Evolutionary History and the Species Problem[1]

ROBERT J. O'HARA

Center for Critical Inquiry in the Liberal Arts and Department of Biology,
University of North Carolina at Greensboro, Greensboro, North Carolina 27412-5001

SYNOPSIS. In the last thirty years systematics has transformed itself from a discipline concerned with classification into a discipline concerned with reconstructing the evolutionary history of life. This transformation has been driven by cladistic analysis, a set of techniques for reconstructing evolutionary trees. Long interested in the large-scale structure of evolutionary history, cladistically oriented systematists have recently begun to apply "tree thinking" to problems near the species level.

In any local ("non-dimensional") situation, species are usually well-defined, but across space and time the grouping of organisms into species is often problematic. Three views of species are in common use today: the biological species concept, the evolutionary species concept, and the phylogenetic species concept. Each of these has strengths and weaknesses, but no matter which is applied, exact counts of the number of species in any extended area will always be ambiguous no matter how much factual information is available. This ambiguity arises because evolution is a historical process, and the grouping of organisms into species always depends to some extent upon expectations of the future behavior of those organisms and their descendants, expectations that cannot be evaluated in the present. The existence and special character of the species problem is itself one of the central pieces of evidence for the fact of evolution.

INTRODUCTION

The word "biodiversity" has spread more rapidly through the scientific community and the popular culture in the last few years than probably any term ever has in the history of science. It did not appear in the 1989 edition of the *Oxford English Dictionary,* and yet by 1992 "biodiversity" was on the lips of scientists, celebrities, and politicians from Ed Wilson to George Bush. Within the scientific community, the term "biodiversity" has come to stand for a mixture of descriptive systematics—what systematists usually call alpha-level systematics (Mayr *et al.,* 1953)—and applied ecology, directed to the problems of biological conservation. That it is an important field goes without saying, and I cannot argue its importance any better than those who have done so

already (National Research Council, 1992; Wilson, 1992).

The role of ecology within biodiversity studies is well known, and the success of nearly all conservation programs depends upon accurate ecological information about the species for which protection is being sought. Less well known is the role of systematics within biodiversity studies, and of the many books and symposia on biodiversity which have appeared in recent years, only one has specially focused on systematics (Eldredge, 1992). In a certain respect this is understandable because the concern of most people within the biodiversity movement is an applied concern: how should we act in order to preserve the greatest part of the earth's natural diversity. But in order to preserve diversity effectively we must first understand that diversity, and understanding the diversity of life—its extent, its distribution, and especially its history—is the object of systematics.

Unfortunately for those who must teach the subject, systematics has been in the midst

of a deep conceptual revolution for the last thirty years, a revolution driven by cladistic analysis, the set of techniques now used for the reconstruction of evolutionary trees. Because of the controversy which has accompanied the development of cladistic analysis, systematics has developed a reputation for combativeness and confusion which is only partly undeserved (Hull, 1988), and which has weakened its intellectual and institutional effectiveness as a discipline. My object in this essay is to review "the species problem" in systematics. The species problem is the observation, made by systematists at least as far back as the early 1800s, that it is often difficult to decide whether two populations that differ slightly from one another, and are geographically separate, ought to be regarded as separate species, or instead as two different varieties (subspecies) of the same species. Because systematics has changed so much in the last thirty years, however, it is not possible to review any part of the field—such as the species problem—in isolation from the whole. I will begin, therefore, with a sketch of the outlines of contemporary systematics in general, and then turn to the species problem in particular. In keeping with the aims of the *Science as a Way of Knowing* symposia, what I present here is primarily a survey, rather than an original contribution. I will however conclude with some argument for my own view of the species problem, which I regard not so much as a solution to it, as a dissolution of it. It is my view that the historical approach to systematics which has been developed over the last thirty years shows that the species problem is not something we need to solve, but rather something that we need to get over. Research that depends upon exact counting of species either across space or through time is probably misconceived, because the historical nature of the evolutionary process imparts an inescapable indeterminateness to the notion of "species."

SYSTEMATICS TODAY: TREES AND HISTORY

The nature of the cladistic revolution

A traditional view of systematics equates it with classification: the terms "systematics" and "classification" (and also "taxonomy" which is more or less a synonym of "classification") have often been used interchangeably, and systematists are commonly thought of as the people who classify animals and plants. But if we examine the history of systematics we can often find these two activities distinguished, with the term classification being applied to the *grouping* of organisms into classes, and the term systematics being applied to the *arrangement* of organisms into some larger whole. This larger whole was often called "the natural system," whence the name "systematics" (O'Hara, 1988*b*, 1991, 1993). The distinction between classifications and systems or arrangements may be compared, on the one hand, to a listing of the counties in a state and the towns within each county, and on the other to a map of the state which arranges the towns and counties in their proper positions relative to one another. Darwin (1859, pp. 420–423) and Wallace (1856) both discussed the distinction between classifications and arrangements, and a number of contemporary systematists have drawn attention to it as well (Griffiths, 1974; de Queiroz, 1988). It was characteristic of systematists who discussed arrangements and systems, as opposed to classifications, to draw diagrams of their research results, and beginning with Darwin these diagrams took the form of evolutionary trees. The only illustration in the *Origin of Species* is Darwin's evolutionary tree, showing his understanding of the notion of the natural system.

The cladistics revolution in systematics in the past thirty years is about these evolutionary trees: how to reconstruct them and how to understand what they represent. It must be remembered that although Darwin did publish a hypothetical evolutionary tree, he offered no prescription for how to reconstruct such a tree for real taxa. In the decades immediately following the publication of the *Origin* considerable attention was given by systematists to the theoretical issues surrounding the reconstruction of evolutionary trees (O'Hara, 1988*b*, 1991; Craw, 1992), but no consensus was reached on how this should be done, and many conceptual issues remained unresolved when interest in phylogenetic issues declined around 1900.
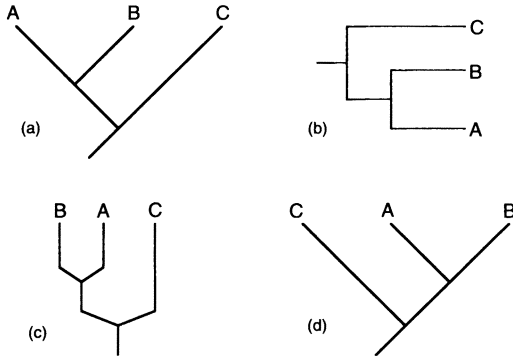
FIG. 1. The evolutionary history of three taxa, A, B, and C. All four of these diagrams are identical in content, differing only in graphical style and arbitrary rotation of branches. A and B taken together with their ancestor make up a clade, and that clade is sister to C. A, B, and C taken together with their most recent common ancestor also make up a clade.
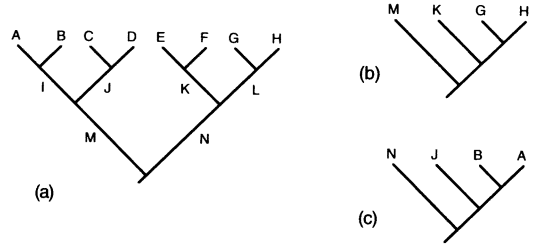

FIG. 2. An evolutionary tree of eight taxa A–H (a), and two of the possible simplified versions of that tree (b–c). The apparent shape of an evolutionary tree—whether balanced or comb-like—may not necessarily reflect anything in particular about evolutionary processes: it may just be the result of the differential simplification (or conversely, differential resolution) of a more complex history.

Interest in phylogeny remained low during the period of the Evolutionary Synthesis of the 1930s and 1940s (Mayr and Provine, 1980), but in the 1950s and 1960s some of the issues that had not been resolved in the late 1800s began to surface again. In particular it became clear that many traditional classifications did not reflect current understanding of phylogeny very well, and in the context of this, owing to the work of Hennig (1966) and others, a new understanding of the relationship between evolutionary trees and character data—the observed similarities and differences among organisms—was developed. This new understanding allowed systematists to reconstruct trees in a consistent and theoretically well-grounded manner for the first time in the history of their discipline.

During the early years of cladistics, in the 1960s and 1970s, the mismatch between cladistically reconstructed phylogenies and traditional classifications gave rise to a great deal of controversy over the relation between trees and classifications, but this controversy has today almost completely withered away. This is because more and more systematists have come to realize that in the evolutionary world the notion of classification as an object of systematics can be largely dispensed with. The point of systematics in an evolutionary world ought not to be the construction of classes, but the reconstruction of history (de Queiroz, 1988; O'Hara, 1988a), and the analogy of systematics to classification is in fact a relict of the pre-evolutionary period, when living diversity was viewed ahistorically. Because I view contemporary systematics in this way, I must with regret dissent from earlier titles in the Science as a Way of Knowing series (e.g., Moore, 1991), which presented classification as the principal object of systematics.

The actual methods of cladistic analysis—the methods now used for reconstructing evolutionary trees—cannot be presented in this short space, but introductions to cladistic analysis, some of them suitable for use with students, are becoming more common and can provide additional information (Felsenstein, 1988; Sober, 1988; Swofford and Olsen, 1990; Brooks and McLennan, 1991, pp. 24–68; Maddison in Mayr and Ashlock, 1991, pp. 274–321; Wiley et al., 1991). Particularly promising for teaching is the computer program MacClade (Maddison and Maddison, 1989, 1992), which permits interactive study of evolutionary trees, and which comes with an excellent introductory text.

How to read a tree

The most important thing to understand about evolutionary trees is that they are *historical* representations: they are *trees of history.* As such, they must not be confused with other kinds of branching diagrams, like

sentence diagrams or directory trees for computer disks, which are not historical, genealogical diagrams of descent, and are of no concern to us. Just as one needs a bit of training to read geographical maps correctly, so also one needs some elementary training to read contemporary evolutionary trees correctly, and confusion often arises among nonsystematists because of a lack of what might be called tree reading skills. Let us consider some elementary diagrams that will illustrate representational principles. It should be noted that these principles apply only to modern cladistic diagrams, and not to diagrams from the earlier history of systematics, which can often be much more difficult to interpret (O'Hara, 1991).

Figure 1a shows the historical relationships of three *terminal taxa*, A, B, and C. This diagram says that A and B have an ancestor in common, represented by the node joining their two branches, that neither of them shares with C, and thus that A and B are more closely related to one another than either is to C. Coordinate branches are called *sister taxa* or *sister clades, clade* being the term for a whole branch of the evolutionary tree. If you were to grab hold of the tree at any point, and cut immediately below your grip—below in the sense of toward the root—the chunk of the tree in your hand would by definition be a clade. In this figure A and B taken together with their ancestor constitute a clade, and that clade is sister to C. A, B, and C as a whole, taken together with their most recent common ancestor, also constitute a clade. Trees often vary stylistically from one author to another, so it is important to understand that *all of the trees shown in Figure 1 are identical in content*: they all illustrate the same historical relationships among the same taxa. Note in particular that branches may be rotated around a node without in any way changing the meaning of a diagram.

The terminal taxa in an evolutionary tree—the end branches—may be individual species (to which we will turn in a moment), but they may also be large complex clades (Fig. 2). This is important to understand because readers often assume that from the shape of a clade—whether it is comb-like, for example (Fig. 2b, c), or more evenly balanced (Fig. 2a)—some conclusion can be drawn about the evolutionary processes that have been at work in the history of that clade. Clade shape *may* tell us something about evolutionary processes, but it may also be entirely an artifact of the way in which a more detailed history was simplified (O'Hara, 1992, 1993).

The importance of the cladistic revolution

Just as the Evolutionary Synthesis of the 1930s and 1940s brought us "population thinking" (Mayr, 1976, pp. 26–29), the cladistic revolution has brought us "tree thinking" (O'Hara, 1988*a*), a way of seeing natural diversity that is based not on classifications and groups but on trees and events in evolutionary time. The historical information supplied by cladistic analysis is proving essential not only to biology generally, but also to nearly every specialty within biology, because in order to explain the similarities and differences among organisms we must first understand the *evolutionary chronicle*—the sequence in which those similarities and differences arose (Fink, 1982; Lauder, 1982; Felsenstein, 1985; Huey, 1987; Coddington, 1988; O'Hara, 1988*a*; Lang, 1990; Burghardt and Gittleman, 1990; Ronquist and Nylin, 1990; Wanntorp *et al.*, 1990; Baum and Larson, 1991; Brooks and McLennan, 1991; Harvey and Pagel, 1991). The importance of phylogenetic information to biodiversity studies is also becoming apparent (Vane-Wright *et al.*, 1991; Stiassny, 1992).

Another consequence of the cladistic revolution—one that is only beginning to be felt—is the abandonment of the ancient concept of taxonomic rank (de Queiroz and Gauthier, 1990, 1992), which is properly understood not as an attribute of nature, but as an artifact of our way of seeing nature (Atran, 1990; O'Hara, 1992). Studies which depend upon actual counts of taxa of a particular rank—on the number of families or genera in a place or over a period of time, for example—and which cannot be recast without these ranks, are probably misconceived. Disputes about how many kingdoms of organisms exist (Margulis and Schwartz, 1988) are similarly meaningless.

What we ought to be disputing, and teaching to our students, are trees, not ranked classifications.

WHAT THE SPECIES PROBLEM IS AND WHAT IT IS NOT

Counting the number of species that occur in an area would seem to be a simple matter. In any particular local situation it usually is. The number of species of birds breeding in Greensboro, North Carolina, can be determined with very little ambiguity by observation, because at any particular location most organisms are segregated into populations within which breeding occurs, but among which it does not. This notion of reproductively isolated populations in a nondimensional situation—at one place and time—is known as the species concept of the local naturalist (Mayr, 1976, p. 503), and it is not problematic. Errors in this sort of counting arise only from failure of observation: counts of bird species on the island of Maui made in the 1960s were in error because at that time the existence of the Poo-uli, *Melamprosops phaeosoma* (Casey and Jacobi, 1974), which lives on the slopes of Haleakala, was utterly unknown.

But as soon as one tries to extend the local naturalist's concept of species as reproductively isolated communities to multidimensional situations—across space and through time—difficulties arise. The Blue Jays (*Cyanocitta cristata*) in North Carolina do not breed with the Red-winged Blackbirds (*Agelaius phoeniceus*) in North Carolina, and thus the two are clearly separate species. But the Blue Jays in North Carolina do not breed with the Blue Jays in Wisconsin, either. Are these two collections of individuals separate species?

Blue Jays do not happen to vary much across their geographical range, so I doubt that anyone would be inclined to call the North Carolina and Wisconsin individuals members of two separate species. But this comparative lack of geographical variation is not characteristic of all organisms. If we ask how many species of birds breed on the Hawaiian Islands as a whole, rather than just on the single island of Maui, for example, we must decide how to count the *Tele-*

spyza finches on Laysan and Nihoa. Are they slightly different forms of the same species (*T. cantans*), as some ornithologists have said, or are they two separate species (*T. cantans* and *T. ultima*), as others have said? *If there is no natural situation in which two forms come into contact in the present then it may be impossible to answer this question with certainty.* It is important to understand that *this ambiguity is not the result of lack of knowledge*: no matter how much we may learn about the birds in question, the ambiguity may remain, because it is not possible to draw "any clear distinction between individual differences and slight varieties; or between more plainly marked varieties and sub-species, and species" (Darwin, 1859, p. 469). This is what is meant by "the species problem." As a result of the species problem, *counts of the number of species in any large geographic area,* such as the United States, or Brazil, or the Hawaiian Islands, *will always involve a measure of ambiguity,* even when extensive factual information is available about individual morphology and distribution.

VIEWS OF SPECIES, OLD AND NEW

The ambiguity that surrounds the notion of "species" was recognized early in the history of systematics. While some systematists believed that "at the beginning to the world, there was created only one single sexual pair of every species of living things" (Linné, 1781, p. 75), the problems of geographical variation and disjunct distributions surfaced quickly (Browne, 1983), and "as long ago as 1747, such facts led Gmelin to conclude that the same species must have been independently created at several distinct points" (Darwin, 1859, p. 365). The complex early history of species concepts has been reviewed by Mayr (1982), Beatty (1985), Atran (1987), and Stevens (1992).

In our time three different views of what species are predominate. These are the biological species concept, the evolutionary species concept, and the phylogenetic species concept. Each of these species concepts has strengths and weaknesses, and each emphasizes slightly different aspects of the evolutionary process. A recent anthology

edited by Ereshefsky (1992) helpfully brings together much of the original literature on these concepts.

The *biological species concept,* developed in the 1930s and 1940s, is probably the most widespread of the three. Under the biological species concept, "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr, 1940). Slight variations in the wording of this definition have appeared from time to time. Paterson has recently argued (1985) that the biological species concept over-emphasizes reproductive isolation among populations at the expense of internal cohesion within populations—although in a certain respect these are two sides of the same coin—and has proposed a "recognition" species concept, closely related to the biological species concept.

One area of criticism of the biological species concept has focused on the notion of potential interbreeding: how can one know whether two allopatric populations have the potential to interbreed under natural conditions, when those natural conditions do not in fact exist? The short answer is that one cannot. (Recall the case of the Laysan and Nihoa *Telespyza.*) The word "potentially" was dropped from some later versions of the biological species concept in response to this criticism, but the notion of potential ability to interbreed is still implicit in the biological species concept: the Blue Jays in North Carolina do not in fact interbreed with Blue Jays in Wisconsin today (no population is instantaneously panmictic), but we include them all in the same biological species because we assume they have the potential to do so.

The *evolutionary species concept* was originally proposed by the paleontologist G. G. Simpson (1961), and it was intended to emphasize the continuity of populations through evolutionary time. According to Simpson, an "evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies." Simpson's definition was slightly modified by Wiley in 1978: "A species is a single lineage of ancestral

descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." The evolutionary species concept places more emphasis on the time dimension than does the biological species concept, but its critics have pointed to expressions like "evolutionary tendencies" and "historical fate" as being vague and not subject to observational test.

The other commonly advocated species concept today is the *phylogenetic species concept* (Cracraft, 1983): "A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent." Nixon and Wheeler (1990) have proposed a slightly modified version of this definition under which a species is "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals." Critics of the phylogenetic species concept point to, among other things, the lack of any limit to diagnosability: if one tries hard enough, characters can be found to diagnose virtually any population, indeed almost any individual organism, especially if molecular techniques are used. The practical effect of the phylogenetic species concept is to greatly increase the number of species in those taxa to which it is applied: using the biological species concept, Mayr (1962) recognized 40 species of Australasian birds-of-paradise (Paradisaeidae), whereas Cracraft (1992) recognized 90 species. It must be emphasized that this difference is *not* the result of the discovery of unknown birds—it is the result of how the known variation is partitioned into species.

HISTORY AND THE DISSOLUTION OF THE SPECIES PROBLEM, OR, TREES UP CLOSE

What is the relation of these various species concepts to the view of contemporary systematics presented above? In particular, how are we to understand these species concepts in the context of evolutionary trees? And can tree thinking clarify our understanding of the apparent difficulties of these concepts?
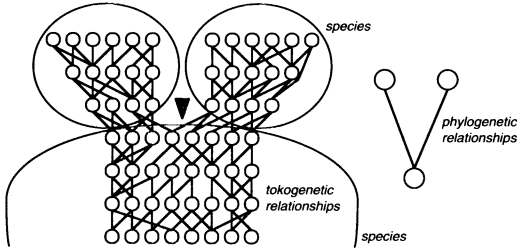
A preliminary answer to the first question

FIG. 3. The branches of a simplified evolutionary tree, resolved to the level of individual organisms. "Tokogenetic relationships" are the reproductive relationships among individuals. Redrawn after Hennig (1966, p. 31, Fig. 6).

might be to say that species are the ultimate terminal taxa in evolutionary trees: within species relationships are reticulate, and between species relationships are branching. This was how the situation was characterized by Hennig (1966), one of the pioneers of cladistic analysis (Fig. 3). This sounds reasonable as far as it goes, but most people would acknowledge that Figure 3 is an overly simplified view of the pattern of descent in real populations. A more realistic view might look something like Figure 4. This diagram will help us to understand the difficulties of all three common species concepts.

Let us suppose that Figure 4 represents the true history of a collection of organisms. How might we group these organisms in the present into species? Under the evolutionary species concept we would have to decide which of the groupings (A–L) share the same historical fate—in other words, we would have to decide which of the several separations among individuals in the last few generations is *temporary,* and which is *permanent.* Groups that are temporarily separated from one another will eventually come back together again, whereas those that are permanently separated will continue to diverge from one another—they will have separate historical fates. How can we determine which separations are temporary and which are permanent? In the case of allopatric populations, *in the present we cannot*: that will depend upon how evolution goes in the future. Judgements of temporariness

and permanence can only be made *retrospectively* (O'Hara, 1993).

What about the phylogenetic species concept? As remarked above, there is no reason to expect that there is any limit to diagnosability, so perhaps even the smallest of the terminal groupings in Figure 4 (D–I) should be recognized as phylogenetic species. (There is an additional difficulty with the phylogenetic species concept, namely that within populations the distribution of diagnostic characters may be overlapping rather than hierarchical [de Queiroz and Donoghue, 1990], but let us set that aside for the moment.) It does seem unwise to recognize every cluster of individuals separated for a few generations as a separate species, and in recognition of this advocates of the phylogenetic species concept have acknowledged that *temporary* isolation does not change the status of individuals within a phylogenetic species (Wheeler and Nixon, 1990). But this brings us back to the question of determining which separations are temporary and which are permanent. And because this depends upon the future, it cannot be determined with certainty in the present.

What about the biological species concept? It does not seem to include any reference to fate, temporariness, or permanence, so perhaps it can be applied unambiguously. The biological species concept does however contain the notion of a "group of interbreeding populations." Are the A, B, and C groupings in Figure 4 interbreeding populations? If we consider their present separations to be temporary then they are, but if their separations are permanent, then their ancestors may have been part of the same group of interbreeding populations at one time in the past, but they themselves are not today. Since no population is instantaneously panmictic, the inclusion of groups of individuals with a population or group of populations contains the implicit assumption that any separations that exist among them in the present are temporary. Thus the biological species concept faces the same problem of retrospective determination: we can only determine for certain whether two allopatric
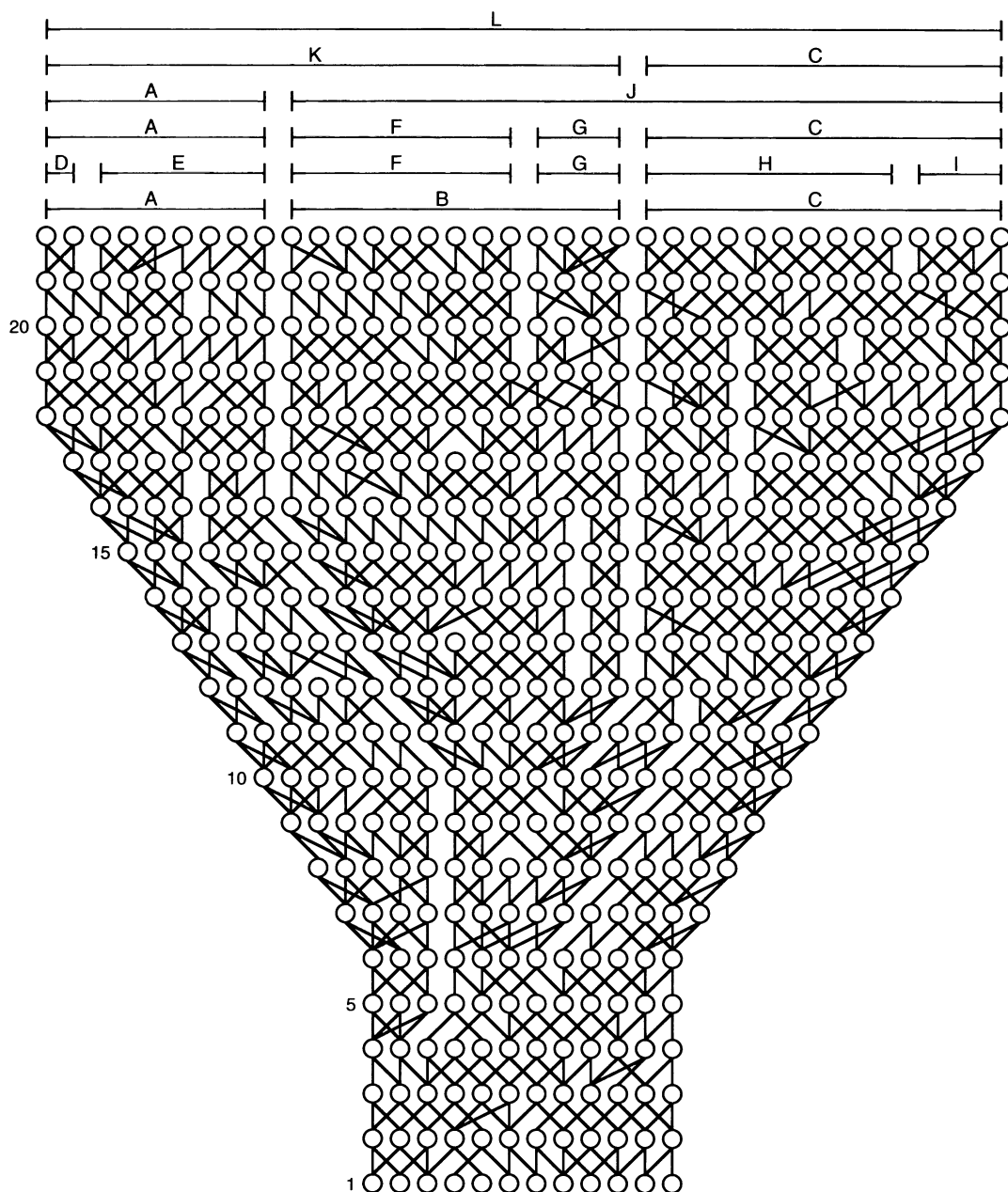
FIG. 4. A more realistic evolutionary tree, resolved to the level of individual organisms. Which of the groupings (A–L) of organisms in the present should be recognized as species depends not only upon factual knowledge of the characteristics of the organisms, but also upon expectations of their future behavior and that of their descendants. Compare de Queiroz and Donoghue (1990, p. 71, Fig. 3).

forms are one species or two by seeing how evolution goes in the future, and whether they either continue to remain separate, or merge back together again.

Theoretical concerns such as these, however, should not blind us to the practical fact that, more often than not, species in nature are easy to delimit, especially in local

situations. If they were not, it would not be possible to publish field guides, checklists, and all manner of similar faunal and floral works. Mayr (1990) has recently shown how successfully the biological species concept can be applied to local floras, and Mayr and Short (1970) had similar success in applying the biological species concept to the North American bird fauna. But as is frequently the case in science, it is the anomalous instances, where commonly applied (and successful) concepts break down, that provide the greatest theoretical insights. Although species are often easy to delimit, they are not always easy to delimit, and in those cases where they are not, the difficulty that arises illustrates well the special *historical* character of the evolutionary process. The particular type of difficulty systematists face in the case of these "doubtful species" (Darwin, 1859, pp. 47–52) is a difficulty that is characteristic of all efforts to write history in the present. This type of difficulty is well known to philosophers of history, and is often called the problem of "future contingents" (Danto, 1985; O'Hara, 1993). If I describe a recent paper by a colleague as "the work that will win her the Nobel Prize" am I correct or incorrect? In the present, the only possible answer is that one cannot tell. It may be correct to say that the Laysan and Nihoa Finches are permanently separate, but then again it may not. It "depends very much on the way the world goes" (Danto, 1985, p. 194).

In writing about species in the *Origin,* Darwin often refers to them as "permanent varieties" (1859, p. 475). I suggest that this is a particularly insightful phrase. Because evolutionary history is something we are still in the midst of, it will not always be possible for us to determine which varieties—which distinctive populations in nature—are temporary and which are permanent, and so our counts of species across space and through time will always have some measure of ambiguity in them that we cannot escape. If there is any consolation in this, it must be that the very existence of this ambiguity—the very fact that some organisms in nature cannot easily be grouped into species—is itself, as Darwin recognized, one of the most important pieces of

evidence for the historical process we call evolution.

REFERENCES

Atran, S. (ed.) 1987. *Histoire du concept d'espèce dans les sciences de la vie.* Fondation Singer-Polignac, Paris.

Atran, S. 1990. *Cognitive foundations of natural history: Towards an anthropology of science.* Cambridge Univ. Press, Cambridge.

Baum, D. A. and A. Larson. 1991. Adaptation reviewed: A phylogenetic methodology for studying character macroevolution. Syst. Zool. 40:1–18.

Beatty, J. 1985. Speaking of species: Darwin's strategy. *In* D. Kohn (ed.), *The Darwinian heritage,* pp. 265–281. Princeton Univ. Press, Princeton.

Brooks, D. R. and D. A. McLennan. 1991. *Phylogeny, ecology, and behavior: A research program in comparative biology.* Univ. Chicago Press, Chicago.

Browne, J. 1983. *The secular ark: Studies in the history of biogeography.* Yale Univ. Press, New Haven.

Burghardt, G. M. and J. L. Gittleman. 1990. Comparative behavior and phylogenetic analysis. *In* M. Bekoff and D. Jamieson (eds.), *Interpretation and explanation in the study of behavior: Comparative perspectives.* Westview Press, Boulder.

Casey, T. L. C. and J. D. Jacobi. 1974. A new genus and species of bird from the island of Maui, Hawaii (Passeriformes, Drepanidae). Occas. Pap. Bishop Mus. 24:216–226.

Coddington, J. A. 1988. Cladistic tests of adaptational hypotheses. Cladistics 4:3–22.

Cracraft, J. 1983. Species concepts and speciation analysis. Current Ornithol. 1:159–187.

Cracraft, J. 1992. The species of the birds-of-paradise (Paradisaeidae): Applying the phylogenetic species concept to a complex pattern of diversification. Cladistics 8:1–43.

Craw, R. 1992. Margins of cladistics: Identity, difference and place in the emergence of phylogenetic systematics, 1864–1975. *In* P. Griffiths (ed.), *Trees of life: Essays in philosophy of biology,* pp. 65–107. Australasian Stud. Hist. Philos. Sci. 11. Kluwer Academic Publishers, Dordrecht.

Danto, A. C. 1985. *Narration and knowledge.* Columbia Univ. Press, New York.

Darwin, C. 1859. *On the origin of species.* John Murray, London.

de Queiroz, K. 1988. Systematics and the Darwinian revolution. Philos. Sci. 55:238–259.

de Queiroz, K. and M. J. Donoghue. 1990. Phylogenetic systematics or Nelson's version of cladistics? Cladistics 6:61–75.

de Queiroz, K. and J. Gauthier. 1990. Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. Syst. Zool. 39:307–322.

de Queiroz, K. and J. Gauthier. 1992. Phylogenetic taxonomy. Annu. Rev. Ecol. Syst. 23:449–480.

Eldredge, N. (ed.) 1992. *Systematics, ecology, and the biodiversity crisis.* Columbia Univ. Press, New York.

Ereshefsky, M. (ed.) 1992. *The units of evolution: Essays on the nature of species.* MIT Press, Cambridge.

Felsenstein, J. 1985. Phylogenies and the comparative method. Am. Nat. 125:1–15.

Felsenstein, J. 1988. Phylogenies from molecular sequences: Inference and reliability. Annu. Rev. Genet. 22:521–565.

Fink, W. L. 1982. The conceptual relationship between ontogeny and phylogeny. Paleobiol. 8:254–264.

Griffiths, G. C. D. 1974. On the foundations of biological systematics. Acta Biotheor. 23:85–131.

Harvey, P. H. and M. D. Pagel. 1991. *The comparative method in evolutionary biology.* Oxford Univ. Press, Oxford.

Hennig, W. 1966. *Phylogenetic systematics.* Univ. Illinois Press, Urbana.

Huey, R. B. 1987. Phylogeny, history, and the comparative method. *In* M. E. Feder, A. F. Bennett, W. Burggren, and R. B. Huey (eds.), *New directions in ecological physiology,* pp. 76–98. Cambridge Univ. Press, Cambridge.

Hull, D. L. 1988. *Science as a process.* University of Chicago Press, Chicago.

Lang, M. 1990. Cladistics as a tool for morphologists. Netherlands J. Zool. 40:386–402.

Lauder, G. V. 1982. Historical biology and the problem of design. J. Theoret. Biol. 97:57–67.

Linné, C. von. 1781. *Select dissertations from the Amoenitates Academicae* (F. J. Brand, transl.). G. Robinson, London. (Reprinted 1977 by Arno Press, New York.)

Maddison, W. P. and D. R. Maddison. 1989. Interactive analysis of phylogeny and character evolution using the computer program MacClade. Fol. Primatol. 53:190–202.

Maddison, W. P. and D. R. Maddison. 1992. *MacClade* (version 3). Sinauer Associates, Sunderland.

Margulis, L. and K. V. Schwartz. 1988. *Five kingdoms: An illustrated guide to the phyla of life on earth,* 2nd ed. Freeman, New York.

Mayr, E. 1940. Speciation phenomena in birds. Am. Nat. 74:249–278.

Mayr, E. 1962. Family Paradisaeidae, birds of paradise. *In* E. Mayr and J. C. Greenway, Jr. (eds.), *Check-list of birds of the world,* 15:181–204. Mus. Comp. Zool., Cambridge.

Mayr, E. 1976. *Evolution and the diversity of life.* Harvard Univ. Press, Cambridge.

Mayr, E. 1982. *The growth of biological thought.* Harvard Univ. Press, Cambridge.

Mayr, E. 1990. A local flora and the biological species concept. Amer. J. Bot. 79:222–238.

Mayr, E. and P. D. Ashlock. 1991. *Principles of systematic zoology,* 2nd ed. McGraw-Hill, New York.

Mayr, E., E. G. Linsley, and R. L. Usinger. 1953. *Methods and principles of systematic zoology.* McGraw-Hill, New York.

Mayr, E. and W. Provine. (eds.) 1980. *The evolutionary synthesis.* Harvard Univ. Press, Cambridge.

Mayr, E. and L. L. Short. 1970. Species taxa of North American birds. Nuttall Ornithological Club, Publication No. 9.

Moore, J. A. 1991. Science as a way of knowing—VII: A conceptual framework for biology, part III. Am. Zool. 31:349–471.

National Research Council. 1992. *Conserving biodiversity: A research agenda for development agencies.* National Academy Press, Washington, D. C.

Nixon, K. C. and Q. D. Wheeler. 1990. An amplification of the phylogenetic species concept. Cladistics 6:211–223.

O'Hara, R. J. 1988a. Homage to Clio, or, toward an historical philosophy for evolutionary biology. Syst. Zool. 37:142–155.

O'Hara, R. J. 1988b. Diagrammatic classifications of birds, 1819–1901: Views of the natural system in 19th-century British ornithology. *In* H. Ouellet (ed.), *Acta XIX Congressus Internationalis Ornithologici,* pp. 2746–2759. National Museum of Natural Sciences, Ottawa.

O'Hara, R. J. 1991. Representations of the natural system in the nineteenth century. Biol. Philos. 7:135–160.

O'Hara, R. J. 1992. Telling the tree: Narrative representation and the study of evolutionary history. Biol. Philos. 7:135–160.

O'Hara, R. J. 1993. Systematic generalization, historical fate, and the species problem. Syst. Biol. 43:231–246.

Paterson, H. E. H. 1985. The recognition concept of species. *In* E. Vrba (ed.), *Species and speciation,* pp. 21–29. Transvaal Mus. Monogr. 4, Pretoria.

Ronquist, F. and S. Nylin. 1990. Process and pattern in the evolution of species associations. Syst. Zool. 39:323–344.

Simpson, G. G. 1961. *Principles of animal taxonomy.* Columbia Univ. Press, New York.

Sober, E. 1988. *Reconstructing the past: Parsimony, evolution, and inference.* MIT Press, Cambridge.

Stevens, P. F. 1992. Species: Historical perspectives. *In* E. F. Keller and E. A. Lloyd (eds.), *Keywords in evolutionary biology,* pp. 302–311. Harvard Univ. Press, Cambridge.

Stiassny, M. L. J. 1992. Phylogenetic analysis and the role of systematics in the biodiversity crisis. *In* N. Eldredge (ed.), *Systematics, ecology, and the biodiversity crisis,* pp. 109–120. Columbia Univ. Press, New York.

Swofford, D. L. and J. Olsen. 1990. Phylogenetic reconstruction. *In* D. M. Hillis and C. Moritz (eds.), *Molecular systematics,* pp. 411–501. Sinauer Associates, Sunderland.

Vane-Wright, R. I., C. J. Humphries, and P. H. Williams. 1991. What to protect? Systematics and the agony of choice. Biol. Cons. 55:235–254.

Wallace, A. R. 1856. Attempts at a natural arrangement of birds. Ann. Mag. Nat. Hist., second series 18:193–216.

Wanntorp, H.-E., D. R. Brooks, T. Nilsson, S. Nylin, F. Ronquist, S. C. Stearns, and N. Wedell. 1990. Phylogenetic approaches in ecology. Oikos 57:119–132.

Wheeler, Q. D. and K. C. Nixon. 1990. Another way of *looking at* the species problem. Cladistics 6:77–81.

Wiley, E. O. 1978. The evolutionary species concept reconsidered. Syst. Zool. 27:17–26.

Wiley, E. O., D. Siegel-Causey, D. R. Brooks, and V. A. Funk. 1991. The compleat cladist: A primer of phylogenetic procedures. Univ. Kansas Mus. Nat. Hist., Spec. Pub. 19.

Wilson, E. O. 1992. *The diversity of life.* Harvard Univ. Press, Cambridge.