

IS THERE A SINGLE OBJECTIVE, EVOLUTIONARY TREE OF LIFE?^{2*}

It is often said that there is just one “objective” tree of life: a single accurate branching hierarchy of species reflecting order of descent. For any two species, there is a single correct answer as to whether one is a “daughter” of the other, whether the two are “sister species” by virtue of their descent from a common parental species, whether they belong to a family line that excludes any given third species, and so on.

The idea is intrinsically interesting. It has consequences for what we should think about the evolutionary origins of *Homo sapiens* as well as other species. The idea also has important connections to the scientific discipline of systematics, which classifies organisms into related groups. The connection to systematics is what has made objectivity a topic of discussion for biologists and philosophers of biology. Cladism, now the dominant school of systematics, places organisms into groups depending just on their place in the tree of life. That is supposed to render classification objective.

In section I, I recite claims to objectivity. In sections II–V, I argue that the apparent objectivity is not what it seems to be. In section VI, I briefly revisit systematics.

I. THE APPEAL TO OBJECTIVITY

Cladistic classification, founded by Willi Hennig, takes into account just relationships of ancestry and descent.¹ The alternative is to take into account evolved similarity. Similarity allows for a multiplicity of permissible classifications. Paul E. Griffiths and Kim Sterelny follow many others in stressing this: “as cladists never tire of pointing out—similarity depends on the traits you measure.”² In some respects, chimpanzees seem more similar to gorillas than to humans. Both are hairy and share a relatively primitive lifestyle. In other respects more obvious to specialists than laypersons, chimpanzees are more similar to humans. Similarity might yield no unique hierarchical representation.

It is supposed to be an “axiom” of cladistic systematics that an unambiguous *historical* hierarchy is available for reference: “nature’s

* For discussion, I am grateful to many, especially Bruce Aune, Brian Bodenbender, and James Walker.

¹ Hennig, *Phylogenetic Systematics* (Urbana: Illinois UP, 1966).

² *Sex and Death: An Introduction to Philosophy of Biology* (Chicago: University Press, 1999), p. 196.

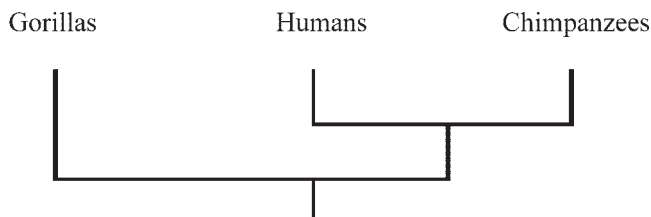


Figure 1: Humans and chimpanzees comprise a *monophyletic* group; gorillas and chimpanzees without humans do not. Monophyletic groups include all descendants of the closest common ancestral species.

hierarchy is discoverable and effectively represented by a branching diagram.”³ With respect to humans, chimpanzees, and gorillas,

History has an objective structure. Suppose we share a more recent common ancestor with the chimp species than it shares with the gorilla species—that the ancestors of the gorillas diverged from a branch ancestral to both chimps and humans. If so, then historical phylogeny should put humans and chimps together in a more closely related group than any including both chimps and gorillas. If not, then it’s just a mistake to think of humans and chimps together alone as a single group.⁴

As it happens, scientists are agreed that humans and chimps do share a common ancestor not shared by gorillas (see figure 1). Because that is all that we need to know to classify the three with respect to one another for cladism, we hear that “Cladistic classification has the advantage of objectivity. The phylogenetic hierarchy exists independently of the methods we use to discover it, and is unique and unambiguous in form.”⁵ Of course, in practice we may have a hard time *discerning* relationships. Still, there is one correct account of the relationships: “One True Tree of Life.”⁶ The state of our information is irrelevant because regardless of that, “It really is true that two species either do, or do not, share a more recent ancestor with each other than with any other species.”⁷

³ I quote from Robert W. Scotland, “Cladistic Theory,” in Peter L. Forey, Christopher J. Humphries, Ian J. Kitching, Robert W. Scotland, Darrell J. Siebert, and David M. Williams, eds., *Cladistics: A Practical Course in Systematics* (New York: Oxford, 1992), pp. 3–13, at p. 3.

⁴ Griffiths and Sterelny, *Sex and Death*, p. 197.

⁵ Mark Ridley, *Evolution* (Malden, MA: Blackwell, 2004, 3rd ed.), p. 480.

⁶ Griffiths and Sterelny, *Sex and Death*, p. 194.

⁷ Ridley, “Can Classification Do Without Evolution?,” in Ridley, ed., *Evolution* (New York: Oxford, 1997), pp. 196–206; this citation is from p. 202. That cladism “allows only one classification: the classification defined by the hierarchy of phylogenetic branching,” as Ridley is always reminding his many readers, is widely accepted: *Evolution and Classification: The Reformation of Cladism* (New York: Longman, 1986), p. 46. See Griffiths, “Cladistic Classification and Functional Explanation,” *Philosophy*

II. SPECIES AND SPECIES CONCEPTS

The alleged uniqueness and absence of ambiguity concerning the phylogenetic hierarchy is exaggerated. I will show in the following sections that different accounts of the familial relationships between species can be acceptable. The notorious species problem is enough to give legitimacy to distinct accounts. In the current section, I rehearse that problem, arguing that no one “species concept,” or account of what a species is, can be discovered to be the correct one at the expense of others. In section III, I go on to argue that if the arguments from section II are sound, then a group of species may allow for many valid accounts of the order of evolutionary branching and the resulting familial relationships. In section IV, I show that appeal to the species problem is dispensable. There are many valid, competing accounts of evolutionary branching even if, contrary to what I argue in section II, there is a single valid species concept. In section V, I discuss the nature and extent of valid diversity in accounts of evolutionary relationships.

As I have indicated, the present section is devoted to the species problem. Biologists make heavy use of the concept or concepts of *specieshood*: they discuss the habits and movements of this or that species, the predators, prey, and parasites of a species, the number of species in an ecosystem, and so on. But there is little agreement about what species are. There are dozens of live species concepts.

Two popular concepts are Ernst Mayr’s *biological species concept* and Joel Cracraft’s *phylogenetic species concept*. According to the biological species concept, species are “groups of interbreeding natural popula-

of Science, LXI (1994): 206–27, at p. 207; David Hull, “The Role of Theories in Biological Systematics,” *Studies in History and Philosophy of Science, Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, xxxii (2001): 221–38, at p. 224; “The Limits of Cladism,” *Systematic Zoology*, xxviii (1979): 416–40, at pp. 437–38; Samir Okasha, *Philosophy of Science: A Very Short Introduction* (New York: Oxford, 2002), pp. 111–12; Ridley, *Evolution*, pp. 475, 479, 481, 490; “The Cladistic Solution to the Species Problem,” *Biology and Philosophy*, iv (1989): 1–16; *The Problems of Evolution* (New York: Oxford, 1985); Donn Eric Rosen, “Cladism or Gradism?: A Reply to Ernst Mayr,” *Systematic Zoology*, xxiii (1974): 446–51, at pp. 447–48; David N. Stamos, *The Species Problem: Biological Species, Ontology, and the Metaphysics of Biology* (Lanham, MD: Lexington, 2003), p. 265; E.O. Wiley, *Phylogenetics: The Theory and Practice of Phylogenetic Systematics* (New York: John Wiley and Sons, 1981), p. 268. Foreshadows of the problems that I raise may be found, in some measure or other, in L.A.S. Johnson, “Rainbow’s End: The Quest for an Optimal Taxonomy,” *Systematic Zoology*, xix (1970): 203–39, at p. 231; Robert O’Hara, “Systematic Generalization, Historical Fate, and the Species Problem,” *Systematic Biology*, xlii (1993): 231–46, at pp. 232–33; and Sterelny, “The Nature of Species,” *Philosophical Books*, xxxv (1994): pp. 9–20 at p. 17, who appears since to have had a change of heart (cf. Griffiths and Sterelny, *Sex and Death*, pp. 194–97): in section V, I indicate that there is something importantly right in each position.

tions that are reproductively isolated from other such groups.”⁸ According to the phylogenetic species concept, “A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent.”⁹ These two concepts both divide the world into natural groups, but often the groups are not the same: the groups recognized by the biological species concept tend to be more inclusive than the narrower groups recognized by the phylogenetic species concept. The biological species concept may group different “races” or “subspecies” because they are interfertile, while the phylogenetic species concept distinguishes them into different “species.” Hence, the biological species concept divides the birds as a whole into an established 10,000 species. The phylogenetic species concept would double that number to 20,000 species.¹⁰

If either the biological species concept or the phylogenetic species concept could be discovered to be the correct species concept, then this could spare witnesses of one unambiguous family tree of species from a source of embarrassment. But it seems hard to believe that either the biological species concept or the phylogenetic species concept could be discovered to be the correct species concept. The decision about whether to adopt the biological species concept or the phylogenetic species concept admits more than one acceptable resolution.

The choice between competing proposals is not completely arbitrary: were it not the case that the biological species concept and the phylogenetic species concept both divide the organic world into groups that are natural and scientifically interesting, there would be no competition between them. But each concept seems to divide the organic world into groups that are natural and scientifically interesting.

⁸ Mayr, “The Biological Species Concept,” in Quentin D. Wheeler and Rudolf Meier, eds., *Species Concepts and Phylogenetic Theory* (New York: Columbia, 2000), pp. 17–29, cited at p. 17. This is a typical statement of the biological species concept. It is repeated word for word in several places: *Evolution and the Diversity of Life: Selected Essays* (Cambridge: Harvard, 1976), p. 518; *Populations, Species, and Evolution: An Abridgment of Animal Species and Evolution* (Cambridge: Harvard, 1970), p. 12; *Principles of Systematic Zoology* (New York: McGraw-Hill, 1969), p. 26. Still, the biological species concept has undergone change over Mayr’s many active decades: see Peter Beurton, “Ernst Mayr through Time on the Biological Species Concept: A Conceptual Analysis,” *Theory in Biosciences*, cxxi (2002): 81–98; and Mayr, “Comments by Ernst Mayr,” *Theory in Biosciences*, cxxi (2002): 99–100.

⁹ Cracraft, “Species Concepts and Speciation Analysis,” in R.F. Johnston, ed., *Current Ornithology* (New York: Plenum, 1983), pp. 159–87, cited at p. 170.

¹⁰ Cracraft, “Species Concepts in Systematics and Conservation Biology: An Ornithological Viewpoint,” in M. Claridge, H. Dawah, and M. R. Wilson, eds., *Species: The Units of Biodiversity* (New York: Chapman and Hall, 1997), pp. 325–39, p. 331; Graham Martin, “Birds in Double Trouble,” *Nature*, ccclxxx (1996): 666–67.

Both concepts have pros and cons. Convenience, the politics of conservation, and other such issues hang in the balance. One salient issue between proponents of different concepts is the issue of whom systematists should serve. An alleged advantage of the biological species concept is that it is user friendly in the field. It takes a laboratory specialist to distinguish species according to the phylogenetic species concept. On the flip side, specialists can more readily convey detailed information to one another if lineages are divided into species according to the phylogenetic species concept. Differences between proponents of the phylogenetic species concept and the biological species concept hinge largely on whether systematists think the discipline should be practiced “as a science dominated by field work or by laboratory investigation.”¹¹ And whether the discipline should be practiced with field work or laboratory work as the first priority is evidently not something that scientists can *discover* an answer to. No one concept seems to trump its competition in such a way that we could learn that it is the single proper answer to the nature of species.¹²

III. A DIVERSITY OF TREES

Just as there may be more than one natural arrangement of a given group of organisms into species, so there may be more than one natural arrangement of a given group of species into historical hierarchies. Consider the common situation in which a controversial lineage qualifies, according to the biological species concept, as a species divided into two subspecies, while for the phylogenetic species concept it counts as two different species. Of course, there is already a need for two different accounts of branching to represent the two options, if all species are to be depicted. One account will recognize two branches, the other just one. But it might be thought that that the problem stops here: that, while there may be subjectivity in determining how *many* species there are, there remains a single correct ordering of whatever species one acknowledges into groups that are united by common ancestry. The problem is not constrained in this way.

The subjectivity in counting species introduces subjectivity in the assignment of which organisms share a common ancestral species to the exclusion of other organisms. Assume that the two sides of the

¹¹ Martin, “Birds in Double Trouble,” p. 667.

¹² For further discussion, see Joseph LaPorte, *Natural Kinds and Conceptual Change* (New York: Cambridge, 2004), chapter 3.

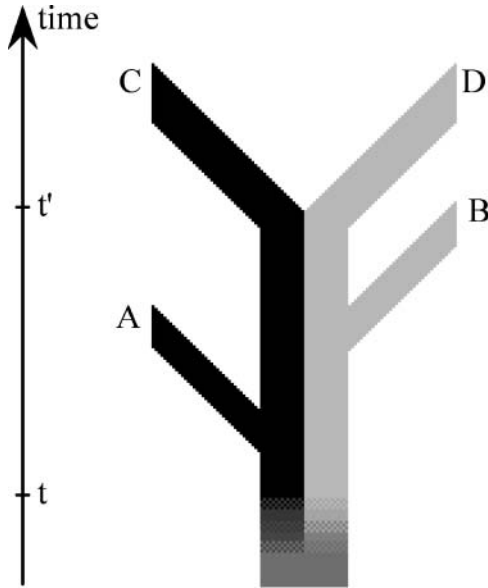


Figure 2: Between t and t' , the trunk is comprised of two borderline species.

trunk in figure 2 begin as one incontrovertible species. Later the species divides into two distinct lineages, represented in light and dark. There is a period of time, between t and t' , in which it is unclear whether the organisms on the trunk should be grouped into one species or two. There are marked differences between the sides, but whether there are enough differences or the right differences depends on whether the biological species concept or the phylogenetic species concept does the delimiting. Eventually, at time t' , the distinct sides separate into two species by any standard. (C) and (D) are the resulting daughter species. Before producing (C) or (D), each side of the trunk generates another daughter: species (A) or (B). These too are distinct species by any standard.¹³

Familial relationships between species (A)–(D) vary depending upon whether the trunk is comprised of one or two species. If the

¹³ This sort of budding from a parental species that survives without much change is probably common: most speciation events probably start with small, isolated founder populations: Mayr, "A Defense of the Biological Species Concept," in Wheeler and Meier, eds., pp. 161–66, p. 164; *The Growth of Biological Thought* (Cambridge: Harvard, 1982), p. 229; Mayr and Peter Ashlock, *Principles of Systematic Zoology* (New York: McGraw-Hill, 1991, 2nd ed.), p. 225.

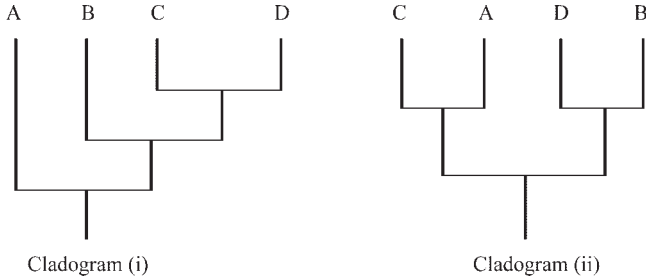


Figure 3: Two different accounts of the monophyletic groups. Cladograms nest groups within groups but give no further information. They do not indicate from which side of a parental lineage a branch issues, as figure 2 does: cladograms rotated at any node will express the same information.

division occurring at around t is only into subspecies, so that the trunk of the tree is still to be counted as one species, then the last two branches, (C) and (D), belong to an exclusive monophyletic group. A wider monophyletic group includes branch (B) and a still wider monophyletic group includes all branches. This interpretation, which favors the biological species concept, is represented by Cladogram (i).¹⁴

On the other hand, if the division prior to t is a division into separate species, in accordance with the phylogenetic species concept, then Cladogram (ii) is the proper one for representing the world. Now (C) and (D) are no longer sister species; rather, (C) is now a sister of (A), and (D) is now a sister of (B). There is no longer any monophyletic group containing just three of the branches. (B) is no longer a sister to a branch culminating in (C) and (D). And (A) is no longer a sister to the group culminating in all of the other branches.

If it is not a matter of discovery as to which species concept is correct, it likewise cannot be a matter of discovery as to which cladogram, (i) or (ii), is correct. There is no single, objectively correct branching diagram depicting the hierarchy of species.

If either the biological species concept or the phylogenetic species concept were the unique correct account of what a species is, contrary to what I have argued, then Cladogram (i) or (ii) might be discovered

¹⁴ What is important is that the two-shaded trunk of the tree is counted as a single species at any one time (before t'). Whether the trunk must be split over time into three species, the endpoints set by branching events, is immaterial, because the order of branching for the species at the tips of cladograms (i) and (ii) is unaffected. I will explain below that for orthodox cladists, the trunk would have to be divided into three species, despite no intrinsic change in its members.

to be correct. So the species issue might be pressed. The most natural reason to hold out for a discovered resolution to the species problem is that one species concept may end up capturing the process or processes that produce and maintain the more or less homogeneous morphological groups of organisms to which biologists attach species names. The phylogenetic species concept might be dismissed on the grounds that it is not even a contender in the race to capture the right processes.¹⁵ It attempts to identify groups that evolution has generated irrespective of the processes behind those groups' production. The biological species concept, on the other hand, might claim a measure of vindication if sexual recombination is sometimes responsible for cohesion. The right account might be a disjunctive one open to different kinds of processes.

This reason to reject the phylogenetic species concept has scant claim to an objective discovery: no one could discover as an objective fact that Cracraft is just wrong in his use of species' names, on the grounds that what should really interest him is the processes producing the groups that he names rather than the groups defined by these processes.¹⁶ Further, just as some theorists call attention to processes

¹⁵ Ridley, "The Cladistic Solution," pp. 3, 5–6, 8.

¹⁶ *Objection*: the issue has been misconceived. The real issue is not whether Cracraft is wrong to name his narrower groups. One can apply names as one fancies. The real issue is whether Cracraft's use of 'species' breaks from traditional use. If there is a break from traditional use, then Cracraft errs in supposing that he is talking about *species*; he is talking about some other kind of group to which he has applied the name. *Reply*: traditional use does not settle in favor of any rival of the phylogenetic species concept. The tradition has long been shared by "lumpers" and "splitters." Both persuasions are reasonable. Over generations, workers of different persuasions have treated the same lineages differently: for examples, see Wiley and Richard L. Mayden, "The Evolutionary Species Concept," in Wheeler and Meier, eds., pp. 70–89, at p. 86; Jody Hey, *Genes, Categories, and Species: The Evolutionary and Cognitive Causes of the Species Problem* (New York: Oxford, 2001), pp. 19–20. The tradition has also long been characterized by different measures to delimit species, including patterns of resemblance, as Darwin indicates in a famous passage:

It is really laughable to see what different ideas are prominent in various naturalists' minds, when they speak of "species"; in some, resemblance is everything and descent of little weight—in some, resemblance seems to go for nothing, and Creation the reigning idea—in some, sterility an unailing test, with others it is not worth a farthing. It all comes, I believe, from trying to define the indefinable (*The Life and Letters of Charles Darwin, Including an Autobiographical Chapter*, Volume 2, F. Darwin, ed. (London: John Murray, 1887), p. 88).

Even the tradition of cladism fails to settle upon a single species concept. Hennig dodges the issue: see section vi. Hennig's most stalwart followers fail to agree on a single concept: cf. D.J. Kornet, "Permanent Splits as Speciation Events: A Formal Reconstruction of the Internodal Species Concept," *Journal of Theoretical Biology*, CLXIV (1993): 407–35; Rudolf Meier and Rainer Willmann, "The Hennigian Species Concept," in Wheeler and Meier, eds., pp. 30–43; "A Defense of the Hennigian Species Concept," in Wheeler and Meier, eds., pp. 167–78; Ridley, "The Cladistic Solution."

that give rise to broad groups, Cracraft could call attention to processes that give rise to the narrow groups that he recognizes, by reworking his statement. In this way, he could continue to split broad groups.

The best way to demonstrate the robustness of the problem may be to expand the discussion. The *ecological species concept*, like the biological species concept, identifies species as groups united by a certain kind of process. Just as sexual processes do, ecological processes sometimes produce groups that are relatively homogeneous, genetically and phenotypically. The organisms thus grouped include not only plants, oaks being the most famous example,¹⁷ but also animals, such as certain species of North American snakes or Darwin finches, for which selection in the environment evidently eliminates hybrids between distinct forms:¹⁸ hence, the recognition of ecologically delimited species.¹⁹

Sometimes, both ecological processes and sexual processes operate to shape the same organisms into groups. For that reason, a large lineage like that represented by the trunk in figure 2 could easily be divided into subgroups, the big group qualifying as a species according to the biological species concept and the narrower subgroups qualifying as separate species according to the ecological species concept, or vice versa. There might be no clear, objective answer as to whether one species concept prevails over the other in characterizing the lineages: "the nature of the evolutionary entity could be inherently ambiguous," as a group of biologists observes in this connection.²⁰

IV. THE MANY TREES FOR ANY SPECIES CONCEPT

In criticizing the proposal that there is one objective hierarchy of species, I have appealed to competing species concepts. But the source of the problem lies deeper. Suppose, contrary to what seems reasonable, that one species concept or another like the biological species concept or the phylogenetic species concept were somehow to have an objective claim to be the sole accurate species concept. Still, there

¹⁷ Alan Templeton, "The Meaning of Species and Speciation: A Genetic Perspective," in Marc Ereshefsky, ed., *The Units of Evolution* (Cambridge: MIT, 1992), pp. 159–83, p. 174; L. Van Valen, "Ecological Species, Multispecies, and Oaks," in Ereshefsky, pp. 69–77, pp. 72–73.

¹⁸ Werner Kunz, "When Is a Parasite Species a Species?," *Trends in Parasitology*, xviii (2002): 121–24.

¹⁹ Van Valen, "Ecological Species"; L. Andersson, "The Driving Force: Species Concepts and Ecology," *Taxon*, xxxix (1990): 375–82; see also Ridley, "The Cladistic Solution."

²⁰ Jody Hey, Robin S. Waples, Michael L. Arnold, Roger K. Butlin, and Richard G. Harrison, "Understanding and Confronting Species Uncertainty in Biology and Conservation," *Trends in Ecology and Evolution*, xviii (2003): 597–603, p. 599.

would be room for doubtful lineages like that shown to give rise to cladograms (i) and (ii).

Take the biological species concept. It may seem that,

The intra-breeding criterion yields only *one* set of groups of living creatures, and the determination of which creatures to assign to the same group and which to different groups is no longer in any sense a matter of choice but only of discovery.²¹

But in fact the distinctness generated comes in degrees. Systematists find it necessary to recognize that distinct species can cross to some degree, despite substantial reproductive isolation. Otherwise, species would be far larger and more heterogeneous than it would be natural to allow. Unfortunately, there would seem to be no fact of the matter as to precisely how much potential for hybridization may be tolerated as species are delimited.²²

Even if systematists were willing to go to extreme measures by lumping otherwise good species that can hybridize into a single species, they could not in this way circumvent the problem of indistinctness.²³ There

²¹ Sybil Wolfram, *Philosophical Logic: An Introduction* (New York: Routledge, 1989), p. 239.

²² A limited amount of hybridization is common among recognized species of both plants and animals: for discussion of examples, see C. J. Hearn, "The Evolution of Citrus Species: Methods to Develop New Sweet Orange Cultivars," *Proceedings of the Annual Meeting of the Florida State Horticultural Society*, cvii (1994): 1–3, p. 2; Daniel Potter, Fangyou Gao, Scott Baggett, James R. McKenna, and Gale H. McGranahan, "Defining the Sources of Paradox: DNA Sequence Markers for North American Walnut (*Juglans* L.) Species and Hybrids," *Scientia Horticulturae*, xciv (2002): 157–70; Douglas J. Futuyma, *Evolutionary Biology* (Sunderland, MA: Sinauer, 1998, 3rd ed.), p. 448. The problem of drawing a line at some point has long been recognized: "the infertility of species when crossed graduates away so insensibly that the two most experienced observers who ever lived have come to diametrically opposite results when experimenting on the same forms," Darwin writes (*Charles Darwin's Natural Selection: Being the Second Part of His Big Species Book Written From 1856 to 1858*), R.C. Stauffer, ed. (New York: Cambridge, 1975), p. 165). The same observation has been made more recently by Theodosius Dobzhansky, *Genetics of the Evolutionary Process* (New York: Columbia, 1970), p. 359; Hey, *Genes, Categories, and Species*, pp. 20–21; Johnson, "Rainbow's End," p. 231; Mayr, *The Growth of Biological Thought*, p. 282; B. Mishler and M. Donoghue, "Species Concepts: A Case for Pluralism," *Systematic Zoology*, xxxi (1982): 491–503, p. 495; Templeton, "The Meaning of Species and Speciation," p. 165.

²³ Cf. Meier and Willmann, "A Defense." This suggestion raises the possibility that the term 'species' be given by stipulation a new use that would make tree construction a repeatable enterprise. Occasions of discord could be *reduced* in this way: even stipulating the biological species concept over the phylogenetic species concept is an improvement. But there is little value in going to drastic measures in this direction to describe a kind of group that, however quirky or biologically meaningless, allows for repeatable ordering. Nor would any algorithm generating an ordering of quirky groups show that there is a repeatable account of the hierarchy of *species*; at best, such an algorithm would show that there is a repeatable account of the hierarchy of some new kind of group deserving a new name. Observe that just as 'species'

is no distinct line at which absolute reproductive isolation can be said to have been achieved: it may be that certain environmental circumstances, for example, preclude any interbreeding even though a change in environment could alter this.²⁴ This and other troubles render the notion *reproductive isolation* unclear and incapable of black and white application.

So even if we restrict our attention to the biological species concept, we are bound to find cases like that depicted in figure 2, in which there is no definitive answer, even in principle, as to whether there are two species present or just one species divided into two subspecies. cursory reflection on the phylogenetic species concept and the ecological species concept indicates that the application of these other species concepts cannot be any more cut and dried than the application of the biological species concept. Still other species concepts fare the same.²⁵ Evolution assures that they do. As the great G. G. Simpson observes, "To insist on an absolute objective criterion would be to deny the facts of life, especially the inescapable fact of evolution."²⁶

V. WHAT IS OBJECTIVE AND WHAT IS NOT?

Not all groups of species permit more than one possible arrangement by order of descent. When does reality uphold just one account? In the present section, I try to clarify this.

When all but a few species are ignored, historical relationships can easily be closed to interpretation. Consider the relationships between any two species of gecko and the lizard-like tuatara species *Sphenodon punctatus*, whose ancestral lineages have been separated from those of all other living reptiles for hundreds of millions of years. Because the tuatara line and the gecko line have been separate for so long, each has myriad common ancestral species that are not shared by the other, *no matter how species are delimited*. Any arrangement according to which the tuatara and one gecko species belong to a monophyletic group that excludes another gecko species is just wrong. Gaps between species produce lots of relationships like these. Wolves and foxes

might be given an artificial, stipulated use that approximates to some extent ordinary use in order to allow for repeatable groupings, so might 'similarity': tellingly, cladists find this trick for achieving repeatability to be arbitrary and to preclude the kind of objectivity in ordering that cladism is supposed to enjoy (Ridley, "Can Classification Do Without Evolution?," p. 199).

²⁴ LaPorte, *Natural Kinds and Conceptual Change*, chapter 2; Philip Kitcher, "Some Puzzles about Species," in Michael Ruse, ed., *What the Philosophy of Biology Is: Essays Dedicated to David Hull* (Boston: Kluwer, 1989), pp. 183–208, pp. 197–98; Ridley, *Evolution*, p. 358.

²⁵ I survey some other concepts in chapter 3 of *Natural Kinds and Conceptual Change*.

²⁶ *Principles of Animal Taxonomy* (New York: Columbia, 1961), p. 152.

separated around five million years ago, but not before they shared tens of millions of years of ancestral species outside the line leading to bears. Humans and chimps share a common ancestor not shared by gorillas. Oranges and lemons share a common ancestor not shared by watermelons. The lesson of this paper does nothing to upset the objectivity of many hierarchies like these.

There is much to be said for objectivity, then. When we prune the tree to a few branches, no two of which share exclusively a closest common ancestor that lies close to the origin of any other branch, then we obtain an ordering that admits of no legitimate dissent, in view of the empirical facts.

But if there is much to be said for objectivity, there is much to be said against it. Relationships are thrown into turmoil when there is no whittling the tree down, or when groups left on the tree have more closely related ancestral species. These relationships can be of great interest, as I will illustrate with an example close to home. A massive amount of effort from multiple disciplines has been expended in the effort to discern the relationships between our own species and our closest relatives in the genus *Homo*.

The genus *Homo* is divided into varying numbers of species, depending on whether differences in specimens at various geographical locations are seen to represent a departure significant enough to warrant the conferral of a distinct species name. Some theorists lump African and Asian specimens of our best-known ancestor all into the same species, which is then called "*Homo erectus*." Others see the differences between African and Asian lineages to be significant enough to warrant different specific designations: these theorists group African specimens into "*Homo ergaster*," reserving '*Homo erectus*' for the Asian lineage. There is no particular reason to suppose that there is an objective answer as to whether there are two species or one here: potential interbreeding is difficult to determine, but it is certainly reasonable to suppose that by one species concept, say the biological species concept, there may be one species divided into two subspecies, while for another concept, say the phylogenetic species concept, there are enough differences between the strains to merit two specific names. As I have indicated, such situations are not rare.

Homo ergaster (or, depending on your perspective, African *Homo erectus*) and the Asian strain of *Homo erectus* are thought to have diverged over a million years ago. Hundreds of thousand of years later, *Homo ergaster* (or African *Homo erectus*) seems to have given rise to the Neandertals, *Homo neanderthalensis*, and then our own species, *Homo sapiens*. Meanwhile, the Asian strain of *Homo erectus* seems to have given rise to the "hobbit" species *Homo floresiensis* that shared the

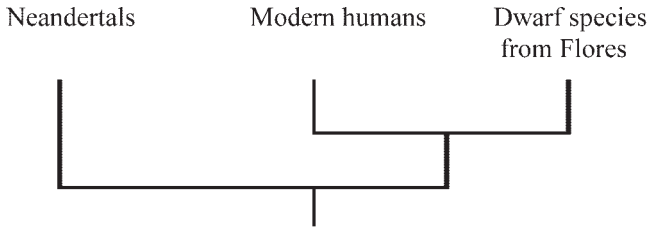


Figure 4

planet with us until only a few thousand years ago. The remarkable discovery of this new species has made headlines in recent months.

No one is quite sure about the precise dates at which these more recent species emerged, or the order in time. But for the sake of illustration, I will suppose that after the split between *Homo ergaster* (or African *Homo erectus*) and the Asian strain of *Homo erectus*, the next split was that which resulted in *Homo neanderthalensis* (from the African line). Sometime after the emergence of *Homo neanderthalensis*, there emerged, in one order or another, both our own species, *Homo sapiens* (from the African line), and *Homo floresiensis* (from the Asian line). This is the correct order of events, for all anyone knows.²⁷

Now let us suppose that the strain that I have been calling “*Homo ergaster* or African *Homo erectus*” is to be counted as conspecific with Asian *Homo erectus*, so that the two comprise the single species *Homo erectus* (between branching events: see note 14). In that event, *Homo neanderthalensis* is the species first to separate from others in the group: it branches off from a species that will go on to generate both *Homo sapiens* and *Homo floresiensis*. *Homo sapiens* and *Homo floresiensis* are more closely related to each other than either is to *Homo neanderthalensis*. This is represented in figure 4 above.

If, on the other hand, the strain that I have been calling “*Homo*

²⁷ *Homo neanderthalensis* is typically thought to be around 400,000 years old and *Homo sapiens* around 200,000 years old. *Homo floresiensis* may be as young as 70,000 years, as preliminary dating for the species indicates, but it could also be much older, perhaps 800,000 years old: Rex Dalton, “Little Lady of Flores Forces Rethink of Human Evolution,” *Nature*, CDXXXI (2004): 1029; see also Marta Mirazón Lahr and Robert Foley, “Palaeoanthropology: Human Evolution Writ Small,” *Nature*, CDXXXI (2004): 1043–44, at p. 1043. If the earlier date is accurate, *Homo floresiensis* may still be younger than *Homo neanderthalensis*, whose roots may lie further back in Africa than the date of origin just mentioned: Chris Stringer, “Human Evolution: Out of Ethiopia,” *Nature*, CDXXXIII (2003): 692–95, p. 693.

Further information might, of course, reveal that the order in which the three species in question emerged is not as I have assumed. But even if my example becomes outdated for this reason, minor alterations could probably render it historically accurate: some other lineage could be substituted in place of *Homo floresiensis* to the same effect. As one of the team leaders responsible for finding *Homo floresiensis*

multiplies when we recognize a more extended family. The species giving rise to early members of *Homo erectus* (or *Homo ergaster*) may have been *Homo habilis*.²⁹ But various authorities split *Homo habilis*, too, into two different species.³⁰ And so it goes.

I have indicated only part of the legitimate variation in tree construction even for the lineages depicted. Some authorities lump Neandertals into our own species, counting them members of *Homo sapiens*.³¹ These authorities see Neandertals as a distinct subspecies of modern humans. It is possible that missing information could, if provided, settle the disagreement: for example, definitive information that there were genetic barriers to interbreeding could settle the issue.³² However, matters could as well be more complicated than that: there is some evidence of *limited* interbreeding where the lineages coexisted.³³ It might be that no amount of information could settle the issue to the satisfaction of authorities in general, since authorities who agree on the empirical facts might simply find it useful to delimit lineages differently, as do authorities on birds who disagree about the number of existing species.

The more we find about species and their close relatives, the more we are bound to find that different trees are permissible. Groups of three or more closely related species are obviously more likely to have closely related nearest ancestral species than groups whose ancestors meet further back. They are more likely to make trouble. The hierarchy is straightforward for lions, bears, and canines; three canine species are another story. The hierarchy is straightforward for pines, watermelons, and citruses; three citrus species are another story.

VI. SYSTEMATICS AGAIN

The observation that there are different legitimate trees has practical interest. And it has obvious bearing on the work of those who are trying to obtain a picture of the whole panorama of life. Both points can be seen in implications for the work of conservationists, as a cursory reflection will indicate. Both points can also be seen in implications for the practice of systematics, as a cursory reflection will *not*

²⁹ Barbara King, *Biological Anthropology: An Evolutionary Perspective, Part I* (Chantilly, VA: Teaching Co., 2002), pp. 164, 170; Monroe W. Strickberger, *Evolution* (Sudbury, MA: Jones and Bartlett, 2000, 3rd ed.), p. 483.

³⁰ King, *Biological Anthropology, Part I*, p. 159.

³¹ An example is Strickberger, *Evolution*, p. 483.

³² King, *Biological Anthropology: An Evolutionary Perspective, Part II* (Chantilly, VA: Teaching Co., 2002), p. 17.

³³ Stringer, "The Evolution of Modern Humans: Where Are We Now?," *General Anthropology*, vii (2001): 1–5, at p. 3.

indicate. I return to the connection to systematics in the present section.

In the practice of systematics, as I have observed, cladists tend to trumpet the need for one legitimate, objective, unambiguous ordering of living groups. Cladists also insist upon cladism's unique capacity to fulfill that need. There is some truth to the claim that the order of evolutionary branching is objective: it is objective if you ignore troublesome species. But that is to ignore a lot of texture in the history of species. It is no wonder, then, that cladists often advertise that one can in principle capture *all* texture down to the level of branching species in a unique, legitimate rendering of the order of species: the objectivity is supposed to start at the level of distinguishing sister species. Hennig is supposed to show how species should be delimited in time in order to allow for objectivity in the phylogenetic hierarchy of species.³⁴

According to Hennig, every species originates with a speciation event and goes into extinction with a speciation event.³⁵ A speciation event is a branching forth of a new species. Each species begins with a forking event and ends when it itself forks into separate species (see figure 6).³⁶ When does speciation occur? Is it, for example, when a species divides into groups that are no longer interfertile that the species goes extinct and new species are born? Hennig has little to say about this.

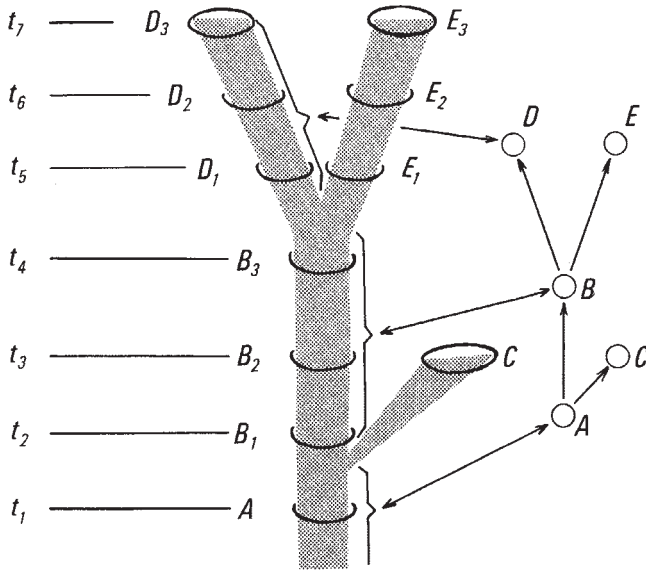
Hennigian constraints on the recognition of species are controversial. Because branching is necessary for speciation, Hennigians cannot recognize *anagenetic* speciation. Thus, species D in figure 6 cannot be divided into more than one species (D1, D2, and so on) no matter how much the D-lineage changes in genetic constitution, breeding habits, and so on, between the numbered segments and no matter how long the time period from each numbered segment to the next; only one species can be recognized because there are no branching events between the segments.

Branching is also sufficient for speciation. This can be awkward if there is little change in a branching lineage: thus, in figure 6, species A goes extinct upon the arrival of C, even though the lineage including A and B does not evolve at all.

³⁴ Kornet, "Permanent Splits"; Meier and Willman, "The Hennigian Species Concept"; "A Defense," p. 167; Ridley, "The Cladistic Solution," pp. 2–4.

³⁵ Hennig, *Phylogenetic Systematics*, p. 66.

³⁶ For the sake of recognizing hybrid species and species that leave no descendants, Hennig's definition must be slightly modified.

Figure 6: Cladistic species.³⁷

In actual practice, authorities are not apt to split species like *Homo erectus* in time wherever there is branching; no one names a new species where *Homo floresiensis* branches off. And authorities do recognize new species without knowledge of branching.³⁸

No doubt there are epistemic reasons for recognizing species' survival through speciation or for recognizing speciation in the absence of branching. One might know that two preserved specimens belong in a common lineage without having much information about whether any speciation events have occurred in the time between the two specimens. Then it might seem to make sense to place the two specimens in a common species, even though there is no evidence one way or the other whether the specimens could fulfill Hennig's criteria for conspecificity. In the same way, one might know that substantial differences distinguish two preserved specimens. In that case, it might seem sensible to place the organisms into different species even if there is not much information about whether any speciation event

³⁷ From W. Hennig's *Phylogenetic Systematics*. Copyright 1966, 1979 by the Board of Trustees of the University of Illinois. Used with permission of the University of Illinois Press.

³⁸ See Strickberger, *Evolution*, p. 483; Lahr and Foley, "Palaeoanthropology"; Stringer, "Human Evolution."

separates the two specimens or whether, instead, the changes between the earlier and later forms came about by way of evolution in a single unbranching line.

Hennigian species are sometimes rejected for reasons having nothing to do with our limited state of knowledge: Mayr complains that Hennigian constraints produce "biological nonsense."³⁹ A look at actual classification indicates that other practicing systematists agree: even where records about branching are very complete, species are often not taken to be delimited in time by branching events.⁴⁰

There are, then, initially plausible considerations *against* Hennigian constraints on the delimiting of species. There are also initially plausible considerations in *favor* of Hennigian constraints on the delimiting of species, as I have indicated: orthodox cladists insist that only the Hennigian species concept preserves the objectivity of the resulting classification. A complete classification of species and their place in the hierarchy of life ceases to be objective if systematists are allowed to make judgment calls about when enough change marks a lineage to legitimate a decision to recognize that a new species has emerged.

A lesson of the foregoing sections is that initially plausible considerations in favor of Hennigian constraints are overstated. The Hennigian species concept does not preserve any single, unambiguous account of species and their relationships to one another. There is no such account, not even in principle.

If Hennigians are to make a decent case for a general adoption of their proposed practice, it will have to be better than the familiar fare. Without such an argument, there is little theoretical barrier to the common practice of delimiting the endpoints of species in other ways.

VII. CONCLUSION

We may whittle a tree of life, paring troublesome branches, in order to portray an ordering that admits of no legitimate dissent. But the history of life can sustain many legitimate arrangements of the same branches. This observation affects relationships of much interest. It undermines a thoroughgoing cladistic systematics.

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³⁹ "A Defense," p. 164.

⁴⁰ Meier and Willmann acknowledge this, citing species of freshwater gastropods: "A Critique from the Hennigian Species Concept Perspective," in Wheeler and Meier, eds., pp. 101–18, p. 105; see also Wiley and Mayden, "A Critique from the Evolutionary Species Concept Perspective," in Wheeler and Meier, eds., pp. 146–58, at p. 157.