

Chapter 6

While reading a book on dinosaurs, you notice that they existed in a time span of about 230 to 65 million years ago in the Mesozoic Era, and you wonder what the first dinosaurs looked like. When you find an artist's rendering of these creatures, you notice that they look similar to modern monitor lizards (such as Komodo dragons), crocodiles, or alligators. Moreover, you are surprised to find out that flying reptiles, marine reptiles, and many other dinosaur contemporaries were not actually dinosaurs. As you read about dinosaurs toward the end of the Mesozoic Era, you also see the phrase "birds are dinosaurs".

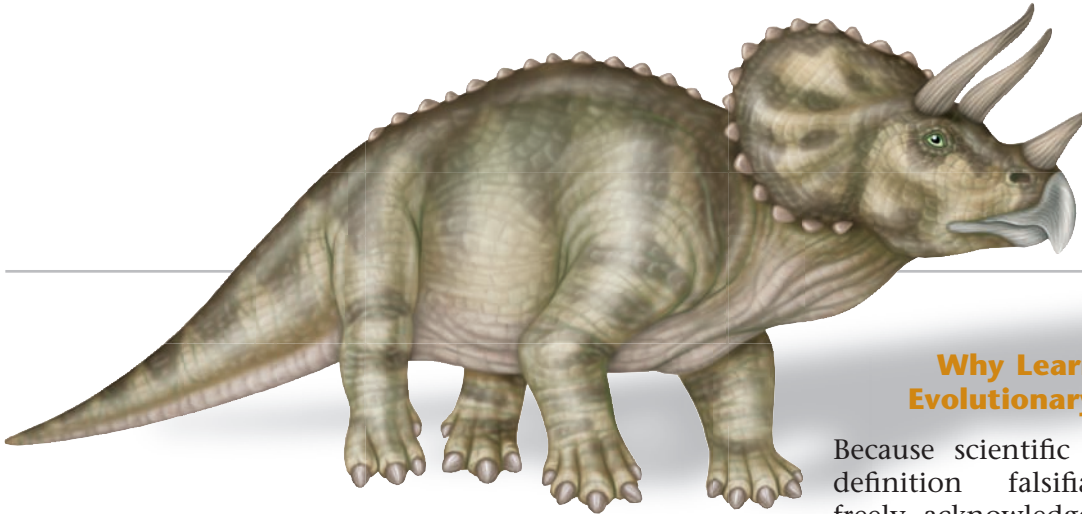
Are dinosaurs, monitor lizards, crocodiles, and alligators related to one another? If so, what common ancestors did they have? What is the basis of the phrase "birds are dinosaurs"? If this premise is acceptable to you, then how are birds related to monitor lizards and crocodiles?

Introduction to Dinosaur Evolution

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Why Learn about Evolutionary Theory?

Because scientific theories are by definition falsifiable, scientists freely acknowledge the possibility that modern evolutionary theory is modifiable. However, the overwhelming amount of evidence supporting evolutionary theory, as well as repeated testing and modification of its numerous interconnecting hypotheses by scientists worldwide during the past 150 years, illustrate its robustness and degree of certainty. In short, no other theory in science has endured and survived as much critical peer review as biological evolution. Consequently, scientists have no rational reason to suppose that evolutionary theory is closer to being incorrect than correct, and they no more “believe” in evolution (in a faith-based sense) than they believe in gravity. Indeed, its factuality is the central pillar of support for understanding the history of life on Earth.



Evolution is both a fact and a theory: evolution and its by-products have been observed, but a theory has also been constructed to explain these observations (Chapter 2).

Dinosaurs represent excellent test subjects for, and examples of, the basic principles of evolutionary theory. The rich history of amniote evolution, which began at least 350 million years ago and continues today, can be used as a framework for understanding the roots of dinosaur evolution. Once dinosaurs had evolved into a definable group in the Mesozoic Era, their proliferation into a wide variety of forms alludes to both the genetic and environmental changes that they experienced throughout their 165-million-year history. Data relating to the genetic components of dinosaur evolution are largely incomplete but can be inferred based on their character traits, the foundation of the phylogenetic (cladistic) classification system (Chapter 5). Broad-scale environmental changes in the Mesozoic, especially those related to plate tectonics (Chapter 4) and paleoclimatology, are well documented as stages for dinosaurs changing as the world changed. Additionally, some researchers have proposed that the evolution of dinosaurs contributed to major evolutionary changes in other organisms. Such hypotheses are supported by intriguing correlations of biological trends, including the origin of the dinosaurs from amniote ancestors that became, at least partially, embedded in the geologic record and continue to be augmented by fossil discoveries made daily. Understanding the evolution of dinosaurs is thus not only important to know as a well-documented process of the past, but is pertinent in the sense that we are connected to the current by-products of dinosaurian interactions with past environments. As ecosystems changed, dinosaurs changed with them and they were active participants in those changes, as part of their role in the web of life.

Basic Concepts in Evolutionary Theory

Part I: Genetics and Natural Selection

Evolution is defined here as the change in a population between generations, where a **population** is a group of interbreeding organisms, such as a species (Chapter 5). Darwin originally summarized this process in the late nineteenth century with the phrase “descent with modification,” which is still apt today, despite much revision of his hypotheses since then. A population that goes through generations, from ancestors to descendants, comprises a **lineage**. Changes that happen to an individual organism during its life do not constitute evolution, although any effects that altered organism confers on its population could have a small impact on evolution of the population. Likewise, changes that happen to an environment surrounding a population also do not represent evolution, although the effects of that environmental shift on that population could influence its evolution.

The evolution of one species into another species is called **speciation**; separate-ness of the two species is defined by **reproductive isolation**, whereby neither species can reproduce with the other to form offspring that also can reproduce. Mules represent an example of reproductive isolation as **hybrids**, in that they are the sterile offspring of two different species, *Equus caballus* (horses) and *Equus asinus* (donkeys). Although speciation is popularly perceived as requiring long periods of time (i.e., millions of years), fast-breeding populations under certain environmental conditions can evolve into different species within a typical human lifespan. This type of evolution has been observed repeatedly, which is one reason why evolutionary theory is a fact, not “just a theory” in the pejorative sense (Chapter 2). Examples of speciation were first documented early in the twentieth century in flowering plants, such as the evening primrose (*Oenothera lamarckiana* to *Oenothera gigas*), and were later observed with various other species of plants, as well as fruit flies, houseflies, and other insects. Moreover, pharmaceutical companies must continuously update formulas for antibiotics because strains of bacteria evolve that are resistant to these treatments. Some insect populations also evolve quickly in response to insecticides, so chemical companies must change their insecticide formulas in response to their decreased effectiveness. Consequently, evolutionary theory is not an esoteric, untested philosophy with little or no real-world applications. The reality of evolution is a social and economic concern for nations, corporations, and individuals worldwide, and practical applications of the principles of modern evolutionary theory help to solve their problems.

Why do people tend to look like their parents? The answer is mostly related to inheritance of physical traits from the parents, which is caused by the passing of **genes** from one organism to the next generation. A gene is a nucleotide sequence in a DNA molecule that provides a code for a protein or part of a protein. The location of a specific gene in a chromosome is its **locus**, and any variation of that gene at the same locus is an **allele**; a pair of genes (or alleles, if the genes vary) constitutes an organism’s genotype at a locus (Chapter 5). The sum total of genes conveyed in a DNA molecule and coding for all of an organism’s proteins is its **genome**, representing the genetic potential of an organism. For example, geneticists defined the human genome in the year 2000. However, the genome is not the same as the **gene pool**, which is the sum total at a given time of all genes in a population and represents different individuals.

The genotype of an organism directly relates to an organism’s physical appearance and behavior, or its phenotype (Chapter 5). People who look like their parents, or in some cases behave like their parents, are simply showing their



phenotype. However, environmental factors acting upon the phenotype could produce a radically different physical form or behavior than anticipated from the original genotype of an organism. For example, tailless mice that acquired their physical trait through severing of their tails (Chapter 5) still have a genotype for a tailed condition, although their phenotype shows otherwise. Their offspring still have tails when they are born, regardless of the environmentally-caused features possessed by the parents. Similarly, a bipedal theropod trackway that consistently shows three digits on one foot and only two on the other foot can be concluded as representing an environmentally-induced condition (probably from an injury or other pathological cause) that was not passed on to any of the dinosaur's offspring (Chapter 14). Behavior also can be greatly influenced by environmental conditions, rather than inherited predispositions. For example, certain breeds of dogs can be bred selectively for aggressive behavior, but breeds that are ordinarily passive also can be taught to attack and be threatening.


Modifications of phenotypes encourage the argument of “nature versus nurture” (inherited characteristics versus acquired characteristics) in examining the physical appearance of an organism. Acquired characteristics cannot be inherited. This hypothesis that promoted the contrary view, articulated by French naturalist **Jean-Baptiste Lamarck** (1744–1829), was critically examined and effectively falsified by the end of the nineteenth century.

Related to the phenotype of an organism is another fundamental property of any individual in a population: it shows **adaptations** to its environment. An adaptation is a physical attribute of an organism that can help it to survive at least long enough to reproduce successfully. Accordingly, a lack of this attribute will decrease an organism's chances of surviving to reproductive age. For example, hadrosaurs had impressive rows of teeth (**dental batteries**) that were well-adapted for the processing of vegetative material, presumably for better digestion (Chapter 11). A lack of these teeth would have considerably decreased their life spans, perhaps to the extent that they would not have reached reproductive age. In evolution, adaptations such as these must be inheritable from one generation to the next. An acquired adaptation is meaningless in the change of a population over generations. An example of an acquired adaptation is the development of a suntan in a normally light-skinned person. Melanin is produced in response to an environmental stimulus (sunlight over time), but this suntan is not inherited by any successive generations coming from this individual. Likewise, a human adult's lifetime habit of dyeing ordinarily dark-brown hair to blonde is perhaps an adaptation used for social enhancement and subsequent reproductive advantage in some societies. However, this adaptation does not necessarily affect whether any offspring of a chronic colorist will also have the same conferred reproductive benefit of blonde hair.

Natural selection, a hypothesis proposed conjointly by Darwin and one of his contemporaries, Alfred Russel Wallace (1823–1913; Fig. 6.1), helped explain why

populations change through time and organisms composing these populations have inheritable adaptations. This explanation was proposed with the following tenets, based on numerous observations in natural settings by Darwin and Wallace:

- Species have variations within their populations that are inheritable.
- Species tend to overpopulate, producing more individuals than will actually survive to reproductive age.
- A struggle for existence occurs within the population, perhaps through competition over resources, habitat, or mates.



*The preceding background information, especially regarding adaptations, is necessary to understand **natural selection**, the central hypothesis of modern evolutionary theory.*

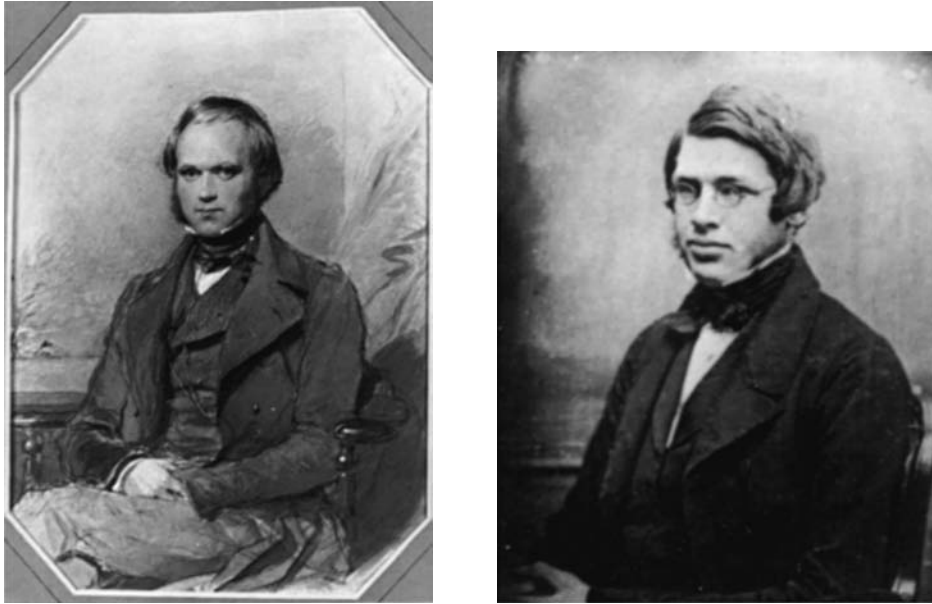


FIGURE 6.1 Main originators of the hypothesis of natural selection, Charles Darwin (left) and Alfred Russel Wallace (right). From Ridley (1996), *Evolution*, 2e, Blackwell Science, Inc., Malden, MA, pp. 9 and 10.


- Those individuals with variations favorable for survival from this struggle (the more adaptable ones) will live to produce offspring that also have these variations, thus changing the population over time with each successive inherited variation and eventually resulting in species different from the ancestral species.

A phrase associated with natural selection is “**survival of the fittest**,” which is potentially misleading because “fitness” is not necessarily related to the popularized idea that “the strong survive and the weak perish.” **Fitness** in this sense actually means “better adapted” or refers to the number of offspring produced by an individual, and thus has little or nothing to do with strength. Mammals of the Mesozoic exemplify this concept, as they were physically weak and small in comparison to their dinosaurian companions but clearly were better adapted than dinosaurs for surviving the environmental changes that resulted in the extinction of the dinosaurs by the end of the Mesozoic (Chapter 16).

The tenets of natural selection have been modified since the time of Darwin and Wallace but still form the foundation of evolutionary theory. The older version of

the hypothesis of natural selection is **Darwinism**. Although Darwin and Wallace knew that certain inheritable variations in organisms translated into adaptations, they did not know the source of the variations or the exact mechanism for their inheritance. Ironically, another scientist at the time, **Gregor Mendel** (1822–84), was providing the answer to this question, but his results were not widely recognized by other scientists until early in the twentieth century. Mainly through cross-breeding pea plants, Mendel discovered the basic factors underlying heredity – genes, alleles, genotypes, and phenotypes. For example, a pair of genes at a locus (comprising

a genotype) is paired because each gene came from a different parent. Consequently, sexual reproduction is responsible for most of the genetic variation in



Neo-Darwinism is a modified descendant that takes into account modern genetics, the study of heredity and variations in organisms.



an organism, because one-half of its genes came from its mother and one-half from its father. This is related to the haploid nature of male and female gametes, formed by meiosis, which combine to form a diploid zygote. Dinosaurs are also presumed, with a high degree of certainty, to have reproduced sexually through male–female pairs and not through parthenogenesis (Chapter 8). This hypothesis is supported by the numerous dinosaur eggs (a few containing embryos) and nests, the sexual dimorphism interpreted from some dinosaur skeletons of the same species, and the sexual reproductive life cycles in their closest living relatives, crocodylians and birds (Chapter 8). Dinosaurs thus had a constant source of genetic variation, as with other sexually reproducing organisms.

Another discovery by Mendel was that one of a pair of genes tends to overshadow the other gene in its physical expression, which affects the phenotype of the organism, so that the **dominant** gene is expressed over the **recessive** gene. An individual with two dominant or two recessive genes at a locus has a **homozygous** condition, in contrast to one with dominant and recessive genes, which is **heterozygous**. A heterozygous condition is defined by alleles, because a pair of genes at the same locus represents variations, or alternatives, of one another. Interestingly, proportions of these dominant and recessive traits can be predicted in offspring from parents with homozygous or heterozygous conditions through probabilities. For example, the gene for brown eyes in humans is dominant over that for blue eyes, but both parents can have brown eyes and a recessive gene for blue eyes, so they will both have a heterozygous condition. The **gene frequency**, which is the frequency of each gene in relation to another gene at its locus, is 0.5 for each allele in a heterozygous condition, which corresponds to a 50% probability for each (otherwise known popularly as “50 : 50”). In contrast, a homozygous condition would have a gene frequency of 1.0 for the single gene, whether it is for a homozygous dominant or homozygous recessive.

Armed with probabilities, geneticists can make predictions about the genotypes and phenotypes of pairings. In the example of eye color, the probability for any one of their offspring to have blues eyes is 25%. Probability is calculated through assigning letters to both the dominant allele (B) and recessive allele (b) in the homozygous pairs and crossing them in a diagram used by geneticists, called a **Punnet square**:

	B	b
B	BB	Bb
b	Bb	bb

The probability of a brown-eyed, homozygous-dominant individual (BB) is 1 in 4, or 25%. The probability of a brown-eyed, heterozygous individual (Bb) is 2 in 4, or 50%. Lastly, the probability of a blue-eyed homozygous-recessive individual (bb) is 1 in 4, or 25%. Therefore, two heterozygous individuals can produce three possible genotypes, but these genotypes can differ in their expression as phenotypes. These probabilities are related as **genotype frequencies** with values between 0 and 1, such as 25% = 0.25, 50% = 0.5, and so on. Notice how the gene frequencies and genotype frequencies are different from one another.

This shuffling of genes produces variation in a population that can be predicted by calculating probabilities for successive generations, based on gene frequencies and assuming random mating with no natural selection. The expected ratio of genotype frequencies in such a case is called the **Hardy–Weinberg ratio**. The ratio was named after its originators, mathematician G. H. Hardy and physician Wilhelm Weinberg, who independently devised a formula describing it early in the twentieth century. For example, the preceding example has two alleles (B and b), which

has three possible genotypes: BB, Bb, and bb. The following binomial equation describes the frequency of each genotype:

$$p^2 + 2pq + q^2 = 1 \tag{6.1}$$

where *p* is the gene frequency of the dominant allele and *q* is the gene frequency of the recessive allele. Thus, *p*² is a result of multiplying the probability of allele B by itself (BB), *q*² is the result of multiplying allele b by itself (bb), and *2pq* is the multiplication of both probabilities (Bb), which is also multiplied by two. Because the total probability for the three genotypes is 100%, then all of the genotype frequencies must have a sum of 1.0. The Hardy-Weinberg ratio is considered as the starting point for discussion of **population genetics**, the study of factors that affect gene frequencies.

Using our example, where each heterozygous parent contributed a gene frequency of 0.5 for each allele, the Hardy-Weinberg formula predicts the genotype frequencies for the first generation of the pairing as:

Step 1. $(0.5)^2 + 2(0.5 \times 0.5) + (0.5)^2 = 1$

Step 2. $(0.25) + (0.5) + (0.25) = 1$

Step 3. $1 = 1$

which corresponds to 0.25 for BB, 0.5 for Bb, and 0.25 for bb in Step 2. Using the formula is a good way to double-check the frequencies derived from crossing them in a Punnet square. Calculated either way, the expected gene frequencies for each generation of offspring can be predicted for all possible pairings by parents with known gene frequencies (Table 6.1). The ultimate result is that observers will expect a 75% probability of the brown-eyed phenotype and a 25% probability of the blue-eyed phenotype in a large population.

However, one of the truisms of statistics is that probabilities do not always translate into certainties. One of the most important facets of evolutionary theory is that expected genotype frequencies can differ considerably from observed genotype frequencies, as represented by the anomaly of more frequent appearances of phenotypes that were not predicted from the original pairings. The primary agent responsible for changing the frequencies is natural selection, which demonstrates the intimate interaction between Mendelian genetics and environmental factors.

TABLE 6.1 All possible mating combinations for a hypothetical male–female pair, crossing for two alleles (B and b) and three genotypes (BB, Bb, bb)



Genotype Crossing	Genotype Frequencies of Offspring
BB × BB	BB = 1.0
BB × Bb	BB = 0.5; Bb = 0.5
BB × bb	Bb = 1.0
Bb × BB	BB = 0.5; Bb = 0.5
Bb × Bb	BB = 0.25; Bb = 0.5; bb = 0.25
Bb × bb	Bb = 0.5; bb = 0.5
bb × BB	Bb = 1.0
bb × Bb	Bb = 0.5; bb = 0.5
bb × bb	bb = 1.0

Modified from Ridley (1992, Table 5.1, p. 94).



INTRODUCTION TO DINOSAUR EVOLUTION

How does all of this genetic theory apply to dinosaurs? Using a dinosaurian example, let us say that a male *Centrosaurus apertus* (a Late Cretaceous neoceratopsian: Chapter 13) with a homozygous dominant gene for a small nasal horn (HH) mated with a female *C. apertus* that had a homozygous recessive gene for an enlarged nasal horn (hh). The expected genotype frequency would have been 1.0 for a heterozygous condition (Hh) in all offspring of the first generation, based on the following Punnet square:

	H	H
h	Hh	Hh
h	Hh	Hh

This means that there was a 100% probability of offspring from this pairing having a phenotype of reduced nasal horns, based on the dominance of the smaller-horn allele. The second generation should have then produced the following genotype frequencies:

	H	h
H	HH	Hh
h	Hh	hh

As a result, HH = 0.25, Hh = 0.5, and hh = 0.25, meaning that the offspring have a 75% chance of having smaller nasal horns (Fig. 6.2). This represents a reduction of 25% from the previous generation; but if it is representative of the population as a whole, smaller-horned *Centrosaurus* individuals will still be more abundant than the larger-horned individuals, as predicted by the Hardy-Weinberg ratio.

Natural selection then could have gone to work, such as through the following potential scenarios:

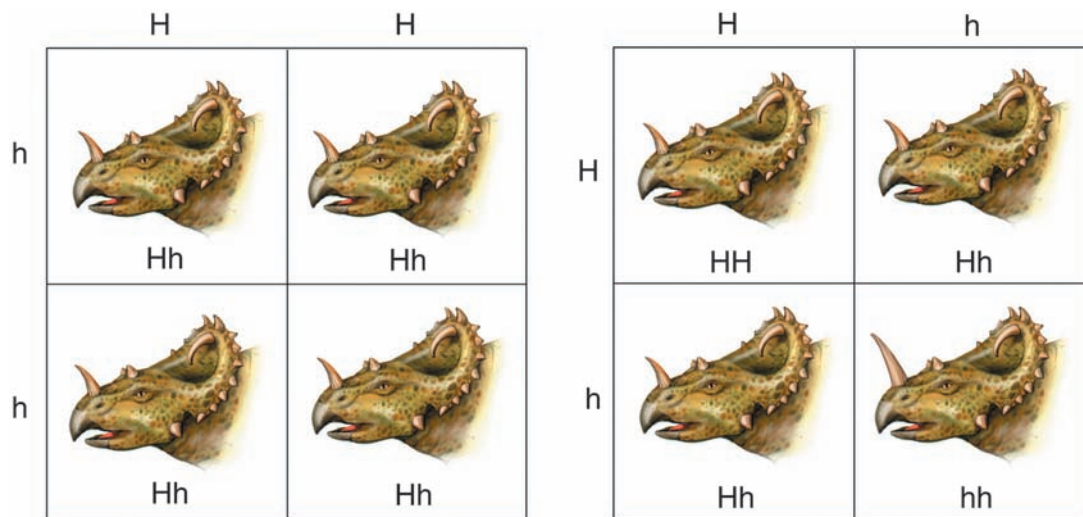


FIGURE 6.2 Hypothetical example of changes in genotype frequencies in the ceratopsian *Centrosaurus* with a dominant allele (H) for a smaller-horned phenotype. (A) First generation, with one parent homozygous dominant and the other homozygous recessive. (B) Second generation, with both parents heterozygous.

- Most other females in the breeding population refused to mate with the smaller-horned male offspring because larger horns in the males serve as better advertisements of their gender and species (a form of sexual selection: Chapter 8).
- Avians that detached parasites from the horns saw the larger horns more often because of their visual prominence, which resulted in more parasitic-borne diseases in the smaller-horned individuals and an increased mortality rate in their juveniles before they reached reproductive age.
- The smaller horn was not as effective in **intraspecific** (within species) competition as the larger-horned condition when males jostled with one another for the attentions of a potential mate. Consequently, the smaller-horned males were out-competed and did not have the opportunity to mate as often as the larger-horned ones.
- The smaller horn was a poor attribute for defense against theropod predators, which caused a higher mortality rate before the smaller-horned individuals reached reproductive age.
- All or any combination of the preceding scenarios could have occurred.

Over enough generations, the end result would have been a reduced frequency of the genotype that caused the phenotype of the smaller-horned condition in *C. apertus*. This circumstance would have happened despite the initial 100% probability from the mated homozygous individuals and the second-generation 75% probability of retaining the phenotypes from the homozygous dominant and heterozygous individuals. Assuming random mating with no natural selection, a population of 1000 *Centrosaurus* individuals should have had about 750 representatives of the smaller-horn phenotype. However, natural selection, through the offered scenarios, would have caused the reduction to a number much less than 750, possibly to zero after enough generations. The reduction of the genotype frequencies for Hh and HH, as well as a decrease in the gene frequency for gene H, was thus facilitated through natural selection that favored adaptations offered by the homozygous recessive (hh, or larger-horned) condition. Part of the natural selection also involved non-random mating, which counters random mating as an assumption of expected frequencies calculated through the Hardy-Weinberg ratio. The example also illustrates an observation in genetics that a dominant gene does not necessarily connote superiority. The word “dominant” unfortunately conveys a sort of hierarchy in genes, which is certainly not the case when a recessive gene is selected over generations.

The change of gene frequencies, added to other inheritable differences, could have caused reproductive isolation and a species different from *C. apertus* if given enough time. Such a small-scale change in gene frequencies in a population is often termed **microevolution**; the larger-scale transitions, such as the evolution of amphibians to amniotes or dinosaurs to birds (Chapter 16), are examples of **macroevolution**. Macroevolution is simply the cumulative effect of microevolution. The *Centrosaurus* example also illustrates **directional selection**, which is a consistent change in a population through time in a particular direction. Directional selections that have been hypothesized for dinosaurs include increased body size in some sauropodomorph lineages (Chapter 10) or reduction of the number of digits in the manus of some theropod lineages (Chapter 9). This type of selection was proposed by Edward Drinker Cope (Chapter 3) in the late nineteenth century through a hypothesis that became known as **Cope’s Rule**, which stated that organisms showed a directional trend toward larger body size in their lineages through geologic time. Numerous exceptions have been demonstrated since Cope’s time that have restricted it to a general trend observed for only some organisms; in other words, Cope based his “rule” on preliminary data from the fossil record, which has



considerably improved since his time. For example, **George Gaylord Simpson** (1902–84), a paleontologist hired originally at the American Museum of Natural History by Henry Fairfield Osborn (Chapter 3), documented the numerous separate species that resulted from the ancestors of horses, a view of evolution that directly contradicted the linear progression for fossil horses proposed by O. C. Marsh (Chapter 3). Simpson's concept has since been applied to other vertebrate lineages, including dinosaurs.

Additionally, directional selection should not be allied with a concept of evolution as a linear trend. Rather, one ancestral population can have many subsequent combined directions that resulted in evolution, making a many-branched "tree" or "bush" (i.e., cladograms: Chapters 1 and 5) rather than a "ladder." Darwin illustrated this concept in a notebook from 1837, where he showed species branching outward from common ancestors in many directions (not just upward) in a "tree of life." His diagram seems amazingly prescient when compared to modern cladograms, but later scientists using cladistics were merely reinforcing Darwin's concept of descent with modification from common ancestors.

Natural selection and Mendelian genetics are currently regarded as the main contributors to changes in the gene frequencies of populations, but other sources of variation can occur through **recombination** or **mutation**. Recombination sometimes happens during meiosis through the exchange of genes between a pair of chromosomes, meaning new allele pairs that previously were unlinked can be formed in one organism's gametes before the contribution of a mate's gamete. Recombination is the basis for applications of recombinant-DNA research, also known as **bioengineering**, which has, for example, resulted in human-manufactured microbes that consume oil spills or produce insulin. Bioengineering has also created genetically altered fruits and vegetables through manipulation of genes in laboratories, and successful **cloning**, which is the production of a genetically identical organism by placing its genetic material from a diploid somatic cell into a gamete (egg). British scientists first achieved cloning of mammals in 1997 when they produced the sheep "Dolly" (1997–2003). Recombinant-DNA research is causing changes in gene frequencies much more rapidly than could be produced through either selective breeding programs or natural selection. The long-term repercussions of this work and of cloning are currently unknown and are a cause of concern among many people, including some scientists. Of course, cloning of dinosaurs has not occurred nor has its possibility been advanced anywhere except in science fiction.

Mutations constitute another source of genetic variation but differ from recombination in how they form. When a cell divides during meiosis or mitosis, its DNA is copied, but like in a photocopier or a computer printer, small errors can happen during the copying that cause the copy to be an imperfect duplicate of the original DNA. In this case, the slightly altered DNA codes different proteins. Mutations are typically caused by environmental factors, such as intense (short-wavelength) electromagnetic radiation or chemicals (often present as pollutants) called **mutagens**. Mutations have their greatest effect when expressed in gametes and many are harmful to an organism, conferring faulty information that will result in selection against the mutated trait. However, some may confer a trait that is advantageous for natural selection in the light of certain environmental factors.

Both recombination and mutation rates are measurable and can be rapid under certain conditions. Whether recombination and mutations occurred in dinosaurs is unknown, but they must be considered as likely because both are common processes in modern vertebrates. No genetic material, which would provide evidence of recombination and mutation, has been recovered yet from a dinosaur, despite some well-supported evidence of proteins (the by-products of DNA coding; Chapter 5) in a few specimens and amino acids in eggshell material (Chapter 8). Some claims of dinosaur DNA were published in peer-reviewed literature, but subsequent

review has resulted in a consensus that modern DNA contaminated the analyzed samples. The reality is that dinosaur remains, with a minimum age of 65 million years, have been considerably altered from their original state (Chapter 7). This means that the direct use of dinosaur DNA for interpreting the population genetics of dinosaurs (let alone for their cloning) is very unlikely. Nevertheless, phenotypes (represented by body fossils), behaviors, paleobiogeography, and paleoenvironmental settings for dinosaurs are well documented, which provide a good framework for understanding the origin and evolution of dinosaurs.

Part II: Mechanisms for Macroevolution

As mentioned earlier, macroevolution has occurred (and is occurring) as a result of the cumulative effects of microevolution. The overwhelming evidence for this process is found in the fossil record. Fossils recognized originally for their biological origin have been placed within a relative age dating scheme (biologic succession: Chapter 4) that has been used by geologists for the past 200 years. The principle of biologic succession is simple – fossils in lower strata are older than ones in the overlying strata (superposition: Chapter 4). Consequently, those fossils with similar forms that show change through time are inferred to have evolved due to changes in their genotypes that eventually affected their phenotypes. Given the millions of years that are often represented by strata in a typical outcrop, geologists and paleontologists can, on any given day in the field, potentially view the numerous records of organisms that underwent descent with modification, and accordingly test hypotheses about biologic succession.

So-called **transitional fossils** are examples of macroevolution that are perceived as “big leaps” in evolution through what may be considered as major changes in adaptations. Examples are:

- *Pikaia*, interpreted as a primitive chordate from the Cambrian Period, represents a transition from invertebrate animals to chordates:
- *Acanthostega* of the Devonian Period is an amphibian derived from lobe-finned fish:
- *Archaeopteryx* of the Late Jurassic is a bird that evolved from dinosaurian ancestors (Chapter 15):
- *Artiocetus* is a whale from about 40 million years ago that shows clear connections to previous generations of legged, land-dwelling mammalian herbivores.

However, all organisms are in transition between generations, meaning that *all* fossils represent transitional forms or, more properly, have transitional features. Whenever a paleontologist is asked to provide an example of a transitional fossil, they can name any fossil of the millions that have been identified and would still be correct. Thus, the term “transitional fossil” (rarely used by evolutionary scientists) is often applied erroneously only to those organisms that, through their adaptations, seem to bridge a gap between habitats, such as water to land, land to water, and land to air. Such a designation consequently confuses descriptions (forms) with interpretations (functions). Using this reasoning, modern animals that could qualify as transitional fossils in the future, assuming favorable circumstances for their preservation, might include the California sea lion (*Zalophus californianus*), “flying lemurs” (such as *Cyanocephalus volans*), and emperor penguins (*Aptenodytes forsteri*), which are adapted to multiple habitats but show adaptations that favor one habitat over another.

Evolution over spans of geologic time is categorized as having occurred in two modes, **phyletic gradualism** and **punctuated equilibrium**. These modes are not



diametrically opposed views, but both have natural selection and Mendelian genetics at their cores. Their difference is in the scale of evolution in its most basic sense, which is change over time. Phyletic gradualism is a hypothesis supported by evidence for small-scale, incremental changes in fossil species over long time periods, where lineages are reconstructed on the basis of morphological changes in similar fossils in a stratigraphic sequence. Darwin promoted this mode of evolution based on his knowledge of the fossil record in the mid-nineteenth century. Fossil evidence discovered since then has not yet falsified this hypothesis for some lineages. In contrast, punctuated equilibrium is characterized by long periods of no morphological changes in a fossil species, followed by rapid change. Evidence from the vertebrate fossil record that supports this hypothesis was noted by George Gaylord Simpson in the 1940s, but then paleontologists **Stephen Jay Gould** (1941–2002) and **Niles Eldredge** named and proposed it as a unified hypothesis in the early 1970s, based on fossil lineages of gastropods and trilobites, respectively. Gould, more than any other scientist of the latter half of the twentieth century, wrote extensively on punctuated equilibrium and all other aspects of evolutionary theory.

So which hypothesis does the fossil record support? The answer is both, in that some fossil lineages show slow, gradual changes and others show periods of stasis followed by rapid change. Hence, lineages should be examined on a case-by-case basis with regard to whether they are interpreted as belonging to either model or as part of a continuum in between them. Controversy exists over whether one hypothesis is more the norm for speciation, and active debate centers on the evidence supporting each. For instance, one criticism of punctuated equilibrium is that it uses its lack of evidence as actual evidence in some cases of the fossil record. Punctuated equilibrium predicts that intermediate fossil forms may not be represented in short, continuous stratigraphic intervals (corresponding to a short time span) between two distinctive fossil species. In such a case, advocates of punctuated equilibrium might propose that speciation was so rapid that most intermediate forms did not become fossilized, which is possible given that conditions must be just right to preserve some fossils (Chapter 7). Gradualists could counter that intermediate forms might still be found in other areas containing the same stratigraphic interval with more favorable conditions for preservation. The incompleteness of the fossil record, as a record of life on Earth during the past 3.8 billion years, may be an issue in this respect, but it is a record that improves every day with each fossil discovery. For example, dinosaur species have been described in ever-increasing numbers over the past few decades, filling previously perceived gaps in their lineages, especially with regard to theropod–bird connections (Chapters 9 and 15).

Regardless of the rates of change in the genotype frequencies of populations over time, the main non-genetic mechanisms that influence natural selection are environmental factors, particularly those related to biogeography. For example, members of a population can be separated geographically through a physical barrier, such as a rise in sea level that isolates an island from a mainland, a river that changes its course after a major flood, or a forest fire that divides a habitat. Separation also can be a result of migration. Members of a population may migrate thousands of kilometers away from their ancestral population, thus no longer mixing their genes with their original population. If separated populations are kept apart long enough for natural selection to cause significant changes in the genomes of each, the reproductive isolation may result in speciation. Such a hypothesis for the origin of species is called **allopatric speciation**; this type of speciation happens when the **gene flow** (the spread of genes through a population by interbreeding) is interrupted.

One version of allopatric speciation is used in the punctuated equilibrium model. When a small subpopulation at the periphery of a species' geographic range is isolated enough, it cannot reproduce with the main population. This

subpopulation, because of natural-selection factors different from the parent population, will undergo rapid changes in its gene frequencies relative to the main ancestral population. The result is a new species within a small number of generations. This specific type of allopatric speciation is **peripheral-isolate speciation**. Evidence from modern biogeography that supports this mode of speciation consists of numerous plant and animal species that have small, isolated populations on islands that are morphologically distinctive (and in some cases are already reproductively isolated) from large, geographically widespread populations on mainland areas adjacent to the islands. Mountains also serve as geographic barriers between populations that began from an ancestral stock, particularly for those organisms that could not fly over them, such as non-avian dinosaurs.

Another important consideration of small populations in evolutionary theory is that they may reflect non-representative (random) samples of a larger population. Picture the following: four people randomly selected from a group of 100 people move to a small Caribbean island to start a new population, but the remaining 96 stay and mate in Kansas, in the midland part of the North American continent. The genotypes and consequent phenotypes from the mating of the four tropically placed people would not represent the group as a whole and the two resultant groups would likely differ considerably in their Hardy-Weinberg ratios after only a few generations. This divergence would happen regardless of the environmental differences between the two localities that might cause natural selection. Such a random change in the gene frequencies is an example of **genetic drift**. The dramatically rapid effect of genetic drift in small populations relative to large ones has been demonstrated in laboratory experiments with fruit flies, and may be a factor in allopatric speciation for other organisms as well. If a large number of these small populations radiate out from a central location and are isolated from one another to form species that demonstrate adaptations distinctive to each of their individual, but geographically separated, environments, then the resulting populations illustrate **adaptive radiation**. Some bird species from closely associated islands that show many “variations on a main theme” probably radiated from an ancestral species and then adapted to their respective **niches**. A niche can be envisaged as the role of an organism in an ecosystem, where it lives in a specific habitat and uses specific resources.

Probably the greatest large-scale factor now recognized as affecting the geographic distribution of populations is plate tectonic activity (Chapter 4). Although it is a much younger theory than evolution, plate tectonics has been successfully integrated with the latter to provide powerful explanations for how fossil populations became geographically isolated from one another and underwent speciation over long periods of time. The study of biogeography (or paleobiogeography) and how it relates to plate tectonics is termed **vicariance biogeography**, where the vicariance is caused by the division of a species’ geographic range by movement of lithospheric plates, such as in divergence. Vicariance biogeography, as an agent for speciation, is supported by major periods of diversification in the fossil record (which presumably reflect increased speciation) that correlate with the splitting of landmasses by continental rifting, occurring at different times during the Phanerozoic Eon (Fig. 6.3). The main hypothesis for this observed higher number of identified fossil species in association with plate divergence is that ancestral populations, especially for organisms inhabiting shallow-marine and continental environments, became increasingly isolated from subpopulations as rifting continued. This separation encouraged speciation as these subpopulations, through major shifts in genotypic frequencies caused by genetic drift and natural selection, became more reproductively isolated from their ancestral populations and adapted to new environments, occupying new niches.

Vicariance biogeography is applicable to dinosaur evolution throughout the Mesozoic Era, as the continents were more or less together (forming Pangea)



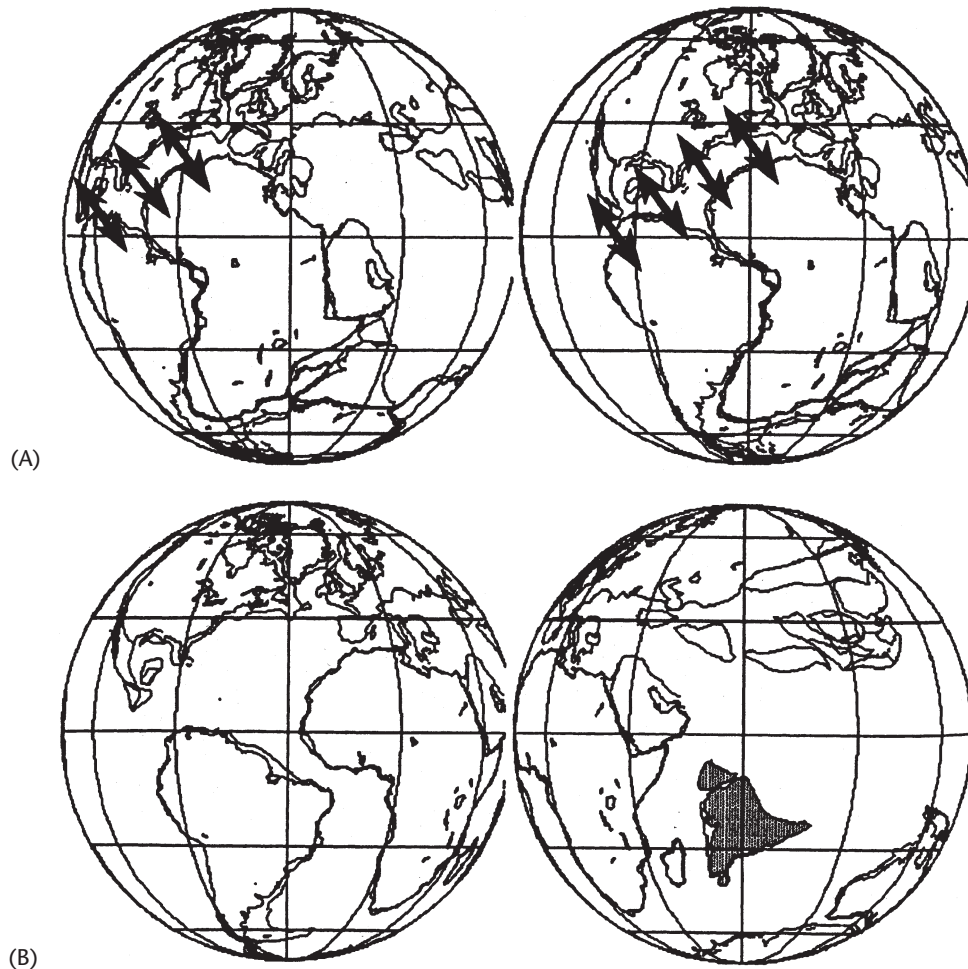


FIGURE 6.3 Continental landmasses during the Mesozoic showing how dinosaur populations became increasingly isolated through time. (A) Late Jurassic (about 140 Ma). (B) Late Cretaceous (about 80 Ma). From Cowen (1995), *History of Life, 2e*, Blackwell Science, Inc., Malden, MA, p. 82, figs. 5.13 and 5.14.

during the Late Triassic Period, when evidence for the first dinosaurs is recorded. Dinosaurs became widespread soon afterward, inhabiting every continent, except Antarctica, by the Early Jurassic (which also reflects their rapid migration rates) before significant splitting up of Pangea. However, as the continents split farther apart by seafloor spreading during the Jurassic and Cretaceous Periods, increased diversification of dinosaurs took place. Some similarities endured within species on still-connected continents, but noticeable differences appeared in those on separate continents. Thus, the most prominent barriers to gene flow and subsequent causes of reproductive isolation and allopatric speciation over time were the oceanic expanses. For terrestrially-bound dinosaurs, this circumstance meant that any of them inhabiting landmasses that later separated from Pangea then formed populations that became distinct from their ancestral populations through time. Additionally, linear mountain systems and inland seas (caused by global sea-level highs) also resulted in geographic barriers that could have been a mechanism for dinosaur speciation (Chapter 13).

However, allopatric speciation through geographic isolation is not the only hypothesis proposed for how species originated in the fossil record. Indeed, reproductively-isolated species with recent common ancestors can have overlapping

geographic ranges. Those closely-related species that occur in the same region have **sympatry**, and the origin of new species from populations within these regions is possibly through **sympatric speciation**. Sympatric speciation is regarded as the result of intraspecific factors, rather than environmental factors such as climate changes or predation by other species. Sexual selection (through competition for mates) is an example of an intraspecific factor that could cause natural selection and subsequent changes in genotype frequencies in a population. This was illustrated through the hypothetical example of the less-endowed *Centrosaurus* earlier. As these differences within a species occur in the same geographic area through time, the increased genetic distance between their inheritable traits is termed **character displacement**. The role of character displacement in dinosaur evolution is poorly understood, but is hypothesized through synapomorphies (connected by cladograms) and speculations about character traits that would relate to this proposed mechanism for speciation. Examples of such characters include horns, head frills, and feathers, which might have served as sexual displays in dinosaurs or were otherwise used for intraspecific competition (Chapters 9, 11, and 13).

Natural selection and the subsequent co-evolution of two or more species that occurs as a result of their interactions are summarized by the **Red Queen hypothesis**. The Red Queen is a character in *Through the Looking Glass*, by writer and mathematician **Charles Lutwidge Dodgson** (1832–98; more popularly known by his pseudonym of **Lewis Carroll**). In the book, Alice meets the Red Queen chess piece, who appears to run across the chess board at high speed, yet never leaves her square: “Now, here, you see, it takes all the running *you* can do, to keep in the same place.” This serves a metaphor for a co-evolutionary process in which two species of organisms continuously match one another’s defenses only to maintain the *status quo*. For example, plants may evolve chemical defenses against insect herbivores, which in turn evolve resistance to the plant’s chemicals, and so on. This type of equilibrium state should cause regular extinctions through time of species with two or more lineages, so the Red Queen hypothesis is scientifically testable. This hypothesis has been proposed to explain some changes in character traits of dinosaurs through time, such as in Cope’s Rule, whereby prey and predatory dinosaurs became progressively larger as a result of their “arms race” interactions (Chapters 9 and 10). Additionally, increased amounts of dermal armor in ankylosaurs and apparent defensive weaponry in stegosaurs comprise other presumed evolutionary responses to pressures from theropod predation (Chapter 12). Although the preceding is a simplistic analogy with regard to modern predators and prey, this hypothesis has also been applied to changes in herbivorous dinosaur dentition and digestive systems in response to changes in vegetation types throughout the Mesozoic Era.

Finally, an important point to keep in mind with natural selection is that some species may have inheritable variations that are “pre-adapted” for a change in either the magnitude or rate of an environmental factor unprecedented in the history of a species. For instance, a large-scale volcanic eruption that deposits ash in only a few weeks over a large area of a forest may favor the reproductive survival of taller adult plants of a species, as the taller plants can still disperse their seeds above the ash layer. The shorter adult plants of the same species, completely covered by the ash, may not survive to reproduce. This chance possession of inheritable traits, favorably adapted for a selective pressure before it happened, is called **exaptation**. Exaptations also are hypothesized as features that had a neutral (non-harmful and non-beneficial) effect on an organism’s adaptation that in later generations become advantageous for survival. This hypothesis for natural selection is especially applicable to explaining the survival of certain lineages of organisms after mass extinctions recorded by the geologic record. The lack of some currently undefined exaptations in dinosaurs at the end of the Cretaceous may have resulted in their demise in the face of a global catastrophe (Chapter 16).



Cladograms that hypothesize macro-evolutionary relationships of dinosaurs and other vertebrates are testable through the fossil record, and new fossil discoveries can change the cladograms. However, a test of cladograms independent of the fossil record is molecular phylogeny (Chapters 5 and 8), which compares relative differences in protein or nucleic acid sequences between extant organisms that are presumed to be descendants from common ancestors. This method is not without controversy, because molecular geneticists who look at these biochemical differences also calculate rates of change in the biomolecules, called **molecular clocks**, under the assumption that these rates do not vary over time. With these molecular-clock models, geneticists are now predicting the divergence times for major clades of organisms, figures that in some cases agree very well with the fossil record but in other cases have discrepancies of tens of millions of years. Despite these disagreements, molecular clocks provide an interesting predictive tool for paleontologists searching the geologic record.

The numerous hypotheses used here to explain how evolution happened in the geologic past, or how it is happening today, do not negate one another. How evolution occurs is not a true-or-false question but a multiple-choice one with the possible answers of “all of the above,” “any of the above,” or “none of the above.” Based on the extensive evidence contributed, at a minimum, by the interrelated sciences of paleontology, geology, biology, and ecology, “none of the above” is the least likely correct answer and “all of the above,” depending on individual circumstances, is the most likely. Of course, all hypotheses in science are subject to falsification, so completely new hypotheses about evolutionary processes that incorporate both old and new information are possible in the future.

Evolutionary Origin of Dinosaurs

Amniote Evolution and Diversification before the Dinosaurs

The origin of dinosaurs could arguably be traced back as far as the origin of life itself, which was about 3.8 billion years ago, but for the purposes of this book the evolution of amniotes is a more reasonable starting point. The development of an **amniotic egg** (one with an **amnion**, or fluid-filled sac surrounding the embryo: Fig. 6.4), from amphibian ancestors for reproduction of offspring outside of aquatic environments, is often heralded as one of the major adaptations in vertebrate evolution. Unfortunately, the first appearance of this defining characteristic of Clade Amniota, which is inferred to have happened during the Carboniferous Period, is currently unknown. No definitive fossil eggs or nests have been interpreted from rocks older than the Late Triassic. This gap in the fossil record, for such a well-established behavior, is likely an artifact of the non-mineralization of eggs before the Triassic (causing a preservation bias), or paleontologists not recognizing nest structures, or a combination of these two factors. However, similarities in the eggs

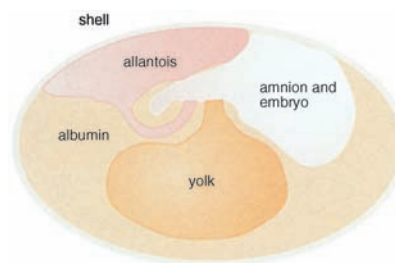


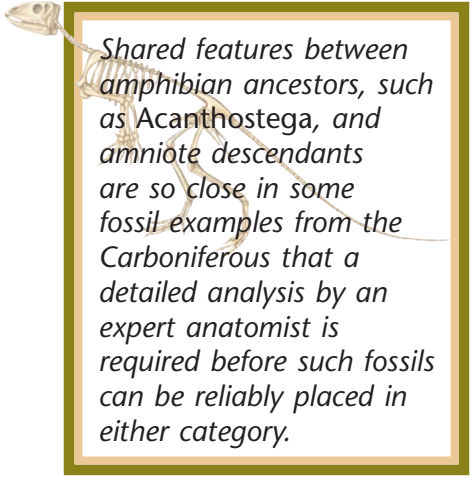
FIGURE 6.4 Components of an amniotic egg, including the eggshell, allantois, yolk sac, amnion, and embryo. Such eggs are a defining character of the clade Amniota, and by extension of dinosaurs. After Cowen (2000), *History of Life*, 3e, Blackwell Science, Inc., Malden, MA, p. 147, fig. 9.12.

of all living amniotes and their close resemblance to fossil eggs argue that this trait is a synapomorphy of amniotes, and it is currently inferred to have evolved just before the skeletal record for amniotes begins.

Despite this lack of evidence, three early species of amniotes in the fossil record are recognized from the Carboniferous Period: *Westlothiana*, *Hylonomus*, and *Paleothyris*. The interpretation of these three small vertebrates as amniotes is based on some anatomical traits distinctive from their amphibian ancestors:

- Dermal bones on the ventral surface of the skull (such as parietals, frontals, and nasals) overlying a bony braincase.
- Reduced head size relative to the overall body size and lightening of the skull.
- Highly modified pelvis consisting of a reinforced pubis and ischium.
- Astragalus and calcaneum in the ankle.

Defining whether some fossils were reptile-like amphibians or amphibian-like reptiles is problematic because of their shared features. Traits of an amniote that differ from that of an amphibian are also more numerous and they summarily reflect adaptations to a terrestrial lifestyle that was increasingly independent of nearby water bodies. As long as aquatic environments were abundant and widespread, amphibians probably did not undergo natural selection that would have favored inheritance of genotypes for sturdier skeletal parts adapted for moving long distances on land away from water.



*Shared features between amphibian ancestors, such as *Acanthostega*, and amniote descendants are so close in some fossil examples from the Carboniferous that a detailed analysis by an expert anatomist is required before such fossils can be reliably placed in either category.*

So as long as aquatic environments were abundant, the buoyancy of water, which helps to relieve gravitational stresses in a vertebrate skeleton, would have negated selection for a heavier skeleton reinforced for extended periods of locomotion out of water. But with changes in environmental conditions to drier climates or the creation of

niches apart from water (such as forests), exaptations or other evolutionary factors favored adaptations of pre-amniotic ancestors toward amniotes. The ability of these non-amniotic ancestors to move about freely on dry land required modifications to their skeletons that supported their weight (that is, a lighter skull, stronger hips, flexible ankles), thus natural selection may have already resulted in amphibians that were divorcing themselves from their dependency on aquatic environments.

The development of an enclosed egg among the descendants of pre-amniotic ancestors was probably the result of natural selection, as only a few eggs (from originally large numbers) had rudimentary membranes enclosing aqueous solutions and prototypes of a yolk sac and **allantois** (respiratory organ for the embryo). Only then would the embryos have survived. Another major evolutionary requirement for the development of amniotic eggs would have been internal fertilization, so sex had to have become more up-close and personal than was previously experienced by amphibians. A few examples of modern amphibians show such a reproductive mode, which means that the same inheritable behavior and anatomical attributes could have been selected in favor of increasing the chances of fertilization. Also, embryos would have been retained within the reproductive tract of the female until a sufficiently protective membrane had developed around them.

The next step in amniotic egg evolution would have been an embryo that underwent growth within the protective membrane to form a miniature version of the adult animal, in contrast to the incompletely developed and intermediate larval (tadpole) stage seen in most amphibians. Although fossil evidence for a sequence



of these adaptations is lacking, the presence of many modern amphibian species that retain their eggs within their bodies for long periods of time, especially in times of drought, attests to the feasibility of this evolutionary scenario. Additionally, some modern salamanders, exemplified by **plethodontids**, lay eggs and their embryos develop completely in non-aquatic environments without any larval stage; among their preferred habitats are inside moist tree trunks or logs. Interestingly, skeletal remains of the Carboniferous amniotes *Westlothiana*, *Hylonomus*, and *Paleothyris* were all discovered within Carboniferous fossil tree trunks, so they may have occupied the same niche as modern plethodontids.

Amniota as a clade is synonymous with the older Linnaean (gradistic) classification of Class Reptilia, but with some qualifications. Under gradistic classification, reptiles, such as lizards, snakes, turtles, and crocodiles, were traditionally regarded as scaly vertebrates; most have four legs (except snakes, of course) and reproduce by laying enclosed eggs. This classification excludes mammals and birds, but cladistics recognizes shared derived characters, meaning that amniotes include all descendants from an ancestral amniote. As a result, Amniota, which includes reptiles, mammals, and birds, is a monophyletic clade. In contrast, reptiles actually comprise a **paraphyletic** group, not a clade, because it does not include all of its descendants, such as mammals and birds. The term “reptile” has been long associated only with lizards, snakes, turtles, alligators, crocodiles, pterosaurs, extinct marine reptiles (such as **euryapsids**, discussed later), and dinosaurs, among others. Nevertheless, change is a part of science (Chapter 2) and part of that change is exemplified through new classification schemes. So now most paleontologists recognize that mammals and birds are also “reptiles” in a cladistic sense.

Once amniotes had developed by the Carboniferous Period, their adaptation into numerous terrestrial ecosystems and consequent diversification was relatively rapid and impressive. The major basis for recognition of their diversification is seen in the arrangement of skull bones, specifically the presence and positions of temporal fenestrae. Amniotes can be subdivided into three major clades on this basis and other characteristics – **Anapsida**, **Synapsida**, and **Diapsida** (Fig. 6.5).

Fossil and modern turtles best represent anapsids, which lack temporal fenestrae. The first reptiles had anapsid skulls, thus turtles exhibit a plesiomorphic trait for amniotes in general. Synapsids and diapsids evidently evolved from a common

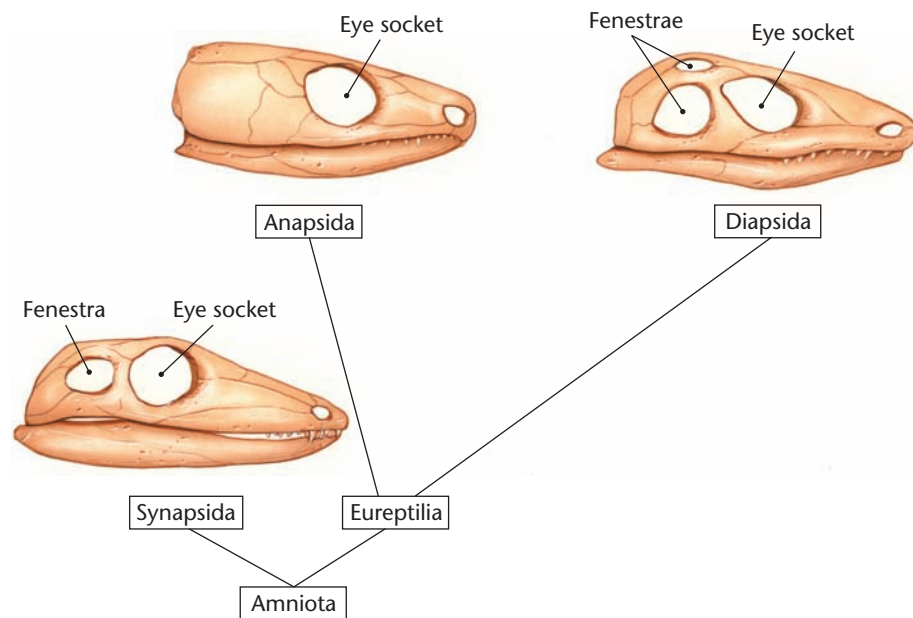
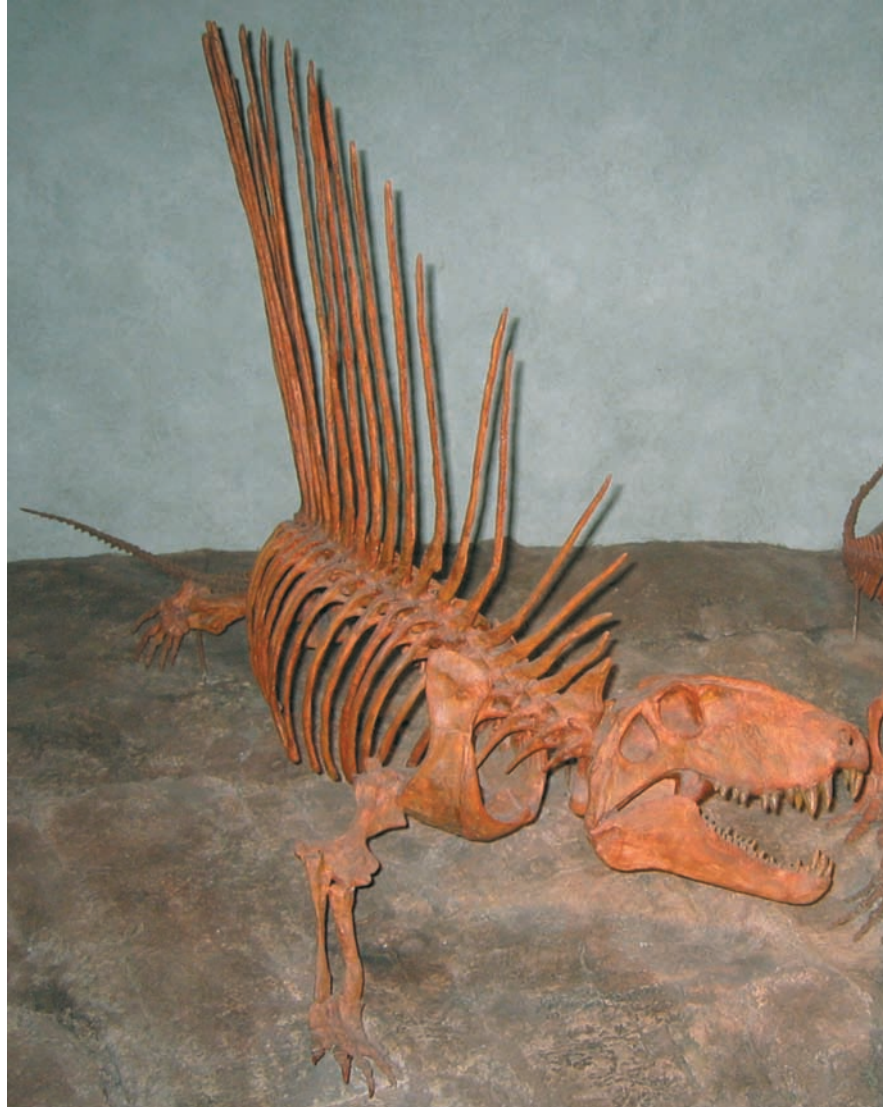


FIGURE 6.5 Three skull types, with positions of temporal fenestra outlined, characterizing the Anapsida, Synapsida, and Diapsida in the context of a cladogram, showing their hypothesized evolutionary relationships.

FIGURE 6.6
Dimetrodon, a Permian synapsid and pelycosaur that was carnivorous, but definitely was not a dinosaur. Denver Museum of Science and Nature, Denver, Colorado.



ancestor of anapsids during the latter part of the Carboniferous, but anapsids and diapsids have been placed in a single clade (Eureptilia) separate from synapsids. Some lineages of synapsids during the Permian included large herbivorous and carnivorous reptiles called **pelycosaurs**. Pelycosaurs had elongated, dorsal vertebral spines that formed sail-like structures, which along with their body size (as long as 3 meters) gave them a formidable appearance that understandably resulted in their popularized but mistaken grouping with dinosaurs (Fig. 6.6). However, synapsids also included lineages that later evolved into **therapsids**, which had some mammal-like characters, and eventually mammals. This means that pelycosaurs are actually more closely related to humans and other mammals than they are to dinosaurs. Mammals are appropriately placed in Mammalia and first show up in the fossil record, at about the same time as the first known dinosaurs, during the Late Triassic.

Diapsida is the clade most pertinent to the discussion of dinosaurs. Diapsids split into two clades, the **Lepidosauria** and **Archosauria**, a divergence of lineages that probably happened during the Permian Period. Lepidosaurians are modern lizards, which includes skinks, geckoes, iguanas, Komodo dragons, and their ancestors. A common misconception about large reptiles, such as alligators and crocodiles, is that they are closely related to lizards such as Komodo dragons, but they are





FIGURE 6.7 *Thalassomedon*, a Late Cretaceous plesiosaur, a marine reptile and an example of a euryapsid. (Euryapsids, and all marine reptiles, were not dinosaurs.) Denver Museum of Science and Nature, Denver, Colorado.

phylogenetically separate, as explained later. Snakes are also lepidosaurs because they share derived characters with lizard ancestors; they even show vestigial pelvic bones. The oldest known snakes in the geologic record are from the Early Cretaceous, thus both lizards and snakes co-existed with dinosaurs during at least part of the Mesozoic (in fact, at least one dinosaur ate a lizard: Chapter 9), and both groups were very successful in later diversification throughout the Cenozoic after the demise of the dinosaurs.

Euryapsids, mentioned previously, are also placed in Lepidosauria because of their inferred common descent from lizard-like ancestors, although they branched into a previously unexplored niche for reptiles, the seas. These diverse, abundant, and often large-bodied marine reptiles of the Mesozoic include the **ichthyosaurs**, **plesiosaurs** (Fig. 6.7), and **mosasaurs**. Among them were the first vertebrates known to have been viviparous, as shown by a few stunning fossil examples of mother ichthyosaurs with their stillborn young. These fascinating and complex reptiles, like many other vertebrates of the Mesozoic, became extinct by the end of the Cretaceous (Chapter 16). They are sometimes confused with dinosaurs because they were contemporaries and overlapped in size with some of the larger dinosaurs. However, dinosaurs were not only anatomically distinct from euryapsids, they were effectively relegated to completely different environments and niches. Probably the

only interactions between these reptilian groups occurred when dinosaur carcasses floated out to sea and were scavenged by euryapsids (Chapter 7).

Archosaur Evolution and Diversification

The Archosauria is defined as having, at minimum, the following characteristics:



Archosauria is the clade often associated with the origin of the dinosaurs.

- Openings anterior to the orbits (antorbital fenestrae).
- Teeth with serrations compressed laterally and none on the palate.
- Dentary fenestrae.
- Differently shaped calcaneum.
- Elongated ilium and pubis.

Some paleontologists place Archosauria within the clades Archosauromorpha and Archosauriformes, the latter originating from the former (Chapter 5). The majority of paleontologists agree upon the designation of Archosauria as a clade that had arrived by the Early Triassic, with members that evolved into lineages, both dinosaurian and otherwise. A group of fossil reptiles, known previously by paleontologists as “**thecodonts**,” was once considered as synonymous with the archosaur group that gave rise to the dinosaurs, crocodylians, and birds. However, cladistic analyses show that thecodonts make up a paraphyletic grouping (such as Reptilia), hence its use as a term is now discouraged in phylogenetic classifications. However, it is commonly mentioned in older literature and represents changing ideas in science.

A likely representative fossil for a common ancestor of the archosaurs is the Early Triassic *Euparkeria* of South Africa (Fig. 6.8). *Euparkeria* was a small (about 1 meter long) but relatively long-limbed reptile that possessed antorbital fenestrae, a key feature of all archosaurs. Clades within the Archosauria, which seemingly descended from ancestors like *Euparkeria*, are the **Crurotarsi** and **Ornithodira**. Crurotarsi includes living crocodylians (alligators and crocodiles), but it encompasses many diverse fossil forms as well. An ankle where the astragalus and calcaneum form a joint between the tarsals and lower part of the limb bones characterizes this clade. Crurotarsans were well-represented during the Middle and Late Triassic by large, crocodile-like carnivorous **parasuchids** (also known as **phytosaur**s) and **rauisuchians** (Fig. 6.9), as well as the armored and herbivorous **aetosaur**s. Rauisuchians were unique among large archosaurs at the time because their forelimbs were considerably shorter than their hind limbs, which suggests that they were capable of walking on two legs. They may have been among the first such archosaurs to evolve this mode of locomotion.

Despite their abundance and success, all species of phytosaurs, rauisuchians, and aetosaur became extinct by the end of the Triassic. However, by the Late Triassic, ornithodirans had diverged into two clades: **Pterosauria** and **Dinosauria**. Pterosaurs, the so-called “flying reptiles,” were among the most famous of the

FIGURE 6.8 Skull of *Euparkeria*, a basal archosaur from the Early Triassic of South Africa, which was not a dinosaur. From Cowen (2000), *History of Life*, 3e, Blackwell Science, Inc., Malden, MA, p. 182, fig. 11.13.

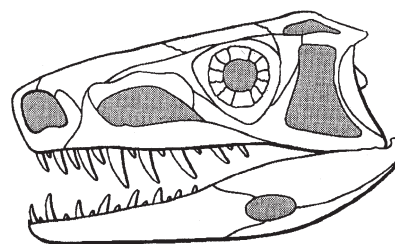




FIGURE 6.9 Cast of *Postosuchus*, a large rauisuchian from the Late Triassic of the southwestern USA: Mesalands Dinosaur Museum, Tucumcari, New Mexico. Despite its very fierce appearance, *Postosuchus* was not a dinosaur.

terrestrial creatures during the Mesozoic, a notoriety related to the interpretation that they were the first vertebrates known to have achieved self-powered flight. Pterosaurs developed a remarkable adaptation whereby digit IV of each forelimb extended far beyond the other digits and had a membrane attached from its distal end to the torso to form a wing (Fig. 6.10). During their time on Earth, which correlated with and was nearly as long as the geologic range of the dinosaurs, pterosaurs evolved into forms as small as a sparrow to the largest animals that ever flew. For example, the Late Cretaceous pterosaur *Quetzalcoatlus* had a wingspan of about 12 meters as it soared over what is now the state of Texas. But in spite of their reputation, grandeur, and chronological association with dinosaurs, the pterosaurs, like many of the other amniotic vertebrates mentioned in this chapter, are still not defined as dinosaurs, although they may have been the closest to having a common ancestor.

Dinosaur Ancestors and the Origins of Dinosaurs

Fame as a dinosaur paleontologist certainly would be justified for anyone who discovered the skeletal remains of the first dinosaurs. However, as shown by the discussion of amniote development, the phrase “first dinosaur” is in itself arguable in the light of evolutionary theory. After all, geologic ranges for fossil lineages are not always static. The possibility that fossils for ancestors of a hypothetical lineage have simply not been discovered yet leads to the concept of **ghost lineages**, meaning that a greater complement of ancestor and descendant species may still be locked away undiscovered in rocks somewhere in the world. For now, paleontologists can define the geologic range of dinosaurs as 228 to 65 Ma (Late Triassic through to the Late Cretaceous) on the basis of discovered specimens, but an understanding

FIGURE 6.10 Cast of the pterosaur *Anhanguera* from the Early Cretaceous of Argentina: Fernbank Museum of Natural History, Atlanta, Georgia. *Anhanguera*, alas, was also not a dinosaur.



of evolutionary theory allows for extrapolating a greater range represented by ghost lineages. Nonetheless, dinosaur remains discovered from Early Triassic rocks would be an extremely significant find, and similar body fossils from Permian rocks would be completely unexpected.

Tracks would be considerably less convincing evidence than skeletal remains for the first dinosaurs or their immediate ancestors, despite the valuable information potentially conveyed by such a find (Chapter 14). Even more suspect evidence would be eggs and nests, minus accompanying skeletal material (Chapter 8). Coprolites, gastroliths, and toothmarks attributable to the first dinosaurs would probably warrant the most skepticism because of the current lack of firm identity attached to such trace fossils (Chapter 14). Consequently, the origin of the first dinosaurs can only be postulated on the basis of skeletal evidence and the stratigraphic position of this evidence, although other indicators or supporting evidence of their existence is possible through trace fossils. The problem with a trace fossil approach for finding evidence of dinosaur ancestors is threefold:

- 1 trace fossils could have been made by tracemakers that had a similar morphology to the first dinosaurs but may have been distantly-related archosaurs;
- 2 the criteria for what constitutes a dinosaur in the fossil record is currently based on anatomical criteria; and
- 3 most dinosaur paleontologists have limited their studies to bones and have not looked for trace fossil evidence.





FIGURE 6.11 Cast of the small dinosauromorph *Marasuchus* from the Late Triassic of Argentina: Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma. *Marasuchus* is not a dinosaur, but is very, very close to being one. Length about 40 cm.

As a result, the body fossil record for dinosaur ancestors is currently considered to be the primary basis for phylogenetic reconstructions of dinosaur lineages.

Based on known lineages of archosaurs before the oldest known dinosaurs found in the geologic record and their anatomical traits, a prediction of the ancestral archosaur, the “mother of all dinosaurs,” can be made. This hypothetical ancestor would have had, at a minimum, the following traits distinctive from other diapsids:

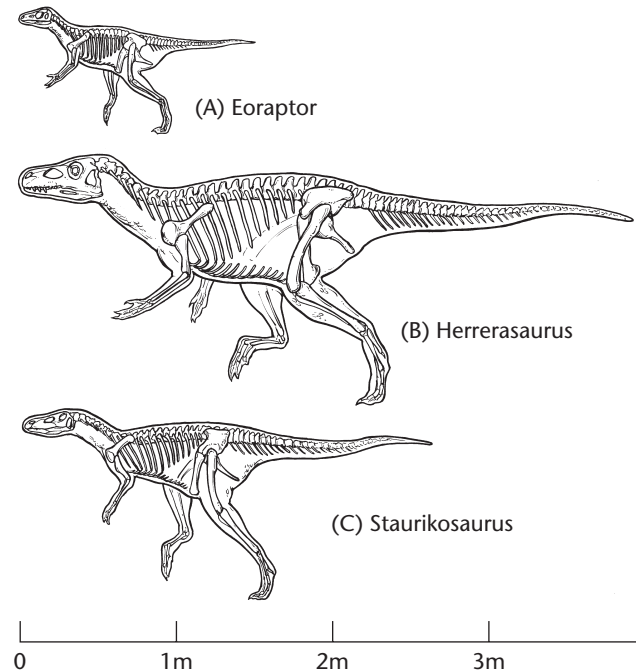
- Bipedal, with long hind limbs relative to the forelimbs.
- Four or five digits on its manus, with digits IV and V reduced in size.
- Long metatarsals and phalanges on its pes.
- Ankle with a hinge developed between the astragalus and calcaneum.
- A tibia–fibula length greater than the femur.

Of fossil finds so far, those closest to this ancestor are *Marasuchus* (Fig. 6.11), synonymous with *Lagosuchus* in some studies, and *Lagerpeton*, which are small but long-limbed reptiles occurring in the Middle Triassic strata of Argentina. *Marasuchus* and *Lagerpeton* were among the first ornithodirans, and their successors could have diverged into either pterosaur or dinosaur lineages. Additionally, small three-toed footprints documented from Early and Middle Triassic strata may be associated with ornithodiran tracemakers that preceded or were contemporaneous with the aforementioned species represented by body fossils.

These possible ancestral forms are succeeded in the geologic record by what are considered by many paleontologists as the earliest known dinosaurs: *Eoraptor lunensis* and *Herrerasaurus ischigualastensis* from the Ischigualasto Formation of Argentina, as well as *Staurikosaurus pricei* from the Santa Maria Formation of Brazil (Fig. 6.12). All three of these specimens are from the earliest part of the Late Triassic (Carnian Age, which was about 221 to 228 Ma); radiometric age dates of $^{40}\text{Ar}/^{39}\text{Ar}$

EVOLUTIONARY ORIGIN OF DINOSAURS

FIGURE 6.12 Three Late Triassic fossil archosaurs proposed as primitive dinosaurs. (A) *Eoraptor lunensis*. (B) *Herrerasaurus ischigualasto*. (C) *Staurikosaurus pricei*. Modified from Paul (1988), Sereno et al. (1993), and Sereno (1994).



from mineral grains gave a minimum age of 227.8 ± 0.3 Ma for the Ischigualasto Formation, which contains the first two species. Of the three species, *Eoraptor* seems to have the most primitive traits, which has led to controversy over whether it actually is a dinosaur. Like many dinosaur species, it is only known from a single specimen. It also was small (about 1 meter long) in comparison to its immediate successors, as well as members of the entire clade of Dinosauria. The other two species, which collectively are represented by more than a dozen specimens, are placed within the clade Herrerasauridae, which is also occupied by the geologically slightly younger *Chindesaurus bryansmalli* of North America. All of these so-called “basal” dinosaurs are regarded as saurischians, and most paleontologists think that they are closely allied with theropods. Interestingly, the lack of agreement on their exact classification probably reflects their basal status.

The only definite ornithischian dinosaur discovered from strata of an age near the apparent “birth of the dinosaurs” is *Pisanosaurus mertii*, which is also from the Ischigualasto Formation of Argentina. Nearly contemporary with the herrerasaurs and *Pisanosaurus* in the Late Triassic was one other saurischian, the prosauropod *Azendohsaurus* from Morocco, and the ornithischian *Technosaurus* from the western USA. Only partial and fragmentary specimens represent both species; in fact, *Azendohsaurus* is only interpreted as a prosauropod on the basis of a single tooth. Hence, these dinosaurs have little to tell us about non-theropod and ornithischian evolution during the Late Triassic. The monophyletic grouping of dinosaurs, which was challenged by Harry Govier Seeley (Chapter 3) through his division of dinosaurs into the Saurischia and Ornithischia, is upheld by synapomorphies of both clades, but an immediate common ancestor for both has yet to be found. For ornithischians in particular, paleontologists have so far only found abundant and well-preserved representatives of this clade beginning in Early Jurassic strata, meaning that:

- 1 ornithischians were uncommon during the Late Triassic;
- 2 taphonomic factors prevented their preservation in Late Triassic sediments; or
- 3 paleontologists are looking in the wrong places for them.



This situation presents a minor evolutionary dilemma for dinosaur paleontologists: if saurischians and ornithischians were already contemporaries during the Late Triassic, when did they diverge from a common dinosaurian ancestor? The most likely answer lies in the Middle Triassic, but unfortunately the body fossil record has not been helpful in this respect. *Marasuchus* is a probable common ancestor for saurischians and ornithischians, showing characteristics (long femur, possibly open acetabulum, long metatarsals) that suggest bipedal adaptations and classification in the clade Dinosauromorpha. However, it was also proposed as a possible common ancestor for pterosaurs and dinosaurs, which would have placed it closer to the node for the clade Ornithodira. Other than *Marasuchus* and perhaps *Lagerpeton*, the other fossils are so poorly preserved or of such uncertain affinity that any declaration of a common ancestor probably would be premature.

Trace fossil data, in the form of distinctive dinosaurian tracks, provide some clues about possible dinosaur ancestors in the Middle Triassic, and some tracks found in strata of this age are similar to undoubted dinosaur tracks. Because the current anatomical evidence related to dinosaur ancestry strongly suggests that primitive dinosaurs were obligate bipeds and developed a pes with three prominent toes, they should have made tracks reflecting this bipedalism. Furthermore, they should have had a track shape that is easily distinguishable from their four-legged predecessors, as well as from other potentially bipedal archosaurs, such as rauisuchians. For example, a reduction in the number of elongated toes seen in theropod tracks from four to three (accompanying a reduction of the hallux) is predicted for the Middle to Late Triassic transition, based on evolutionary changes reflected by the skeletal record. Considering the abundance of tracks left by a living, mobile animal (maybe thousands) versus its body (one), there should be many examples of dinosaur tracks from soon after the time that they evolved (Chapter 14). However, paleontologists who are skeptical about the identity of trackmakers may first insist on correlation of footprint morphology with appendicular skeletons of known tracemakers in same-age strata. Only then might they agree that such evidence is indicative of dinosaur ancestors or dinosaurs themselves in the Middle Triassic.

Once they evolved, dinosaurs rapidly filled niches in their terrestrial environments during the Late Triassic. The extinction of large, abundant, and diverse archosaurs by the end of the Triassic coincided with the increased diversification and abundance of dinosaurs, which is reflected by their body fossils and tracks. Additionally, a prosauropod nest with eggs interpreted from the Late Triassic of Argentina indicates that dinosaurs were already reproducing in ways familiar to paleontologists who have made similar finds in Jurassic and Cretaceous rocks (Chapter 8). The change in archosaurian faunas was originally interpreted as a result of **interspecific** (between species) competition, where dinosaurian domination over other terrestrial vertebrates was ensured by their upright stance and increased speed associated with bipedalism. However, an extinction event that affected some eureptilian groups and herrerasaurids alike near the beginning of the Late Triassic (at about 225 Ma) suggests that other factors, such as environmental change, were more likely contributors to dinosaurian hegemony, which was clearly in place by the end of the Late Triassic (about 206 Ma: Chapter 16).

Possible Genetic and Environmental Causes for the Origin of Dinosaurs

For dinosaurs to have evolved from archosaur ancestors, a combination of genetic and environmental factors had to combine in just the right way to result in the fossil forms that we define as dinosaurs at least 230 million years after. Before considering what factors may have influenced the origin of dinosaurs, a review of some

character traits that define dinosaurs (Chapters 1 and 5) provide a framework for how the traits reflect adaptations, which will be revisited later:

- Three or more sacral vertebrae.
- Shoulder girdle with backward-facing (caudally pointing) glenoid.
- Asymmetrical manus with less than or equal to three phalanges on digit IV.
- Acetabulum with open medial wall.
- Tibia with cnemial crest.
- Astragalus with a long ascending process that fits into the anterior part of the tibia.
- Sigmoidally shaped third metatarsal.
- Postfrontal absent.
- Humerus with long deltopectoral crest.
- Femur with ball-like head on proximal end.

Eight of these ten traits are related to modification of the appendicular skeleton that shows adaptations to bipedalism, a mode of life well-suited to nearly all subsequent theropods (Chapter 9). Discussion of the early evolution of dinosaurs should therefore focus on these adaptations, which occurred through an interaction of genetic and environmental factors.

Probably the most difficult task in figuring out dinosaur origins is evaluating the genetic factors that contributed to evolution of the characteristic traits. Nearly as difficult is discerning the environmental factors that affected a selection of these same traits. Geneticists and ecologists have problems in defining the interactions of modern populations, their genetics, and ecosystems, so why should understanding the Mesozoic be any easier? Fortunately, the skeletal record for dinosaurs and their ancestors, along with their associated geologic information, provide enough clues that a general hypothesis for the origin of dinosaurs has been proposed, tested, and refined with new information and insights.

Through cladistic analyses of Early, Middle, and Late Triassic archosaurs, the probable genetic relationships between different fossils have been well established, although cladograms are often modified with the discovery of each new fossil species or re-interpretations of previously described species. Genetic relationships between Triassic archosaurs are based on phenotypes as reflected by skeletal features interpreted as synapomorphies (Chapter 5). However, some paleontologists will acknowledge that a single specimen of a fossil species may be unrepresentative of most phenotypes in its species at that particular slice in time. Uncertainty is inevitable because some features in a body fossil may be acquired characteristics, and thus not representative of an organism's genome.

Nonetheless, the regularity and predictable occurrence of most features in a body fossil, testable through discovery of multiple specimens of a presumed species, provides a valid reason for assuming that these features are indeed reflecting inheritable traits. Such traits can be as simple as, for example, four limbs. We can safely assume that a fossil tetrapod showing four limbs does not represent a mutation inherited from an ancestor that normally had three limbs. A close examination of changes in details of the anatomy reveals what changes occurred in lineages through time, such as synapomorphies documented for typical Triassic archosaur traits – hind limbs lengthening more than fore limbs, reduction of digits IV and V, elongation of metatarsals and phalanges on the pes, etc.

Because synapomorphies are assumed in the majority of cases as representative of an archosaur's genome, morphological variations within an archosaur lineage also can be interpreted on the basis of how these features may be similar or different in time-equivalent strata. For archosaurs, this interpretation obviously



depends on the sample number of specimens and the completeness of the individual specimens; hence taphonomy (Chapter 7) sets conditions on interpretations once again. Excellent examples of dinosaur species, which were abundantly preserved so that genetic variation in a population can be estimated, are provided by two Late Triassic dinosaurs, the theropod *Coelophysis* (Chapter 9) and prosauropod *Plateosaurus* (Chapter 10). In these two species, many individuals can reflect a population structure, especially if found in the same locality and deposit. Indeed, for *Coelophysis*, a proposed population structure includes juveniles to adults, although in this case too much data can mean more complications, because some of the adult variations may actually be attributable to sexual dimorphism (Chapters 8 and 9). Nonetheless, statistical descriptions of the population provide a sample of at least a few parameters of the original gene pools for *Coelophysis* and *Plateosaurus*.

As mentioned earlier, biogeography is a key facet of evolutionary theory because a close proximity of similar species is additional evidence suggesting their relatedness. The same applies to dinosaurs – because of the abundance of Late Triassic dinosaurs and their immediate ancestors in South America, the origin of dinosaurs is currently attributed to that continent, which was part of Gondwana during the Late Triassic (Chapter 4). Assuming that this was the general location for the birth of dinosaurs, the split between saurischians and ornithischians also may have happened in this area, probably about 230 Ma or slightly earlier.

Why this divergence occurred and why it was so rapid, geologically speaking, are both good questions. Because so little evidence exists for fossils showing intermediate features between dinosaur ancestors and basal dinosaurs, paleontologists hesitate to state whether this apparently rapid evolution was a result of:

- 1 phyletic gradualism that is simply missing parts of the lineages;
- 2 punctuated equilibrium; or
- 3 some combination of the two.

One form of natural selection invoked for dinosaur evolution, as a type of Red Queen hypothesis, is that early dinosaurs successfully competed with other archosaurs for habitats and resources throughout the Triassic, which eventually resulted in crurotarsans becoming extinct and ornithomirans (including dinosaurs) thriving by the end of the Triassic. However, some paleontologists doubt this hypothesis because re-examination of the archosaur fossil record does not show gradual inverse trends between dinosaur abundance and demises of other archosaurs. As mentioned previously, Late Triassic extinctions of archosaurs, other than dinosaurs, began before the end of the period, meaning that they may have encountered many different and changing environmental factors that selected against their survival.

Some evidence of environmental change and its effects on biota during the Late Triassic is indicated by extinctions of marine invertebrate organisms about 220 Ma, which coincided with the beginning of the breakup of Pangea (Chapter 4). Divergence of the continental masses from this supercontinent would have caused gradual changes in oceanic and atmospheric circulation patterns, which not only would have affected marine habitats but overall global climate. **Climate** is often synonymized with **weather**, but they differ considerably in their time frames. Climate is persistent long-term trends and patterns of weather, whereas weather is daily, short-term changes in atmospheric conditions. For example, if most of the years in a million-year period had low amounts of rainfall in an area, these data would allow for defining an arid climate for that area.

At any rate, climate affects evolutionary processes, in particular natural selection, and climate did indeed change during the Late Triassic. These changes are indicated by Late Triassic **evaporite deposits**, which are thick accumulations of minerals such as halite (NaCl) and gypsum ($\text{CaSO}_4 \times 2\text{H}_2\text{O}$) that form in sedimentary

basins over long periods of time under predominantly arid conditions. A hypothesized effect of arid climates is that terrestrial plant communities, through natural selection, would have adapted so that drought-resistant species should have become more common. A change in plant communities meant that herbivores would have had to adapt to new food sources, and those species that could not adapt would become extinct. Likewise, carnivorous species that preyed upon the maladapted herbivores then also would have gone extinct, in the sense of an ecological domino effect (discussed in Chapter 16). Sure enough, this change in plant communities in accordance with the onset of arid climates has been observed with fossil plants from the Late Triassic, which in turn corresponds with faunal changes, justifying a cause-and-effect hypothesis.

Other than changes in climate, another possible consequence of Pangea breaking up in the Late Triassic was habitat fragmentation, which would have caused geographic isolation of dinosaur and other archosaur faunas, translating into conditions favorable for allopatric speciation and adaptive radiation that was perhaps facilitated through genetic drift. As mentioned earlier, diversification of fossil faunas seems to correspond with times of continental breakup throughout the Phanerozoic Eon, a correlation that is attributed to the formation of new habitats. Consequently, new niches also should have opened up for species that had the genetic capability to adapt. Dinosaurs certainly represented novel adaptations in archosaur lineages during the Late Triassic, which is perhaps related to their fitting into new niches caused by continental rifting and the emptying of those niches by extinct archosaurs. So rather than dinosaurs “out-competing” other archosaurs, they may have simply replaced them.

The worldwide dispersal of dinosaur faunas by the end of the Triassic, within 25 million years of their origin, is remarkable in itself, but other aspects of dinosaurs in the latter part of the Late Triassic argue for how they had already made their mark on the world. Three trends in particular are notable:

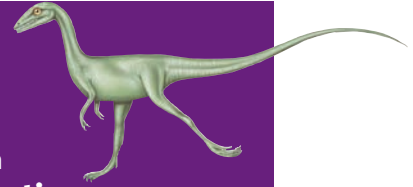
- 1 increased body size (corroborated by larger dinosaur tracks in same-age strata as larger dinosaurs);
- 2 increased number as a percent composition of terrestrial vertebrates; and
- 3 increased diversity with time.

Within those 25 million years, saurischians in particular increased in size, from the 1-meter long *Eoraptor* to the 11-meter long prosauropod *Riojasaurus* of Argentina. Meanwhile, dinosaurs went from about 6% of terrestrial amniote species to as much as 60%. The abundance of some dinosaur species is worth mentioning; interestingly, the dinosaur species most abundantly represented in the fossil record is the Late Triassic *Coelophysis*, but most dinosaurs (such as *Apatosaurus*, *Tyrannosaurus*, *Stegosaurus*, and *Triceratops*) lived much later in geologic time. Paleontological information suggests that *Coelophysis* was not only abundant, but had already developed social behavior, traveling together in large groups (Chapter 9). Likewise, *Plateosaurus* and other prosauropods represented a pinnacle of herbivore evolution in body size by the Late Triassic, anticipating the sauropod leviathans that would emanate from their common ancestors later in the Mesozoic (Chapter 10). The diversity of dinosaurs is indicated by the large number of species described from strata formed toward the end of the Late Triassic in comparison to the few species known from the beginning of the Late Triassic (Table 6.2).

Dinosaurs also survived one of the most well-documented mass extinctions in the geologic record, an extinction that eliminated all aetosaurs, phytosaurs, rauisuchians, and some other formerly successful archosaurs by the end of the Triassic. Compatriots of the early dinosaurs that survived this mass extinction included some euryapsids, anapsids, pterosaurs, and mammals. Various hypotheses proposed



TABLE 6.2 Dinosaur genera of the Late Triassic: (A) earlier part of the Late Triassic, Carnian Age (228–221 Ma), (B) latter part of the Late Triassic, Norian through Rhaetian Ages (221–206 Ma). Notice that some genera (*Blikanasaurus*, *Euskelosaurus*, *Melanorosaurus*) span both intervals, but these genera do not extend into the Rhaetian.



GENUS AND CLADE	PLACE OF DISCOVERY
A. Carnian Dinosaurs	
Saurischians	
<i>Eoraptor</i> (?Theropoda)	Argentina
<i>Staurikosaurus</i> (Theropoda)	Brazil
<i>Herrerasaurus</i> (Theropoda)	Argentina
<i>Azendohsaurus</i> (Sauropodomorpha)	Morocco
<i>Blikanasaurus</i> (Sauropodomorpha)	South Africa
<i>Euskelosaurus</i> (Sauropodomorpha)	South Africa
<i>Melanorosaurus</i> (Sauropodomorpha)	South Africa
<i>Saturnalia</i> (Sauropodomorpha)	Brazil
Ornithischians	
<i>Pisanosaurus</i> (Uncertain)	Argentina
<i>Technosaurus</i> (Uncertain)	Western USA
B. Norian–Rhaetian Dinosaurs	
Saurischians	
<i>Antetonitrus</i> (Sauropodomorpha)	South Africa
<i>Coelophysis</i> (Theropoda)	Western USA
<i>Chindesaurus</i> (Theropoda)	Western USA
<i>Liliensternus</i> (Theropoda)	Germany
<i>Syntarsus</i> (Theropoda)	Zimbabwe, western USA
<i>Blikanasaurus</i> (Sauropodomorpha)	South Africa
<i>Camelotia</i> (Sauropodomorpha)	England
<i>Coloradisaurus</i> (Sauropodomorpha)	Argentina
<i>Euskelosaurus</i> (Sauropodomorpha)	South Africa
<i>Melanorosaurus</i> (Sauropodomorpha)	South Africa
<i>Mussasaurus</i> (Sauropodomorpha)	Argentina
<i>Plateosaurus</i> (Sauropodomorpha)	Europe (Germany, France, Switzerland)
<i>Riojasaurus</i> (Sauropodomorpha)	Argentina
<i>Sellosaurus</i> (Sauropodomorpha)	Germany
<i>Thecodontosaurus</i> (Sauropodomorpha)	England
Ornithischians	
None known.	

for causes of this mass extinction (one of six indicated by the geologic record) include:

- 1 interspecific competition;
- 2 changing climates;
- 3 habitat fragmentation from the continued breakup of Pangea; and
- 4 a meteorite impact.

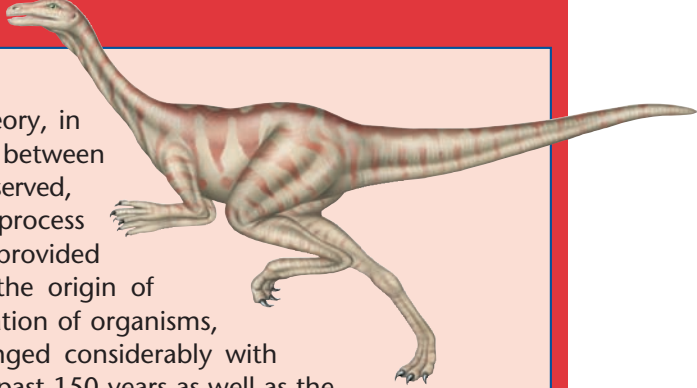
SUMMARY

All of these factors are similar to those implicated in the downfall of dinosaurs at the end of the Cretaceous Period (Chapter 16).

The survival of dinosaurs through what must have been a significant change in global ecosystems in the Late Triassic indicates that dinosaurs may have had exaptations that gave them evolutionary advantages, despite whatever factors (genetic or environmental) might have eliminated other species. A similar probability of exaptations in bird lineages, which most likely evolved out of theropods during the Jurassic Period (Chapters 9 and 15), must have allowed some of them to survive the extinction at the end of the Cretaceous.

The reason for dinosaur survival through a major extinction and their subsequent worldwide dominance of terrestrial faunas is that they had the right genetic makeup for adaptations to new niches and consequent diversification in environments of the forthcoming Jurassic and Cretaceous Periods. The 140-million-year span of the Jurassic and Cretaceous, often hailed as the reign of the dinosaurs, thus followed the foundation of an already diverse and successful Late Triassic dinosaurian fauna. Dinosaurs were, and still are, by-products of an evolutionary process that continues today.

SUMMARY



Evolution is both a fact and a theory, in that the change in a population between generations of species has been observed, but the explanation for how this process happens is still evolving. Darwin provided the first unified explanation for the origin of species and descent with modification of organisms, although his hypothesis has changed considerably with more fossil discoveries during the past 150 years as well as the addition of Mendelian genetics, which was further elaborated through the study of population genetics. Nevertheless, the basic tenets of Darwinian theory (natural selection through inheritable variations, overpopulation, struggle for existence, and survival of the better-adapted) are still applicable to understanding how environmental and intraspecific factors change genotype frequencies and phenotypes, causing speciation. Speciation that happened over longer periods of time and caused considerable changes within lineages (macroevolution) is attributed to either phyletic gradualism or punctuated equilibrium, depending on the timing of the changes. Evidence supporting both of these hypotheses comes from the fossil record, with possible mechanisms of allopatric and sympatric speciation, adaptive radiation, and vicariance biogeography, among others. Molecular phylogeny is an independent method used more in recent years to test phylogenetic relationships established through fossil lineages, although cladistic analyses based on characteristic traits still determine hypotheses for how dinosaurs evolved.

Dinosaur evolution can be evaluated by examining the fossil record for amniotes as a whole and archosaurs in particular. The development of a cleidoic egg from amphibian ancestors probably happened during the Carboniferous Period as a result of both genetic and environmental factors that favored this mode of reproduction. Subsequent diversification

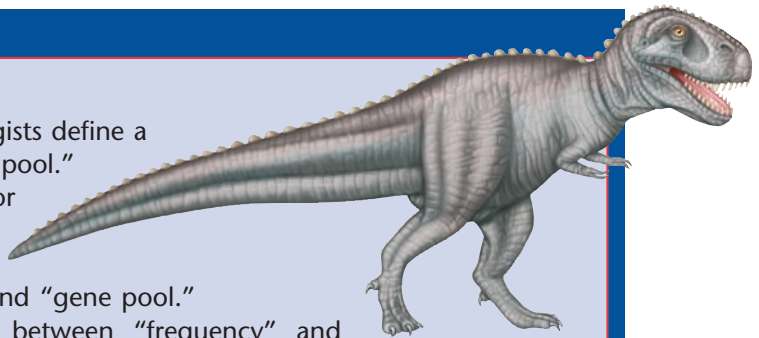


SUMMARY Continued

of amniotes resulted in the origin of anapsids, synapsids, and diapsids well before the end of the Permian; diapsids gave rise to archosaurs, which proliferated throughout the Triassic. Among the archosaur lineages was the ornithomirans, which include dinosaurs and their contemporaries, the pterosaurs. Dinosaurs probably originated during the Middle Triassic, as suggested by both body and trace fossil evidence, and their increased diversification and abundance developed rapidly within the last 25 million years of the Late Triassic, particularly for saurischians (theropods and prosauropods). Although genetic factors were certainly involved, the diversification may have been prompted by the opening of ecological niches left by other archosaurs (such as rauisuchians, phytosaurs, and aetosaurs) that went extinct toward the end of the Triassic. Additionally, the onset of arid climates and the beginning of continental rifting in the supercontinent Pangea through the same time span may have contributed to changes in the roles of plants, herbivores, and carnivores in terrestrial ecosystems. Regardless of the exact evolutionary mechanisms responsible for their ascendancy, dinosaurs had become the dominant vertebrates by the end of the Triassic and they would have a magnificent reign that would last for the next 140 million years, until the end of the Cretaceous.

DISCUSSION QUESTIONS

1. Some evolutionary biologists define a species as a "closed gene pool." Justify this description or criticize it on the basis of definitions given in the chapter for a "species" and "gene pool."
2. What is the difference between "frequency" and "probability"? How are these statistical expressions related to population genetics?
3. A hypothetical female theropod with a homozygous recessive gene for a reduced hallux mated with a male theropod with a heterozygous condition that has a normal-sized hallux as the dominant trait.
 - a. What was the probability of their offspring having the phenotype of a reduced hallux?
 - b. What is the probability for the next generation (the offspring of the offspring) having the phenotype of a reduced hallux?
 - c. What is the assumption of the preceding probabilities? In other words, what factors could change the expected gene frequencies?
4. Out of all of your friends, think about how representative one of them might be for the phenotype of *Homo sapiens* if he or she was randomly picked as a "type specimen."



DISCUSSION QUESTIONS Continued

- a. How much variation would your friend have in his or her living appearance?
 - b. Out of those observed variations, what inheritable features do you think would be evident in the fossil record that might define them as typical of your species?
 - c. What acquired features do you think would be unrepresentative of their genome and thus would be a source of confusion for paleontologists of the future (whatever their species might be)? For example, do they have dyed hair, tattoos, piercings, or other modifications?
5. Explain how the evolutionary development of a cleidic egg for amniotes could have occurred through the following models:
 - a. Allopatric speciation
 - b. Sympatric speciation
 - c. Phyletic gradualism
 - d. Punctuated equilibrium
 - e. Character displacement
 - f. Red Queen
 6. Based on the information presented in the chapter, make your own cladogram showing the ancestry of the following modern reptile groups: turtles, snakes, lizards, crocodiles, and alligators. Which pair among these five groups seems to be the most related and which pair seems the least related?
 7. The overall average height of humans has increased in the past 1000 years, based on measurements of skeletons from that time span as well as data taken from living people. Is this increase in height an example of directional selection (Cope's Rule)? Why or why not?
 8. Given the primitive dinosaur traits of bipedalism, think about the following:
 - a. How could natural selection have caused some descendants of the first dinosaurs, such as prosauropods, to go to quadrupedalism as a mode of locomotion?
 - b. What are some environmental factors that might have favored quadrupedal postures? What evidence in the geologic record would be needed to corroborate your hypotheses?
 - c. What are some possible intraspecific factors that might have caused sympatric speciation in such a direction? What evidence in the geologic record would be needed to corroborate your hypotheses?
 9. Of the amniotes mentioned in the chapter, which ones did you mistakenly think were dinosaurs before reading this book? How would you go about convincing someone else that these animals were not dinosaurs?
 10. How could a meteorite impact have caused problems for ecosystems during the Late Triassic? List some of the effects of an impact that are unlike the more gradual changes that might have been caused by continental rifting.



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