On Systematists' Single Objective Tree of Ancestors and Descendants

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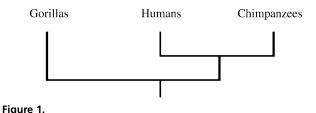
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Abstract

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. This position is not right. 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 of species. The same can be said about other taxonomically relevant groups besides species, such as "Least Inclusive Taxonomic Units" (LITUs), so the basic claim survives even if we abandon traditional species. Similarly, the claim survives even if we distinguish between synchronic and diachronic groups, even if we consider polytomies, even if we distinguish between models and the world modeled, and even if we recognize an objective world. Nor is the claim merely an epistemic one.

Keywords

BSC, cladism, Paul Griffiths, paraphyletic, polytomy, PSC, Mark Ridley, species, Kim Sterelny, systematics



Humans and chimpanzees comprise a monophyletic group.

Cladistic classification, founded by Willi Hennig (1966), takes into account just relationships of ancestry and descent. The alternative is to take into account evolved similarity. Similarity allows for a multiplicity of permissible classifications. Griffiths and Sterelny (1999: 196) follow many others in stressing this: "as cladists never tire of pointing out—similarity depends on the traits you measure." Consider whether chimpanzees are more similar to gorillas or to humans: there might be no unique answer. But genealogical relationships are supposed to be different.

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. (Griffiths and Sterelny 1999: 197)

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" (Ridley 2004: 480). Of course, in practice we may have a hard time *discerning* relationships. Still, there is just one correct account of the relationships: "One True Tree of Life" (Griffiths and Sterelny 1999: 194). 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" (Ridley 1997: 202).

In this article, I briefly present arguments that there is no single, objective tree of life of the foregoing sort: a tree that honors a single order of genealogical relationships between species. My central claim has been the target of more opposition than I would have expected (sometimes the opposition has been more violent than I would have expected, too, even for a discipline as notoriously bellicose as systematics). Some interesting objections were aired at the "Edges and Boundaries" conference, work from which is published here; other interesting objections have been aired in other professional venues or presented to me by friends in personal communication. I make no attempt in this short work to cite in any comprehensive way the biologists and philosophers to whom I react; nor do I cite all who have provided me with reactions.¹ I just address salient objections that have been brought to my attention, especially those that seem common or natural.

In the first section, I rehearse central arguments (presented at the "Edges and Boundaries" conference and more fully in other published work: LaPorte 2005). In the second section, I respond to worries. This gives me the occasion to expand a little on points implied but not stated earlier, in order to express claims more sweeping than those originally stated in the first section.

The Basic Case

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, at least if the problem is as recalcitrant as I think it is. I will not here defend my position 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, but I *will* argue that if this is right, then a group of species may allow for many valid accounts of the order of evolutionary branching and the resulting familial relationships. I will then suggest that appeal to the species problem is dispensable. I also discuss the nature and extent of valid diversity in accounts of evolutionary relationships.

A Diversity of Species Trees

Consider some species concept that is popular with lumpers, like Mayr's biological species concept (BSC), and another species concept that is popular among splitters, like Cracraft's phylogenetic species concept (PSC): these are two popular construals of "species," one of which would cut the organic world into fewer species than the other. Again, my assumption here is that neither concept trumps the other: there may be more than one natural arrangement of a given group of organisms into groups traditionally called "species" (for support, see LaPorte 2004: 70-76). What I will argue here, on the basis of this assumption, is that just as there may be more than one natural arrangement of a given group of organisms into "species," so there may also 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 BSC, as a species divided into two subspecies, while for the PSC 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

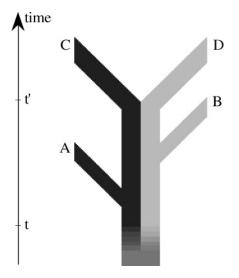


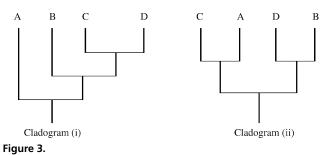
Figure 2. Between t and t', the trunk is comprised of two borderline species.

are to be depicted. One account will recognize two branches, the other just one. But it might be thought 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 trunk in Figure 2 begin as one incontrovertible species.

Later the species divides into two more-or-less distinct lineages, represented in pale 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 BSC or the PSC 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.

Familial relationships between the species A–D vary depending upon whether the trunk is comprised of one or two species. If the division occurring at around t is only into subspecies, so that the two sides of the trunk of the tree are still to be counted as belonging to just 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 BSC, is represented by Cladogram (i). On the other hand, if the division prior to t is a division into



Two different accounts of the monophyletic groups.

separate species, in accordance with the PSC, then Cladogram (ii) is the proper one for representing the world. (Cladogram [i] and Cladogram [ii] are represented in Figure 3.) Now C and D are no longer sister species, and there are other distinct changes.

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 of the cladograms is correct. There is no single, objectively correct branching diagram depicting the hierarchy of species. Similar considerations show that even given a single species concept, we will sometimes find that a group of organisms fails to privilege straightforwardly just one cladistic tree, since it is unclear how to apply the species concept in view of somewhat distinct subgroups within the relevant group of organisms (see LaPorte 2005, §IV). Thus, even if we restrict our attention to the BSC, we are bound to find cases like that depicted in Figure 2, in which there is no definitive answer as to whether there are two species present along the trunk or just one species divided into two subspecies. Cursory reflection on other species concepts indicates that their application is no more cut and dried than the application of the BSC. As the great G. G. Simpson (1961: 152) observes, "To insist on an absolute objective criterion would be to deny the facts of life, especially the inescapable fact of evolution."

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 line of ancestors has been separated from that of any other living reptile for hundreds of millions of years. Because the relevant lineages have been separated for so long, the two gecko species share myriad common ancestral species that the tuatara does not share, on any account of how species are delimited. Gaps between species produce lots of relationships like these. 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 article does nothing to upset the objectivity of many hierarchies like these.

There is something 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 can expect to obtain an ordering that admits of no legitimate dissent, in view of the empirical facts.

But if there is something to be said for objectivity, there is something 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 (and these relationships can be of great interest, as I illustrate with a detailed example elsewhere: LaPorte 2005, \S V).

Worries

In this section, I canvass salient objections that have been brought to my attention.

Objection From Paraphyly

"It is supposed to be *indeterminate* whether the dark and pale sides of the trunk in Figure 2, call them 'Trunk_d' and 'Trunk_p,' are different species. Yet once we have the information that the branching events would occur as Figure 2 shows, then we should say that the split between Trunk_d and Trunk_p happened before t', where Figure 2 shows that they separate by any standard. Any proper account of species ought to respect this earlier split, in order to avoid paraphyly. Paraphyly would otherwise come because the species represented by the trunk, call it 'Trunk_{d+p},' would share its closest common ancestor with an outsider, namely A (we may ignore the other branches in Figure 2), which is not conspecific. Trunk_{d+p} would not be a legitimate genealogical group, which a species has to be. So the proper diagram is (2) not (1)."

This is an interesting objection; but the sort of species concept to which the objection tacitly appeals seems doubtful. It is probably too stringent. We could suppose, in the extreme case, that there is nothing at all to distinguish the two sides of the trunk in Figure 2 except geography. If we reject paraphyletic species, we must even so recognize two distinct species on the trunk, $Trunk_d$ and $Trunk_p$: but then we would seem to be replacing traditional use of "species" with a related but distinct notion.

The foregoing objection seems flawed, at least as an account of *traditional* species. Even so, the essence of the objection can perhaps be preserved with a little reformulation. Suppose we are willing to speak of two "species" on the trunk, according to some updated use of "species," even if the two sides of the trunk are just geographically isolated. Or suppose that we are willing to give up on species altogether. In either case, we might do well to refine the foregoing objection, proposing something like the following:

Objection From the Irrelevance of Traditional Species

"Let us focus on strict genealogical groups of organisms: lineages, not species (according to a traditional understanding of 'species'). Now the correct diagram is again (2), not (1)."

This objection lets us reconstruct what was really central and compelling about claims to objectivity without worrying about the baggage attending the traditional notion of species. Proponents might favor populations rather than species, or what are sometimes called "Least Inclusive Taxonomic Units" (LITUs) or what not.

Unfortunately, however the objection is formulated in its details, it faces a basic, debilitating problem. Trunk_d and Trunk_p, from Figure 2, are supposed to be *borderline* species. But *any* type of natural, genealogical group is going to admit such borderline cases, which could be represented by the two shades of the trunk. One should not see the pale and dark on the trunk as representing two clearly defined groups, of whatever type we are discussing; the point of the image is to depict the contrary.

Suppose then that we are interested in stable lineages, regardless of what maintains them, even if it is mere geographical isolation. We get familiar problems. Geographical isolation obviously comes in degrees. So again, the trunk could be an intermediate case, for which there is a very small amount of crossing or very occasional crossing: it could be a matter of discretion whether we should say that we have one genealogical group or two between Trunk_d and Trunk_p. Think, for example, of a peninsula or an island separated from the mainland by currents that usually prevent crossing but that can also relax. If a semi-isolated group on a peninsula or island is represented by Trunk_p, say, which colonizes different islands from which arise new species B and D in Figure 2, we get the familiar results.

Objection From a Distinction Between Synchronic and Diachronic Groups

A third objection that, like the former two, alleges that I have somehow mischaracterized the relevant groups, goes something like this: "Perhaps the proposal that there are different live options, in the form of (1) or (2), for representing the relevant situation in Figure 2, rests on a confusion between something like a time-slice of a species (or genealogical group) and a species as it is spread out in time. At a time the matter resolves itself; it is only when we consider groups over time that we get ambiguity. So we should be considering synchronic groups, not diachronic groups."

This objection is unsuccessful, because to find a correct ordering of groups at a time, provided that these are arranged by historical relationships, one clearly has to take into account different times. Take a given time, say t'', which is the last

moment depicted in Figure 2: all branches A–D have speciated from the trunk. No one disputes that A, B, C, and D are separate species (genealogical groups, what have you) at this time, but of course this was not supposed to be problematic: the Cladograms (i) and (ii) agree in recognizing these distinct groups. Still, there is a choice to be made between Cladograms (i) and (ii): and the selection will depend on how many species (or genealogical groups) one recognizes at *other* times, including, say, the moment after A splits. Do we have two prongs then (A and Trunk_{d+p}) or three prongs (A, Trunk_d, and Trunk_p)? If we say there are two prongs, then we reject Cladogram (ii) as a correct ordering at later time t''. If we say there are three prongs, then we reject Cladogram (i) as a correct ordering at later time t''. So different times matter to deciding the correct representation at a time.

Perhaps it is time to try a different sort of objection. The foregoing objections all raise trouble with the way I have characterized groups. But even if there is no problem with the groups that I have recognized, there may be some single hierarchical ordering of the groups represented by Figure 2. Here is a natural suggestion:

Objection From Epistemicism

"The two depictions, represented by (1) and (2), of the order of division into species (or genealogical groups, or what have you) can be resolved by more information. So it is really just an epistemic problem."

On the contrary, no amount of information will resolve the matter. The peninsular subgroup Trunk_p giving rise to B and D is just a borderline member of the larger group comprising the entire trunk: there is some crossing, but it is infrequent enough that it gives rise to difficulties with attempts to say whether there is one species here (or what have you) or more. All the relevant information to be found will simply provide details to confirm this: e.g., details according to which Trunk_p is seamlessly united with Trunk_d in such and such millennium but then is isolated for the next several millennia, except when six specimens cross to the mainland at time t^n to cross with such and such population in Trunk_d , and so on. More information here confirms or could confirm the unclarity of the matter; it does not clarify. So the hierarchy depicting the order of speciation remains unclear.

Let us try yet a different tack to put pressure on the thesis in question. We might say that since there are different ways to go, what we have is an unresolved case or a tree with *just one node*: a polytomy.

Objection From a Third Interpretation of Figure 2

"The correct ordering is represented not by Cladogram (i) or (ii) but by Cladogram (iii), as depicted in Figure 4."

Scientists often use polytomies to represent unresolved relationships, where more information is needed. But let us

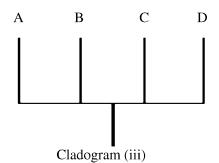


Figure 4. Yet a third account of the monophyletic groups from Figure 2.

set aside this merely epistemic appeal: it is irrelevant to the case at hand, as I have explained (see the foregoing discussion of the Objection from Epistemicism). Is it straightforwardly true that the correct tree, in view of all relevant information (again, not just the known information), is Cladogram (iii) in Figure 4? No. There could be clear cases in which Cladogram (iii) in Figure 4 is the right depiction of the order of species (or what have you); but there could also be borderline cases. Figure 2 represents a borderline case.

An example of a polytomy that does straightforwardly represent all relevant information might be one representing, say, a group of several cichlid species that has speciated at once from a common ancestor: cichlids speciate rapidly. But in other cases, it is not clear that more than two species split off at once, either because it is clear that they do not split at once, or because it is unclear how to describe the case. In the event that it is just an unclear case, one might claim justifiably on one basis that two groups share an ancestor to the exclusion of a third even though on some other basis one might claim justifiably that they do not, but rather that a *different* two groups in that same trio do the exclusive sharing (I present these options in Figure 3). Yet other considerations would favor saying that in such debatable circumstances the best conclusion is that none of the groups excludes another, so that a polytomy is the proper representation: but this third choice for compromisers amounts to yet one more option to choose from, if the case is truly unclear, in the manner in which I have stipulated. So I do not exhaust in Figure 3 all of the possible representations of the organisms in Figure 2: we could add Cladogram (iii) from Figure 4 and indeed we could extend still further the list of cladograms to choose from, though I will not do so here.

The foregoing objections are more or less theoretical in nature. Perhaps a look at scientific practice can generate a better objection.

Objection From Scientific Appeal to Individuals and Characters

"Scientists do not talk much about what species or group comes from what species or group. Their cladistic trees often order just a few representative *individual* organisms on the basis of certain genetic characters, say. So scientists could settle on Cladogram (i) or Cladogram (ii) and be right, even in view of the situation depicted in Figure 2, depending on the individual organisms and the genes or characters considered."

This objection seems beside the point. My claim is one about systematics and the ordering of groups of organisms into hierarchies of species (or other groups). That cladistic trees can be used for other purposes, with or without problems or conflict, is not relevant.

My aim is not to criticize the ordinary construction of cladistic trees. It is a criticism of ambitious appeals to some single cladistic tree that represents the history of species or other taxonomically relevant groups (genealogical groups, LITUs, and so on: see the Objection from the Irrelevance of Traditional Species). Thus, when Ridley (2004: 479) says "in a cladistic classification sister species are classified together. The branching hierarchy of ancestral relations is a unique hierarchy," it is a mistake. It is a *natural* mistake when one compares cladistic systematics with phenetic systematics, but it is still a mistake.

A final sort of objection appeals to the hard-headed conviction that, after all, there is just one way that the world is. I consider two related objections.

Objection From a Distinction Between Models and the World Modeled

"Where different *models* might represent the organisms in Figure 2, there is just one history of the world: so different models cause no problems for the claim that there is a single order of speciation represented by one or another possible model."

I would agree that there is just one history of the world in all of its detail. But that does not make for just one history of species or similar groups: something like *this* is what an ambitious systematist needs in order to claim that one particular model is the right one for representing the hierarchy of species. Of course, if the objection is softened to the claim that lots of models might represent the hierarchy of species differently, each with its legitimate point of view, even though there is just one history of the world in all of its detail, then the objection concedes my central claim.

Objection From Appeal to an Objective World

"There is one history of the world in all of its detail: that has just been granted. But then the unclarity at issue is not *ontological*: so it has to be merely epistemic after all, contrary to previous conclusions."

The foregoing objection suggests a false dichotomy. I deny that the problem is merely epistemic (see the reply to the Objection from Epistemicism). But this leaves room for different accounts of what sort of problem it is: some of these accounts are more ontologically oriented than others. A reasonably good account is probably this: the problem rests in the nature of our *language*, which is not up to the task of representing the world clearly. God could give a molecule-by-molecule account of the state of the world at any given moment or over any given time period. This could include all that we need to be able to give an intelligent account of the "species" or "salient groups" into which the history of life divides. But this does not mean that everyone must give the same answer, after all the information is in, to the question, "what is the order of speciation?" So the problem is not that there is no way that the world is. The problem is that the way that the world is does not lend itself to neat accounts of "species" in the required way. And that, we can say, is a problem of our representation in language: "species" lacks precision.²

Conclusion

There is no unique tree of species embracing life forms in general. A look at salient objections confirms and clarifies this point, and allows me to extend the point beyond species to lineages of different sorts. My central point does not signal trouble for our conviction that there is a way that the world is, in all its detail. But it does create trouble for claims on behalf of a single objective hierarchy of species or other such groups to which systematists might be beholden.

Notes

1. I will mention just three respondents who have raised especially intelligent and detailed criticisms and observations: Joel Velasco, Marc Ereshefsky, and Matt Haber. Elsewhere (2005) I cite sources to whom I myself respond.

2. A parallel might help: consider strength instead of species. Anyone in the National Football League could be placed above your average dweller in a nursing home, for strength. But when we compare certain harder sets of individuals, we will find "strength" to be ill-defined: some individuals will be better at the dead lift and others at the bench press, say, or some will have the strength to budge a heavier load than others who can budge less but lift more to the end of their reach. So different workers with the same information about what people can lift and how, could produce somewhat different representative hierarchies, when it comes to giving an account of strength for players in the NFL, say. The reason that a multiplicity of representative hierarchies arises is that a command to represent "*the* hierarchy according to *strength*" is not a precise one. The reason is not that no detailed account could in principle be provided about who can lift what, how high, and under what circumstances.

Of course, the problem *is* ontological insofar as the world does not present a single, straightforward hierarchy of the ill-defined sort in question. Strictly speaking, it might be best to say that there is no such thing as "strength" or "species," "lineages," and so on, until we *precisify* in a context, at least where borderline cases are in question.

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