



Population thinking and tree thinking in systematics

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Two new modes of thinking have spread through systematics in the twentieth century. Both have deep historical roots, but they have been widely accepted only during this century. Population thinking overtook the field in the early part of the century, culminating in the full development of population systematics in the 1930s and 1940s, and the subsequent growth of the entire field of population biology. Population thinking rejects the idea that each species has a natural type (as the earlier essentialist view had assumed), and instead sees every species as a varying population of interbreeding individuals. Tree thinking has spread through the field since the 1960s with the development of phylogenetic systematics. Tree thinking recognizes that species are not independent replicates within a class (as earlier group thinkers had tended to see them), but are instead interconnected parts of an evolutionary tree. It lays emphasis on the explanation of evolutionary events in the context of a tree, rather than on the states exhibited by collections of species, and it sees evolutionary history as a story of divergence rather than a story of development. Just as population thinking gave rise to the new field of population biology, so tree thinking is giving rise to the new field of phylogenetic biology. © 1998 The Norwegian Academy of Science and Letters

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Introduction

The history of systematics in the twentieth century can be broadly divided into two periods. The first is the period of population systematics, which began at the turn of the century and flourished especially through the years of the Modern Synthesis of the 1930s and 1940s and beyond (Mayr & Provine 1980). The second period is the period of phylogenetic systematics which began during the 1960s and which continues to flourish today (de Queiroz 1997).

During the period of population systematics much of the work of the systematics community was directed toward studies of geographical variation, speciation, and microevolutionary processes, and a great many practical and theoretical advances were made in all of these areas. The theory of allopatric speciation was comprehensively developed, especially for vertebrates; large series of specimens for the study of geographical variation were assembled in museums; the application of statistical techniques became widespread; and studies of cytological and biochemical variation began to be added to traditional studies of gross anatomical variation.

The period of phylogenetic systematics, beginning in the 1960s, has seen a shift in emphasis toward larger questions of evolutionary history and the structure of the evolutionary tree, and, just as in the earlier period, this newer phylogenetic era has seen and continues to see many advances in systematic theory and practice. The development of all the tools and concepts of cladistic analysis has been the most important advance of this period; the distinction between ancestral and derived character states;

the application of computational techniques for reconstructing trees; the increasing availability of data on molecular anatomy to supplement the data of gross anatomy; and more recently the application of phylogenetic information to problems in many other biological fields from ecology to physiology to embryology to behavior.

The distinction between the two periods of population systematics and phylogenetic systematics is not sharp, of course, and there continues to be much fine work done today in population systematics, just as there were important contributions to the study of phylogeny before the 1960s. But the general distinction between these two periods is real, and it captures a variety of important practical, theoretical, and disciplinary developments in the history of twentieth-century systematics.

At the broadest level, beyond the development of particular techniques or concepts, each of these two periods may be characterized by the introduction and spread of new ways of thinking about systematic and evolutionary problems, ways of thinking that correspond in scope to the scientific "themata" described by Holton (1973) for the physical sciences. Distinctive of the period of population systematics was the spread of what is commonly called "population thinking" (Mayr 1959, 1975), and distinctive of the period of phylogenetic systematics has been the spread of what may be called "tree thinking" (O'Hara 1988). My aim here is to outline the components of tree thinking, as a way of understanding some of the larger changes that have taken place since the 1960s. Before we consider tree thinking, however, let us look at the idea of population thinking by way of comparison.

Population thinking

The term "population thinking" was coined by Ernst Mayr in 1959. In coining the term Mayr did not claim to be describing something new; rather he intended to capture with the term a way of thinking that had swept through systematics and evolutionary biology generally in the first half of the twentieth century. (Mayr in fact traces the idea of population thinking back to the early 1800s, but I think it is fair to say that its hold within systematics did not become widespread until early in the twentieth century.)

To understand the idea of population thinking it is necessary to contrast it with the mode of thought it replaced, which Mayr calls typology or essentialism. In simple terms, an essentialist sees individual variation within a species as *error*. An essentialist would in no way deny the existence of individual variation; it obviously does exist. But for an essentialist every species has a natural form, a true type, and individual variation within that species represents accidental deviation from that true type caused by external environmental influences. In the absence of external influences that cause individuals to deviate from their true type all individuals of a species would be forever the same, because each species' type remains fixed through time.

The French naturalist Buffon expressed the essentialist view well in his *Histoire Naturelle* in 1753 (Sloan 1987: 121):

"There is, in nature, a general prototype in each species upon which each individual is modeled, but which seems, in realizing itself, to be altered or perfected by circumstances. So that, relative to certain characteristics, there is an unusual variation in the appearance in the succession of individuals, and at the same time a constancy in the species as a whole which appears remarkable. The first animal, the first horse, for example, has been the external model and the internal mold upon which all horses which have ever been born, all those which now exist, and all which will arise, have been formed. But this model, which we know only by its copies, has been able to be altered or perfected in the communication and multiplication of its form. The original impression subsists in its entirety in each individual, but although there might be millions of them, none of these individuals is similar in entirety to any other, nor, by implication, to the impressing model."

Elliott Sober (1980, 1994) has provided a very thorough examination of the idea of essentialism as it applies to species, drawing on what he calls the "natural state model" of Aristotle, and I recommend his work to all who are interested in this subject. Sober's discussion can be fruitfully compared with those of Toulmin (1961) and Kuhn (1977) on the conceptual framework of early chemistry and physics.

In contrast to the essentialist, the population thinker rejects entirely the idea that species have "types" or "natural states". Individual variation within a species is not deviation from a natural state under the influence of external forces, a natural state to which the species will return if the forces are removed. Rather, the range of individual variation within a species is the result of ongoing processes of mutation and recombination, the production of phenotypes in the available environments, and then the selection of those phenotypes from generation to generation. Nothing remains invariant across time because new individuals are not produced from some permanent "internal mold", but instead are produced directly from their

parents, and they incorporate new heritable variations in each generation. This allows species to "depart indefinitely" (Wallace 1858) from their ancestors, and in so doing it dissolves the idea of an enduring species type altogether.

In passing it is worthwhile to note that even though population thinking has by now thoroughly permeated systematics and evolutionary biology generally, there are other biological fields, most notably medicine, where it has made little headway. Medical notions of health and disease have strong essentialist overtones, and as medicine has come to focus more on the genetic traits of individuals (as opposed to external agents of infection) there is a tendency on the part of medical practitioners to pathologize normal variation in human populations, and in so doing to resurrect the idea of a "natural type" for *Homo sapiens*, an idea long ago rejected by evolutionary biology.

Tree thinking

If the spread of population thinking characterized the period of population systematics, then the spread of what we may call "tree thinking" (O'Hara 1988; Maddison & Maddison 1989; de Queiroz 1992; Doyle & Donoghue 1993; Wake 1994) has characterised the period of phylogenetic systematics. Tree thinking is in no sense a successor to population thinking, which is just as important today as it has ever been. Tree thinking is simply the phylogenetic counterpart to population thinking, and like population thinking it has brought a more completely evolutionary perspective to systematics (de Queiroz 1988, 1992, 1997; O'Hara 1988, 1992, 1996).

What constitutes tree thinking, and more especially what constitutes the absence of tree thinking? If population thinking is contrasted with essentialism, then with what should we contrast tree thinking?

Tree thinking may be contrasted with two other ways of thinking about systematics and large-scale evolutionary phenomena. The first of these I call "group thinking," and the second I call "developmental thinking." Let us consider each in turn, and consider how tree thinking differs from them.

Group thinking has been a long-standing way of thinking in systematics, and group thinking equates "systematics" with "classification." Just as we can classify many kinds of objects—landforms, books, minerals, stars—so in the same way can we classify species, says the group thinker. Group thinking in systematics (and classificatory thinking in general) treats each member of a particular group as an independent replicate, and this is key. Each neutron star, for example, is an instance of the class of neutron stars, an independent replicate that can teach us something about the nature of neutron stars as a class. Each drumlin is an independent replicate of the landform group "drumlins" and can give us insight into the common causes of drumlins—the common processes responsible for the formation of all drumlins. The goal is to abstract from the replicate instances a general picture that will describe all members of the class and account for their existence.

Group thinking of this kind—seeing members of a group as replicate instances—is quite appropriate for many kinds

of scientific inquiry, such as the study of stars or landforms, but it breaks down when we try to apply it to species. It breaks down for the fundamental reason that species are *not* independent replicates: they are parts of a connected tree of ancestry and descent, and they *inherit* most of their attributes in a way that stars and landforms, for example, do not.

Tree thinking, in contrast to group thinking, considers species in a phylogenetic context, not as independent replicates but as parts of a single phylogenetic tree. If we seek to understand common causes acting in evolution then the replicates we need to examine are not species, but the evolutionary *events* that are of interest in a particular study, and this can only be done by plotting those events on a tree. If we are interested in why 10 species in a larger group exhibit a particular trait (say a trait that is correlated with the occupation of a certain environment) then we must first ask, in the context of a tree, whether this situation represents 10 independent originations of the trait, or eight with two subsequent speciations, or five, or three, or perhaps only one independent origination event with the 10 separate species all retaining the trait through inheritance. These questions can only be answered in the context of a tree.

The focus on explaining evolutionary events rather than the states of supposedly replicate species, and on determining where the events occur on a phylogeny, is central to tree thinking. This new phylogenetic orientation has in recent years opened the door to a whole range of important studies of adaptation, ecology, physiology, and other areas that have long been approached from ahistorical, synchronic perspectives (Fink 1982; Lauder 1982; Felsenstein 1985; Huey 1987; Coddington 1988; Ronquist & Nylin 1990; Wanntorp *et al.* 1990; Brooks & McLennan 1991; Harvey & Pagel 1991; Vane-Wright *et al.* 1991; Stiassny 1992).

Although tree thinking as I have described it is an aspect of systematic biology, the idea of tree thinking isn't necessarily tied to living things—all it requires is descent and inheritance. A fascinating inorganic example of tree thinking can be found in a recent paper on the motion of asteroids (Milani & Farinella 1994), an example which makes use of many of the same ideas I have just outlined. In examining the orbits of asteroids it is often possible to identify groups of asteroids that have motion characteristics in common. One might be tempted to assume that there is something about the composition of this group of

asteroids or about their location that causes this common "phenotype" (if you will) to exist. But Milani and Farinella have shown that these asteroids do not share certain characteristics of motion because of some common set of external forces acting on them; they share common patterns of motion because they literally inherited that motion from an ancestral asteroid of which they once were parts and which subsequently broke up into the pieces we now see. The asteroids in this group are not independent replicates that constitute a class, but rather are parts of a tree of inheritance and their common characteristics can be explained by reference to their shared history.

There is another aspect of group thinking that tree thinking is supplanting, and that is the traditional inclination to regard taxa of equal rank within certain large groups as equivalent and comparable in some sense. (This is a higher level version of the species-as-replicates perspective.) An example concerns the traditional orders of birds, the largest of which is the Passeriformes which by itself contains about half of all bird species, with the other 30 or so traditional orders containing all the rest. The ornithologist Robert Raikow wrote a paper called "*Why are there so many kinds of passerine birds?*" (1986) in which he argued in part that this question is misplaced because it assumes that the various "orders" of birds are in some way comparable groups when in fact they are not. And further, even if we frame a more precise comparison between the Passeriformes and their sister clade, and ask why each of these two groups differs in species richness, here the validity of the question will depend upon the internal structure of the passeriform tree (Fig. 1). Framing these questions in the context of a tree is essential if progress is to be made, a point that some of Raikow's commentators did not appear to fully grasp (Raikow 1988).

Let us now turn from group thinking as contrasted with tree thinking, to what may be called "developmental thinking" and contrast this also with tree thinking.

By "developmental thinking" I mean thinking that sees evolutionary history as a story of individual development or unfolding—a story of "evolution" in the original sense of the word. There is a long-standing tradition in evolutionary writing of describing the course of evolution as a developmental course running from monad to man. This tradition pre-dates evolution certainly; the evolutionary version is really a temporalization of the ancient idea of the Chain of Being (Lovejoy 1936).

Evolutionary histories of the developmental type don't

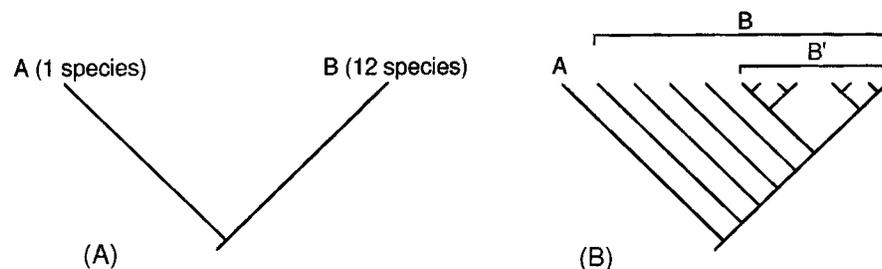


Fig. 1. Two sister taxa differing in species richness (A). One might be inclined to assume that the speciose taxon possesses a "key innovation" that has caused it to speciate at a greater rate than its sister taxon. Such an assumption may or may not be warranted depending upon the internal structure of the speciose clade. If the internal structure is as shown in (B) then it is unlikely that clade B possesses any special innovation, although its sub-clade B' may.

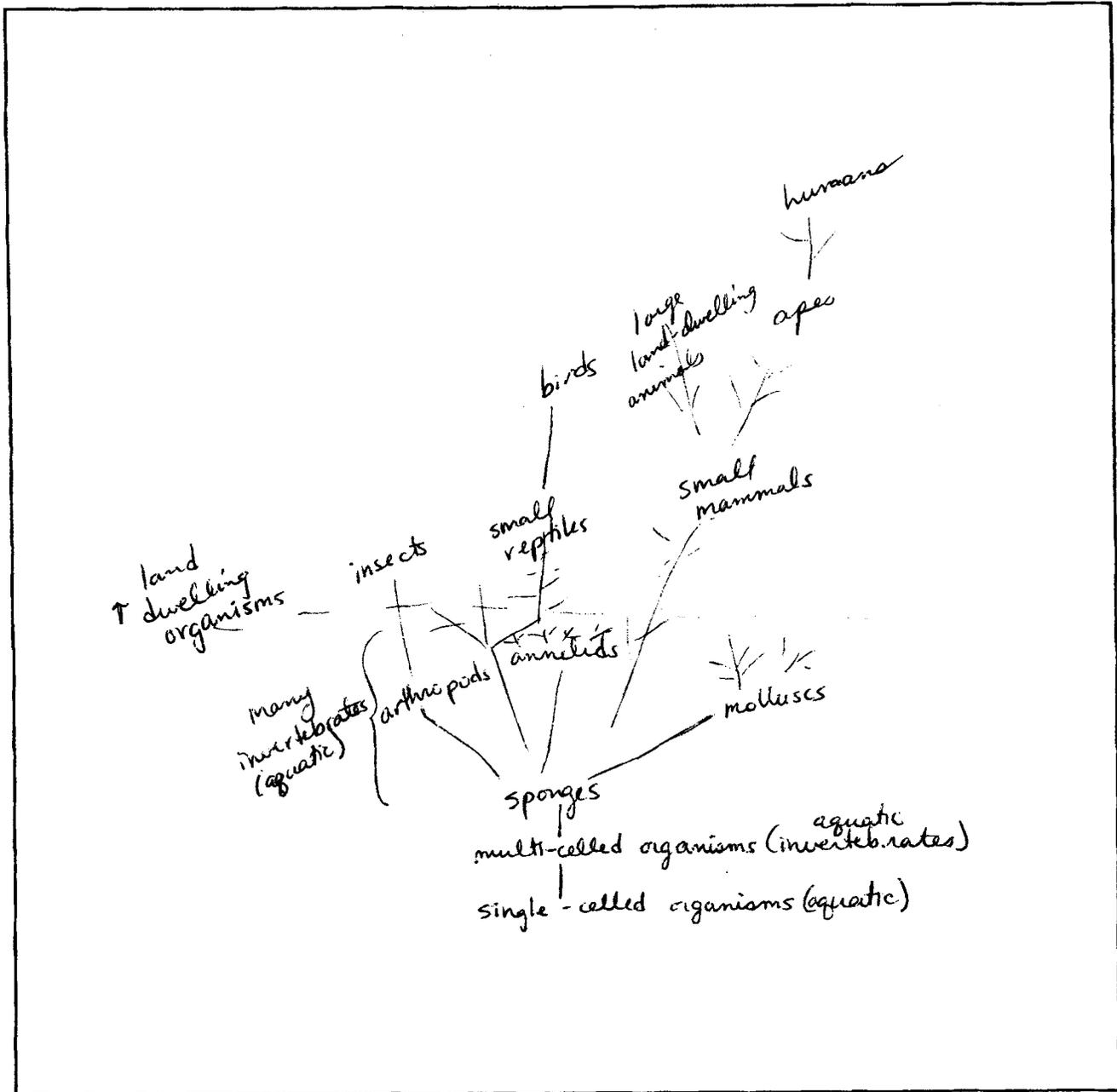


Fig. 2. An evolutionary tree drawn by an undergraduate biology student at the University of Wisconsin-Madison. At the beginning of a course each student was asked to "sketch an evolutionary tree of life, and label as many branches as you can. Don't worry if your tree is not perfect or if you can't remember technical terminology; this is not a graded exercise, and you should not even put your name on the page." Most trees the students produced have as their longest branches the ones leading humans or to mammals or vertebrates generally.

narrate a tree—a branching history—they select one important endpoint (usually us) and then trace up from the root through the tree to that endpoint, employing a variety of narrative and nomenclatural devices that minimize the branching aspect of evolution. In other papers (O'Hara 1988, 1992, 1993) I have discussed in detail the narrative and graphical devices that have traditionally been used to minimize the branching aspect of evolutionary history and to thereby create a linear, developmental aspect.

Tree thinking, in contrast to this sort of developmental thinking, emphasizes the divergent character of evolutionary history and the complexity and irregularity of the evolutionary tree. I'm sorry to say, however, that while many contemporary systematists no longer think of evolution as a developmental story and no longer draw diagrams that show humans as the pinnacle of life, most of the general public and most of our students still do. A survey of beginning biology students' understanding of evolutionary history almost invariably produces images of the developmental type with a long main line reaching to vertebrates, mammals, or humans (Fig. 2). One of the main objectives of the systematics community for the next decade should be the preparation of educational materials for beginning students to teach them to become tree thinkers (O'Hara 1994). Just as beginning students in geography need to be taught how to read maps, so beginning students in biology should be taught how to read trees and to understand what trees communicate (Figs 3 and 4). One effective method of jarring students out of the traditional pattern of developmental thinking is to show them trees that are purposely drawn from a different evolutionary perspective (Fig. 5), although few such trees are now available.

Systematics and palaeontology

When William Whewell, the nineteenth-century polymath, compiled his comprehensive survey of all the sciences (Whewell 1847), he placed systematic zoology and systematic botany along with mineralogy in the category "classificatory sciences." Elsewhere in his survey, however,

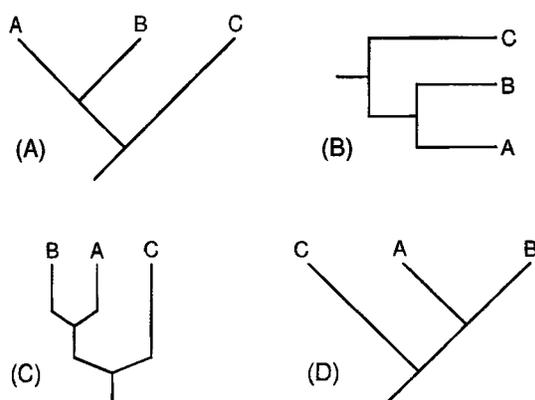


Fig. 3. A phylogeny of three taxa shown in four different graphical styles (A–D), from O'Hara (1994: 14). All four of these diagrams convey exactly the same information about the three taxa. Non-specialists and beginning biology students need to be taught to read modern evolutionary trees just as beginning students of geography need to be taught to read maps.

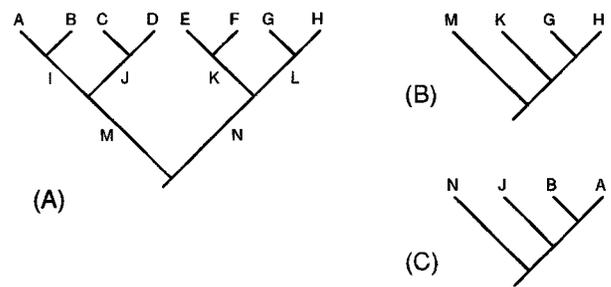


Fig. 4. A phylogeny of eight taxa (A), and two simplified versions of that phylogeny (B–C), from O'Hara (1994: 14). If students and non-specialists are to become tree thinkers they must learn to recognize how trees can be differentially simplified (or differentially resolved) to show the details of particular branches.

Whewell created a new class of sciences which he called by the awkward name "palaeontological sciences"—the sciences of history and historical causation. Into this new category Whewell put such seemingly disparate fields as geology and comparative philology, fields he saw as united by their common aim of historical reconstruction (O'Hara 1996). Charles Lyell's geological work, which was new at the time, helped to shape Whewell's characterization of the palaeontological sciences. When Charles Darwin began to work seriously on the species question he didn't take as his model the approaches of the classificatory sciences; he took as his model the palaeontological science of Lyell. Indeed, the *Origin of Species* is almost a casebook of the palaeontological principles that Whewell had outlined. Darwin in effect took systematic biology out of the classificatory sciences and placed it squarely among the palaeontological sciences, and in so doing he set for us a range of historical problems the full implications of which are still being discovered today (de Queiroz 1988; O'Hara 1988, 1992, 1993; de Queiroz & Gauthier 1992, 1994; Williams 1992).

"As buds give rise by growth to fresh buds," wrote Darwin in one of his more literary passages (1859: 130), "and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications." The tree of life has proven to be a subtle construct, more subtle perhaps than Darwin suspected. But the spread of tree thinking throughout systematics in the last 30 years, and its more recent spread from systematics to other fields, has brought a new clarity to our understanding of the tree of life, an idea that is fundamental to all of evolutionary biology.

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