Incipient and Complex Features. Several hypotheses can account for the first stages of the evolution of features that, when fully developed, serve a clear adaptive function.

1. **Upon first appearance, the feature is sufficiently well developed** to provide an advantage. The major mutations in the wing pattern of mimetic butterflies, discussed above [pp. 680-681], provide examples. The pattern produced by the initial mutation, although resembling an unpalatable model, is sufficiently similar to it to provide a selective advantage. It is refined by additional substitution of alleles with small effects.

2. **The new feature is not adaptive initially, but it is a developmental by-product of other adaptive features.** At some later point, it becomes modified to serve an adaptive function. For instance, by excreting nitrogenous waste as crystalline uric, insects if I lose less water than if they excreted ammonia or urea. Excreting uric acid is surely an adaptation, but the white color of uric and acid is not however, pierine butterflies such as the cabbage white butterfly (*Pieris rapae*) sequester he uric acid in their wing scales, imparting to the wings a white-collar that plays a role in thermoregulation and probably in other functions.

3. **One of several an ancestral functions of the feature becomes accentuated,** especially if another feature takes on its other original functions. In the synapsid ancestors of mammals, for example, a the lower jaw, articulating with the skull by the articular and quadrate bones, received sound vibrations that were transmitted via the jaw joint to the inner ear. As then dentary-squamosal articulation of the jaw evolved, the articular and quadrate bones became smaller, looser, and functionally specialized for sound transmission, and now form to of the middle ear ossicles of mammals (see Chapter 6).

4. **A change in the function of a feature alters the selective regime, leading to its modification.** Already recognized by Darwin, this is one of the most important principles of macroevolution (Mayr 1960), and every group of organisms presents numerous examples. The wings of auks and several other aquatic birds are used in the same way in both air and water; in penguins, the wings have become entirely modified for underwater flight (Figure 24.6). The ability of an electric eel (*Electrophorus electricus*) to kill prey and defend itself by electric shock is a an elaboration of the much weaker electric fields generated by other fishes in the same family (Gymnotidae, knifefishes), which use their electricity for orientation and communication in murky waters. The hairs, or setae, on the surface of insect's bodies universally serve functions that depend on registering changes in, pressure such as proprioceptio and detection of air currents, but they have been modified to serve many other functions as well (Figure 24.7). For example, the flattened, scalelike setae of moths and butterflies enable them to escape spiderwebs (by shedding scales and fluttering free) and bear the pigments that provide their wing patterns.
Intermediate steps in the evolution of complex features are generally advantageous. Most new features are modifications of pre-existing structures with altered functions, as we have just seen. Although in its later stages of modification a structure may be highly complex, with its function depending on the intricate coordination of many parts, it is a mistake to think that only such complexity can provide an adaptive advantage. Wings provide an example of this principle; so do eyes. Vertebrates and cephalopods (squid, octopus) have remarkably similar eyes that are the epitome of complex organs. Darwin acknowledged, in The Origin of Species: "that the eye, with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection seems, I freely confess, absurd in the highest possible degree." But he then proceeded to supply examples of animal's eyes as evidence that "in numerous gradations from a perfect and complex eye to one very imperfect and simple, each grade being useful to its possessor, can be shown to exist; if further, the eye does very ever so slightly, and the variations be inherited, which is certainly the case; and if any variation or modification in the organ be ever useful to the animal under changing conditions of life, then the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, can hardly be considered real." Since Darwin's time a great deal of information on the photoreceptive organs the various animals has been amassed (Salvini-Plawen and Mayr 1977; Osorio 1994). these organs are exceedingly diverse in structure and function, ranging from small groups of merely light sensitive cells to the complex structures, capable of registering precise images, found in many arthropods, some molluscs, and vertebrates. Many protists, such as dinoflagellates, have an "eyespot" consisting of an aggregation of visual pigment associated with the chloroplast or the base of the flagellum. These organisms can move in response to change in light intensity. This photoreceptive structure resembles that of ciliated photosensitive cells that are widely distributed among the animal phyla.

In few instances has the phylogenetic sequence of photoreceptor evolution been clarified; in its place, we can recognize grades of complexity among unrelated animals that show the adaptive feasibility of each stage (Burggren and Bemis 1990). The simplest grade is a mere aggregation of a few or many other photosensitive cells, found in some flatworms, rotifers, annelid worms, vertebrates (lamprey larvae), and others. The next grade is a simple epidermal cup lined with photic cells; this structure, which can provide some information on the direction of a light source through the differential illumination of different parts of the cup, has evolved independently in numerous lineages of flatworms, cnidarians, molluscs, polychaetes, cephalochordates, and others (Figure 24.8a). from this grade, there are numerous transitions series to "pinhole eyes" and dense to "closed eyes" in which translucent cells or cell secretions (vitreous mass) act as a rudimentary lens. Closed eyes, usually with some kind of lenslike structure, have evolved independently in cnidarians, snails, bivalves, polychaete worms, arthropods, and vertebrates. A close eye with a lens enables the organisms to more accurately determine the direction of incident light and to orient by it, to detect movement of objects, and, by the principle of the pinhole camera, to form at least elementary images. Image formation reaches its apogee in insects, in which each element (ommatidium) of the compound eye subtends a small angle of the field of view, enabling the many elements together to provide a detailed mosaic image; and in cephalopods and vertebrates, in which muscles move the lens or alter its shape in order to focus.
In Chapter 23, we described the experimental results indicating that a homologous gene initiates eye development in both insects and vertebrates. Insect and vertebrate eyes as such are surely not homologous, since they differ so greatly in structure. It is likely instead, that this gene primarily had the more general function of governing the differentiation of photosensitive cells, a which are so widely distributed among the animals that they doubtless predate the divergence of the animal phyla. In various filing, other genes that to organize it the development of our structures came under the control of this "master" gene. Salvini-Plaw and Mayr (1977) estimated that at least 15 lineages have independently evolved eyes with a distinct lens. The evolution of eyes is apparently not so improbable! Each of the many grades of photoreceptors, from the simplest to the most
complex, serve an adaptive function. Simple epidurm photoreceptors and cups are most common in slowly moving or borrowing animals; highly elaborated structures are typical of more mobile animals. The mystery of how a simple eye could be adaptive is no great mystery after all.

**Functional integration and complexity.** The parts of an organism are often functionally interdependent, so the selective value of variation in any one character must often depend on the state of other features. For this reason, many biologists feel that evolutionary theory must be framed not only in terms of population genetics, with its focus on simple models of a few genes or characters, but also in terms of whole organisms (Wake and Roth 1989). By its nature, complexity is difficult to understand and to describe with a few simple principles. Nonetheless, we must ask how it evolves, in what its evolutionary consequence may be.

**Complex functional design.** Advantageous changes in organismal design may not occur until constraints have been relieved. Some constraints may reside in genetically controlled patterns of development, as we saw in Chapter 23. Other constraints are functional. The greater the number and agree of functional integration of interacting parts, the more stringent constraints on evolution are likely to be, and the rarer will be evolutionary "breakthroughs" to new organismal designs. Thus the evolution of a complex design often limits severely the variety of evolutionary pathways that a lineage can subsequently take. In most salamanders, for example, the hyobranchial bones and muscles that support the tongue also move the floor of the mouth, forcing air into the lungs. Many salamanders catch prey with their sticky tongues, but can extrude the tongue only slightly, because of a conflict between the respiratory and feeding functions of the hyobranchial apparatus (Wake and Roth 1989). Thus structural coupling of different functions can act as a constraint.

**Key innovations** frequently lift functional constraints. The term "key innovation" (or key adaptation") is used differently by various authors. Usually it refers to an evolutionary change that (1) provide adaptations to one or more new ecological niches or adaptive zones and (2) enables a lineage to diversify greatly (Mayr 1960; Liem 1973). the continuously growing incisors of rodents (the largest order of mammals) are an example. yet another criterion is that the change set in motion the evolution of other, functionally interacting, features (Levinton 1988). The evolution of feathers of sufficient size for flight (as in Archaeopteryx) set the stage for the many other flight-related features of later birds. [...] Two mechanisms by which functional constraints may be lifted are functional divergence of redundant elements and decoupling of functions and structures.