Introduction

What Is a Missing Link?

In colloquial language a "missing link" is generally considered to be a connecting species between higher taxonomic categories, such as between a fish and an amphibian or between an ape and a human. Most people tend to think of a missing link as a single kind of animal, at the exact midpoint between two quite different animal groups. It is sometimes thought of as a special kind of organism that represents a "quantum leap" in evolution. In fact, links between major organismal groups were no different from any evolutionary connection in life's history, except by virtue of what came after them.

Every living organism is a member, at the same time, of a breeding group, a population, and a species. Humans are members of the species *sapiens* in the genus *Homo*. Conventionally this is expressed as the species *Homo sapiens*. The genus is a level that includes related species, all of which presumably evolved from a common ancestor. A species includes only individual organisms, arranged in populations of breeding groups. Genera (the plural of genus) can be grouped into families, families into orders, orders into classes, classes into phyla, and phyla into kingdoms. These represent higher levels, or scales, in a standard organismal classification. Humans appear to have evolved from apes; this represents a link at the family scale — between the Pongidae and Hominidae (if we follow a classification that treats these as separate families; some do not). Both families are in the mammalian order Primates. The link between dinosaurs and modern birds represents a considerably more distant connection. It seems there should be something different about links at these different scales, but it is just an illusion.

Individual living humans have unique family histories, but they eventually blend with other humans as we go back far enough in time. Every human alive today is likely descended from a single human ancestor at some point in the past. So there are links even within the single human species. The history of parental and offspring descent that represents the genealogical tapestry of humans is known by biologists as a *lineage*. Many lineages are known in the fossil record, and some are millions of years old. It is now understood that populations of individuals making up a lineage can change, or evolve, through time. We call this kind of change *phyletic change*, or *phyletic evolution*. So, how does this all bear on the concept of a missing link?

First, it is important to realize that all taxonomic units above the level of the species are artifacts of our need to make order out of the universe. A "genus" is not a real biological unit, nor is a "family." These terms simply ally sets of related species in an ever-enlarging family tree. The names become more inclusive as we progress farther back in time and include more common ancestors and their descendants, until we have created a complete family tree and named, for our own convenience, a variety of descriptive and helpful higher taxonomic categories (Figure I.1). *Thus links, missing or otherwise, can only be individuals.* There is nothing else in nature. We do not look for the link between ancient fishes and modern amphibians (frogs, salamanders, etc.) to be qualitatively any different than the link between apes and humans, despite the fact that the links in which we are interested are at different taxonomic scales. Expressed another way, links include only two categories: the individuals in a lineage (= a species) and the individuals that connect different lineages.

Furthermore, to the extent that lineages change, a missing link is not just a single organism, but all the individuals within the species that change. Thus, we often identify *Archaeopteryx lithographica* as an example of a missing link between early theropods and birds, but there were likely many hundreds or even thousands of individuals with slightly less and slightly more bird-like features in the link from dinosaurs to birds. Some existed within one lineage and others in different species that make up the full connection between dinosaurs and birds. We might believe that there must at least be a *quantitative* difference between links at different taxonomic scales, maybe more species at the higher scales. Perhaps there are more species linking dinosaurs with birds, or fishes with amphibians, than apes with modern humans. But there is no evidence for this of which I am aware, nor any reason why it should be so. Each transition includes individuals within species and must be considered on its own merits, taking place under its own unique environmental conditions. Actually, the number of links one identifies can depend on the way the particular question is phrased. For example, the system defined by the question "What are the links between fishes and modern humans?" obviously includes more links than one defined between fishes and amphibians, for the simple reason that in the former case we are asking a question about two groups that did not directly evolve into one another, but included a series of groups in between.

Evolution is a process designed to facilitate two basic activities in organisms; the consumption of energy and reproduction (leaving genetic material to the next generation). Evolution is opportunistic, and any mechanism or organismal trait that promotes energy consumption and reproduction will be favored. Because the underlying basis of all

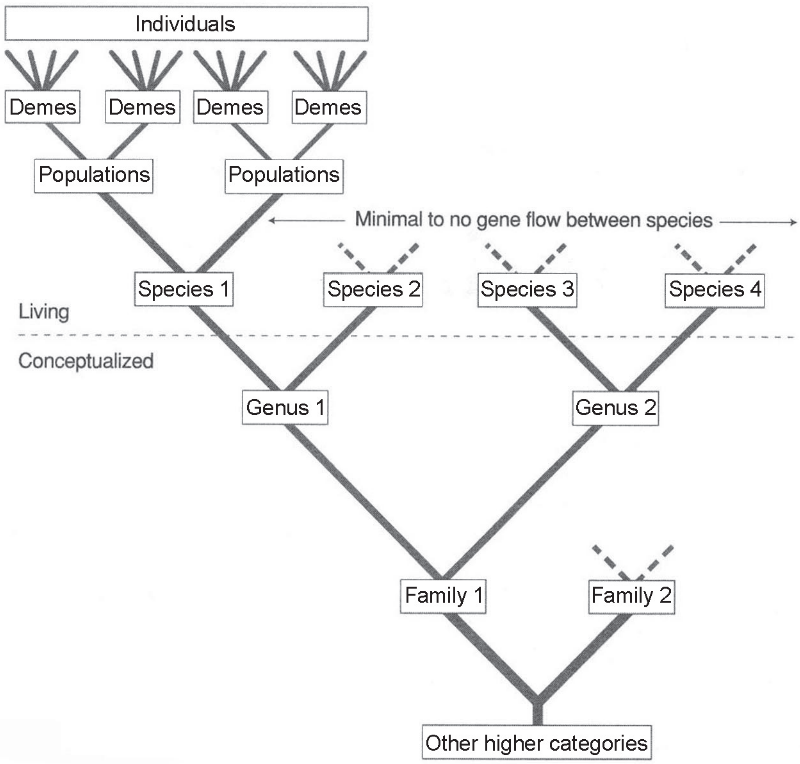

Figure I.1. A genetic/hierarchical organization representing living (above the line) and conceptualized associations. The conceptualized associations, of course, if interpreted correctly and including information from the fossil record, can provide the basis for a classification and a history of genetic connections among related groups. (Courtesy of Jones & Bartlett, Sudbury.)

evolutionary change is genetic, translated to the adult organism through development, in order to understand how organisms change we must understand how heredity and development work. This has not been so easy, and we make new discoveries in these fields regularly. From simple Mendelian inheritance we now have mutations, linkage, pleiotropy, "jumping" genes, polyploidy, introns and exons, and homeotic complexes. Haeckel's "ontogeny recapitulates phylogeny" has been supplanted with a robust developmental theory incorporating the expression of D'Arcy Thompson's and Thomas Henry Huxley's allometric responses of body form through *Hox* regulatory genes and embryonic enzyme gradients. We now have a pretty good idea of how major types of organismic body form, termed life's *disparity*, came about. Documenting the appearance of these changes is another matter entirely, for primary evidence of evolutionary change must come from the fossil record, which is very imperfect. But paleontology, too, makes progress, and we now have many dense fossil histories, often spanning millions of years, recording change through time (Darwin's "descent with modification"). Imprints of feathers in dinosaurs tell us that many reptilian groups were experimenting with this mode of thermoregulation, although feathered flight seems to have developed in only one group. But we still have much to learn. We know that some structural arrangements have been remarkably stable in animal groups, whereas other features show continuous, albeit sometimes jerky, change. Because the fossil record is frustratingly fragmentary, we do not yet quite know what this means. Some paleontologists argue that most significant morphological (anatomical) change originates rapidly in species, followed by little change, whereas others suspect this apparent stability is an illusion created by incomplete sampling, or perhaps by the nature of the preserved parts. After all, why would anatomy critical to the survival of an organism change regularly? These questions are the sign of a healthy science, operating properly and always self-regulating, assuring that more links will be discovered and that our understanding of them will continue to improve. Missing links, then, are all the individuals in the one great tree of life that we have not yet found as fossils. We won't find them all, but every day we add a few more and through this process slowly reconstruct our amazingly improbable history.