

CHAPTER 3

LIFE TODAY: SPECIES, DIVERSITY, AND CLASSIFICATION



The perspective of evolutionary biologists is very broad because their concern is with the origins of organism diversity across the whole of the biosphere, and there are two obvious questions. First, how should one make sense of the diversity of life today and, second, what are the origins of this diversity. This chapter mainly focuses on the first of these questions, and only provides a summary answer to the second. The rest of the book provides a fuller answer.

Making sense of the diversity of organisms alive today primarily means working out how to group the different types of organisms into logical categories. The first task is therefore deciding on how to distinguish one group of organisms from other, similar groups, and it is generally agreed that the essential unit for eukaryotic, sexually reproducing organisms is the species. This is ideally defined by the interbreeding criterion: if the males and females from two different groups cannot interbreed to produce fertile offspring, they belong to different species; if they can, they are viewed as members of the same species. Thus, if members of two apparently different populations can interbreed to produce fertile offspring, they are subspecies of the same species. This functional test works well in the context of contemporary speciation and is particularly important in theoretical discussions on the evolution of novel species. This is because the reproductive isolation that derives from a species' inability to breed with related species drives future diversity.

The definition works less well in other contexts. First, as one can only rarely undertake breeding experiments, such a test cannot usually be applied to living species and never, of course, to extinct ones or those that reproduce asexually. Second, the definition can lead to apparently counterintuitive results: as all canines can interbreed to produce fertile offspring, this definition means that all domestic dogs, jackals, dingoes, coyotes, and wolves have to be viewed as members of the same species. It seems odd to include in the same species an animal such as a pug that is about 30 cm high and with a very short jaw with a Great Dane that can be more than 1 m tall with a very long jaw. It is unlikely that they would be considered a single species if the only data for analysis were their fossilized skeletons. Third, plants form fertile hybrids far more readily than animals – plants seem to be much more tolerant of polyploidy and genetic variation in cross-breeding for reasons that are still not fully clear. The boundaries between plant species are thus often more blurred than those between animal ones.

In practice, the appropriate definition for a species depends on its context and, for evolutionary discussions, is usually based on noteworthy morphological differences when one is discussing the fossil record or those that reproduce asexually, on interbreeding

abilities for detailed speciation in living organisms, and on niche adaptation for exploring the early stages of separation (Coyne & Orr, 2004). What does need to be remembered in cases where the interbreeding test is not possible is that separate species can only be viewed as being closely related if their differences clearly derive from shared features that were possessed by a recent common ancestor (Chapter 5).

The numbers of species today

The numbers of living species so far identified is very large: the catalog of life database (www.catalogueoflife.org) includes information on about 1.1 million living species of which the very great majority (~920,000) are arthropods. These databases are still being added to and there are certainly many more species that are known informally but have yet to be officially cataloged. What is clear, however, is that we are a long way off having a full list of species.

The world-wide investigations by naturalists over the last few centuries have certainly led to the identification of the very great majority of the larger species (**Table 3.1**), and many of the smaller ones, but, as one goes down in scale to the small invertebrates, tiny plants, and fungi that are barely visible to the naked eye, there will inevitably be many yet to be discovered. A recent estimate of biodiversity, or the number of eukaryotic species on earth, is 8.7 ± 1.3 million; if this is correct, less than 20% of the distinct organisms with which we share the planet have been identified (Mora et al., 2011). One reason why this number is so large is that we have little idea of the number of parasites that are specific to each species. There is a standard joke that goes as follows: “Which phylum has the most species?” The answer is the nematodes (round worms). This is because every other species has a nematode parasite, although most have yet to be cataloged (hence the wide range seen in Table 3.1). There are, however, many, many other species-specific parasitic organisms that remain unknown and their identification will increase the total. Another reason is that we are unlikely to have cataloged all the single-celled and other very small eukaryotic organisms; indeed, it is unlikely that we ever will: there will always be odd niches that we will have neither the resources nor the imagination to investigate. Furthermore, evolution has not ceased and groups of existing variants are always making the transition to becoming new species.

Such reasons also help explain the unexpectedly low number of prokaryotic species so far identified: the PubMed taxonomy database includes only ~18,000 bacterial and ~800 archaeal species. The prokaryotic populations of most habitats and organisms, other than

Table 3.1: Numbers of cataloged species in various groups of eukaryotes (numbers are approximate because different sources give different numbers)

Species	Number
Monocotyledonous plants	~5 K
Flowering plants	~300 K
Nematode worms	80–1000 K
Beetles	~450 K
Fishes	~28 K
Birds	~10 K
Mammals	~5 K

humans, have not been systematically investigated, so there are bound to be many more prokaryotic species to be discovered. It is, however, harder to define a prokaryotic than a eukaryotic species. Because bacteria divide asexually, a morphological rather than a breeding criterion is normally used, but there is a limited number of possible shapes for a single-cell organism, so individual species in each morphological group have to be distinguished partly by their DNA differences and partly on the basis of the hosts to which they are restricted (Wayne, 1988; Oren & Garrity, 2014). We may have to accept that the differences within groups of bacteria reflect a continuum rather than a set of distinct species (note that a similar problem occurs in eukaryotes in what are known as ring species; see Chapter 15). As to the viruses, their effects are usually organism-specific and can only be identified if they lead to some disease. As we care little about the diseases that affect the great majority of organisms, the ~3400 virus species cataloged in 2014 is bound to be a gross underestimate of the full number.

Scale: from microns to meters

One of the most remarkable features of the biosphere is the range of sizes of multicellular organisms. Living vertebrates, for example, extend from *Paedophryne amauensis*, a small frog less than 8 mm long, to the blue whale, *Balaenoptera musculus*, which is up to 30 m long (the volume ratio is about 1:10¹⁰). Flowering plants extend from less than 1 mm (*Wolffia globosa*, a duckweed that weighs about 150 mg) to almost 100 m in height (for example, the giant sequoia, *Sequoiadendron giganteum*, and the fig, *Ficus benghalensis*, which both weigh well over 1000 tons). The length ratio of the two trees to *Wolffia* is about 1:10⁷ and the weight ratio about 1:10²⁰. Going down to the level of a bacterium that is about 2×10^{-3} mm in diameter and weighs about 10⁻¹¹ g or a single-cell eukaryotic yeast, which can be as little as 3×10^{-3} mm across and weighs about 3×10^{-11} g, it is clear that the scale of life is almost inconceivably large.

When one compares the smallest with the largest, the differences are more than obvious, but the similarities should not be ignored. The organ systems in the frog and the whale are remarkably similar, and the range of cell types in the two is thus much the same. This is, of course, because their last common ancestor was a late amphibian with the same set of organ systems. The most important types of cellular organization in vertebrates are epithelia, which cover external surfaces and line internal tubes and are essentially two-dimensional sheets; mesenchyme, which forms most tissue three-dimensional masses (such as dermis, muscles, bones, tendons, cartilage); neurons and their support cells (such as glia and astrocytes); and the many subtypes of blood cells. Other, more specialized cells are subtypes of these main classes. At this level of discussion, the main difference between vertebrates and invertebrates is that the latter have a more restricted set of mesenchymal cells: they lack bones, fascia, and a sophisticated set of blood-cell types.

As to the plants, the similarities between *W. globosa* and the fig tree are particularly apparent in their respective reproductive systems as both have the flowers, pistils, stamens, and seeds characteristic of flowering plants. The differences are in the supporting tissues. Comparison of the fig or sequoia with a small woody shrub called *Salix herbacea*, which is only a few centimeters high, shows that it is hard to discover any differences in the anatomical entities or cell types that make up the plant – the differences are merely of scale and minor morphological detail. Naturally, our eye looks for differences, and inevitably focuses on the exterior rather than on the organism as a whole. Most of an

organism's tissues are on the inside and, if scale is set aside, are usually similar to most other organisms in the same phylum.

Variation within a species

If one excludes the minority of eukaryotic species that reproduce by parthenogenesis (asexual reproduction, for example water fleas such as *Daphnia* and many single-cell eukaryotes) or are essentially hermaphroditic (organisms carrying both male and female reproductive cells, a group that includes many examples of plants, slugs, mollusks, and nematodes), reproduction involves mating, and this implies the presence of members of the opposite sex. In other words, when one speaks of a species, one is implicitly talking about a population, and the individual members of that population are never identical – variation is normal. Even identical twins, which start off the same and with the same DNA, soon develop small differences. This is owing to the fact that, for all the DNA error-correcting molecular machinery in cells, a few such somatic mutations are incorporated into the genome of the daughters every time a cell divides. However, such mutations are not inherited as they are not in the germline.

The major, immediate sources of variation within a population come from the essentially random combinations of genes that occur during reproduction (genetic drift). This has two sources: first, the homologous combination between pairs of chromosome that occurs during meiosis arbitrarily assort the genes, after allowing for linkage effects; second, mating brings together two arbitrarily chosen sets of genes. Any additional copying errors that occur during meiosis or development just add a further small amount of randomness, albeit that they are inherited, together with any future mutations that appear in the next generation of sperm and eggs.

Such resulting phenotypic variation within a population reflects the effects of the mutations that make minor changes to protein function and tend to have minimal effects on individuals and their reproductive abilities. Cases where a heritable or germline mutation has a more dramatic effect fall into two classes: those whose effects are deleterious to the individual are likely to be lost, particularly if they generate congenital abnormalities; those that enhance the ability of the organism to thrive and reproduce in a particular environment will be kept and may slowly spread through the population. They may even be candidate genes for facilitating novel speciation, although these are just about impossible to identify.

Within any population there is thus a broad spectrum of unique genotypes with the phenotype of each individual, other than of very young identical twins, being different. If we just look at humans, the major areas where we immediately notice the distinctiveness of an individual are in overall size, pigmentation patterns (skin, hair), and minor differences in the relative size of particular features, notably in the face; in terms of the various anatomical bits and pieces, all humans are essentially identical. The molecular basis for minor differences in phenotype between individuals is discussed in Chapter 11.

The anatomical differences between species

Before considering how organisms are classified into the various taxonomic levels on the basis of their anatomy, it is worth taking a brief look at the origin of the differences among them. In taxonomies, more basic differences are reflected in the criteria used for high-level taxa, such as phyla and classes, and smaller differences for low-level ones, such as species and subspecies. Nevertheless, the grouping of cetaceans and ungulates shows that taxonomies can sometimes have an odd feel about them in terms of the underlying biology. It is

therefore necessary to take a slightly deeper look at how the differences across groups of similar organisms arise and why the hierarchies are less arbitrary than they sometimes seem.

The fundamental point here is that differences among organisms reflect the different ways that embryos and larvae develop and so produce the adults; very few distinguishing features reflect events taking place during the growth phase that follows morphological development in the embryo and larva. The key insight that helps in making sense of these events came from von Baer almost 200 years ago (see Chapter 10 for details), and seems obvious today. This was that basic features, such as the body plan, emerge early in embryonic development, while more minor interspecies differences appear much later, building on what is already there. Although embryological stages are not precisely linked to taxonomic classifications, they provide the basis for them as early events reflect higher taxonomic levels and later events, lower ones (Davidson & Erwin, 2009).

The key distinctions between high-level taxa lie in the basic body patterns, and reflect distinct patterning events in the early embryo. These define the ~60 eukaryotic phyla; examples are mollusks (an external mantle and a radula for eating), arthropods (invertebrates with a segmented body, a chitin exoskeleton, and jointed limbs), and gymnosperms (seeds develop from leaves or leaf derivatives such as cones). Within a phylum, the next stages of development of most members are often similar, with interspecies differences appearing later. If one considers the vertebrate subphylum: all go through a series of early stages that lead to an elongated bilateral embryo with a notochord, a rod just ventral to the neural tube, and a segmented mesodermal body musculature. The latter separate into those that do have a proper head and those that do not (these are the lancelets which lack neural crest cells – Chapter 10).

Those with heads then develop backbones, their shared feature, and go on to produce paired lateral outgrowths. If these become fins, the animals are fish, but if these outgrowths develop into limbs, the result is usually a land vertebrate, with subsequent developmental features distinguishing amphibia, reptiles, birds, and mammals. In each of these taxa, subsequent changes in, say, head morphology produce further subdivisions of classes and families. Later in development, minor differences appear that distinguish the various species within a family. Typical areas where such terminal differences occur include size, tooth morphology, and the details of skin patterns.

The taxon of Eutherian (placental) mammals illustrates this. The essential disparities among them are not particularly impressive in the greater scheme of things: they all have, to a close approximation, the same body form and the same cell types. Their primary differences reflect their evolutionary adaptations to different environments. Comparisons between mouse and man show that the obvious differences are in size, hair coverage, a tail, and brain complexity, but these are as nothing compared with the internal similarities. Both have very similar cardiovascular, liver, reproductive, sensory, alimentary (gut), neuronal, and other organs systems, and it is very hard to tell under the microscope whether a cell is from a mouse or a man. This is, of course, why the mouse is such a good model system for man. This is not to underplay the differences but to show where they lie and what they are. In considering lines of evolutionary descent, it turns out that similarities are just as important as differences.

It has already been noted that all multicellular organisms are made of a very similar set of cell types that include epithelial cells that form sheets and tubes, neurons, muscle cells, pigment cells, reproductive cells, and the like. Similarly, there is a short list of cells for plants that includes support cells, transporting cells, storage cells, and reproductive cells.

What is wonderful about nature is that small permutations on a limited number of themes can lead to such a wonderful range of variants.

Taxonomy and the grouping of species

It is immediately obvious that the diverse species of life today can be grouped into families or taxa (a taxon is a collection of organisms grouped on the basis of shared characteristics and can include one or more levels). Similar taxa can be grouped into broader taxa on the basis of shared properties, and so on upwards (**Box 3.1**). Membership of a particular taxon at a particular level is defined by the possession of a set of properties, with higher ranks having a smaller number of defining properties than lower ones and so including more organisms. Thus, for example, the taxon of marsupial mammals sustains the later development of their early-born offspring in a pouch, the taxon of placental mammals sustains the fetus to birth through a placenta, and the taxon of monotremes produces eggs whose yolk provides food for their embryos. These three taxa are members of a higher-level taxon, the mammalia, whose membership is defined by the possession of milk-producing mammary glands.

A classification based on such similarities is known as a taxonomy, and the essential feature of the current taxonomy is a graded hierarchy of classes whose highest level is generally considered to have three members: eukaryotes and the two prokaryotic taxa, eubacteria and archaeobacteria. Below these are kingdoms and these reflect the expansion of the various classes of eukaryotes, although the classification of single-celled eukaryotes is still contentious. A level lower are the phyla, a taxon based on body plan. Within each phylum, there are lower ranks of taxa that include class, order, family, genus, species, and subspecies, together with other intervening levels that are sometimes inserted because they have been deemed convenient (see Box 3.1). Although such classifications go back to Aristotle, the credit for modern approaches to the subject is given to Linnaeus through his book *Systema Naturae*, published in 1735. Species are, following Linnaeus's practice, given a double name written in italics: the former is the genus or family name, the latter the species name; thus *Pan paniscus* and *Homo sapiens* are the species names for bonobos and humans, respectively. Subspecies have a third name so that, for example, the Sumatran tiger is *Panthera tigris sumatrae*.

In systems terminology, such a taxonomy is a series of embedded classes linked by the relationship <A> <is a subclass of> , normally shortened to <A> <is a> , and can be

Box 3.1: Classic taxonomic description of the domestic cat

According to www.ncbi.nlm.nih.gov/Taxonomy, the full taxonomic hierarchy (with *taxonomic* levels) for the domestic cat is:

cellular organisms; Eukaryota (*domain*); Opisthokonta; Metazoa (*kingdom*); Eumetazoa; Bilateria (*subkingdom*); Deuterostomia (*infrakingdom*); Chordata (*phylum*); Craniata; Vertebrata (*subphylum*); Gnathostomata (*infraphylum*); Teleostomi; Euteleostomi; Sarcopterygii; Dipnotetrapodomorpha; Tetrapoda (*superclass*); Amniota; Mammalia (*class*); Theria (*subclass*); Eutheria (*infraclass*); Laurasiatheria (*superorder*); Carnivora (*order*); Feliformia (*suborder*); Felidae (*family*); Felinae (*subfamily*); *Felis* (*genus*); *Felis catus* (*species*).

In more formal, systems terms, this 27-level hierarchy is a series of embedded classes or sets linked by the relationship <is a subclass of> (abbreviation: *is a*). Thus, <my cat, Coco> <is a> <*Felis catus*> <is a> <*Felis*> <is a> <Felinae> <is a> <Felidae> <is a> <Feliformia>, etc.

visualized as a hierarchical tree or as sets of embedded circles (Chapter 5, Appendix 1). It is important to realize that such a hierarchy, even where it is based on the interbreeding abilities of living organisms, says nothing about evolutionary descent. Even where taxa include extinct, fossilized organisms with timings, they still say nothing explicit about evolution. One reason is that the dates associated with a particular fossilized species are rarely precise as to when that species evolved, what were its descendants, and when it became extinct, unless the latter date coincided with a major extinction. The more important reason, however, is that time is not a link that describes evolutionary descent; for this, one needs the details of anatomical change.

Evolutionary hierarchies or cladograms, which will be discussed in subsequent chapters, are different from taxonomic hierarchies for two important reasons. First, the link that connects terms is *<descended with modification from>* rather than *<is a>* (Chapter 5). Second, in evolutionary hierarchies, every link connects, in principle at least, two species of organisms, the parent and the child, although it can be hard to identify the original parent species. In Linnaean classifications, all higher levels reflect groups of organisms, alive or extinct, that share features; such classifications carry only an implication of common descent. For Linnaean classifications even to be consistent with evolutionary hierarchies, further information needs to be added.

It is worth noting that, because a pair of taxa may share some common features, this does not necessarily imply that they are closely related evolutionarily: the common features could just reflect a common adaptation to a particular environment. Thus, for example, although cactuses and desert euphorbias can look very similar because both are succulents with spikes and thick layers of cuticle, they are only distantly related taxonomically. Similarly, sabre teeth have arisen independently many times (Chapter 5). In fact, there are many examples of very similar morphological features that have evolved independently as adaptations to a particular environment rather than through common descent. These are known as homoplasies and reflect what is known as convergent evolution (McGhee, 2011); their existence emphasizes the importance of using a broad range of phenotypic characteristics in making taxon assignments.

It used to be difficult to assign organisms that looked very similar to a particular taxon as it was not always clear whether the similarity derived from convergence or close inheritance. DNA analysis usually solves such problems today, and is widely used to confirm the validity of Linnaean classifications. Comparative DNA sequencing of a particular gene across a group of organisms shows which of its members are closely related and which only distantly. Thus, analysis of the various 18S ribosome RNA genes was important in showing that there was an early and high-level subdivision of the animal kingdom into protostomes and deuterostomes (Peterson & Eernisse, 2001; Giribet, 2008). It was also used to confirm that the subdivision of the protostomes into molting Ecdysozoa and non-molting Lophotrochozoa reflected a high-level, and hence a very old, evolutionary separation. The origins of the phyla are discussed briefly in Chapter 4 and more thoroughly in Chapter 9.

A difficulty with today's standard class taxonomy is that it tries to solve two problems. It aims to group species on the basis of physical similarity and to include within particular subhierarchies species with a common evolutionary ancestor, and the latter requirement can lead to some surprising results. Thus, for example, the ungulates were originally mammals that walked on their toes and whose nails evolved into hooves; it has now become clear on the basis of DNA analysis that not only have hooves evolved more than once, but also that the cetaceans (whales, dolphins, and other sea mammals) have the same

common ancestor as modern even-toed ungulates such as pigs, sheep, and camels. Although they were originally considered as unrelated groups, the class taxonomy had to be changed so as to include both within a single class. Today, the cetaceans are now grouped with these even-toed ungulates in a higher-level class, the Cetartiodactyla (Chapter 7). Although there are occasional such changes, the current taxonomy can now be viewed as fairly stable.

Classifying life today

The domains at the top level of the current taxonomy of living organisms are the eubacteria (anuclear prokaryotes with a membrane containing glycerol-ester lipids), the archaeobacteria (anuclear prokaryotes with glycerol-ether lipids), and the eukaryotes (with nucleated cells). Below the domains is the taxon of kingdoms, which particularly subdivides the eukaryotes. The two major ones are the Archaeplastida (subkingdoms: red algae, green algae, and plants, all of which have chloroplasts with double membranes), and the opisthokonts (subkingdoms: animals, fungi, and some single-celled eukaryotes, all of whose motile cells such as sperm have a single flagellum); there are also several minor kingdoms, most of which are single-celled eukaryotes (see Chapter 9).

The next important level down is the phylum and it has an important biological meaning: each phylum includes all species possessing the same body plan; the taxon includes 35 animal, six fungal, 11 plant, one moss, 52 bacterial, and five archaeal members. Well-known examples are the arthropods and the flowering plants (note: plant phyla are sometimes called divisions). **Table 3.2** shows 22 of the main animal phyla (the omitted 15 or so minor phyla are protostomes). Four are radiata, which have rotational symmetry and are diploblastic; this means that the embryos have two layers, an external epithelial ectoderm and an inner epithelial gut, with any muscles forming later in development. The rest are bilateria, which have basic mirror-image symmetry and are all triploblasts, having an intervening layer of mesoderm between the ectoderm and endoderm that makes muscles and other cell types not seen in diploblasts. The bilateral phyla are divided into two major groups on the basis of embryonic development: most are protostomes (the first cavity in the early embryo becomes the mouth and the second the anus) and only three are deuterostomes (the roles of these cavities are reversed, other than in amniotes where the evolution of the large yolk changed the way that the gut formed in fishes and their descendants). The chordates are the major deuterostome taxon and their most important subgroup is the vertebrates.

A phylum was initially defined solely on the basis of morphology, but this can be ambiguous, as the example of the echinoderms shows. Adult echinoderms such as starfish have essentially radial symmetry, normally with five arms, but their larvae, which are triploblastic, initially show bilateral symmetry. Later in their development, these larvae undergo a major and very rapid reorganization as internal rudiments in the larva rapidly restructure it, producing limbs and even rebuilding the gut (Wray, 1997). For the purposes of classification, the larval form with its three layers and bilateral morphology is a better indication of the nature of the organism than the adult morphology with its radial symmetry. Echinoderms are therefore included in the bilateria.

Today, the most successful phylum on the basis of cataloged numbers is that of the arthropods (see Table 3.1); these invertebrates, which possess a chitin exoskeleton and jointed limbs, have flourished from the Cambrian Period onwards. The famous evolutionary biologist J.B.S Haldane is said to have replied to a question from a theologian about what the

Table 3.2: The main living animal phyla: most of those excluded are worm protostomic phyla with few species					
Superphylum	Phylum	Common name	Distinguishing characteristic	Species described	
Radiata	Cnidaria	Coelenterates	Nematocysts (stinging cells)	~11,000	
	Ctenophora	Comb jellies	Eight "comb rows" of fused cilia	~100	
	Placozoa		Small (1 mm), flat, and featureless	1	
	Porifera	Sponges	Perforated inner wall	5000+	
Bilateria	Deuterostomes	Chordata	Hollow dorsal nerve cord, notochord, pharyngeal slits, endostyle, postanal tail	~100,000+	
		Echinodermata	Echinoderms	Fivefold radial symmetry in living forms, mesodermal calcified spines	7000
	Proto-stomes	Hemichordata	Acorn worms, pterobranchs	Stomochord in collar, pharyngeal slits	~100
		Arthropoda	Arthropods	Chitin exoskeleton	1,134,000+
		Kinorhyncha	Mud dragons	Eleven segments; each with a dorsal plate	~150
		Loricifera	Brush heads	Umbrella-like scale at each end	~122
		Nematoda	Round worms	Round cross section, keratin cuticle	80–1000 K
		Nematomorpha	Horsehair worms	Nonfunctional gut	~320
		Onychophora	Velvet worms	Legs tipped by chitinous claws	~200
		Priapulida	Penis worms	Eversible proboscis	16
		Tardigrada	Water bears	Head and body with four segments	1000+
		Annelida	Segmented worms	Multiple circular segments	17,000+
		Brachiopoda	Lamp shells	Lophophore and pedicle	300–500
		Bryozoa	Moss animals, sea mats	Lophophore, no pedicle, ciliated tentacles	5000
Entoprocta	Goblet worms	Anus inside ring of cilia	~150		
Mollusca	Mollusks/molluscs	Muscular foot and mantle round	112,000		
Nemertea	Ribbon worms		~1200		
Phoronida	Horseshoe worms	U-shaped gut	11		

living world tells us about God by saying, “If one could conclude as to the nature of the Creator from a study of creation, it would appear that God has an inordinate fondness for stars and beetles.”

As to the prokaryotes, bacteria are subdivided into about 50 phyla on the basis of morphology; they mainly have outer membranes that contain glycerol-ester lipids and peptidoglycan (Cyanobacteria, an important bacterial phylum, contain cellulose rather than peptidoglycan). The rarer Archaea have cell membranes that contain glycerol-ether lipids and are subdivided into four phyla. Archaea were originally known as extremophiles because they were found in what were considered unfriendly environments, such as those with high salt concentrations (the halophiles), high temperatures (up to 105°C; the thermophiles), high acidity or alkalinity, and those lacking oxygen (the methanogens). More recently, however, and because the search has been widened, Archaea have been found in almost every environment that has been studied. The relationship between Archaea and bacteria is discussed in more detail in Chapter 9.

The taxonomic levels between the phylum, defined by body plan, and the species, defined by the interbreeding criterion, are essentially artificial constructs based on morphological criteria that indirectly reflect the development of the organisms within a phylum; in general, higher taxonomic levels reflect early developmental events and lower ones much later events. The Integrated Taxonomic Information System (www.itis.gov/) shows that the domestic cat hierarchy has 27, the honey bee has 18, and the garden daffodil has 12 levels between kingdom and species. There is little that is contentious in these levels between the phylum and the species, albeit that names occasionally change (for example, the family of legumes used to be called the *Leguminosae* but are now called the *Fabaceae*).

In considering whether to assign different living organisms to distinct species when breeding experiments are impractical, the main criteria are the external characteristics, such as size, skin patterns, feather details, and coloring. An example is Darwin’s classic work on how specific finches flourished on individual islands in the Galapagos: it is now clear that a key distinguishing feature is beak morphology and its adaptation to particular island-specific food resources (**Figure 3.1**). As the finches are still on their respective islands, this example of speciation is still accessible for study (Abzhanov et al., 2006; Abzhanov, 2010; Rands et al., 2013). Extinct taxa can, however, only be studied on the basis of fossilized tissues: these mainly reflect the tough exoskeleton of invertebrates, the hard tissues of plants, and the bones and teeth of vertebrates. Paleontologists have to know anatomy in very great detail and be able to recognize quite small differences between sets of fossilized remains if they are to produce convincing arguments that similar tissues represent different species.

The full current taxonomy is now so large and complicated (see Box 3.1) that it can only be held in a database and viewed online, and there are several versions (these include www.itis.gov/ and www.ncbi.nlm.nih.gov/taxonomy/). While the higher levels represent abstract groupings and are inevitably generalizations, they do try to capture a structural, an evolutionary, and, implicitly, a developmental relationship. Each species represents a group of real organisms and the numbers in some of the phyla are very large (see Table 3.1). The key reason for this is that natural variation allows organisms to explore new habitats. Every small region on the planet affords organisms an opportunity to invade it and, once there, not only change themselves and form a new species, but also to change that habitat (for example, it may deplete one source of food while offering itself as another). This may allow further organisms to invade the territory, to adapt and make a living there – and so further speciation occurs!

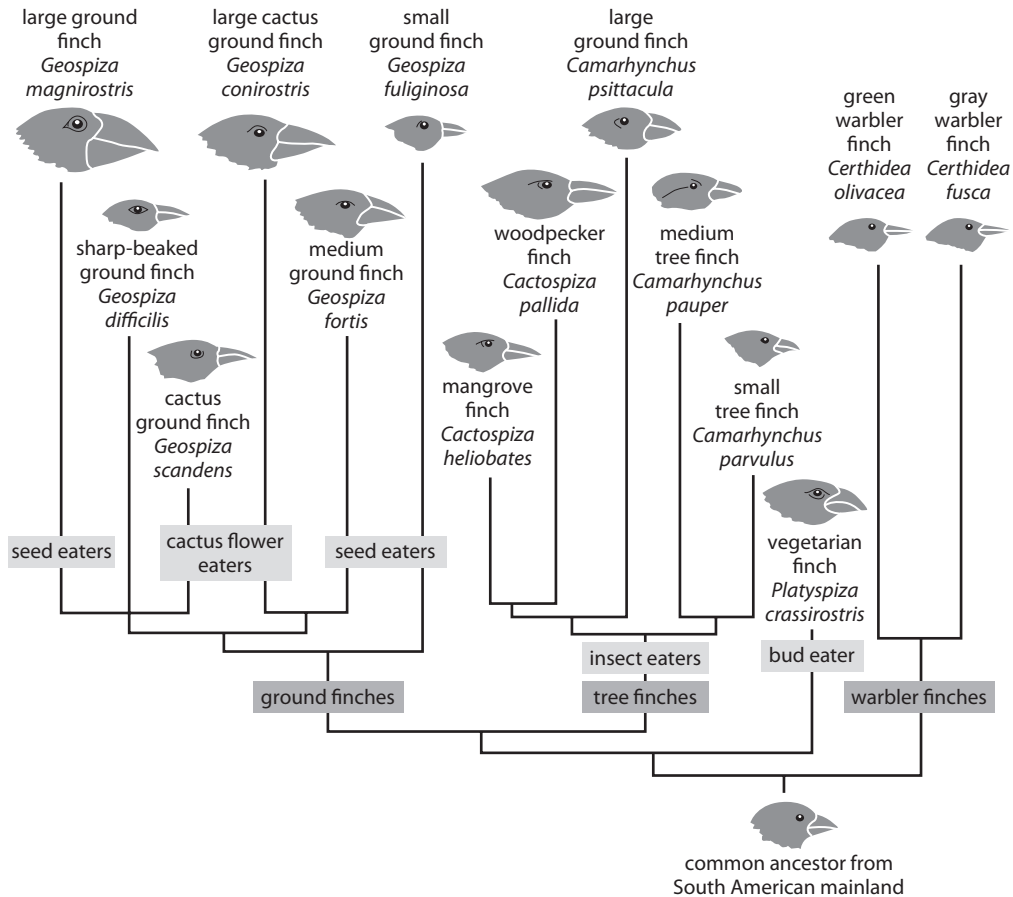


Figure 3.1 A taxonomic representation of Darwin's finches.

The mechanisms of speciation – a summary

The diversity of contemporary species discussed in this chapter raises two important and related problems for the evolutionary biologist. The first concerns the historical origins of this diversity; the second is the mechanism by which change happened. The solution to the first comes from the fossil record, where it exists, and from the analysis of homologous DNA sequences in related organisms, as this shows how they are grouped and hence when they last shared a common ancestor. The second is more difficult because it highlights an apparent contradiction. If a species is defined as a population of organisms that is reproductively isolated, it does not seem possible that it can generate another population that is also reproductively isolated not only from all other species, but also from the parent species.

There is a good solution to the problem of how species originate, but it was not easy to discover. The problem was initially posed by Darwin (1859), and his answer was that natural selection acted on variation, but he knew nothing of the origins of variation nor anything about genes and inheritance. Some of the answers become clear in the 1950s with the exploration of the implications of population genetics, although a full understanding of the actual role of genes awaited the discovery of DNA coding and molecular genetics

in the 1950s–1970s, while it is only recently that the ways in which mutation affects the phenotype have become clear. Providing the data to explain the mechanism by which new species form occupies the major part of Section 3 (Chapters 12–15). Here, a summary of the four stages that lead to speciation is given.

Stage 1: Reproductive isolation

The first active step on the way to novel speciation occurs when a small subpopulation becomes reproductively isolated in some new habitat different from that in which its parent population lived, and there are many ways in which this can happen. Because this new population is small, its distribution of genotypes and phenotypes will be slightly different from those of the parent population, owing to genetic drift (random sampling).

Stage 2: Novel phenotypes appear

The effect of this reduced and unbalanced gene profile is the appearance of novel phenotypes, partly due to the Wahlund effect that increases the proportion of recessive phenotypes (Chapter 14), and partly due to the increased frequency of rare alleles because of genetic drift. Over time, these effects together with that of continual mutation leads to further variation, with change being relatively rapid.

Stage 3: Selection

As a result of this different phenotype distribution and because the selection pressures in this new habitat are different from those in the original one, individuals in the new population will do better or worse in the new habitat than those in its parent population might have done. The subpopulation that, as a whole, does worse in the sense that it cannot maintain its numbers will eventually be lost. If, however, there are individuals in the subpopulation with appropriate phenotypes that allow them to produce more fertile offspring, then they will flourish (this is the definition of fitness).

Underpinning these events at the phenotypic level is a different set of events at the genotypic level. The gene pools of the parent and new populations start by being slightly different because of genetic drift. As further mutations and gene distributions accumulate over time, changes to existing traits appear in the phenotype and are available for further positive or negative selection. As a result, the population becomes ever better suited to its new habitat.

At this stage, changes in both the phenotype and genotype distributions in the new population have amplified its original differences from the parent population. Because the two populations are reproductively isolated, there can be no equalizing of genes between them and, as time passes, they become increasingly different. At this stage, however, there is unlikely to be any genetic barrier to interbreeding because the accumulating genetic differences represent minor mutational changes – the two populations are now variants (this is essentially what happens in artificial breeding).

Stage 4: Speciation

Speciation is the process that leads to genetic incompatibility between the two populations, and occurs as a result of three types of further genetic change. The first and second are relatively fast and can overlap; the third takes much longer. The first affects the phenotype and results in individuals in one population becoming unwilling to mate with those

in the other (prezygotic isolation). The second derives from mutation that decreases the likelihood of pregnancy and the fertility of any hybrid that results from such a mating through the build-up of genetic incompatibilities.

The third type of change results from the slow accumulation of structural changes to the genome (e.g. chromosomal rearrangements). As these accumulate, they make hybrids increasingly less fertile because their chromosomes become unable to pair up during meiosis. Thus, although horses and donkeys are distinct species with 64 and 62 chromosomes respectively, they are close enough to be able to interbreed. But their offspring, mules and hinnies with 63 chromosomes, are normally infertile, there being a single published exception (Ryder et al., 1985). Eventually, and this may take millions of years, these structural changes accumulate to the extent that fertilization and mitosis fail through nondisjunction of chromosomes. At this stage, the two populations have finally become separate species. As a result, the new species cannot be absorbed back into its parent community; it can only maintain itself and generate further novel species. Thus, speciation represents a one-way mechanism to future diversity.

One reason why evolution is so hard to study is that the genetic changes that lead to speciation are of very low probability and can take thousands, even millions of generations to occur first in groups of individuals and then to spread throughout a population. The next chapter discusses the history of life, the origins of today's diversity, and the glacial speed with which evolutionary change occurs.

Key points

- There are more than a million known species distributed across about 50 phyla (basic body forms) with vertebrates varying in size from less than 1 cm (a frog) to more than 30 m long (the blue whale). Plants likewise show a similar size range.
- There is no definition of a species that is appropriate in all contexts, but, where appropriate, the best is that a species is a group of organisms that cannot breed with other groups.
- Where a definition of species based on breeding cannot be used (for example, for extinct organisms), species are usually distinguished on the basis of their morphology, habitat or DNA profile.
- Groups of organisms can be arranged in hierarchical trees on the basis of anatomical features with broader features having higher levels than more specific ones (a Linnaean taxonomy). This hierarchy roughly reflects the order in which the events of development take place.
- Within any population, variation is normal and mainly derives from gene assortment during meiosis and mating.
- Novel speciation builds on this variation.

Further reading

Gaston KJ & Spicer JI (2004) *Biodiversity: An Introduction*. Blackwell Science Ltd.

Polaszek A (ed.) (2010) *Systema Naturae 250 – The Linnaean Ark*. CRC Press.

Ruse M & Travis J (eds) (2009) *Evolution: The First Four Billion Years*. Harvard University Press.

