



CHAPTER

3

Similarity and Patterns of Evolution

CHAPTER SUMMARY

Structures with an underlying similarity found in different species share their essential similarity (homology) because the species share a common ancestor. Structures not related through a common ancestor arise by independent evolution and so are not homologous. Essentially, three patterns of evolution exist: (1) common descent because of similarity based on homology; (2) parallelism, the evolution of similar features in related lineages; and (3) convergence, the evolution of similar features in independent lineages. Many evolutionary biologists are actively involved in identifying and separating these different patterns of evolution in order to determine evolutionary origins and relationships.

Careful anatomical dissections and comparisons of adults and of embryos provided the basis upon which late nineteenth and twentieth century biologists identified species and constructed detailed evolutionary trees. Similarities among vertebrate embryos during early developmental stages provided evidence for their common evolutionary past.

Because in almost every instance fossils differ from present-day forms, fossils provide the hard physical evidence for evolution (**END BOX 3.1**). Horses comprise one of the most complete and continuous fossil records of the evolution of an animal lineage. From the fossil record, we know that horses evolved from a small, four-toed leaf-browsing animal to a large,

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single-toed animal with continuously growing teeth, adapted to chewing tough grasses. In some instances, the fossil record contains forms with features of two major extant groups of organisms. Perhaps the most famous of these is *Archaeopteryx* (“ancient wing”), which has features of both reptiles and of birds. Other ancient lineages, often described as “living fossils,” persist with minimal morphological changes to the present day. The coelacanth (*Latimeria chalumnae*) is a notable example of a living fossil fish, the Ginkgo (*Ginkgo biloba*) of a living fossil tree.

INTRODUCTION

At least four (and in fact many more) species concepts are in use, reflecting different types of evidence used to identify a species. These species concepts also reflect speciation as an ongoing process; species are classified at various stages during speciation or when speciation is complete. Because evolutionary change differs in intensity and duration, temporally and spatially (especially when environments are changing rapidly), some organisms are difficult to classify.

Members of a species are identified by their similarity derived from a shared history. Although a species name indicates a distinct group with shared characters, the individual members of a species display variation. Because classification and evolution inevitably emphasize different aspects of organisms, the basis on which similarity is determined is a central issue. Two aspects of this issue are discussed below in the context of evolutionary patterns seen when we compare organisms with different degrees of shared relatedness and evolutionary history. The first aspect considers how similarity of features is determined. The second deals with two classes of evidence—comparative embryology and the fossil record—used to compare organisms.

SIMILARITY: KNOWING WHEN CHARACTERS ARE THE SAME OR DIFFERENT

In general, the more similar features shared by a group, the more likely the group descended from a common ancestor. Once again, a classic example lies in the evolution of horses and the reduction in their number of toes over the past 60 million years (My). (MacFadden, 1992; Vila et al., 2001). We can readily recognize and equate the parts of the horse skeleton at the ends of the feet as toes, even when the number decreased over time from four to one (FIGURE 3.1). The fossil record is detailed, enabling us to reconstruct evolutionary changes, recognize now extinct lineages, and identify the lineage that led to the modern horse. The evolutionary record is rarely as complete as it is for horse evolution, however.

Greater difficulties in interpretation occur when similar characters arise in different lineages, as seen in organisms that evolve to mimic another species in their environment. Examples include palatable insects that mimic a poisonous insect species, moths that mimic leaves, and seahorses that mimic seaweeds or corals (FIGURE 3.2). Organisms in far-flung parts of the globe may evolve in parallel or by convergence, even though they do not share gene flow or a recent common ancestor. Examples include placental and marsupial “tigers” or “wolves” (FIGURE 3.3), marsupial, placental, and monotreme “anteaters,” and African euphorbs and American cacti (FIGURE 3.4). These examples bring us face to face with the “apples and oranges” problem (FIGURE 3.5). How can we tell whether similarity reflects evolutionary origin from a common ancestor or independent evolution? When does similarity mean sameness and when does similarity mean close resemblance?

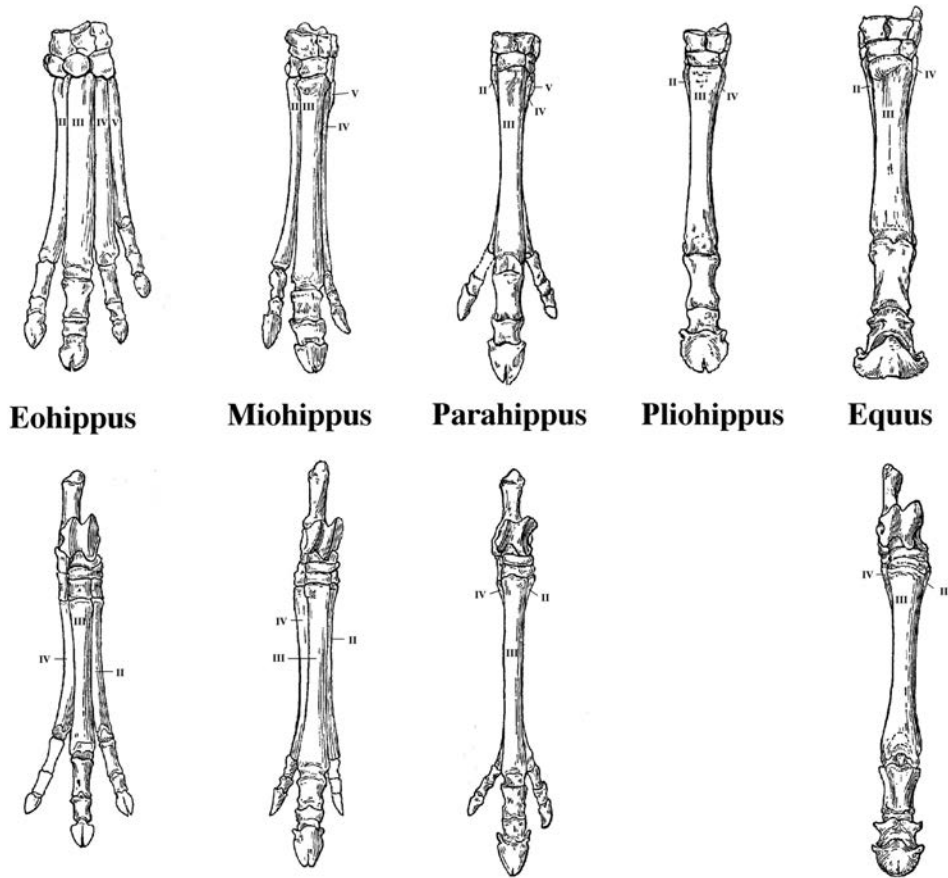


FIGURE 3.1 Reduction of the toes from four to one in both forelimbs (top row) and hindlimbs (bottom row) in horses from the Eocene “dawn horse,” *Eohippus* (*Hyracotherium*), to the modern horse genus *Equus*, which appeared in the Pleistocene and has persisted to today. Digit III is retained in all, digits II and IV are reduced to splint bones in *Parahippus* and *Equus*, while digits I and V (the outer digits) were lost as early as *Miohippus*. (See also Figure B3.1.)

[Modified from Gregory, W. K., 1951. *Evolution Emerging. A Survey of Changing Patterns from Primeval Life to Man*. Two Volumes. The Macmillan Company. New York.]



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FIGURE 3.2 Mimicry. (a) The pygmy seahorse *Hippocampus bargibanti*, which is no more than 2.5 cm in length, mimics the sea fan coral (*Muricella* sp.) in which it resides. (b) Many moths mimic leaves as shown in this example of the lappet moth (*Gastropacha quercifolia*) that mimics dried oak leaves. (continues)



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(c)



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(d)



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(e)

FIGURE 3.2 (continued) (c) Many flowers mimic insects. In this example the upper petals resemble antennae, the iridescent blue mimics the blue luster of the wings of a fly, while the two glistening patches mimic eyes. (d) The leafy (Glauerts) sea dragon (*Phycodurus eques*) mimics seaweed. (e) The giant Devil's Flower Mantis (*Idolomantis diabolica*) mimics flowers.

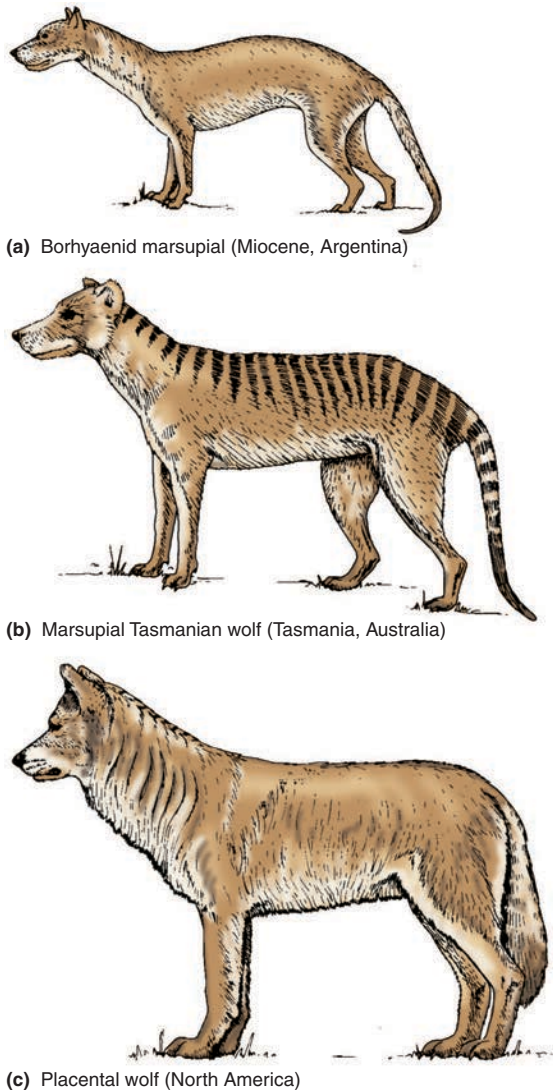


FIGURE 3.3 Striking examples of parallel evolution involving independent evolution of the “wolf” phenotype on three continents. (a) *Prothylacynus patagonicus*, a marsupial from the early Miocene in southern Argentina. (b) *Thylacynus cynocephalus*, the recently extinct marsupial Tasmanian wolf. (c) *Canis lupus*, the placental North American wolf.

[Adapted from Marshall, L. Q. Marsupial paleogeography. In L. L. Jacob (ed.), *Aspects of Vertebrate History*. Museum of Northern Arizona Press, 1980.]

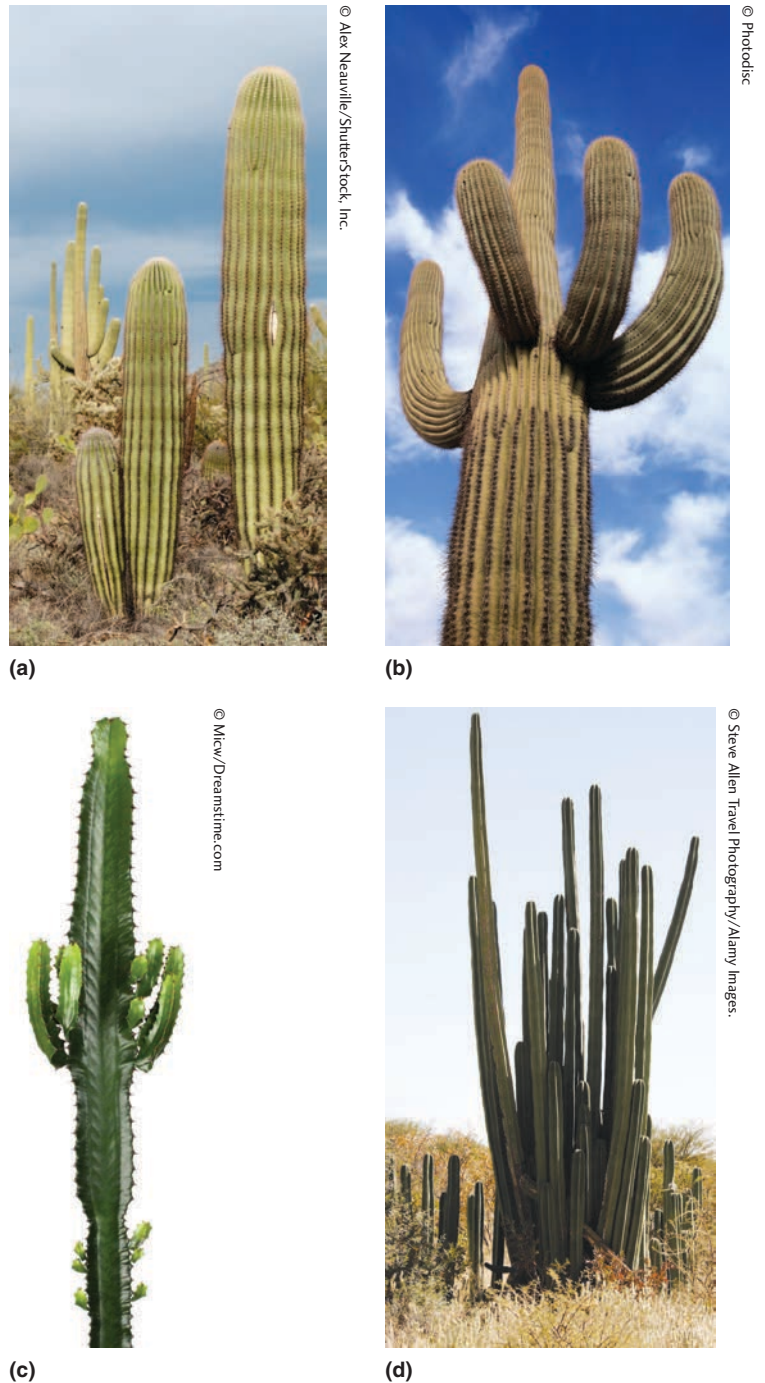
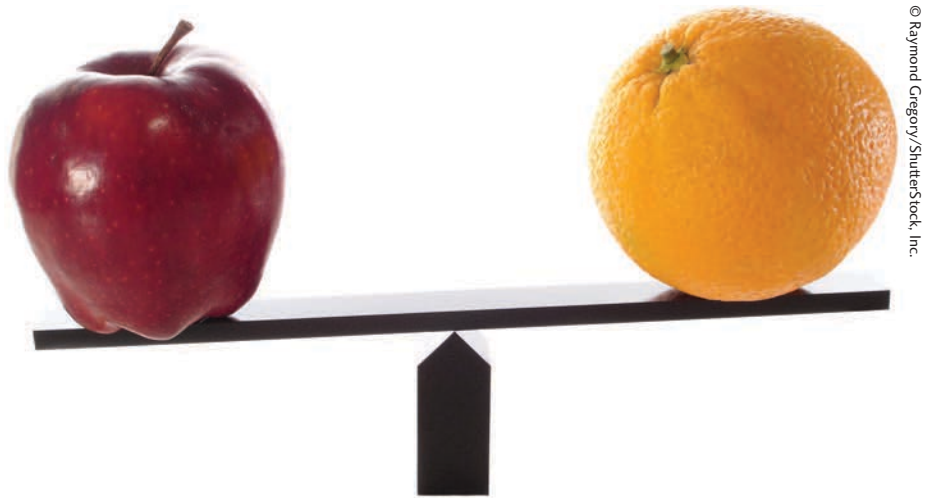


FIGURE 3.4 Convergent evolution between representative desert species of American Cactaceae, illustrated by the American saguaro (a, b) and African Euphorbiaceae, illustrated by two species of African euphorbs (c, d).

FIGURE 3.5 When weighed on the balance of homology an apple is an apple and an orange is an orange.



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SIMILARITY AND PATTERNS OF EVOLUTION

Phenotypes may be similar (1) because of recent shared ancestry; (2) because similar characters arose in groups with a more distant shared ancestor; or (3) because similar evolutionary patterns arose independently in different lineages.¹ Three concepts and terms were proposed in the mid-nineteenth century to deal with these situations.

1. **Homology: similarity resulting from shared ancestry:** when similarity of a feature arises because organisms in two species or lineages share a recent common ancestor that possessed the feature, the features are **homologous** (FIGURE 3.6).
2. **Parallelism: similarity based on shared genes or developmental pathways:** when similar features arise in related lineages whose common ancestor lacked them, the features are considered to have evolved independently and in **parallel**. Because of the shared earlier evolutionary history of the two lineages, parallel features normally develop using similar genetic or developmental pathways (Figure 3.6).
3. **Convergence: similarity resulting from evolution in independent lineages:** when a feature arises independently in unrelated organisms because of similar responses to the same selective pressures, we regard the features as **convergent**. Convergent evolution also is known as homoplasy. Because the lineages have independent evolutionary histories, convergent features usually develop using different genetic or developmental pathways (Figure 3.6). Similarity or dissimilarity of development is therefore a key criterion separating parallelism from convergence, although distinguishing parallelism from convergence can be subjective. There are no rules that specify how far in the past one should search for a common ancestor in parallel evolution, and even convergent lineages have common, albeit very distant, ancestors (Hall et al., 2003, Hall, 2006; Wake et al., 2011).

Each of these patterns of evolution is now treated in more detail.

HOMOLOGY

Derived from terminology introduced in the 1840s by the English comparative anatomist Richard Owen (1804–1892), organs identified as the same, even if serving different functions, are considered homologous. The humerus in the upper arm of a climbing monkey is homologous with the humerus in the forelimb of a digging mole, even though put to different uses by the two animals. Studies of similar bones in a wide range of vertebrates—the

¹ See Hall (1994, 2003, 2006) and Scholtz (2010) for discussions.

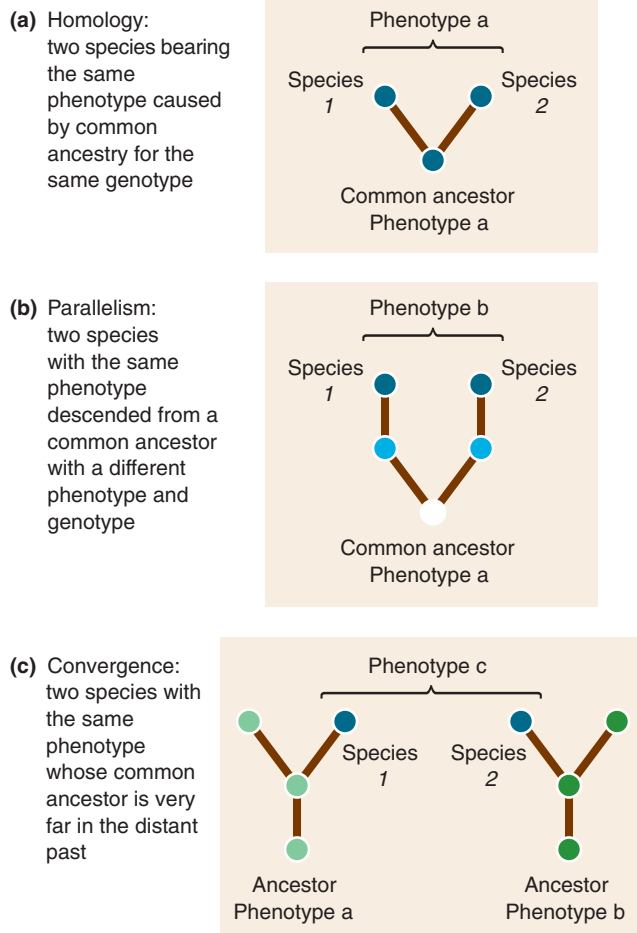


FIGURE 3.6 Homology, parallelism, and convergence diagrammed for two species (1, 2) that share a similar phenotypic character (phenotype a, b, c).

humerus in the upper arm, radius and ulna in the lower arm, digits—demonstrated that the forelimbs of widely different vertebrates are homologous, albeit with such different functions as walking, flying, and swimming (**FIGURE 3.7**). Homology can be applied at different levels in the biological hierarchy; for example, to individual bones (the humerus) and to parts of the body (the forelimbs). **Organs that perform the same function in different groups but do not share a similarity of structure are analogous.** Wings of bats or birds, which are built around a bony skeleton, and the wings of insects, which are based on an exoskeleton associated with a network of veins, do not show a common underlying structural plan and so are analogous, not homologous (**FIGURE 3.8**). Because analogues are found in organisms that do not share a recent common ancestor², analogous features develop by convergence.

COMPARATIVE ANATOMY is introduced elsewhere in this text as a major means of identifying morphological species.

HOMOLOGY STATEMENTS

Toes of a 60-My-old horse are recognizable and easily identified as toes (Figure 3.1). Toes are homologous throughout the lineages of horse evolution because they arose from an ancestor that had the same features in the same position.

²Of course, if we trace evolutionary history far enough back and construct evolutionary trees we find that all organisms share a common ancestor, and that some genetic and developmental processes are very ancient indeed and have persisted.

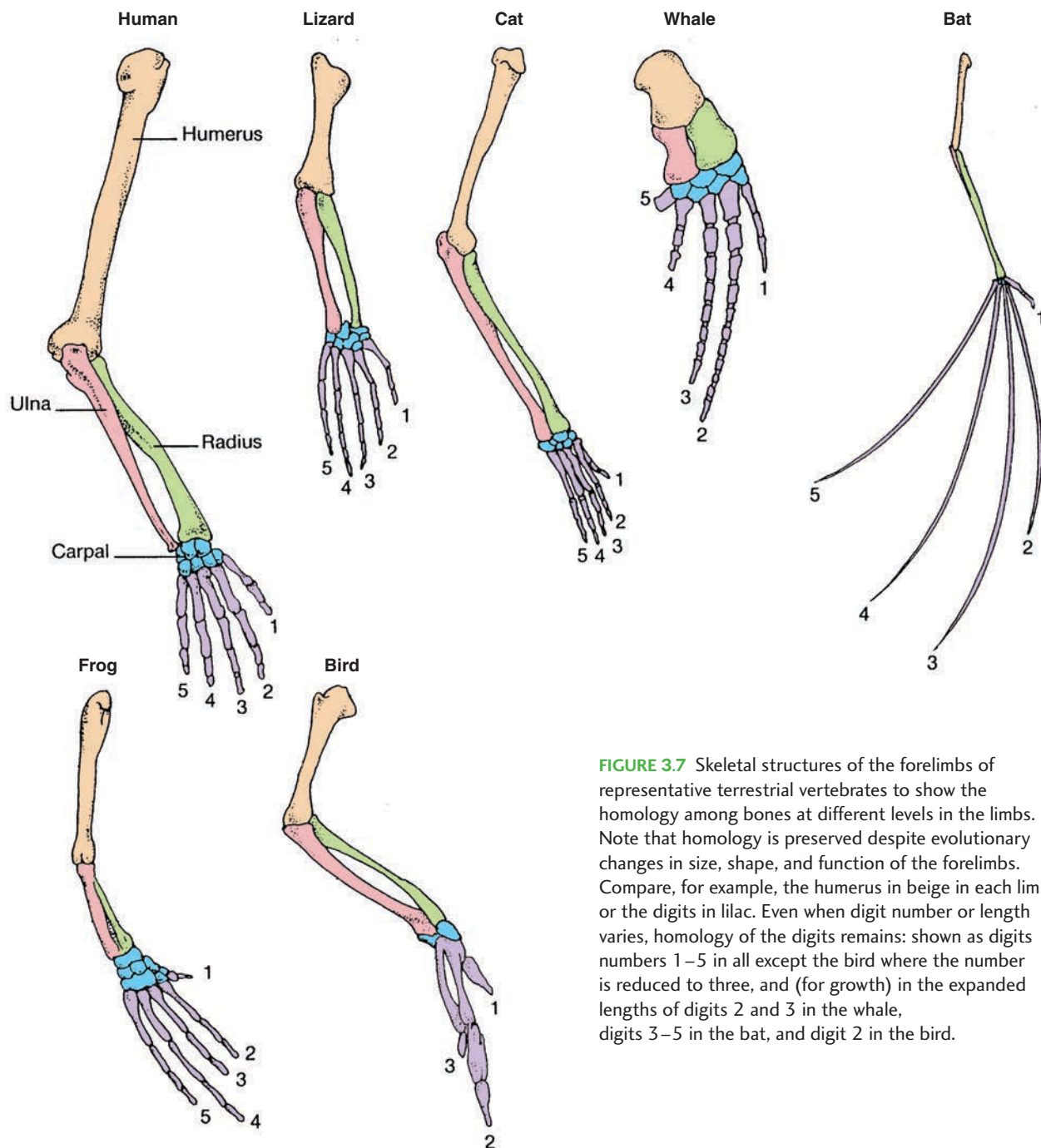


FIGURE 3.7 Skeletal structures of the forelimbs of representative terrestrial vertebrates to show the homology among bones at different levels in the limbs. Note that homology is preserved despite evolutionary changes in size, shape, and function of the forelimbs. Compare, for example, the humerus in beige in each limb, or the digits in lilac. Even when digit number or length varies, homology of the digits remains: shown as digits numbers 1–5 in all except the bird where the number is reduced to three, and (for growth) in the expanded lengths of digits 2 and 3 in the whale, digits 3–5 in the bat, and digit 2 in the bird.

Statements of homology make no comment about features having to be identical or even to look the same to be homologues. The similar features in the forelimb skeleton of the different vertebrates shown in Figure 3.7 are homologous because they arose from the same feature in a common ancestor. They are homologues even though they have changed in appearance with the evolution of wings in birds, flippers in seals, and so forth. As Charles Darwin wrote in Chapter 14 of *The Origin of Species*:

What can be more curious than that the hand of man formed for grasping, that of a mole, for digging, the leg of a horse, the paddle of a porpoise and the wing of a bat, should

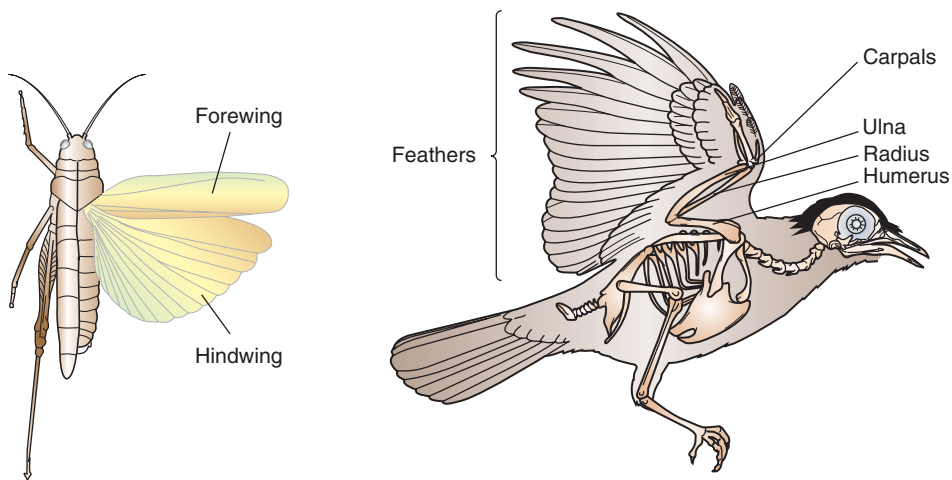


FIGURE 3.8 Comparison of insect and bird wings to show their analogy.

all be constructed on the same pattern and should include similar bones and in the same relative positions?

Just as it is easy to see homology in the toes of ancestral and descendant horses, it is more difficult to see wings and flippers as homologues. Compare Figures 3.7 with **FIGURE 3.9** to see the essential similarities.

An additional source of evidence for homology, one used to considerable extent by Darwin, is the presence of vestigial features in descendant species that are more fully developed in their ancestors. Examples of vestigial feature or **vestigis** may be found in **BOX 3.1**.

LEVELS OF HOMOLOGY

Whenever a statement about homology is made, *the level at which the comparison is being made should always be specified*: forelimbs are homologous as forelimbs or as the anterior set of paired appendages; humeri are homologous as the single bone located in the

The **LARGEST KNOWN SNAKE**, a Paleocene relation of the *boa constrictors*, 13 m in length and with an estimated weight of 1,135 kg, was described in 2009.

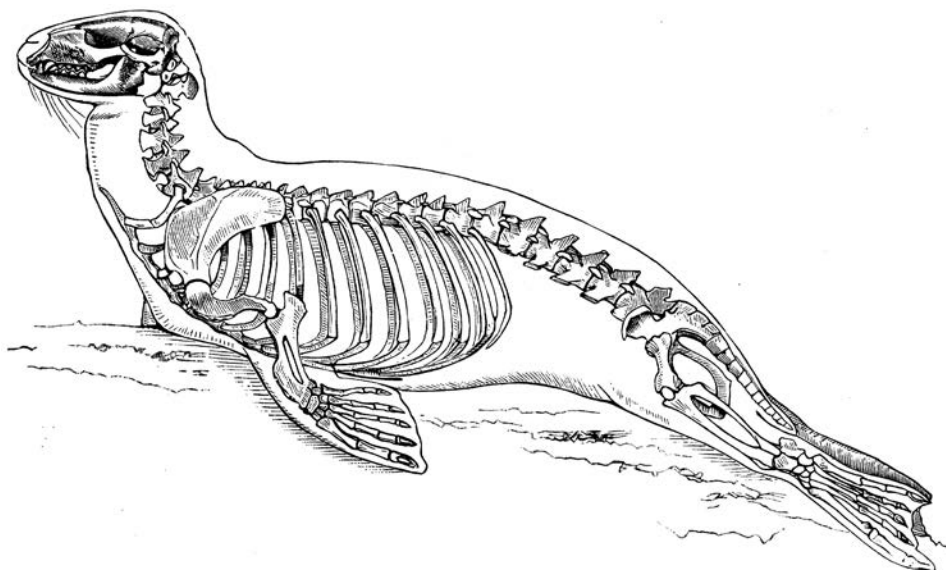


FIGURE 3.9 Skeleton of a harbor seal, *Phoca vitulina*, showing how the homology of the bones in the flippers relates to the limb bones of the other tetrapods shown in Figure 3.7.

[Adapted from Romanes, G. J. *Darwin, and After Darwin*. Open Court, 1910.]

Comparative anatomy and embryology come together in various ways, one of which is the study of **vestigial** structures that seem to have lost some or all of their ancestral functions (**FIGURE B1.1**).

From an evolutionary viewpoint, rudimentary or vestigial organs occur when an organism adapts to a new environment without losing some previously evolved structures (Hall, 2003). As evolution continues, structures that are no longer used tend to diminish, showing only traces of their former size and function. Examples are the rudiments of hind limb and pelvic girdle bones in some species of whales and snakes (**FIGURE B1.2**), even though hind limbs and pelvic girdles were lost in both groups when they diverged from limbed ancestors. (Although to speak of snakes with legs may seem paradoxical, the direct ancestors of modern-day snakes had legs. At least

four genera of limbed fossil snakes are now known: *Haasiophis*, *Pachyrhachis*, *Eupodophis*, and *Najash*.)

Adult whales and dolphins have forelimbs (flippers) but no hind limbs. Flippers develop from flipper buds in early embryos. The existence of vestigial of hind limb skeletal elements indicates that hind limb buds must occur in whale and dolphin embryos, which they do (**FIG. B1.3**; Bejder and Hall, 2002; Hall, 2007).

Organisms that have evolved in dark environments such as caves also provide evidence that obsolete structures gradually become rudimentary. Cave-dwelling crustaceans possess only reduced eyestalks, and some Mexican cavefish have eyes so reduced that the fish are blind. In such cases, other sensory organs assume a greater role to compensate for the lack of vision.

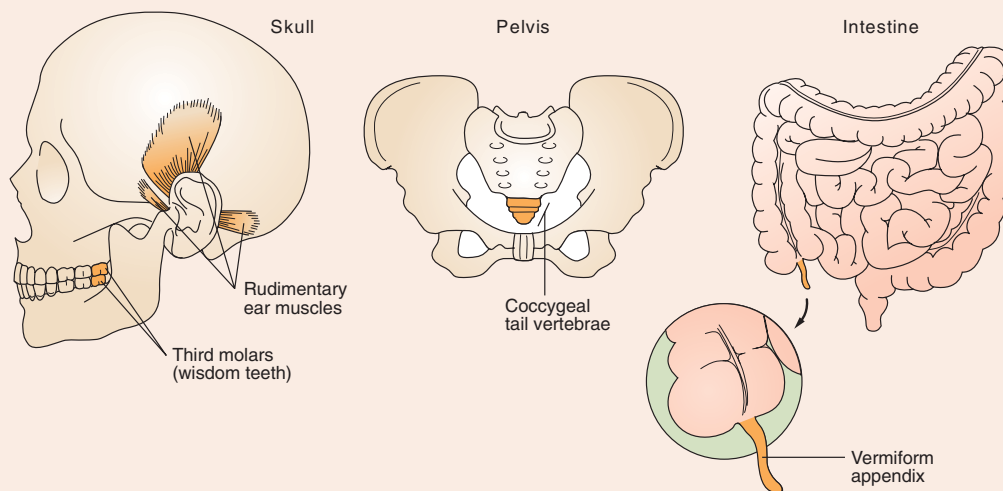


FIGURE B1.1 Vestigial (non-functioning) structures found in humans include the third set of molar (wisdom) teeth, muscles that move the ears in other mammals, ear muscles, tail vertebrae, and the appendix.

[Adapted from Romanes, G. J. *Darwin, and After Darwin*. Open Court, 1910.]

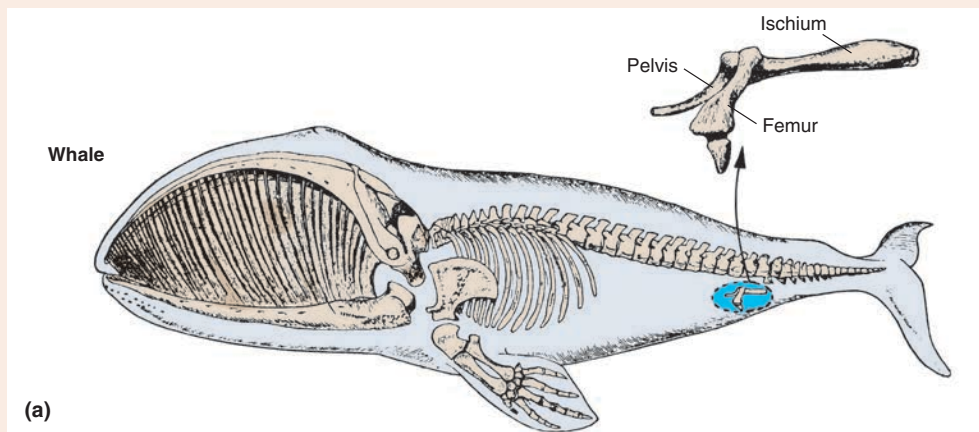


FIGURE B1.2 (a) Rudimentary hind limb (femur) and elements of the pelvic girdle (pelvis, ischium) in a bowhead (Greenland) whale, *Balaena mysticus*. (continues)

[Adapted from Romanes, G. J. *Darwin, and After Darwin*. Open Court, 1910.]

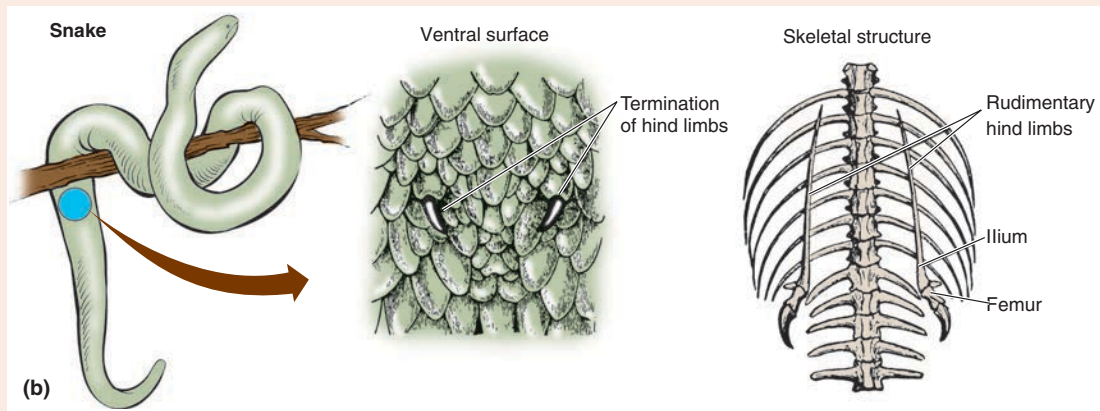


FIGURE B1.2 (continued) (b) Spurs at the termination of the hind limbs, represented by a vestigial femur and pelvic girdle elements (ilium) in a python.

[Adapted from Romanes, G. J. *Darwin, and After Darwin*. Open Court, 1910.]



(a)

Courtesy of Erin Green, Crown Copyright, Dept. of Conservation, NZ



(b)

Thewissen Lab, NEOMED



(c)

Thewissen Lab, NEOMED

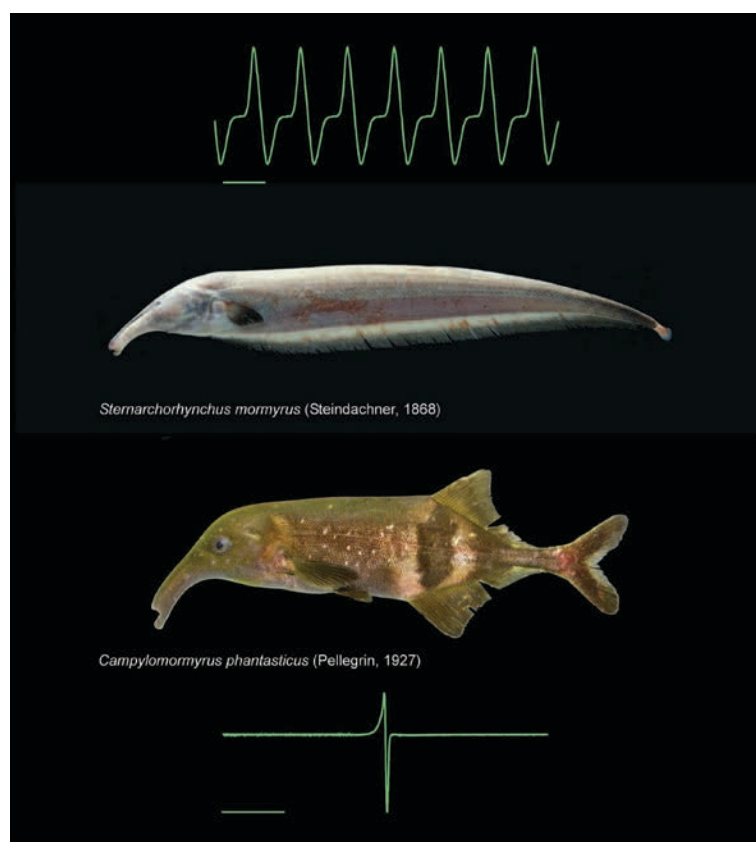
FIGURE B1.3 (a) Hector's dolphin, *Cephalorhynchus hectori*, showing the well-developed flippers and absence of hind limbs. Embryos of the spotted dolphin, *Stenella attenuata*, at 24 (b) and 48 (c) days of gestation to show the well-developed flipper buds (f) and the rudimentary hind limb buds (h).

forelimb between shoulder girdle and elbow. If in one species two bones were found in the position occupied by the humerus, one of the bones would not be a homolog of the single bone in other species. Indeed, such an occurrence (no such specimen has ever been found) would lead us to suspect that the organism containing the two bones had an independent evolutionary history from those organisms containing a single humerus. The two bones would be given different names and not be considered homologous. Furthermore, features of organisms that are not homologous as structures (limbs and genitalia in terrestrial vertebrates, for example) may share genes or gene pathways that are homologous. **Homology is a hierarchical concept that takes into account the fact that evolutionary change at different levels (genes, development, structures) need not, and often does not, occur in tandem.**

Features are not only the morphological or structural aspects of organisms, but the physiological, developmental, behavioral, molecular, or genetic aspects as well. Behavioral characters, for example, patterns of grooming in rodents, stand as homologous features in their own right. When the heritable basis of behavior is conserved, homologous behaviors are based on homologous features (forepaws and whiskers used by rodents in grooming) that, in turn, may be based on homologous developmental processes. However, as the developmental basis of behavior is both heritable and evolvable (Stamps, 1991), the structural and developmental basis of homologous behavior need not be the same.

Importantly, dissimilarities between organisms do not render behaviors non-homologous; homology at one level does not require homology at the levels upon which the homology is based. For example, consider the homologous behavior of sharks that produce an electric shock to stun their prey. Although the electric organs of all sharks produce an electric shock, electric organs may be modified muscles or modified nerves depending on the taxon, as shown in **FIGURE 3.10**. Homology at one level (stunning prey with electric organs) does not imply homology at another level (the developmental origin of the electric organs).

FIGURE 3.10 Independent evolution of electric organs (and ventrally curved jaws) in electric fish from South American (*Sternarchorhynchus mormyrus*) and African waters (*Campylomormyrus phantasticus*) results in different patterns of electrical discharge.



Courtesy of Carl D. Hopkins and John P. Sullivan

HOMOLOGY OF MOLECULES

With the discovery and comparison of the molecular sequences underlying proteins and nucleic acids, the term homology was extended from features of the phenotype to features of the genotype (Hillis, 1994). Genes *shared between species* because of shared species ancestry are called **orthologous genes** (orthologues). **Paralogous genes** (paralogues) are genes *duplicated within a species*; that is, they are extra copies of a gene, rather like the extra vertebrae discussed below as an example of serial homology (Fitch and Margoliash, 1967).

SERIAL HOMOLOGY

Parts repeated in an individual are liable to vary in number, structure, and/or function in response to natural selection. The term **serial** (iterative) **homology** is used for similarities among parts of the same individual; for example, similarities between neck and tail vertebrae, as shown in Figure 3.9, or variants of hemoglobin molecules (α , β , γ chains). Serial homology often reflects the duplication of a gene responsible for producing or affecting a particular structure. Duplication of globin genes led to the large number of hemoglobin variants present in organisms today. Serial homology also can reflect duplication of a particular structure, such as the duplication of vertebrae. Such duplicates may have originally had similar features, but subsequently evolved independently of each other, as illustrated by the independent evolution of neck (cervical) and tail vertebrae in mammals.

PARALLELISM

Parallelism is the evolution of similar features in lineages that are related but do not share a most recent common ancestor. Examples cited above include marsupial and placental “tigers” and “wolves” (Figure 3.3) and the anteater-like features found in several lines of mammals, each of which descended from a non-anteater mammalian group³ (FIGURE 3.11). As with homology and convergence, parallelism can occur in both the phenotype and the genotype.

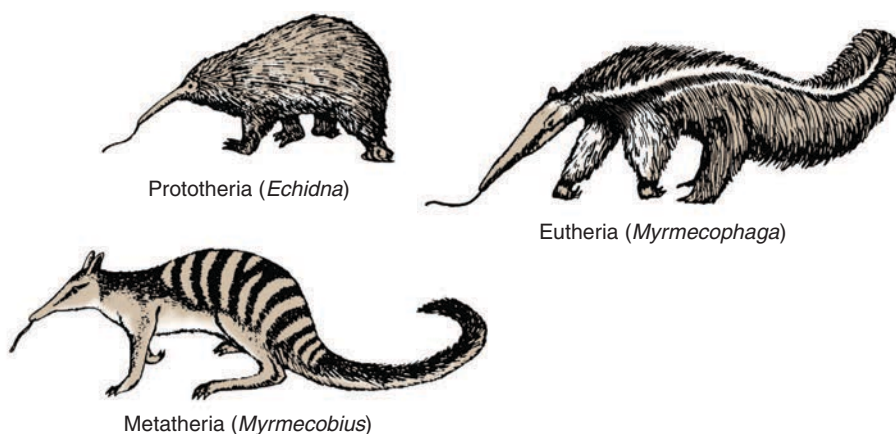


FIGURE 3.11 Similar phenotypic features—long snout, long tongue, powerful claws—among anteaters that evolved independently within each of the three major groups of extant mammals.

³For an assessment of parallel evolution in early mammals, see Z.-X. Luo (2007), Transformation and diversification in early mammal evolution. *Nature*, **450**, 1011–1019.

As discussed above, organisms are organized hierarchically, with information building upon the level(s) below. New emergent properties arise at each level and, importantly, cannot be predicted from the properties of the level below. If evolution is constrained—for example, by processes that limit variation—we might expect to find parallel features based on similar genetic or developmental processes.

CONVERGENCE

As the examples of parallel evolution of the “wolf” phenotype on three continents (Figure 3.3) illustrate, why we need to understand evolutionary relationships in order to separate parallelism from convergence. In parallelism, similar features evolve in related lineages, based on similar genetic or developmental processes. In convergence (convergent evolution), similar features evolve in independent lineages, based on different genetic or developmental processes. Euphorbs and cacti are a good example of convergence (Figure 3.4). The two types of plants look a great deal alike, and share a number of physiological and metabolic features; however, cacti evolved in South America, and euphorbs evolved in Africa. Cacti and euphorbs converged on a number of features through adaptation to their respective environments, but the features are based on different underlying processes.

The number of examples of convergence in evolution is evidence that responses to similar environmental conditions can, and often do, lead to functionally similar anatomical structures in different evolutionary lineages (Figure 3.3). Evolution of wings in insects and in vertebrates is an example of convergence, as two independent lineages of animals are responding to selection for flight through modification of existing but different appendages. Wings of birds and bats are homologous as limbs with digits; they share an ancestor that possessed limbs with digits, built using similar regulatory processes. However, neither bat nor bird wings are homologous to insect wings, because no common ancestor has a feature from which both types of wings could have been derived.

Likewise, the structural similarity of squid and vertebrate eyes does not come from an ancestral visual structure in a recent common ancestor of mollusks and vertebrates, but from convergent evolution; similar selective pressures led to similar organs that enhance visual acuity. What is shared deep in metazoan ancestry is the ability to form light-gathering cells or organs.⁴ From this ability, such convergences arose independently in numerous animal lineages subject to similar selective visual pressures (because of such selective pressures, even butterflies and primates have evolved color vision photopigments with overlapping absorption spectra, based on similar amino acid sites, despite the large separation between the two lineages [Frentiu et al., 2007]).

Modification of shared genetic or developmental, long postulated as underlying, convergence is now being demonstrated. Convergence in the relative length of the limbs in lizards in the genus *Anolis* is based on repeated modification of early stages of limb development (Sanger et al., 2012). Independent evolution of a single gene underlies the convergent evolution of the loss of abdominal legs in spiders and insects; knocking out the genes results in spiders with an extra pair of legs—a 10-legged spider (Khadjeh et al., 2012).

Having discussed how similarity of features is determined, we turn to two classes of evidence that have been used to compare organisms (animals in these examples) and assess evolutionary relationships for close to 200 years. The first is comparative embryology, the second the fossil record. (Genetic and molecular evidence for evolution are discussed elsewhere in this text.)

⁴ Interestingly, genetic studies indicate that a similar inherited factor (the *Pax-6* gene) regulates the development of anterior sense organ patterns in invertebrates and vertebrates. Nevertheless, despite some common regulatory features, specific cellular pathways in embryonic eye development differ substantially between squid and vertebrates. Squid photoreceptor cells derive from the epidermis; vertebrate retinæ derive from the central nervous system.

COMPARATIVE EMBRYOLOGY AS EVIDENCE FOR SHARED SIMILARITY AND EVOLUTION

Comparative embryology is the study of relationships among anatomical structures in the embryos of different species. Animal species have long been the targets of active comparative embryology research, though similar knowledge informs our understanding of plant evolution.⁵

Early in the nineteenth century the Estonian comparative embryologist Karl von Baer (1792–1876) discovered remarkable **similarities among the embryos of vertebrates whose adult forms were quite different from each other**. The earlier in development the comparisons were made the more similar the embryos were found to be. von Baer generalized his findings into a “law”: *early embryos of related species bear more common features than do later, more specialized developmental stages*. Throughout his life and in his publications (even after Darwin’s *The Origin of Species* was published), von Baer’s views remained comparative and taxonomic, not evolutionary; he used categories of embryos to erect a scheme of classification, not evolutionary lineages.

One of Darwin’s major insights was to use comparative embryology as evidence for evolutionary change. As he stated in *The Origin of Species*:

In two groups of animals, however much they may at present differ from each other in structure and habits, if they pass through the same or similar embryonic stages, we may feel assured that they have both descended from the same or nearly similar parents, and are therefore in that degree closely related. Thus, community in embryonic structure reveals community of descent (p. 481).

In 1861 (after *The Origin of Species* had been published) and in a lifetime of publications and lectures, German embryologist, naturalist, philosopher, and artist Ernst Haeckel (1834–1919) used von Baer’s research on comparative embryology to propose **that during their development animal embryos repeat the evolutionary history of the groups to which they belong. For Haeckel, developing embryos were stages of evolution, and evolution could be studied in embryos (FIGURE 3.12)**. In this way, Haeckel integrated comparative embryology with evolution in what became known as the **biogenetic law**.

Ontogeny [development of the individual] is a short rapid recapitulation of phylogeny [the ancestral sequence]... The organic individual repeats during the swift brief course of its individual development the most important of those changes in form that its ancestors traversed during the slow protracted course of their paleontological evolution according to the laws of heredity and adaptation.⁶

To Haeckel, this meant that the tadpole developmental stage of an extant frog reflected, or recapitulated, a *tailed frog ancestor*.

We now understand, however, that early stages of embryonic development recapitulate only *early ancestral developmental stages*, not ancestral adults (Hall, 1999, 2002). Juvenile stages of ancestral organisms can be retained in the adult forms of their descendants, as, for example, in the preservation of juvenile ape features in adult humans. This observation directly contradicts the Haeckelian notion that descendants retain ancestral adult features. Rather, organisms that share common descent make use of common underlying embryological patterns. Further, related organisms use shared genes and gene networks to produce characteristic developmental stages that have persisted for tens of millions of years. Evidence from genetics, molecular and developmental biology, and from the integration of evolutionary and developmental biology (evo-devo) provide strong support for this view.

⁵ See Niklas (1977), Hall (1999), and Hall and Olson (2003) for further information.

⁶ E. Haeckel (1866). *Natürliche Schöpfungsgeschichte*. Reimer, Berlin. See Richards (2008) for the authoritative scientific biography of Haeckel.

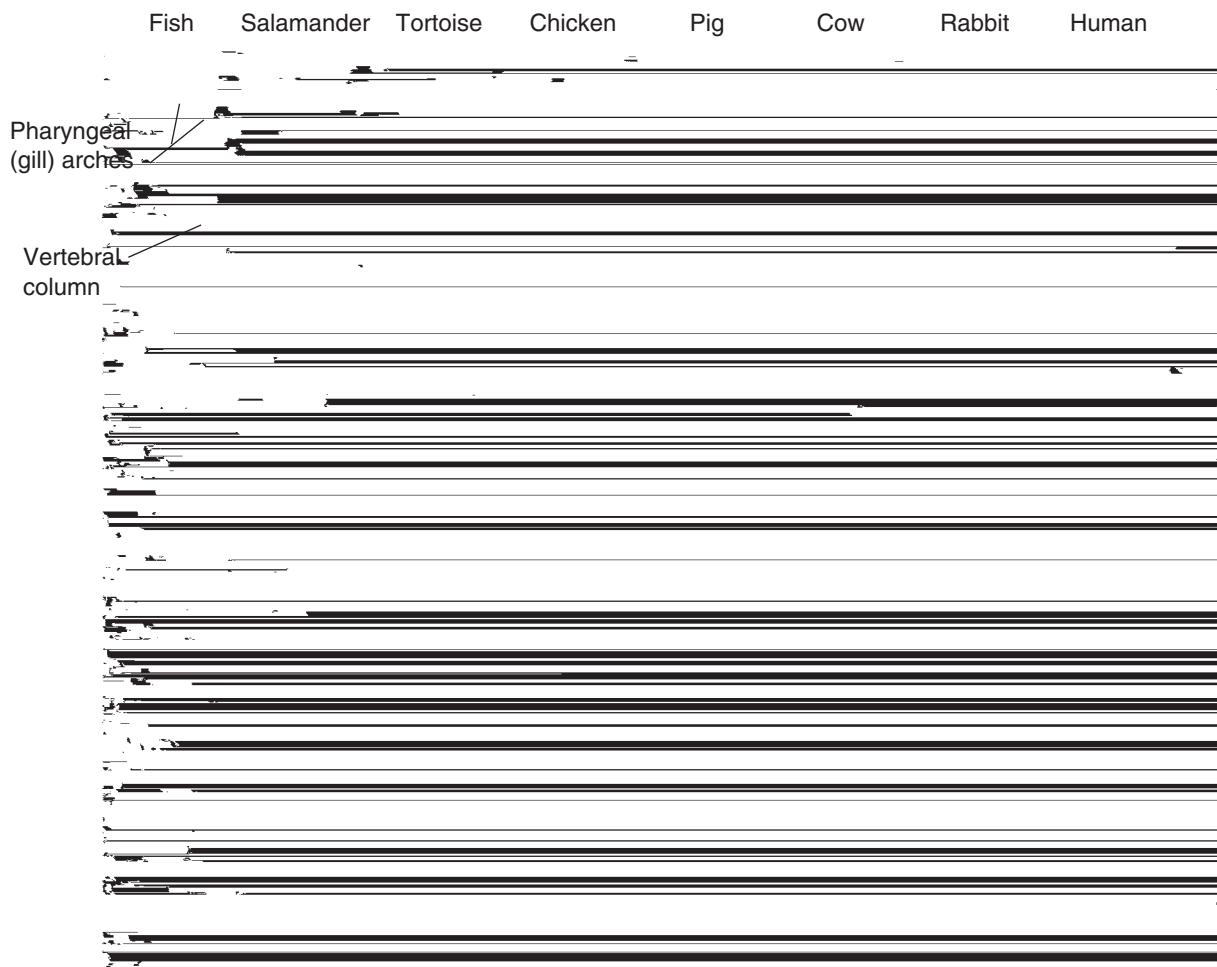


FIGURE 3.12 One of Haeckel's classic nineteenth century illustrations of different vertebrate embryos at comparable stages of development. Although Haeckel took some liberties in drawing these figures, the earlier stages are more similar to one another than later stages are to one another. Embryos in the different groups have been scaled to the same approximate size so that comparisons can be made among them.

[Adapted from Romanes, G. J. *Darwin, and After Darwin*. Open Court, 1910.]

FOSSILS AS THE PHYSICAL EVIDENCE OF EVOLUTION

Discovery of the fossil record of life gave us a rich source of data with which to understand relationships among organisms. It led to the hypothesis that Earth's surface and the organisms on it had existed for a long time, and to the conclusion that organisms succeeded one another through time (Fortey, 2002; Rudwick, 2005).

End Box 3.1 contains a brief history of the recognition that fossils are the remains of past life, as well as a discussion of how fossils form.

Charles Lyell (1797–1875), a contemporary and close friend of Charles Darwin, broke with the popular theories that catastrophic or miraculous events (**catastrophism**) were responsible for Earth's geological structure. In the mid-nineteenth century, Lyell and others began to consider that species may have changed in concert with changes in Earth's geology. He developed the principle of **uniformitarianism** (BOX 3.2), that the natural laws and processes functioning in the universe today, and the rate at which they

BOX 3.2

How Rocks Are Deposited: Catastrophism and Uniformitarianism

Georges Cuvier (1769–1832) was one of the most gifted French comparative anatomists and the founder of modern paleontology. In the late 1700s and early 1800s, his theory of catastrophism was commonly believed to explain the formation of geological structure. Transition from catastrophism to an alternate theory—uniformitarianism—had profound effects on our understanding of the natural world. It helped liberate scientific thinking from the concept of a static universe powered by unexplainable changes to one that is dynamic and understandable in natural terms.

CATASTROPHISM

According to catastrophism, sharp discontinuities in the geological record—stratifications of rocks, layering of fossils, transition from marine to freshwater fossils—were evidence of sudden upheavals caused by glaciations, floods, and other catastrophes. Fossils were recognized as extinct species whose place has been taken by species alive today. Swiss paleontologist, geologist, naturalist, and founder of the Museum of Comparative Zoology at Harvard University Louis Agassiz (1807–1873) proposed that there may have been as many as 100 successive special divine creations.

UNIFORMITARIANISM

Jean-Baptiste Lamarck was introduced elsewhere in this text when discussing his theory of the inheritance of acquired characters. In contrast to Cuvier's catastrophist position, Lamarck proposed that geological discontinuities represented gradual changes in the environment and climate to which species were

exposed. Through environmental effects on organisms, these changes led to species transformation.

This uniformitarian concept, that the steady, uniform action of the forces of nature could account for Earth's features (foreshadowed by Buffon and others), was strongly developed in the work of the Scottish geologist James Hutton (1726–1797). Later, Charles Lyell offered the *uniformitarian reply to catastrophism* with the following hypotheses:

1. Sharp, catastrophic discontinuities are absent if geological strata are examined over widespread geographical areas. Most often, a widely distributed stratum shows regularity in its structure and composition. Only in specific localities do rapid shifts seem to appear, as a response to local changes.
2. Changes in the geological record arise from the action of erosive natural forces such as rain, wind, volcanic activity, and flood deposits. The laws of motion and gravity that govern natural events are constant through time. Therefore, past events were caused by the same forces that produce phenomena today (although the extent of phenomena, such as volcanism, might have fluctuated in the past). Consequently, all natural explanations for phenomena should be investigated before supernatural causes are used to explain them.
3. Earth must be very old for so many geological changes to have taken place by such gradual processes.

Thus, uniformitarianism did not exclude sudden geological changes such as floods, volcanic eruptions, and meteorite impacts—events that were of common or recorded knowledge. Instead, it led to the position that even such “catastrophes” could be natural and rationally explained.

operate, have not changed since the beginning of time. However, Lyell did not explicitly identify the changes in Earth's geology and climate as a selective pressure that could drive evolution of life. Indeed, he struggled with the ideas put forth by Darwin and Wallace, which connected species change with (a) interactions between organisms and (b) interactions between organisms and their environment, and which proposed a mechanism for species change—evolution by natural selection.

In the mid-nineteenth century the known fossil record was sporadic, the result of serendipitous collecting and random finds. Nevertheless, during Darwin's lifetime a few paleontological findings came to light that strongly supported his theory of descent with modification. One was the discovery in 1861 of what had been proposed as a true “missing link,” in this case, an animal that was interpreted as intermediate between reptiles and birds. As shown in **FIGURE 3.13**, this fossil, *Archaeopteryx*, had a number of reptilian features, including teeth and a tail of 21 vertebrae. However, it also had a number of bird-like features, such as a wishbone and feathers. English biologist and Darwin-proponent Thomas Henry Huxley argued convincingly that *Archaeopteryx* was a “cousin” to the lineage running from reptiles (dinosaurs) to birds. He believed that such “primitive” forms were predictable consequences of evolution that helped prove the theory. An even more

Analysis of mtDNA from 22 fossil horses has revealed **TWO NEW SPECIES OF HORSES** and revised the patterns of relationships known previously only from the fossil record (Orlando et al., 2009).

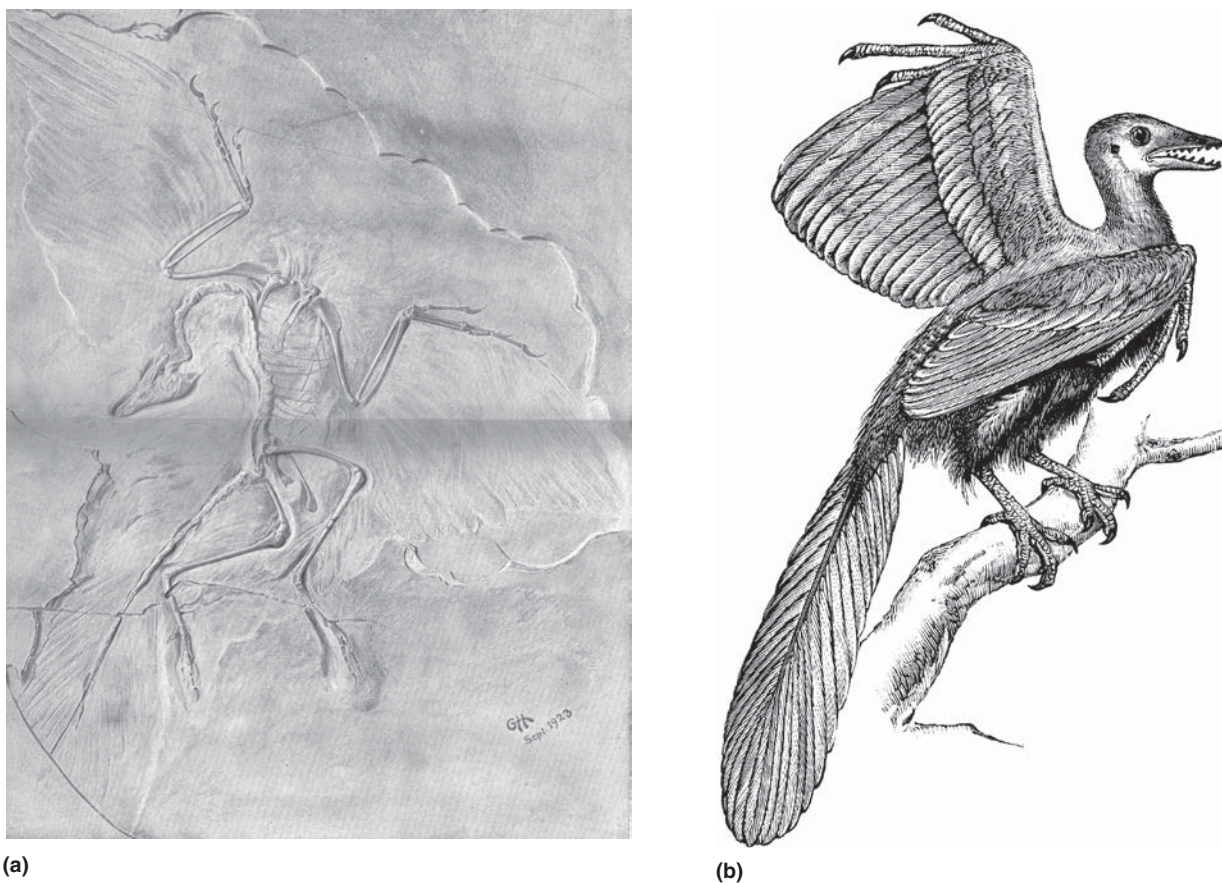


FIGURE 3.13 (a) The Berlin specimen of *Archaeopteryx*. (b) (Gerhard) Heilmann's reconstruction of what *Archaeopteryx* may have looked like in real life.

[Reproduced from Heilmann, G. *The Origin of Birds*. Appleton, 1927 (Reprinted Dover Publication, 1972).]

complete history of the evolution of a lineage exists and, once again, we return to the evolution of horses, which was discerned through the fossil record. The finely detailed phylogeny of horses is one of the best illustrations of some of the realities and complexities of evolution.

EVOLUTION OF HORSES

EOHIPPIUS is an alternate but later genus name for *Hyracotherium*. Priority goes to *Hyracotherium*.

One year after the publication of *On the Origin of Species*, Richard Owen (1804–1892) described the earliest known horse-like fossil, first called *Hyracotherium* but often referred to as *Eohippus* (the dawn horse). *Hyracotherium* was some 50-cm high (about 20 inches, the size of an average Border Collie) and weighed about 23 kg (50 pounds). It had four toes on its front legs and three on its hind legs, adapted to walking on soft, moist forest floors, and simple teeth adapted for browsing on soft vegetation (FIGURES 3.1 and 3.14). Later fossil finds revealed that *Hyracotherium* was actually a number of herbivorous species present from North America to Europe, some no larger than an average-sized modern-day fox; this is an excellent example of parallel evolution in the horse lineage.

In the approximately 60 My after *Hyracotherium* arose, horses changed radically. Today, horses have only a single toe on each foot (Figure 3.1). They show special adaptations for running on hard ground. Their elongated legs are built for speed, bearing most of the limb muscles in the upper part of the legs, enabling a powerful, rapid swing. This arrangement, coupled with a special set of ligaments, provides them with a pogo-stick-like

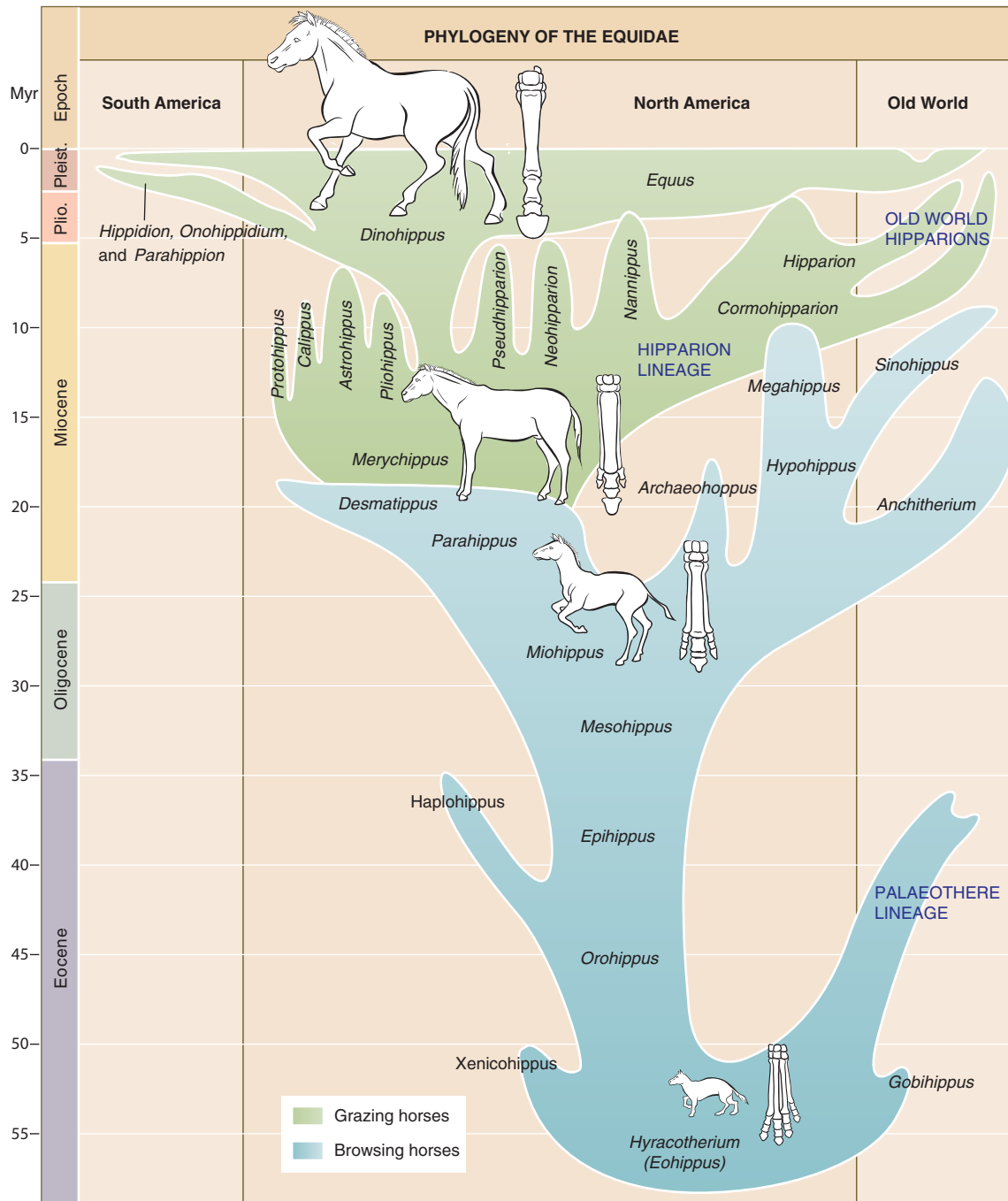


FIGURE 3.14 Evolutionary relationships among various lineages of horses, with emphasis on North American and Old World groups. Sample reconstruction of the digits ("toes") of the hind feet of some fossil horses and of the extant horse *Equus* are shown. The number of digits declined from four to one during evolution of the lineage. These horse lineages show both branching and non-branching patterns of evolution.

[Adapted from MacFadden, B. J. *Fossil Horses: Systematics, Paleobiology and Evolution of the Family Equidae*. Cambridge University Press, 1992.]

springing action while running on hard ground. Horses also show adaptations for chewing tough, silica-containing grasses; their teeth are much longer than the teeth of other grazing animals.

By the 1870s, paleontologists such as America's Othniel C. Marsh (1831–1899) were able to use fossils of North American and European horses to present a now classic example of various transitional stages of evolutionary change (Figure 3.14). Remarkably, we now know almost all the intermediate stages between *Hyracotherium* and the modern horse, *Equus*. These include transitions from low- to high-crowned teeth, from browsers to grazers, from pad-footed to spring-footed, and from small- to large-brained. As shown in Figure 3.14, evolutionary changes among these forms did not proceed in a single direction, being better represented as a “bushy” family tree. Horses adapted to their habitats in different ways, with some lineages maintaining distinct structures until they went extinct.

Although all occupied the same general area, separate horse lineages made use of different environmental resources (*resource partitioning*). Some species became grazers, feeding on grasses. Others remained browsers, feeding on shrubs and trees. Others both grazed and browsed. Still others became grazers, and then reverted to browsing, as occurred in some Florida species. Differences in feeding habits can be deduced from dental scratches (resulting from grazing) and dental pits (resulting from browsing). Testing the carbon isotope ratios ($^{12}\text{C}/^{13}\text{C}$) in fossil teeth can also give us information about the individual's diet: grasses and shrubs have different $^{12}\text{C}/^{13}\text{C}$ ratios, which affect the $^{12}\text{C}/^{13}\text{C}$ ratios in teeth.⁷

Rates of evolution were not constant for any particular trait among the various horse lineages. Size, for example, underwent relatively few changes for the first 30 million and the last few million years of horse evolution. Even when evolution was proceeding rapidly, as it did during the Miocene, both small- and large-sized species evolved. No continuous linear trend is present in the fossil record.

LIVING FOSSILS

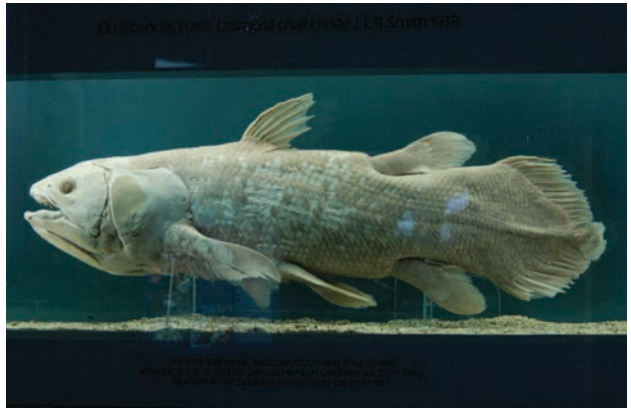
Interestingly, some ancient lineages have persisted to the present day with minimal morphological changes. Evolution seeks to explain such examples of persistence as well as explaining examples of descent with modification.

The fossil record provides us with information about organisms that went extinct many ages ago. Occasionally, species are discovered that are so remarkably similar to these extinct organisms that they are called “**living fossils**”: sturgeons, lungfish, horse-shoe crabs, *Lingula* (a brachiopod), and ginkgo trees.

About 200 Mya, one lineage of lobe-finned fishes evolved (FIGURE 3.15) into terrestrial vertebrates. The fossil record of another lineage, coelacanths, begins in the Devonian about 380 Mya and ends 80 to 100 Mya, indicating extinction of the species in the late Cretaceous. However, in 1938 a museum curator in South Africa found a coelacanth specimen amongst a fisherman's daily catch. Still today, fishermen find live coelacanths in deep waters off the eastern coast of South Africa (Thomson, 1991). The coelacanth is a living fossil.

Aside from such rare “living relics,” fossils in almost every instance differ from present-day forms, often in proportion to their age. More recent geological strata contain forms more like the present than those in older strata. Fossils provide the hard evidence of evolution.

⁷B. J. MacFadden, N. Solounias, and T. E. Cerling, 1999. Ancient diets, ecology and extinction of 5-million-year-old horses from Florida. *Science*, **283**, 824–827; J. T. Eronen et al., 2009. The impact of regional climate on the evolution of mammals: a case study using fossil horse. *Evolution*, **64**, 398–408.



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(a)



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(b)



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(c)

FIGURE 3.15 Representative “living fossils.” **(a)** The coelacanth (*Latimeria chamulnae*). **(b)** Leaves of the ginkgo tree (*Ginkgo biloba*). **(c)** The Atlantic horseshoe crab (*Limulus polyphemus*).

KEY TERMS

analogy
biogenetic law
catastrophism
convergent
convergence
homology
living fossils

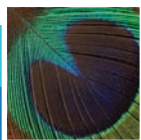
orthologous genes
parallelism
paralogous genes
serial (iterative) homology
uniformitarianism
vestigial organs
vestigial

EVOLUTION ON THE WEB

Explore evolution on the Internet! Visit the accompanying website for *Strickberger's Evolution, Fifth Edition*, at go.jblearning.com/Evolution5eCW for exercises and links relating to topics covered in this chapter.

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END BOX 3.1

Fossils as Evidence of Past Life

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SYNOPSIS: This is a brief history of our understanding of the nature of fossil evidence that explains *succession*—the replacement of one form of organism by another—as an explanation of why complete sequences of fossils are rarely found.

The discovery and study of fossils provides an essential basis for understanding evolutionary relationships between past organisms and for appreciating their lengthy history. During the sixteenth and seventeenth centuries, fossils were regarded as “naturally formed” images of God’s creation, placed on Earth for man’s admiration (Rudwick, 2005; Ruse and Travis, 2009).

It had long been known that the fossilized bones or shells in exposed riverbanks, in mines, and on eroded surfaces did not resemble extant species (FIGURE EB1.1), and that seashells could be found in most unlikely places, such as mountaintops. Ancient Greeks were aware of such fossils, and a number of ancient writers, including Herodotus (484–425 BC), hypothesized that they could be explained by changes in the positions of sea and land. Studies by English physician and naturalist Robert Hooke (1635–1703) and Danish anatomist and geologist Nicolaus Steno (1638–1686) concerning the reality of fossil species led to naturalistic proposals to understand fossil origins. The frontispiece of Charles Lyell’s 1830 *Principles of Geology* is a portrait of the three remaining columns of the ruined Temple of Serapis in Pozzuoli, Italy, which show evidence of historical rise and fall in sea level. A three-meter section of these columns contains holes bored by gastropods, indicating that the bases of the columns were once submerged (FIGURE EB1.2).^a

When arranged by stratigraphic age, with deeper strata signifying older ages than superimposed strata, older fossils show greater morphological differences from extant species than do later fossils. This evidence of change over time provided the foundation for a “law of succession” in which one form replaced another.

FOSSIL FINDS

Fossil remains are predominantly found in sedimentary rocks, which originated as a succession of deposits in seas, lakes, riverbeds, or deserts (FIGURE EB1.3). Even in appropriate sedimentary environments, many dead organisms decompose before they fossilize or, if they have fossilized, are destroyed by erosion.

Because isolation of populations encourages and sustains their differences, we rarely find intermediate forms in the same place as the original forms. Consequently, a complete evolutionary progression of fossils from most ancient to most recent has never been found in a single locality. Nevertheless, fossils provide the hard evidence for evolution. One of the most complete fossil sequences is the evolution of horse lineages. Many of the fossils in this sequence were discovered soon after Darwin published *The Origin of Species*.^b

Fossils are not always the result of organisms’ remains; other forms such as footprints can be enormously informative. The earliest land-dwelling vertebrate (tetrapod) fossils are dated to the Late Devonian Period, whereas fossil trackways left by tetrapods date to the early Middle Devonian, some 18 My earlier (Niedzwiedzki et al., 2010). Further, the trackways attest to life in coral reef lagoons whereas the first fossilized remains imply that the first tetrapods lived in a river delta or lake environment (Markey and Marshall, 2007). Burrows and disturbed sediments provide us with the evidence for Precambrian adult animal life, while multicellular Precambrian embryos demonstrate the antiquity of animal development and of animals themselves (Chen et al., 2009). Even single-celled organisms have left traces of their existence as far back as 1.8 Bya (Matz et al., 2008). Finally, molecular signatures reveal the presence of life billions of years ago.

^aLyell used such an image through 12 editions of his book as an example of gradual geological change.

^bSee Fortey (2002), Hall (2002), and Rudwick (2005) for three perspectives on the fossil record.



END BOX 3.1

Fossils as Evidence of Past Life (Cont...)

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FIGURE EB1.1 Succession of fossils as revealed when geological strata are exposed in a quarry or canal.

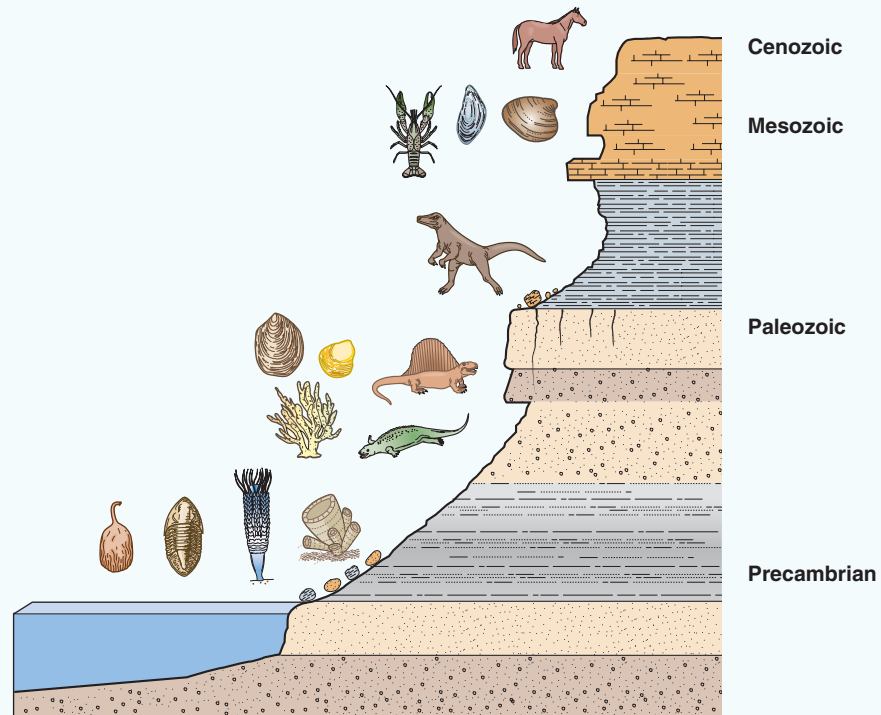
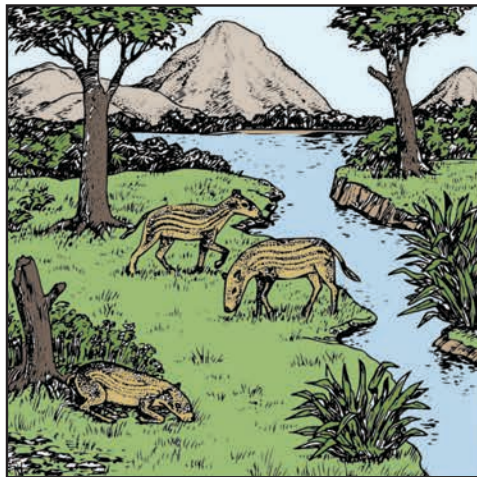


FIGURE EB1.2 A contemporary photograph of the three remaining columns of the ruined “Temple of Serapis” in Pozzuoli, Italy, showing that they had been historically subjected to rise and fall in sea level. A dark, three-meter section of the columns is filled with holes bored by marine organisms, evidence that the columns were once partly submerged.



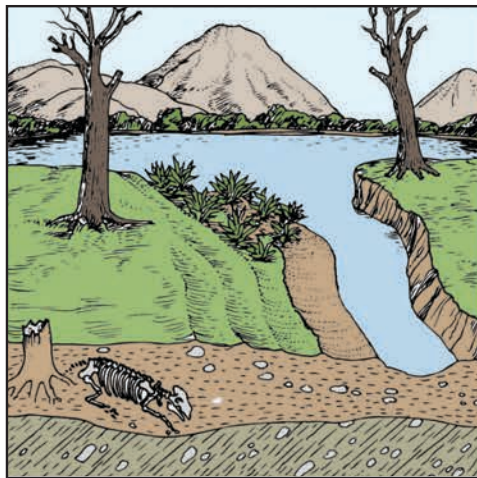
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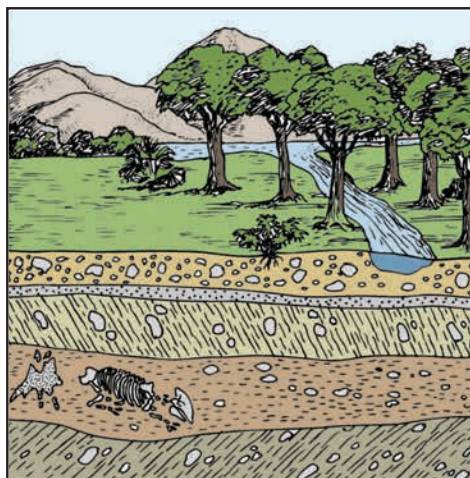
(a)



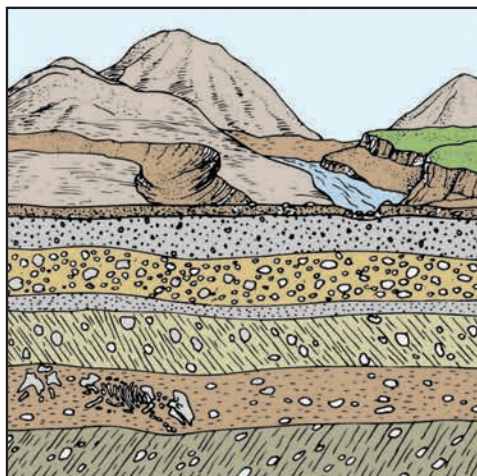
(b)



(c)



(d)



(e)



(f)

FIGURE EB1.3 The process of fossilization in which an organism (in this case, an animal) **(a)** dies in a watery environment that protects it from scavengers. Reduced oxygen levels in deeper water further resist deterioration **(b)**. The remains are gradually silted over **(c)** and eventually covered by successive layers of soil that compact into sedimentary rock **(d)**. In time, because of erosion, the fossil surface may become exposed **(e)**.

[From Kardong, K. V., 2006. *Vertebrates: Comparative Anatomy, Function, Evolution*, 4th ed. McGraw-Hill, New York. © The McGraw-Hill Companies, Inc.]



END BOX 3.1

Fossils as Evidence of Past Life (Cont...)

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