

Chapter 13 Death by Decree

In the same paper in which Richard Owen coined their name, he also claimed that dinosaurs are extinct, in an effort to disprove the idea of evolution^{1,2}. But with so much evidence linking birds and dinosaurs, why have so many evolutionists, from Huxley to Ostrom, agreed that dinosaurs are extinct?

The revolution catalyzed by Darwin's theory of evolution shed a bright new light on dinosaurs. Dinosauria represented a lineage that could evolve. Using *Compsognathus* and *Deinonychus*, Huxley and Ostrom showed that dinosaurs not only *could* evolve, but that they *did* evolve both bird-like size and bird-like features. So, if birds *did* evolve from Mesozoic dinosaurs, as the preponderance of evidence suggests, how can we say that dinosaurs are extinct?

The belief that dinosaurs are extinct is one of the great ironies of paleontology. Richard Owen is sometimes reviled for fighting throughout his life against evolution. Yet, even though modern science recognizes Darwin as the victor in this battle, the world did not go on to adopt a Darwinian view of dinosaurs. If Owen is looking down from the Hereafter, he must be gratified despite the bad press. Most people still accept his anti-evolutionary view, that dinosaurs are extinct.

Linnaeus and the Linnaean System of Nature

This paradox arose as scientists tried to map the evolutionary history of various lineages using the pre-evolutionary Linnaean system of classification and nomenclature, which for centuries was about the only system available. Up until this point in the book, we have followed a system that is strictly hierarchical and that attempts to plot all available information onto a single map of relationships, using cladistic mapping techniques. As we saw earlier, shared evolutionary novelties are the basis for phylogenetic mapping, and the map of dinosaur history that we followed to this point is our best current approximation of their relationships. But the system that we have been following up to this point was not always in use, and in its place was the Linnaean system of classification³.

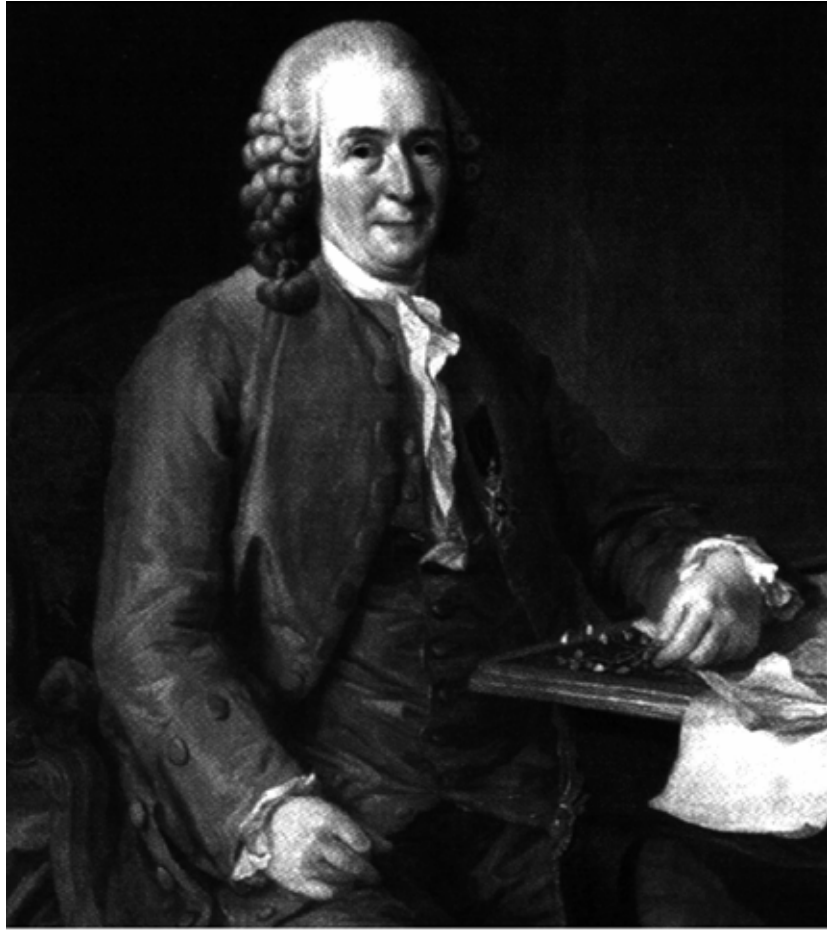


Figure 13.01 Carolus Linnaeus (1707-1778), the founder of the Linnaean system of classification, published his first great classification 101 years before Darwin's *On the Origin of Species* appeared in print.

As beginning graduate students, the prospect of studying the “science” of classification loomed before us like a barren desert of endless boredom. There were countless unpronounceable Latin names to learn and regurgitate, along with the many ranks -- genus, family, order, phylum, etc. – that were assigned to each clam, leaf, or bone fragment that we came across in an exam or on a field trip. But it was a desert that we had to cross in order to reach the professional world. The classification of organisms is the basic language that scientists use to communicate about dinosaurs and all other organisms, and we couldn't participate in that world without mastery of its lingo. Like any other language, the system of animal classification has complex rules, countless

exceptions to the rules, and a vast vocabulary. Moreover, classification systems inevitably change over time and for many technical terms an intricate maze of implied meanings has evolved over the years. So, we had to understand not only modern classification, but also the history of classifications. The only way to make it through the exams, and to get a foothold in the professional world, was to muscle your way through - memorize the glut of arcane terms and rules that had accumulated over the centuries and that could not easily be categorized and dealt with more efficiently.

The system of classification used by Owen, with which he both founded Dinosauria and proclaimed it extinct, was developed in the previous century by the great naturalist Carolus Linnaeus (1707-1778). Linnaeus (figure 13.01) was a botanist, and he became as famous as Newton and Galileo for the resounding endurance of his influence. Even during his lifetime Linnaeus was enormously famous and influential. He may be the only scientist whose death and service to his country were recorded by a European sovereign in a speech from the throne. In 1778 King Gustavus III of Sweden eulogized Linnaeus at his funeral in Uppsala, saying “I have lost a man, whose renown filled the world, and whom his country will ever be proud to reckon among her children. Long will Upsal remember the celebrity which it acquired by the name of Linnaeus.”⁴ A medal was struck in honour of Linnaeus, and his picture still appears on Swedish currency.

As his system of plant classification⁵ developed, Linnaeus’ extended his interest to practically all organisms known at the time. Linnaeus called his classification *Systema Naturae*⁶, the Natural System, although just what he meant by ‘natural’ was never clear. Before Linnaeus and for many years after, natural historians argued over what criterion should be used to classify organisms. For animals, some argued that fur or feather color was best. Others maintained that the number of fingers and toes should be used. Still others proposed that habitat or way of life were best. The problem is that different criteria produced different classifications. Late in his life, Linnaeus admitted that he had spent decades trying to articulate criteria and principles for classifying organisms, but that he had failed⁷. In the absence of clear guidelines, intuition had been his guide.

The Linnaean system grouped organisms that basically look alike and, given some key character, it established a naming system to help naturalists discuss nature in a precise and efficient fashion. Referring to groups based on their names, instead of listing

all their various characters, created a shorthand for scientific communication. For example, Linnaeus coined the name 'Mammalia' for a group of organisms whose members possess an extensive and unique suite of characteristics. In defining the name, Linnaeus enumerated what he considered to be the essential characteristics: "Mammals have a heart with two auricles and two ventricles, with hot red blood; that the lungs breathe rhythmically; that the jaws are slung as in other vertebrates, but 'covered,' i.e., with flesh, as opposed to the 'naked' jaws of birds; that the penis is intromittent; that the females are viviparous, and secrete and give milk; that the means of perception are the tongue, nose, eyes, ears, and the sense of touch; that the integument is provided with hairs, which are sparse in tropical and still fewer in aquatic mammals; that the body is supported on four feet, save in the aquatic forms in which the hind limbs are said to be coalesced into the tail."⁸ It is obviously easier to use the word 'mammal' than to list all these features every time you want to refer to the group. Of course, this only works if everyone in the conversation shares a common understanding about what the name means⁹.

In the Linnaean system, named groups are also given ranks based on their distinctiveness. The categories genus, family, order, class, phylum, and kingdom form a successively more inclusive hierarchy of ranks. A cluster of similar species would be grouped together in the same genus, whereas species that are sufficiently different would be placed in a separate genus. Similar genera would be ranked together in the same family, similar families grouped under a single order, and so on. If a species proved especially distinctive, it might also be placed in its own genus and family, or perhaps even order, to highlight this distinctiveness. The more distinctive the group, the higher the rank, and the more subjective the process became. Birds and mammals were each assigned the rank of Class to emphasize how distinctive and different these two groups are. So long as groups are assigned ranks, they need not be arrayed in a strictly hierarchical scheme based on shared inherited features. For example, the kingdoms *Plantae* and *Animalia* were regarded as fundamental divisions that are entirely separate but equal in rank. Before scientists understood that species are linked genealogically, there was no reason to unite all Life into a single hierarchy of relationships.

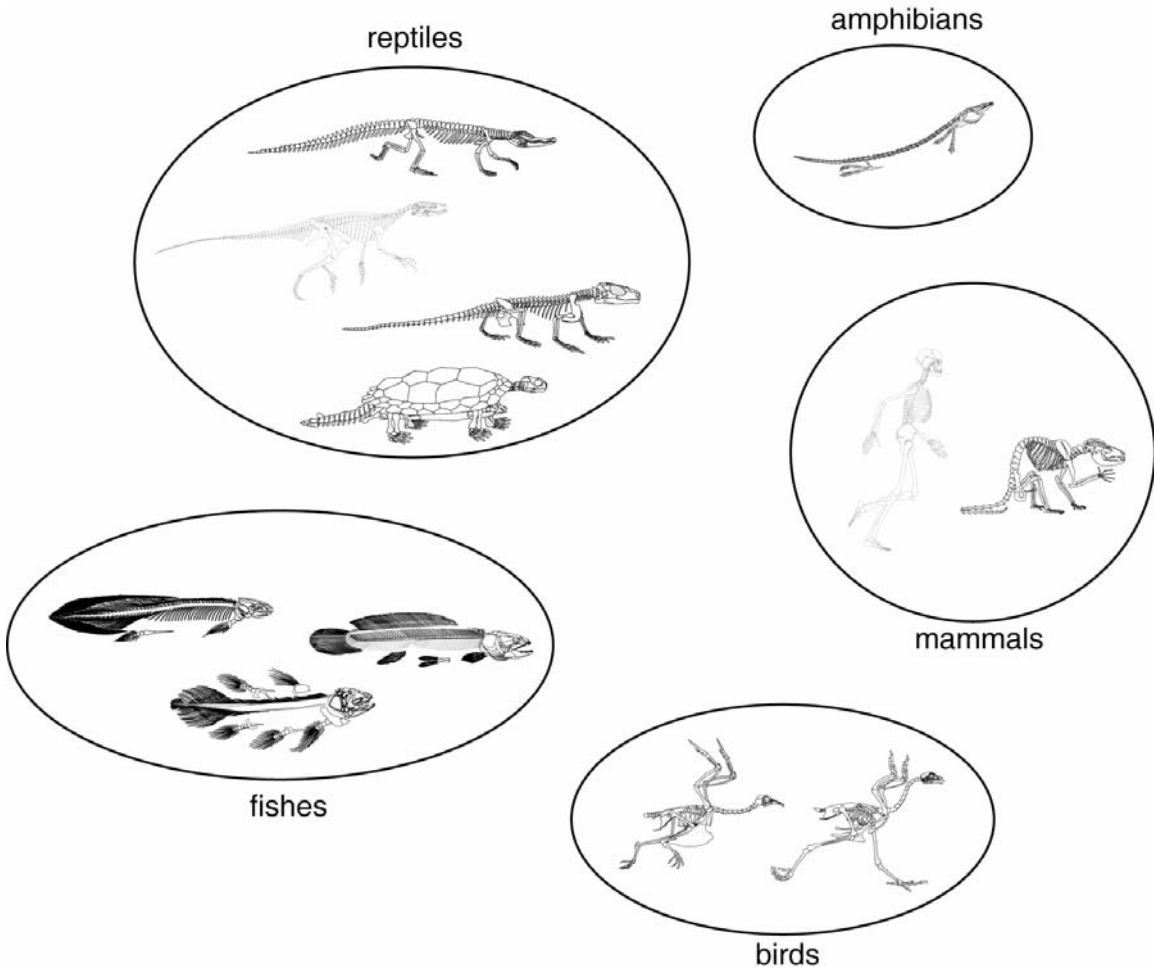


Figure 13.02 The Linnaean classification divided vertebrates into five non-overlapping Classes. While this does pigeonhole all the vertebrates into a convenient filing system, it is a poor reflection of their relationships to one another.

The Linnaean ranking scheme depends on the idea of fundamentally distinct types of organisms--groups that are separate but equal in rank. Among vertebrates, for example, Linnaeus recognized the Class Osteichthyes, Class Amphibia, Class Reptilia, Class Mammalia, and Class Aves, to be non-overlapping categories representing separate but equal Classes⁶. Membership was defined by distinctive features, like fur and mammary glands for mammals, scales and cold blood for reptiles, and feathers for birds. Linnaeus strove to discover the characteristics of essential importance to the group. But without clear principles for guidance, biologists fought bitterly over what a natural classification really represented and which criteria should be regarded as essential in

building a classification. And, without some objective measure of difference, they also fought over what ranking should be assigned to any given group. The result has been continual turmoil and revision in our system of classification. Consequently, ever since Linnaeus' day, many scientists have claimed that classification is mere pigeonholing, and that the arguments over how to classify any particular organism generate only heat, not enlightenment. Systematics and classification are for stamp collectors, not scientists.

The Linnaean system is what was available to Darwin as a student. Even after the Darwinian revolution was underway, the Linnaean system remained enormously successful because it was at least partly hierarchical. It provided a convenient means of conveying nature's diversity. After Linnaeus' death, naturalists expanded Linnaean classification to include newly discovered living species as well as fossils. The classification became all-inclusive and rapidly grew into one of the most general tools in the naturalist's repertoire. For more than two centuries, the Linnaean system of classification has provided a basic language for communication about Nature's diversity. And, this pre-evolutionary system was still in general use when we entered graduate school.

Darwin and natural classification: the roots of conflict

Darwin noted that, even in the most ancient written records, humans recognized that organisms resemble one another to varying degrees¹⁰. They classified organisms into smaller groups contained within larger groups. Primates are placed within the larger group Mammalia, which in turn is contained within Amniota, Tetrapoda, Vertebrata, and so on. But unlike the constellations of stars, this arrangement of groups is not entirely arbitrary. Species that look most alike are grouped together, and those that are different are grouped separately.

To pre-Darwinian naturalists, the classification of species was simply a scheme for arranging living objects that looked most similar, a convenient tool to 'sort out' organisms. To Darwin, much more was implied by the shared resemblances of organisms. A shared history of descent, the one known cause of close similarity in organic beings, is what the general system of classification revealed. The bond among members of a group is relationship, "propinquity of descent", though it can be hidden in

various degrees by the modifications which make the different groups so distinctive. To Linnaeus and Owen, organisms were grouped together simply because they looked alike. But to Darwin and his followers, organisms are grouped together because they are descendants of a common ancestor.

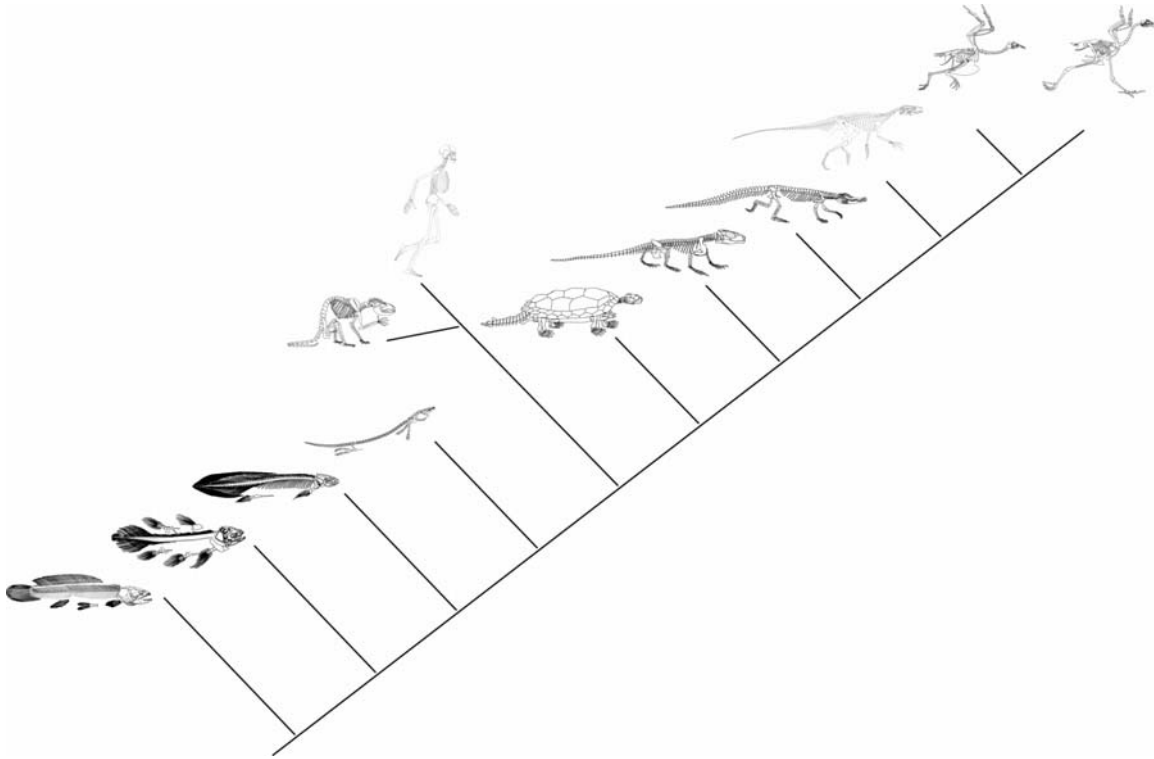


Figure 13.03 This is a map of vertebrate phylogeny showing the relationships among all its members.

The Darwinian view cast a very different light on what classified groups represent and on how to build classifications¹¹. The groupings were generally seen to represent the branches of the evolutionary family tree. The “naturalness” that Linnaeus groped for but failed to identify is genealogy. Ever since Darwin, scientists have worked to see that each group, whether it be a genus, family or higher group, contains only related forms. But as this work has progressed, it has become clear that the Linnaean system of classification can never provide a completely accurate representation of relationship, because it is not completely hierarchical. It was never intended to reflect evolutionary relationship. Thanks to the newly developed maps of vertebrate phylogeny, we have realized that many of the groupings established through Linnaean methods fail to depict

genealogy. Instead, they reflect ecology, geography, or some other criterion (figure 13.02- 13.03).

The Linnaean classification would work perfectly well if the gaps between groups were always distinct. For example, if only one group were designed for life in the water, one for life on land, one as a predator, one as a flyer, and so forth, classification would be a simple process. But the variability among organisms inevitably seems to cross these convenient boundaries. Some tetrapods still live mostly in the water, while other tetrapods never go near it. Lungfish can live buried in their burrows at the bottom of dried ponds and breathe air for years, while other fish will quickly suffocate outside water. Rarely can a group be defined by a single character shared among all its members and no other species. Even when groups seem highly distinctive and sharply separated from each other, as living birds differ from lizards and crocodylians, the distinction often becomes blurred when fossils are considered. *Archaeopteryx* is the classic example. Nineteenth century scientists asked, “Is it a feathered reptile or a reptile-like bird?” Fossils blurred the seemingly sharp and objective boundary. Under the Linnaean system *Archaeopteryx* can not be *both* a reptile and a bird, even if birds have reptilian ancestors (figures 13.04 - 13.05).

Naturalists had long noted that gaps exist between groups of equal rank, and as we saw earlier the existence of these gaps represented a basic challenge to the theory of evolution. But when fossils narrowed the gaps and offered evidence in support of Darwin’s theory, it posed a real dilemma for Linnaean classification. Whether *Archaeopteryx* was segregated into its own class or lumped into either Reptilia or Aves, the solution was an uncomfortable one, because either approach arbitrarily broke the genealogical bond. Some scientists advocated splitting, some lumping, and the two camps fought bitterly over how to handle any particular case.

This argument is important because, if classifications are to represent genealogies, the problem of splitting versus lumping taxa poses a problem that directly affects our understanding of history. Classifying *Archaeopteryx* as a bird in the Class Aves breaks its connection to reptiles. Classifying it within the Class Reptilia severs its connection to birds. Placing it in a Class by itself would tear apart both connections. Paleontologists sometimes comment that they are fortunate that so many distinct gaps still exist between

different groups, for without them classification would be impossible. Reading between the lines, what they are also admitting is that Linnaean classification is stronger when based on less information. When used as an evolutionary tool, Linnaean classification has a difficult time dealing with new discoveries like *Archaeopteryx*.

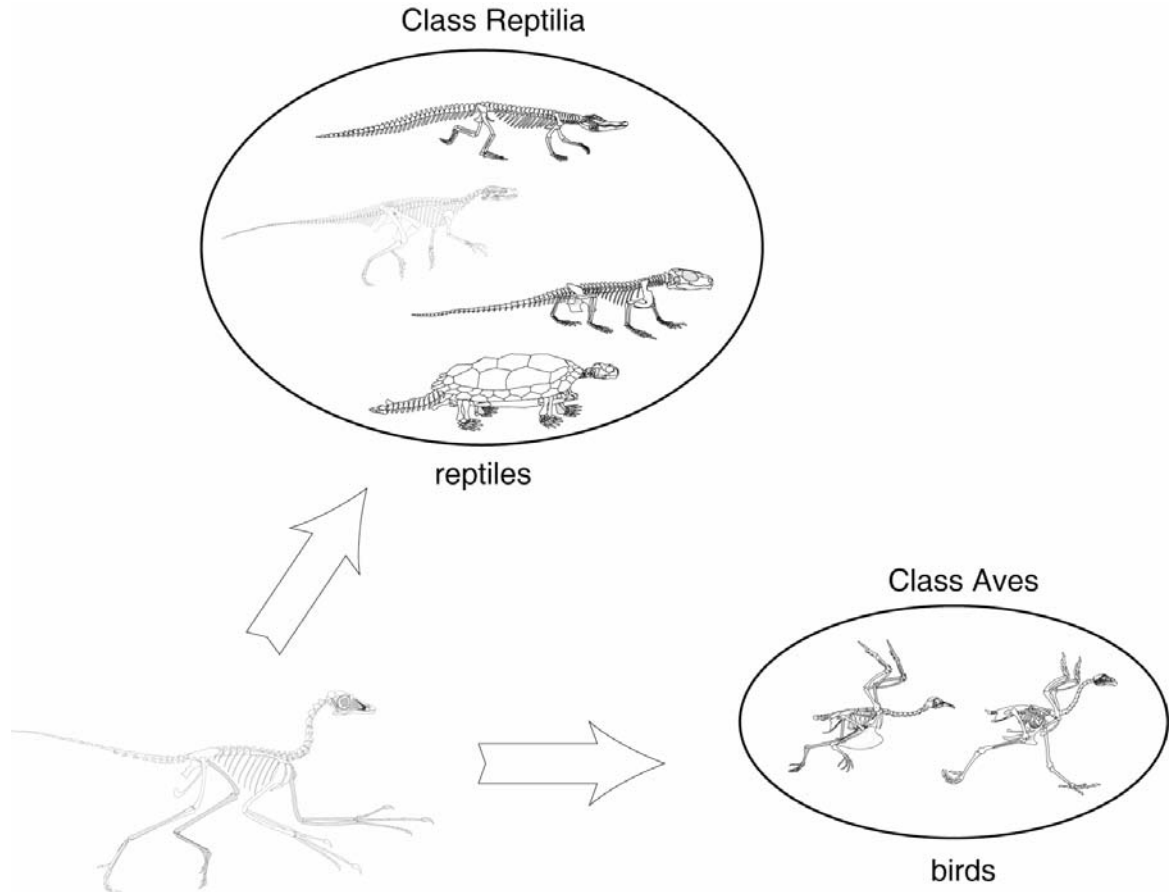


Figure 13.04 In the Linnaean system of separate but non-overlapping ranks, *Archaeopteryx* could be either a reptile or a bird, but it couldn't be a member of both classes despite its genealogical tie to both.

Implications of Evolution

Darwin's theory has become the most central principle of biology, and today virtually all biologists interpret classifications to reflect evolutionary history. Since Darwin's time, scientists have discovered the mechanism of inheritance. With computers they can decipher the structural features of double helix DNA molecules and use DNA itself as evidence for classifying organisms. DNA evidence is even used routinely in the

British and American legal systems. Where would modern medicine be if DNA had never been discovered? Genetic engineering and cloning are now possible. Their future potentials are so vast that we can't foresee where biotechnology, which transplants genetic information from one species into the genetic mechanism of another, will have taken us a century from now. So transformed is humankind by the theory of evolution, that it is difficult to imagine what our lives might be like today in the absence of the cascading discoveries it has spawned.

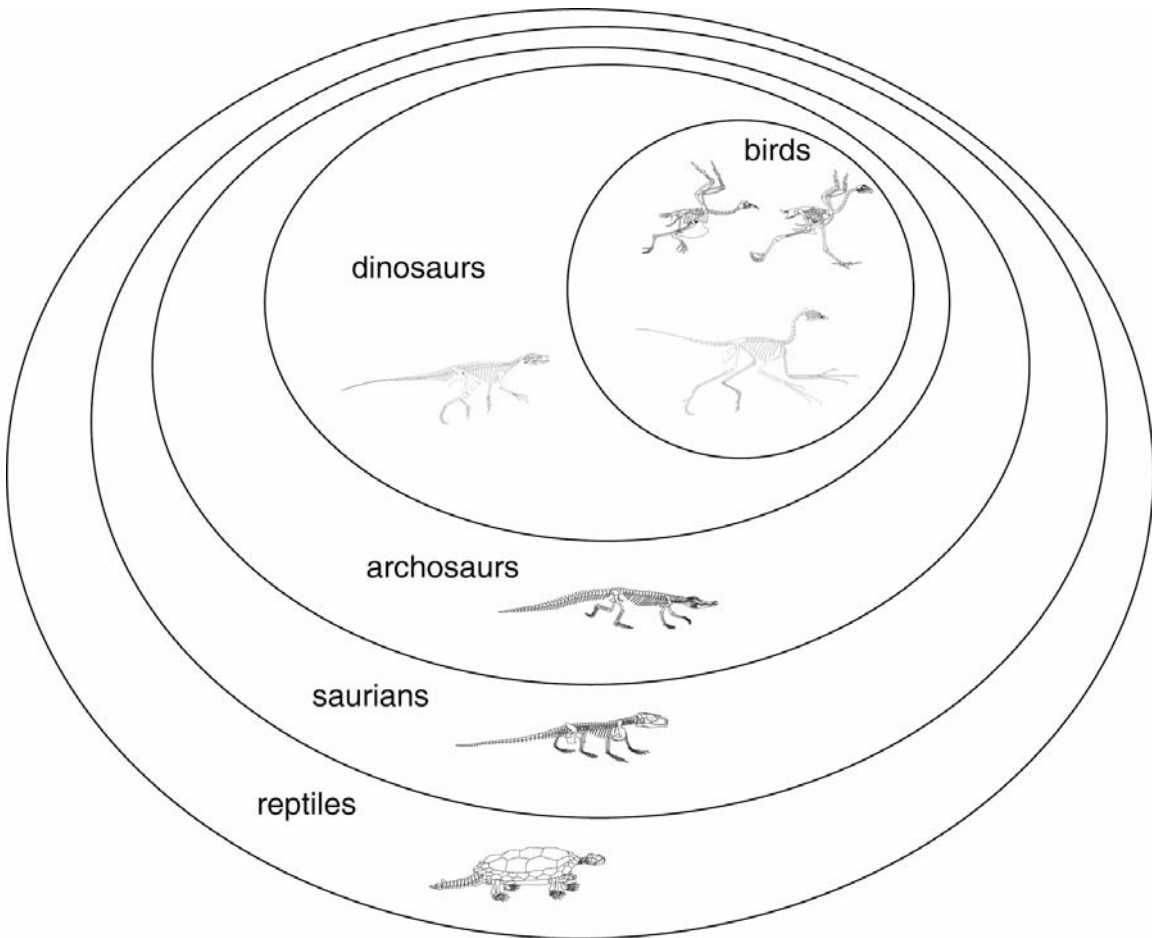


Figure 13.05 In the phylogenetic system, *Archaeopteryx* is a bird, a dinosaur, an archosaur, a saurian, and a reptile.

All the same, a number of influential 20th century biologists have commented that the Darwinian revolution did not lead to a similar revolution in the way organisms are classified, despite acceptance that classification should reflect genealogy. We had learned of this paradox as undergraduates and we had read about some attempted

solutions. But the solutions seemed only to introduce new problems, and we shared the general scientific response to the entire issue, which was to ask, “so what?” And then we met a Berkeley graduate student named Kevin de Queiroz. Now a curator of Herpetology at the Smithsonian Institution, de Queiroz had a resounding influence across our community as he explored the paradox in the way evolutionary biology was studied. Most evolutionary biologists have continued to use Linnaean methods, lumping organisms together based on overall similarity, and splitting groups into different ranks to reflect their differences. Even though they may express their ideas in evolutionary terms, their methods for detecting the underlying pattern of relationship were devised long before Darwin’s theory emerged. Other scientists had argued that a classification designed optimally to reflect evolutionary relationships would be a far better tool than traditional Linnaean classifications, but de Queiroz showed us how powerful such a tool could be.

Before Darwin’s theory of evolution, which stipulated that species could transform, there was no reason to develop a system that depicted the dynamic properties of lineages. To better reflect what we have learned about evolutionary history, the Linnaean system has been tinkered with, modified, revised, and overhauled. New rules for classification have been added, and a Linnaean Commission has published a Code of Taxonomy for more than a century. Since Darwin’s *Origin* was published, the Code has evolved into a governing system for classification that rivals the American tax code in its mind-boggling complexity. But despite countless alterations, it remains painfully evident that the Linnaean system was designed to classify static, unchanging objects. To Linnaeus, organisms were separately created and ‘permanent.’ He had no idea that species could become extinct, much less that they could transform as part of evolutionary lineages. Darwin’s *Origin* was still a century in the future when Linnaeus published the basic structure of his classification system. Kevin de Queiroz argued that it was time to develop a system designed for studying evolution, using the idea of descent with modification as axiomatic, and deriving from that axiom the best evolutionary tools possible¹¹.

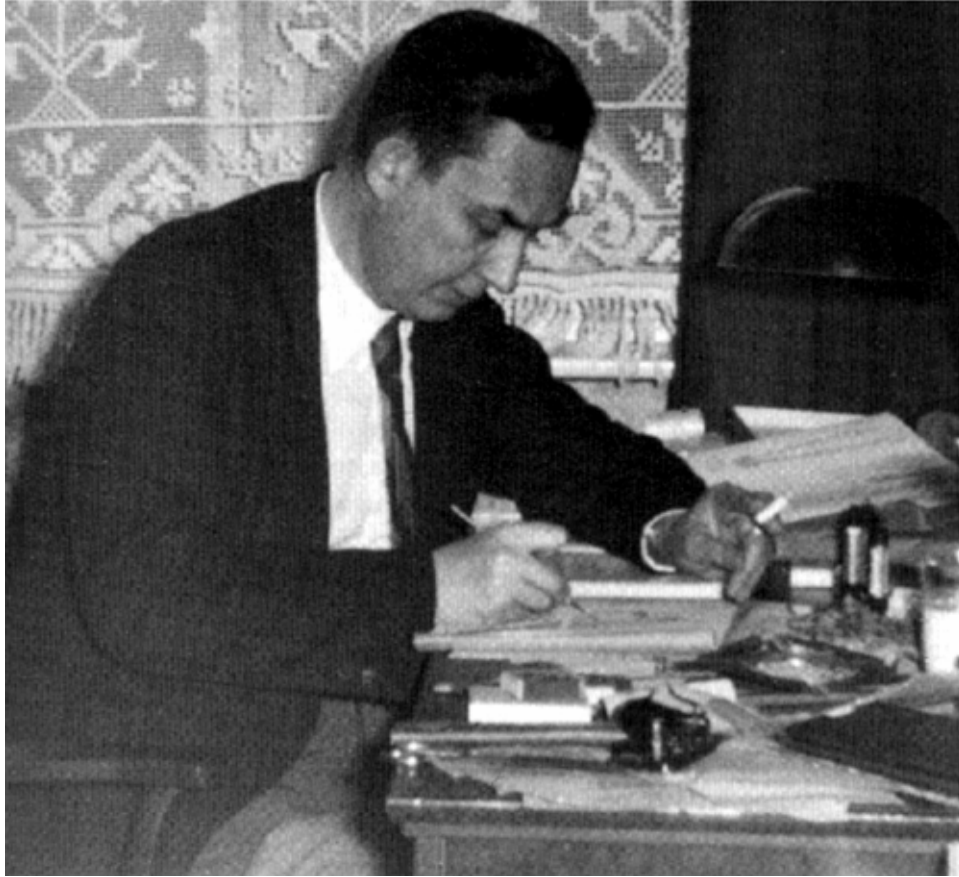


Figure 13.06 Willi Hennig, who founded phylogenetic systematics. It took about 30 years for Hennig's view to catch on, but it is now the most widely used method to reconstruct genealogy. (from: R. Lewin 1997. *Patterns in Evolution: the New Molecular View*. Scientific American Library)

The Phylogenetic System

Berkeley became a hotbed for overthrowing the Linnaean system while we were graduate students there. The hierarchical map of genealogy that we have been using in this book, known as the *phylogenetic system*, is what was proposed in its place. The German naturalist Willi Hennig (figure 13.06) had founded the field of phylogenetic systematics in works on insect relationships that he published in the 1950's. In 1966, his major book on phylogenetic systematics¹² was translated into English, and over the next decade his methods were refined, mostly by a small group of ichthyologists led by Colin Patterson and associates at the British Museum (Natural History), and by Donn Rosen, Gareth Nelson, and their associates at the American Museum of Natural History.

At first the movement was no more than a small network of a few dozen scientists scattered across the US and Europe. Kevin de Queiroz and Jacques Gauthier were among its first supporters at Berkeley, often to the dismay of some of the faculty, whose careers were deeply rooted in the Linnaean system. But by applying phylogenetic methods to some long-standing problems in reptile evolution, they were able to offer compelling demonstrations of the difference between the two systems. de Queiroz worked on mapping the relationships among modern lizards, while Gauthier focused on the phylogeny of dinosaurs and the origin of birds¹³, and the two collaborated in a great deal of this research. They argued that by merely superimposing a secondary evolutionary interpretation on top of a Linnaean classification, biologists were risking many mistakes, and Dinosauria was a classic example. As Gauthier put it, explaining why Dinosauria became extinct is like explaining why Napoleon crossed the Mississippi. The Linnaean system had misled scientists into seeking an explanation for something that had never happened. Gauthier and de Queiroz argued that it was time to break with the past and construct a phylogenetic system to reflect Darwin's concept of evolution¹⁴.

Ancestry, rather than overall similarity, formed the fundamental basis of the phylogenetic system of classification. Many Linnaean names, like Dinosauria, Saurischia, and Theropoda, are preserved to provide a linkage to historical Linnaean schemes. However, the meaning behind those names shifted from a static concept based on physical characteristics to a dynamic one based on ancestry, and the practice of ranking lineages was abandoned entirely. In the phylogenetic system, groups must include the last common ancestor of a lineage plus all its descendants, no matter what form the descendants might eventually assume through evolution. Whereas the Linnaean system was only partly hierarchical, the phylogenetic system is exclusively hierarchical. In the phylogenetic system, anything born to a vertebrate is a vertebrate, anything born to a tetrapod is a tetrapod, and anything born to a dinosaur inherits that name, plus all the others.

A system based on ancestry is at least potentially stable, because organisms can't escape their history. One's ancestry can never be altered, and the phylogenetic system remains loyal to Darwin's fundamental evolutionary concept--all species share common ancestry. And by linking particular names to particular ancestors, the precise meanings

of the names is potentially stable. Discovering ancestors and historic relationships--the process of phylogeny reconstruction--is a different question, and it is not always a simple task. The phylogenetic map of organisms is still under construction, as we will see in the chapters ahead. But despite the difficulties that face phylogeny reconstruction, the basic idea that ancestry provides a stable criterion for an evolutionary system of classification is now being put into practice on a global scale.

This was a radical shift in perspective and one that was deeply upsetting to many scientists when we were graduate students. It would mean, for example, that dinosaurs are not extinct! And similar revelations faced researchers studying many other lineages. At about the same time as the war over an asteroid impact at the K-T boundary was under way, a debate over the phylogenetic system stormed across the community, although it obviously didn't gather nearly the same level of media coverage. At Berkeley the debate was so strong that it led to several formal seminars that involved students and faculty from many different departments. One of the seminars was led by Kevin Padian, who carried an historic perspective that brought Richard Owen into the spotlight of our discussions. As the group discussed the phylogenetic system, Gauthier discovered the striking similarity of the modern debate to the debates that had raged in England a century before. Not only was the relationship between birds and Mesozoic dinosaurs once again being challenged, but the very role that the theory of evolution should play in science was again at stake.

A Rose by Any Other Name?

Owing to the fundamentally non-evolutionary design of the Linnaean system, even evolutionists like Thomas Huxley and John Ostrom, were trapped into arguing that dinosaurs are extinct. But instead of dying out, dinosaurs were merely defined out of existence. In the Linnaean system, with its foundation of defining characteristics, only birds could have feathers, and birds belonged to a Class entirely separated from reptilian dinosaurs. The name Dinosauria, as originally defined by Richard Owen, referred only to giant extinct Mesozoic species, and Owen refused to believe that they could transform into something with feathers. But, under the phylogenetic system this doesn't necessarily mean that the dinosaurian lineage is extinct. It may be true that living descendants are

not so “fearfully great” as *Megalosaurus* or *Iguanodon*. But beneath their feathers, they retain many attributes that were inherited from their Mesozoic ancestors. Consequently, birds have legitimately inherited the evolutionary titles of their ancestors. We now tell our students that birds are card-carrying avialian, maniraptoran, coelurosaurian, tetanurine, theropod, saurischian dinosaurs, and don't you forget it! Because in doing so, you would be denying them their rightful claims to a proud and distinguished ancestry.

So, not all dinosaurs became extinct at the end of the Cretaceous. The avian dinosaurs flew over whatever it was that affected their huge cousins at the K-T boundary. Subsequently, dinosaurs evolved into the most speciose lineage of land-living vertebrates ever to appear. Today, living dinosaur species outnumber those of all the other major branches of the tetrapod family tree. Once an icon for obsolescence, Dinosauria now appears as one of Mother Nature's greatest success stories.

This isn't simply a question about what names to apply to which organisms. Once the relationships of a lineage have been phylogenetically mapped out, the next step is to re-evaluate interpretations of its history that were based on Linnaean classifications. Dinosauria is a marvelous example of how Mother Nature can turn science on its head. Mapping the phylogenetic relationships of dinosaurs indicated that Owen's original conception of dinosaurs as huge, lumbering, extinct reptiles is only partly correct. Some dinosaurs fit that bill, but in fact, the majority do not.

To explore the implications of this new interpretation of dinosaurs, we now return to the map of dinosaur phylogeny and follow it to the present. The evolutionary evidence represented by anatomical signposts on the map will show that a diversity of dinosaurs probably crossed the K-T boundary unscathed, and that only recently have they been threatened with mass extinction.

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Figure captions for Chapter 13

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Figure 13.02 The Linnaean classification divided vertebrates into five non-overlapping Classes. While this does pigeonholed all the vertebrates into a convenient filing system, it is a poor reflection of their relationships to one another.

Figure 13.03 This a map of the relationships among vertebrates.

Figure 13.04 In the Linnaean system of separate but non-overlapping ranks, *Archaeopteryx* could be either a reptile or a bird, but it couldn't be a member of both Classes despite its genealogical tie to both.

Figure 13.05 In contrast to the Linnaean system, the phylogenetic system, *Archaeopteryx* is a bird, a dinosaur, an archosaur, a saurian, and a reptile.

Figure 13.06 Willie Hennig, who founded phylogenetic systematics. It took about 30 years for Hennig's view to catch on, but it is now the most widely used method to reconstruct genealogy. (from: R. Lewin 1997. *Patterns in Evolution: the New Molecular View*. Scientific American Library)