or lesser degrees, not necessarily better or worse.

Natural selection, on the other hand, is a separate theory about one of several mechanisms that might drive an episode of diversification. Darwin identified several other mechanisms as well, such as sexual selection and what he called blending inheritance. Because genetics and genes had yet to be discovered, some of Darwin's ideas about evolutionary mechanisms, like blending inheritance, have been refuted by later researchers. Identifying which mechanisms have operated in particular evolutionary cases has always been the most problematic and controversial aspect of Darwinian evolution. Even Darwin's strongest supporters, including Thomas Huxley, had a hard time accepting the slow, gradual mechanism of natural selection, and with good reason as we will see in a later chapter. But Darwin's basic tenet of evolution, descent with modification, remains the grand unifying theory of biology. Of course in the mid-19th century these issues were far less clear. By the time Darwin published his theory in 1859, numerous theories had been advanced and refuted. After all, Owen had been correct in refuting the progressive evolution of Lamarck. Any new theory about evolution should be met with healthy skepticism.

One of the earliest and greatest tests of Darwinian evolution involved the fossil record. All debaters agreed that today's diverse species are not arrayed into a complete continuum of form, and that Nature is instead divided into distinctive clumps of species separated by wide gaps. Green plants are unmistakably different from animals, turtles from birds, and so on. Within larger groups, smaller groups and gaps are also discernible. Among birds, humming birds, woodpeckers, and ducks are readily distinguished. The critics of evolution asked, if today's diversity emerged by gradual modification from some common ancestral form, why do these gaps exist?

In response, Darwin's ally, Thomas Huxley (fig. 10.8), argued that "We, who believe in evolution, reply that these gaps were once non-existent; that the connecting forms existed in previous epochs of the world's history, but that they have died out."[8]

Living lineages, however distinctive and different from one another, should be connected in the past through their fossil records.

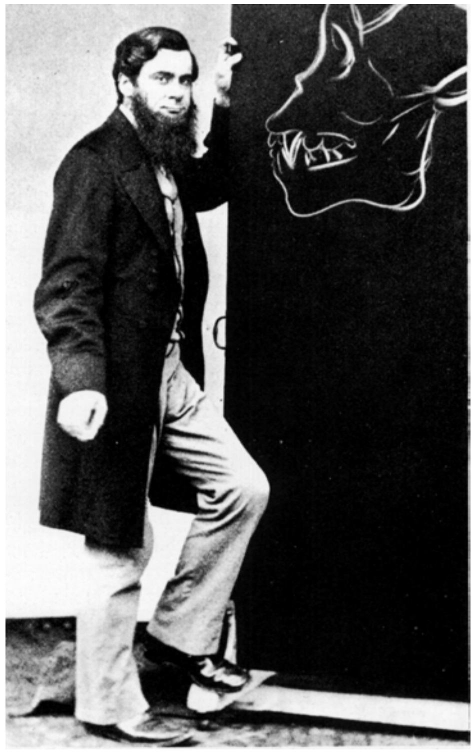

Figure 10.8. Thomas Huxley, one of Darwin's greatest supporters and the first great promoter of the dinosaur-bird hypothesis. (from: Desmond, A., and J. Moore, 1991, Darwin - the life of a tormented evolutionist. Warner Books, fig. 63).

Testability was the standard for Darwin's scientific theory, as it had become for the geological sciences in the decades preceding publication of the *Origin*. Naturally, evolutionists were challenged to produce evidence of the extinct transitional forms that Darwin's theory predicted. But just as incompleteness of the rock record compromises our ability to test between catastrophic and gradualistic explanations for the K-T extinction episode, incompleteness also compromises our ability to connect lineages back through time. Darwin appreciated this and explained that we should expect such gaps.[7] Fossilization is an exceptional process. Only a minute fraction of the organisms that have lived on Earth are preserved as fossils; far fewer yet have been discovered by naturalists. So, our record of ancient life is highly incomplete.

Darwin’s critics labeled this as an excuse to cover another fundamentally flawed theory of evolution. And without any transitional fossils to counter this claim, they might just as well have been right.

The Problem with Birds

When *The Origin of Species* hit the newsstands, one of the most glaring gaps in the fossil record was the early history of birds. Birds are highly distinctive. Nobody would mistake a bird for any other animal. But in the mid-19th century their fossil record appeared to begin abruptly during the Tertiary. Some naturalists argued that some three-toed Mesozoic trackways were made by more ancient birds. But some of these were much too large for known birds to make, so most naturalists agreed with Richard Owen that these "Foot-prints alone....are insufficient to support the inference of the possession of the highly developed organization of a bird of flight by the creatures which have left them."[1]

The earliest known fossil birds were already very highly modified, having wings and the ability to fly. And at their first appearance in the fossil record, there were already a number of different lineages. To Owen, this reflected the pattern of creation. Darwinians, however, viewed this as an artifact of an incomplete fossil record. They predicted that a long pre-Tertiary history of fossil birds linking the various bird lineages together through common ancestors would eventually be found, as well as fossil "protobirds" linking birds with other tetrapods. But if this is true, where were the fossils?

Compounding the incompleteness problem, birds are so distinctive that evolutionists weren’t sure which other tetrapod represented their closest living relative. With their warm-bloodedness, feathers, and flight, birds seemed as different from other tetrapods, as tetrapods are from fish. All tetrapods, including birds, mammals, crocodylians, lizards, turtles, and amphibians, could be distinguished from fish by their four limbs. Turtles, lizards, and crocodylians were all cold-blooded and had scales. So they belonged to a group within tetrapods called reptiles. But that was as far as general agreement went.

This limited understanding was reflected in the classification system used at that time. Owen and Darwin were basically still using Linnaeus' system. Birds, mammals, reptiles, amphibians, and fishes were each placed in a separate Class, a Linnaean rank denoting a large group that looks very distinct from other animals. Class Aves, for birds, was equal to but entirely separate from Class Reptilia, Class Mammalia, and Class Amphibia. While this allowed all animals to be properly classified in the Linnaean system - it ignored the critical genealogical question: are birds more closely related to mammals, reptiles, or amphibians?

Working in 1763, Linnaeus had no idea that species were related, so he never attempted to design a system of classification that reflected genealogy. But as the Darwinian Revolution swept across the scientific community, naturalists began to search for the closest relative of birds. Most naturalists speculated that birds were most closely related to reptiles, but which reptiles? Some allied birds with turtles, based on the shared presence of a toothless, horn-covered bill or beak. Other naturalists allied birds with crocodylians or lizards. Richard Owen classified animals based on "unity of type" not genealogy. His solution to the problem was to classify birds and mammals together based on warm-bloodedness. But if Darwin was right about all species being related, these possibilities could not all be true. There could be only one true, historic set of relationships. Who were the closest living relatives of birds? Who were the ancestors of birds among extinct organisms?

Archaeopteryx and Evolution

Two years after publishing *On The Origin of Species,* Darwin was under attack in both the scientific and popular press. And then, *Archaeopteryx* was discovered. It was an instant scientific sensation as both evolutionists and anti-evolutionists claimed it as their prize, and used it to open a new battlefront in the escalating war over evolution.

It is difficult to imagine a more highly charged atmosphere than the one existing when *Archaeopteryx* was discovered. Its Late Jurassic age fitted Darwinian predictions perfectly. The feather impressions looked like modern bird feathers down to their microscopic detail. But *Archaeopteryx* also had a long bony tail, more like the cold-blooded reptiles than any living birds. In addition, the three fingers of its hand (or wing) were separate, with claws on the end. Modern birds have three fingers that fuse into a single bone to help strengthen the wing. And who ever heard of a bird with claws on its hands? Were these the primitive features expected in a Mesozoic intermediate between birds and other tetrapods?

On November 9, 1861, Professor Andreas Wagner, a distinguished German paleontologist, announced the discovery of what would become known as the London specimen at a meeting of the Royal Academy of Sciences of Munich. However, the real issue of Wagner's address was evolution. Wagner had never actually seen the skeleton, so he relied upon a report by a lawyer named Witte who had seen it in Karl Häberlein's possession. As Owen later recounted the story, "Upon the report thus furnished to him, Professor Wagner proposed for the remarkable fossil the generic name *Griphosaurus*, conceiving it to be a long-tailed Pterodactyle with feathers. His state of health prevented his visiting Pappenheim for a personal inspection of the fossil; and, unfortunately for palaeontological science, which is indebted to him for many valuable contributions, Professor Wagner shortly after expired."[9]

Wagner's terminal scientific thought that night was a shot at evolution: "In conclusion, I must add a few words to ward off Darwinian misinterpretation of our new saurian. At the first glance of the *Griphosaurus* [Wagner's proposed name for *Archaeopteryx*] we might certainly form a notion that we have before us an intermediate creature, engaged in the transition from the saurian to the bird. Darwin and his adherents will probably employ the new discovery as an exceedingly welcome occurrence for the justification of their strange views upon the transformation of animals but in this they will be wrong."[10]

Archaeopteryx: Bird or Feathered Reptile?

Was *Archaeopteryx* a feathered pterosaur or some other kind of feathered reptile? Was it really a reptile-like bird--a transitional fossil like Darwin's theory predicted? Grasping instantly its pivotal importance to the debate over evolution, Owen snatched up the specimen for the British Museum. It arrived in London in 1862.

Now, with both the specimen and one of the world's premiere skeleton collections to compare it with, Owen wasted little time in responding to the speculations of evolutionists, who had never even seen it. In 1863 he published a thorough description, masterfully crafted to rebut the publicity *Archaeopteryx* had already received as a potential link between birds and reptiles.

The skeleton is divided between two halves of the split slab. Prior to burial, the skeleton became partly dismembered, and the skull and jaws were apparently lost. But most of the skeleton and many feathers were preserved. As Owen described it, "The remains of *Archaeopteryx*, as preserved in the present split slab of lithographic stone, recalled to mind the condition in which I have seen the carcase of a Gull or other sea-bird left on an estuary sand after having been a prey to some carnivorous assailant. The viscera and chief masses of flesh, with the cavity containing and giving attachment to them, are gone, with the muscular neck and perhaps the head, while the indigestible quill-feathers of the wings and tail, with more or less of the limbs, held together by parts of the skin, and with such an amount of dislocation as the bones of the present specimen exhibit, remain to indicate what once had been a bird."[9]

Along with its size, proportions, and feathers, the skeleton showed many other resemblances to modern birds, including a wishbone or *furcula* (fig. 10.9). Among living species, the furcula is known only in birds and had never before been discovered in a fossil reptile. It represents a fusion of the right and left collar bones or *clavicles*. As a young bird embryo develops, the collar bones form separately, reflecting the condition found in most adult tetrapods. But by hatching time, the avian clavicles fuse to form the highly characteristic U-shaped furcula. Once fused, the wishbone acts as a spring to help power the flight stroke and may also facilitate breathing during flight. Because the furcula is absent in flightless birds like ostriches, some naturalists have argued that it must be an essential component of flight. Who else but a fully volant bird would have a furcula?

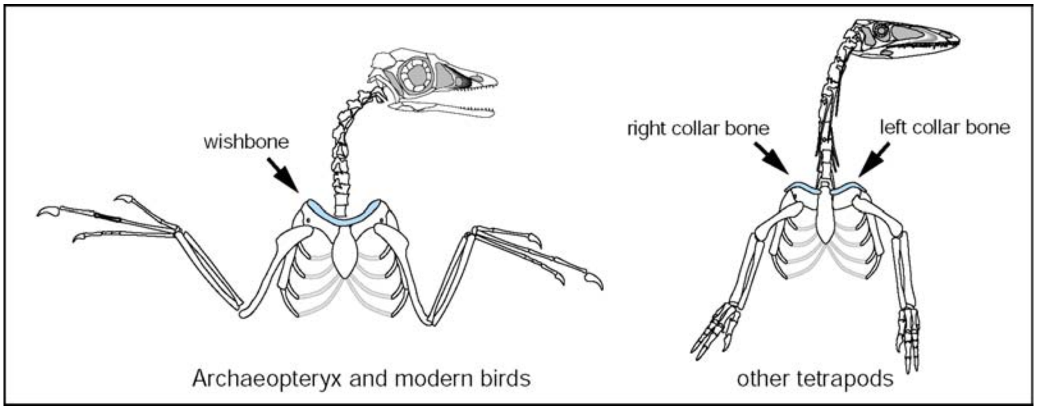

Figure 10.9. *Archaeopteryx* has what Owen considered to be definitive avian features, like the wishbone or furcula, which forms when the two collar bones become fused together.

Also bird-like (fig. 10.10) are the shoulder and arm of *Archaeopteryx*. The wrist has the half-moon-shaped semilunate carpal, just like *Deinonychus*. The hand proportions, the three fingers, and the relationships of the wing feathers to the fingers are also bird-like. Owen went to great length to show that pterosaur wings found around Solnhofen are different from *Archaeopteryx*. The pterosaur wing's membrane of skin often forms an impression on the lithographic stone. The membrane supported by the fourth finger, a digit that is entirely absent in *Archaeopteryx* and adult living birds. This was clearly no feathered pterosaur, as Andreas Wagner had claimed.

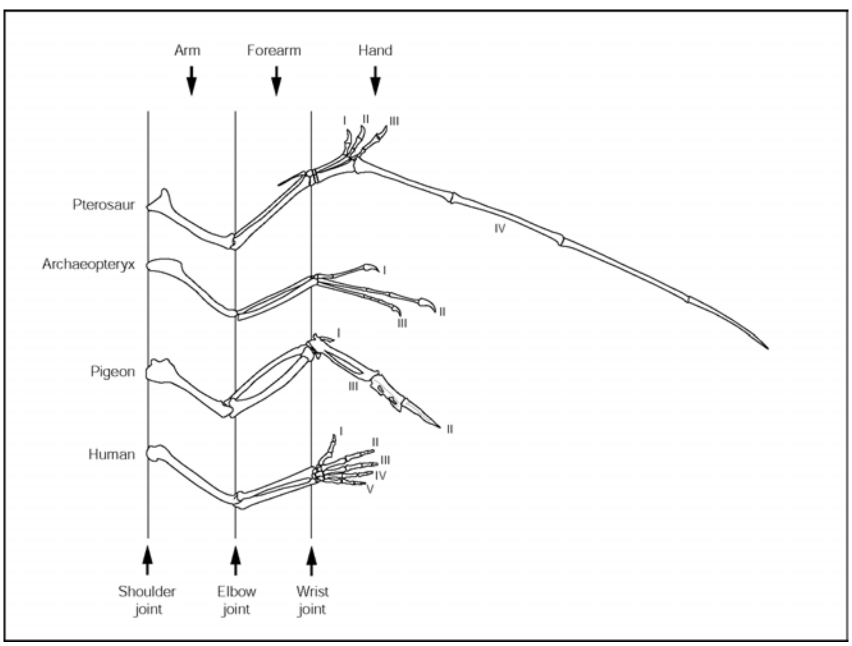

Figure 10.10. The arms of a pterosaur, *Archaeopteryx*, a modern bird, and a human compared.

Owen reported that the pelvis and hindlimb are especially bird-like. One of the most important resemblances is in the sacrum, and the pelvis that attaches to it. The sacrum is composed of separate vertebrae whose short and massive ribs attach to the inside of the pelvis, anchoring the backbone to the hindlimb. The elongated sacrum in *Archaeopteryx* and modern birds is massive and reinforced to withstand the forces generated in landing. The inner wall of the hip socket is perforated (fig. 10.11). The head of the thighbone is bent sharply to fit deeply into the hip socket, in characteristically avian fashion. Even more bird-like, the bones of the ankle are fused together, some to the end of the shin, others to the top of the foot, producing a hinge-like ankle. The upper foot bones, the metatarsals, are partially fused as well for both strength and stability. Three toes point forward, while the first toe is turned backwards so that it can grasp against the other three. Does this sound familiar?

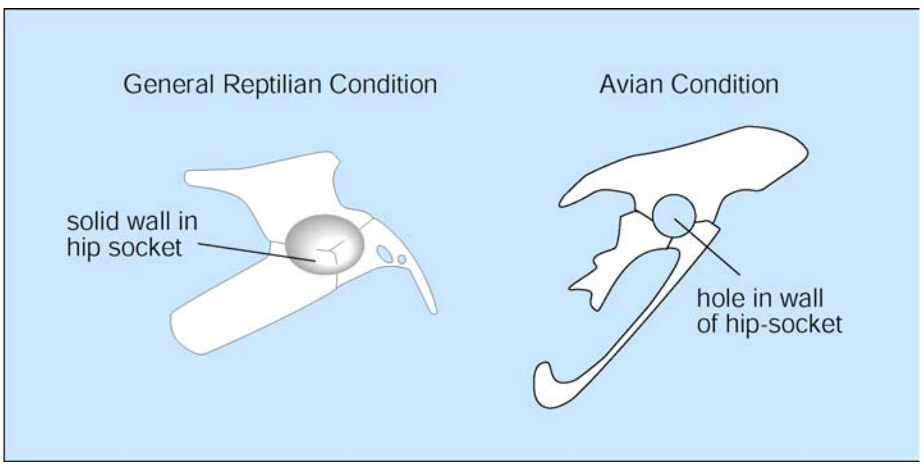

Figure 10.11. The hip socket or acetabulum is perforated in *Archaeopteryx* and other birds, contrasting with the general reptilian condition in which there is a solid wall inside the socket.

Owen noted that the limb bones in *Archaeopteryx* are hollow, thin-walled tubes. Modern birds have an expanded lung system that extends throughout much of the body as a series of air sacs. They enhance the efficiency of oxygen extraction by the lungs and lighten the skeleton. Some air sacs actually extend into the hollows of the bones. The first clues to this remarkable lung system were discovered a century before Owen set eyes on *Archaeopteryx*. In 1758, John Hunter, a leading British physician and naturalist, discovered the unique connection. After tying closed the windpipe of a domestic fowl, he cut through the humerus, the bone between shoulder and elbow, and "found that the air passed to and from the lungs by the canal in this bone. The same experiment was made with the os femoris [the femur] of a young hawk, and was attended with a similar result."[11] Hunter had demonstrated that birds' bones contain air, not marrow, and that the air spaces are connected to the respiratory system. The hollow skeleton of *Archaeopteryx* was further evidence that it is a bird.

But Owen noted striking differences between *Archaeopteryx* and modern birds, and it is these features that caused the sensation surrounding its discovery. Its peculiar hand had three separate fingers, two of which were equipped with claws. The unusual, eight-inch-long, bony tail was composed of sixteen vertebrae, and impressions indicated that the quills of the tail feathers were attached to the vertebrae by thin ligaments. In modern birds, there are only a few vertebrae at the base of their stubby tail, and the tail feathers attach to a plow-shaped bone at the end of the backbone known as the *pygostyle*. Were the evolutionists right that these are transitional features, or was *Archaeopteryx* just another bird ?

Utilizing his understanding of embryology, Owen downplayed the importance of these potentially transitional features. He pointed out that the embryonic pygostyle forms from separate cartilages, like the separate vertebrae in *Archaeopteryx*, before they fuse to form the adult pygostyle (fig. 10.12). Similarly, the avian hand forms from the fusion of the second and third fingers, which are separate in early development. To Owen, both the hand and tail of *Archaeopteryx* were minor developmental variants of the basic avian plan; similar variants are seen in the tails of bony fishes and other vertebrate groups. And the presence of claws, Owen argued, was highly variable in living groups. Even some modern birds, like the Kiwi, have a claw on the end of one finger in the hand.

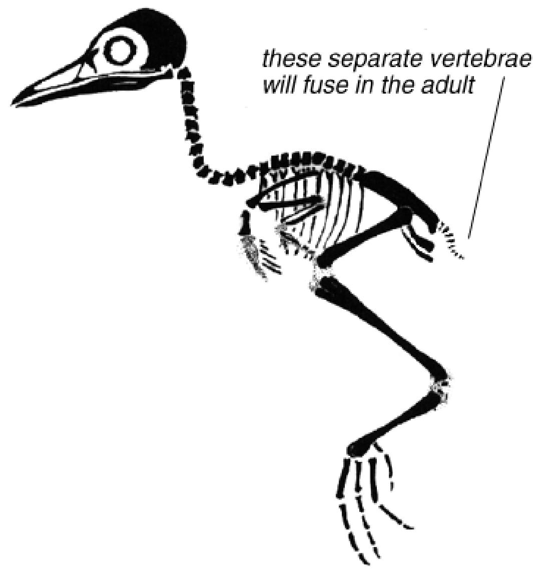

Figure 10.12. In embryonic birds and young hatchlings, the tail is made up of several separate bones or cartilages, like the adult tail of Archaeopteryx. In modern birds, these separate elements eventually fuse to become the adult pygostyle. (from Gill, F. B., 1995, Ornithology. W. H. Freeman & Co., New York, figure 5-11)

In summation, Owen counterattacked against Darwin, "Thus we discern, in the main differential character of the by-fossil-oldest known feathered Vertebrate, a retention of a structure embryonal and transitory in the modern representatives of the class, and a closer adhesion to the general vertebrate type.... The best-determinable parts of its preserved structure declare it unequivocally to be a bird, with rare peculiarities indicative of a distinct order in that class."[9] The differences between *Archaeopteryx* and other birds were minor compared to the overall similarities in the skeleton and the presence of feathers. In Owen's view, *Archaeopteryx* fell squarely in the Class Aves; it was not transitional between birds and reptiles.

Bridging the Gap

But to an equally famous evolutionist like Thomas Huxley, *Archaeopteryx* looked like a perfect transition between birds and reptiles, suggesting that one Class could "transmute" into another.[12] Furthermore, Huxley loathed Owen, and relished the opportunity for a fight. Their personal acrimony spilled out into the tabloids, and the debate became highly adversarial.

Unlike Owen, Huxley compared *Archaeopteryx* to fossil reptiles as well as to living birds, noting that today "no two groups of beings can appear to be more entirely dissimilar than reptiles and birds. Placed side by side, a Humming-bird and a Tortoise, an Ostrich and a Crocodile offer the strongest contrast, and a Stork seems to have little but animality in common with the Snake it swallows."[13] He then asked, "How far can this gap be filled up by the fossil records of the life of past ages? This question resolves itself into two: - 1. Are any fossil birds more reptilian than any of those now living? 2. Are any fossil reptiles more bird-like than living reptiles?"[13]

Huxley answered both in the affirmative. For a fossil bird more reptilian than any modern bird, Huxley of course pointed to *Archaeopteryx*. Like reptiles, the digits of the hand are unfused, and two of them have claws, whereas in living birds there is never more than one claw. The long tail made up of separate vertebrae is also reptilian. Owen's objection that these were merely embryonic and transitory structures notwithstanding, Huxley concluded "it is a matter of fact that, in certain particulars, the oldest known bird does exhibit a closer approximation to reptilian structure than any modern bird."[13]

In answering the second question, Huxley slapped Owen's face by turning to Dinosauria, the very group Owen had discovered. In the two decades since Owen named Dinosauria, great new discoveries of dinosaurs had been made in Britain, Germany, and North America. They showed that some dinosaurs walked on their hindlimbs like birds. Mesozoic trackways confirmed this and showed, moreover, that both huge animals and tiny ones were walking bipedally. In Bavaria a nearly complete skeleton as old as *Archaeopteryx* was described and named in 1861 by Andreas Wagner, shortly before his death.[14] *Compsognathus longipes* is only about two-thirds of a meter long. Wagner recognized it as a reptile, but failed to see what kind.

The brilliant German anatomist and evolutionist Carl Gegenbaur studied *Compsognathus* (fig. 10.13) soon after its discovery.[15] He observed that its ankle closely resembled the ankle of birds, one of the features Owen had used to place *Archaeopteryx* within birds. Huxley instantly concurred with Gegenbaur, adding that "there can be no doubt that the hind quarters of the Dinosauria wonderfully approached those of birds in their general structure, and therefore that these extinct reptiles were more closely allied to birds than any which now live."[16] Huxley also recognized that *Compsognathus* must be "placed among, or close to, the Dinosauria; but it is still more bird-like than any of the animals which are ordinarily included in that group."[13]

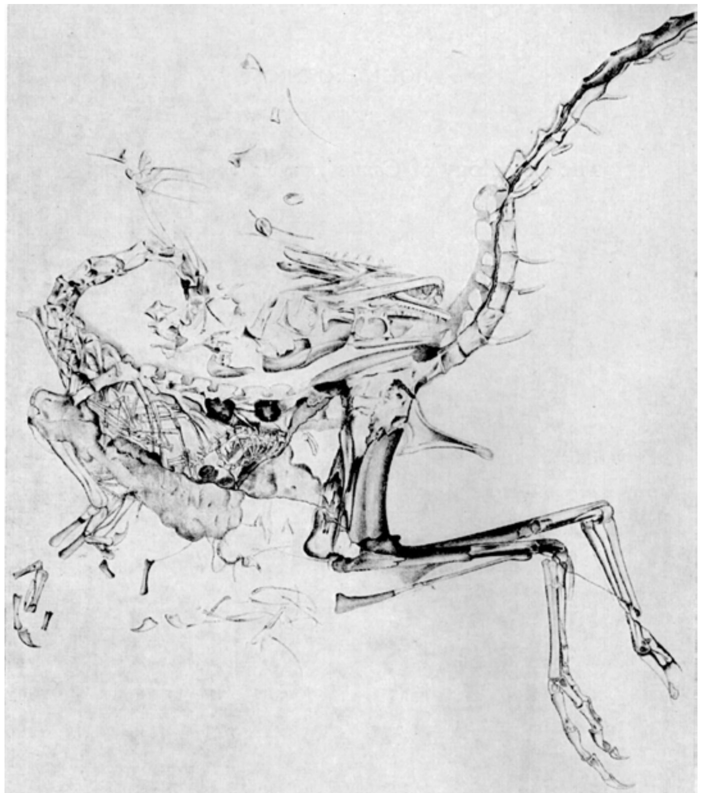

Figure 10.13. The skeleton of *Compsognathus* was found in the Solnhofen Limestones at about the same time as Archaeopteryx. It led the great German anatomist and developmental biologist to discover the connection between Mesozoic dinosaurs and modern birds. (lithograph courtesy of John Ostrom).

Huxley next turned to embryology, highlighting a special similarity between dinosaurs and young embryonic birds. Expanding on Gegenbaur's observations, he described the leg and ankle of a young Dorking fowl, concluding that if "found in the fossil state, I know not by what test they could be distinguished from the bones of a Dinosaurian. And if the whole hindquarters, from the ilium to the toes, of a half-hatched chicken could be suddenly enlarged, ossified, and fossilized as they are, they would furnish us with the last step of the transition between Birds and Reptiles; for there would be nothing in their characters to prevent us from referring them to the Dinosauria."[16]

Many characters that Huxley used to identify *Compsognathus* as a dinosaur were the same ones Owen had used to define Dinosauria, and Huxley must have appreciated the irony of it. The fact that two specimens of *Archaeopteryx* were long mistaken for

Compsognathus further highlights the degree of resemblance. *Compsognathus* has the sacrum and hip of a dinosaur but the foot more like that of a bird. The major difference is that the metatarsal bones remain separate in *Compsognathus*, whereas they become fused in birds. It was surprising to find these features in such a small animal, however. Dinosaurs were supposed to be huge. But other paleontologists quickly saw the resemblance, and the idea of a close connection between birds and dinosaurs found a wide following over the next few years.

Huxley even inferred that the physiology of dinosaurs might have achieved a level found in modern birds. "Birds have hot blood, a muscular valve in the right ventricle, a single aortic arch, and remarkably modified respiratory organs; but it is, to say the least, highly probable that the Pterosauria, if not the Dinosauria, shared some of these characters with them."[17] Huxley and Owen had both seen bird-like features in extinct dinosaurs.

The Theory of Homoplasy or Independent Evolution

Showing that there were tiny, more birdlike dinosaurs closed the gap between birds and reptiles even more than *Archaeopteryx* had, by linking birds with a particular kind of reptile. For both Huxley and John Ostrom a century later, it was also the critical step in connecting birds to dinosaurs.

So what happened to the connection? Why did *Deinonychus* resurrect the point Huxley apparently won a century before? What changed the scientific world's mind in the last quarter of the 19th century?

Owen's protégé, Harry Seeley proposed the argument at one of Huxley's lectures before the Geological Society of London (fig. 10.14). Huxley cited the similarities in the hindlimb of birds and dinosaurs as evidence of a close evolutionary relationship. At the end, as recorded by the secretary of the society, Seeley rose and noted “that the peculiar structure of the hinder limbs of the Dinosauria was due to the functions they performed rather than to any actual affinity with birds.”[16] Later, he enlarged on the idea: “All the characters whereon are based the claim of dinosaurs to be regarded as the ancestors of birds are only related to the power of keeping an upright position upon the hind feet.”

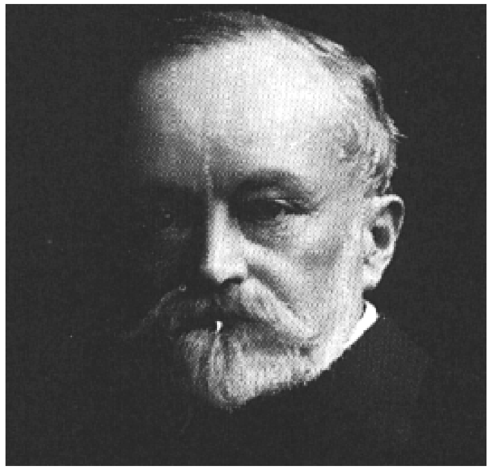

Figure 10.14. Harry Seeley, who first articulated what was later known as the theory of homoplasy. (from Desmond, A., 1982, Archetypes and Ancestors. London, Blond and Briggs).

Seeley claimed that the resemblances between birds and dinosaurs, like running on the hind limbs, could have evolved independently. No close evolutionary connection was necessary. Natural selection might possibly shape comparable evolutionary solutions in distant relatives, owing to comparable demands of the environment. Seeley in addition believed that the linking together of extinct lineages, as Huxley was trying to do with birds and dinosaurs, was virtually impossible. Lastly, he noted that only some, not all, dinosaurs have the bird-like resemblances. There was a mosaic of characters distributed among these fossils that he argued were best interpreted as independent acquisitions.

This notion was eventually termed the *theory of homoplasy*.[18] Homoplastic features are corresponding and similar parts in different organisms whose similarity is not inherited from a common ancestor. Independent acquisitions like the wing of a bird and a bat are said to be homoplastic because, based on what we know about their relationships, we can conclude that their wings evolved independently. The last common ancestor shared by birds and bats did not fly.

The theory of homoplasy was widely accepted by naturalists. Those who supported dinosaurian ancestry complicated the problem by arguing over which dinosaur was the ancestor. Some would derive birds from the carnivorous dinosaurs while others argued that it was the herbivorous forms like *Iguanodon* that held the ancestry of birds. Even Huxley later straddled the fence. Although he derived birds from reptiles, he did not subscribe to the direct derivation of birds from dinosaurs, stating "It may be regarded as certain that we have no knowledge of the animals which linked reptiles and birds genetically, and that the Dinosauria, with *Compsognathus*, *Archaeopteryx*, and the struthious birds only help us to form a reasonable conception of what these intermediate forms may have been."[16]

The $64 Question

What Huxley had originally resolved into two questions, paleontologists now resolved into one: are birds directly descended from dinosaurs or not? Huxley had answered the question with a strong affirmative to an initially warm reception. But his following in the scientific community on this point steadily diminished toward the end of the century. One reason is that no known dinosaur presented a suitable ancestor. The particular mosaic of characters observed in known fossils seemed to disqualify each one of them. One seemingly insurmountable problem was that no dinosaur was known to have clavicles - the collar bones - and without the clavicles where could the furcula come from? Several influential paleontologists argued that complex features like the clavicles, once lost, could never reappear. *Dollo's Law*, as it was called, seemed to put the last nail in the coffin for dinosaurs as the ancestors of birds. According to Dollo's law, once complex features like a clavicle have evolved and then been lost, they were unlikely to ever reappear. As we will see, there are many exceptions to Dollo's law, which has been discarded. But for a time it seemed to offer a more accurate explanation for the actual patterns observed in the paleontological record. Birds and dinosaurs evolved as separate lineages arising from some earlier, common ancestor. Any advanced similarities they might share must have arisen numerous times.

Several additional discoveries were taken to support this view. The discovery of part of the head and jaws of *Archaeopteryx* on the London slabs must have embarrassed Owen, who had seen the bones but dismissed them as belonging to a fish. The jaws had teeth, but the braincase was indicative of a big brain, like living birds. The Berlin *Archaeopteryx* came to light at about this time, confirming the presence of teeth in a fossil bird. The discovery of additional toothed Mesozoic birds by O. C. Marsh in the Cretaceous chalks of Kansas seemed to add support to the homoplasy theory. His two most complete finds were *Hesperornis* and *Ichthyornis*, both of which were aquatic, and had a mosaic of characters best explained as having evolved independently from the comparable features in dinosaurs. The common ancestor for the two groups must have existed in the early Mesozoic, or before.

In Robert Broom's hands, the Early Triassic *Euparkeria* became the perfect candidate for the ancestor from which birds and dinosaurs split off. It was almost uniformly primitive. Crocodylians, birds, dinosaurs, and pterosaurs could all have evolved directly from *Euparkeria* or from something very much like it. There were several other primitive archosaurs, all poorly known, of Triassic age, that became grouped together with *Euparkeria*. Somewhere within this assemblage of primitive archosaurs, named Thecodontia, was the ancestor. The thecodont ancestry of birds was the most popular view from then on, or at least until *Deinonychus* raised its distinctive bird-like head.

By the time Ostrom began to suspect that *Deinonychus* was more than just another dinosaur, the homoplasy theory had even been carried to Dinosauria itself. Some paleontologists were arguing that the resemblances Owen had originally noted between the various dinosaurs were also homoplastic, and the things we call dinosaurs had evolved these features several times. Not only were birds not derived from dinosaurs, but the dinosaurs themselves did not form a natural group and were instead separately evolved from different thecodont ancestors.

The many new discoveries since 1841 only seemed to complicate our picture of the past. Did the discovery of *Deinonychus* take us a step backwards or a step closer to answering whether birds and dinosaurs are related? By the time our first year of graduate school at Berkeley had ended, it seemed that the only thing paleontologists all agreed on is that dinosaurs are extinct.

Notes and References

1) Owen, R., 1842. Report on British Fossil Reptiles, 1841. Report of the Eleventh Meeting of the British Association for the Advancement of Science, held at Plymouth in July, 1841: 60-204.

2) Halstead, L. B. and W. A. S. Sarjeant, 1993. *Scrotum humanum* Brookes - the earliest name for a dinosaur? Modern Geology, 18: 221-224.

3) Halstead, L. B. and W. A. S. Sarjeant, 1993. *Scrotum humanum* Brookes - the earliest name for a dinosaur? Modern Geology, 18: 221-224.

4) Halstead, L. B. and W. A. S. Sarjeant, 1993. *Scrotum humanum* Brookes - the earliest name for a dinosaur? Modern Geology, 18: 221-224.

5) Buckland, W., 1824. Notice on the *Megalosaurus* or great Fossil Lizard of Stonesfield. Transactions of the Geological Society, London, (series 2)1: 390-396.

6) Mantell, G., 1825. Notice on the *Iguanodon*, a newly discovered fossil reptile, from the sandstone of Tilgate forest, in Sussex. Philosophical Transactions of the Royal Society, 115: 179-186.

7) Darwin, C., 1859. The Origin of Species by means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life. London, John Murray, first edition.

8) Huxley, T. H., 1868. On the animals which are most nearly intermediate between Birds and Reptiles. Annals and Magazine of Natural History, 2: 66-75.

9) Owen, R., 1863. On the *Archaeopteryx* of von Meyer, with a description of the fossil remains of a long-tailed species, from the lithographic stone of Solenhofen. Philosophical Transactions of the Royal Society of London, 153: 33-47.

10) Wagner, A., 1862. On a new fossil reptile supposed to be furnished with feathers. Annals and Magazine of Natural History, (third series)9: 261-267.

11) Schmidt-Nielsen, K., 1971. How birds breathe. Scientific American, 225 (December): 72-79.

12) Cracraft, J., 1986. The origin and early diversification of birds. Paleobiology 12: 383-399; Desmond, A., 1982. Archetypes and Ancestors. London, Blond and Briggs.

13) Huxley, T. H., 1868. On the animals which are most nearly intermediate between Birds and Reptiles. Annals and Magazine of Natural History, 2: 66-75.

14) Wagner, A., 1861. Neue Beiträge zur Kenntnis der urweltlichen Fauna des lithographisches Schiefers. II. Schildkröten und Saurier. Abhandlungen der (Könighichen preussischen) Akademie der Wissenschaft, Munich 9: 65-124.

15) Gegenbaur, C., 1863. Vergleichend - anatomische Bemerkungen Über das Fusskelet der Vögel. Archiv für Anatomie, Physiologie und Wissenschaftliche Medicin 1863: 450-472.

16) Huxley, T. H., 1870. Further evidence of the affinity between the dinosaurian reptiles and birds. Quarterly Journal of the Geological Society of London, 26: 12-31.

17) Huxley, T. H., 1867. On the classification of birds; and on the taxonomic value of the modifications of certain of the cranial bones observable in that class. Proceedings of the Zoological Society of London 1867: 415-472.

18) Osborn, H. F., 1900. Reconsideration of the evidence for a common dinosaur-avian stem in the Permian. American Naturalist, 34: 777-799.