Title: Species Concepts Should Not Conflict with Evolutionary History, but often do

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Abstract: Many phylogenetic systematists have criticized the Biological Species Concept (BSC) because it distorts evolutionary history. While defenses against this particular criticism have been attempted, I argue that these responses are unsuccessful. In addition, I argue that the source of this problem leads to previously unappreciated, and deeper, fatal objections. These objections to the BSC also straightforwardly apply to other species concepts that are not defined by genealogical history. What is missing from many previous discussions is the fact that the Tree of Life, which represents phylogenetic history, is independent of our choice of species concept. Some species concepts are consistent with species having unique positions on the Tree while others, including the BSC, are not. Since representing history is of primary importance in evolutionary biology, these problems lead to the conclusion that the BSC, along with many other species concepts, are unacceptable. If species are to be taxa used in phylogenetic inferences, we need a history-based species concept.

Keywords: Biological Species Concept, Phylogenetic Species Concept, Phylogenetic Trees, Taxonomy

1. Introduction

A central task in the field of biological systematics is the development of a theory to guide our taxonomic practices in constructing biological classifications. Systematics today is dominated by the phylogenetic perspective – the view that evolutionary history is of primary importance when delimiting taxa. These taxa are the formally named groups, such as *Homo sapiens*, that are hierarchically arranged in a classification system.

Reconstructing the history of these groups – the project of phylogenetic inference – involves discovering where particular organisms fit on the Tree of Life. Because of this goal, groups like the traditional Reptilia, which cannot be properly placed on a tree, cannot be taxa. Similarly, groups such as the birds plus the bats, a group we might call "flying tetrapods"[1], which have no unique history, cannot be taxa. Yet, in spite of the dominance of the phylogenetic perspective, a number of non-phylogenetic (or non-history based) species concepts remain popular among biologists. One of them is the so-called "Biological Species Concept" (BSC). This and other non-phylogenetic species concepts lead systematists to make the same type of errors as those engendered by Reptilia and "flying tetrapods". These errors are not mere logical possibilities; they arise frequently in biological practice.

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[1] The pterosaurs, an extinct taxon closely related to dinosaurs, were also flying tetrapods.

The goal of this paper is to argue for the necessity of a phylogenetic species concept. I do this by arguing that a set of views and a set of practices, both widely endorsed by biologists, are incompatible. The argument is essentially as follows:

1) A species concept determines the parent-offspring (or genealogical) relationship between species (via its implied definition of speciation).
2) A phylogenetic tree represents genealogical relationships between groups and is used to make inferences about evolutionary history.
3) When we use a non-phylogenetic species concept, and these groups are placed on phylogenetic trees, the tree has false implications about evolutionary history.

Therefore, 4) We need a phylogenetic species concept.

It is an unquestionable fact that a central part of modern evolutionary theory is the use of phylogenetic trees to make inferences about evolutionary history. However, in this paper I give no argument that we <u>must</u> place the groups we call “species” on trees to make historical inferences rather than having separate systems for classification and for use with trees. Rather, I simply point out that if we do place species on trees, as is the common practice, and we use trees to make the kinds of inferences that we typically do make, then we must have a phylogenetic species concept.

2. Phylogenetic Trees

The argument in this paper depends in crucial places on properly understanding what a phylogenetic tree represents and how we make phylogenetic inferences using trees. In addition, important concepts, such as what a monophyletic group is, are easier to understand by referring to trees. For these reasons, I will provide a fairly substantial introduction to "tree thinking" before developing the key arguments of this paper. Figure 1 displays the relationships of several vertebrate groups placed at the tips of a tree. These groups share a common ancestor deep in the past. As time passes, we move up the tree and single lineages divide into descendant lineages – for example, at the first node, node y, one of these lineages eventually leads to the sharks while the other leads to the other four groups.

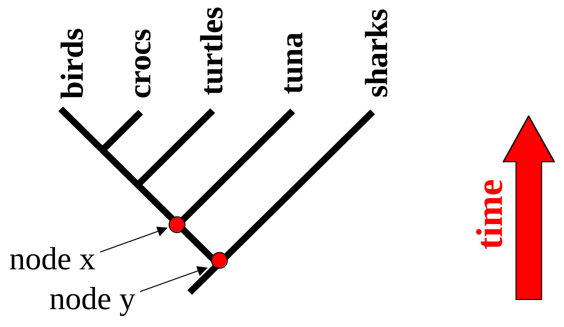

Figure 1. A phylogenetic tree depicting the genealogical relationships between various groups of vertebrate animals.

Groups shown on a phylogenetic tree are understood to be related to each other genealogically in the same way that individual organisms within a family tree are. You are more closely related to your first cousins than to your second cousins since you and your first cousins share grandparents rather than just great-grandparents. Similarly, tuna are more closely related to birds than they are to sharks since tuna and birds share a common ancestor at node x, while tuna and sharks share an ancestor at node y (which is earlier in time). There is an ancestor shared by tuna and birds (at node x) that is not an ancestor of sharks; on the other hand, every ancestor shared by tuna and sharks is also an ancestor of birds. By generalizing this example, one can see that horizontal distance among the tips on a tree means nothing when it comes to degree of relatedness. Though it may seem that tuna and sharks share many properties that might lead you to believe that they are closely related, it is recency of common ancestry, not morphological similarity, that defines genealogical relationships.

An essential concept for phylogenetics is that of a monophyletic group. A monophyletic group consists of an ancestor and all of its descendants. Two nested monophyletic groups are depicted in Figure 2a. Birds + crocs form a monophyletic group within the larger monophyletic group composed of birds + crocs + turtles.[2] Groups are called "paraphyletic" when they include an ancestor, but not all of its descendants. Groups that include multiple groups of organisms, but that do not include their common ancestor are called "polyphyletic". The most recent common ancestor of tuna and sharks is also an ancestor of birds. This means that tuna + sharks is not monophyletic.

A key fact about monophyletic groups that partially explains their importance is that in a purely diverging tree (i.e., one in which branches split but never join), a single

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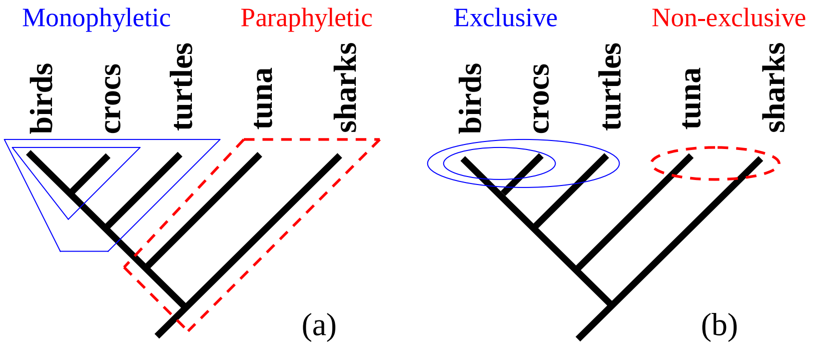
[2] There is some ambiguity in this standard definition of monophyly. The group that is truly monophyletic is the most recent common ancestor of birds, crocs, and turtles together with all of its descendants. This would include lizards, snakes, tuataras, and various extinct taxa, but they are not on this tree. What matters is that neither tuna nor sharks are nested in this group.

time-slice of a monophyletic group forms a group that is genealogically exclusive – members of the group are more closely related to each other than any of them is to anything outside the group (see Figure 2b). Non-monophyletic groups do not lead to exclusive groups. Exclusive groups can serve as valid tips of trees since there is a branch on the Tree of Life that leads to them and only to them.

Figure 2. A monophyletic group is composed of an ancestor and all of its descendants. A paraphyletic group includes only some of those descendants. An exclusive group is a contemporaneous group of organisms more closely related to each other than to anything outside the group.

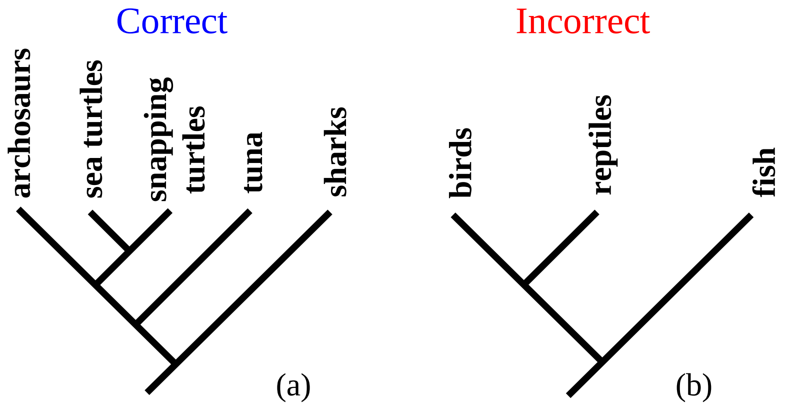


Because monophyletic groups share a unique history not shared by anything outside the group, it is possible to take a monophyletic group and “collapse” it into a single exclusive tip with a single lineage leading to it. For example, the “birds” tip in Figures 1 and 2 is already a collapsed lineage of over 10,000 species, but it could be further combined with the crocodiles to form the “archosaurs” – the group that includes the dinosaurs (see Figure 3a). This is acceptable since everything outside of the archosaurs (for example, the turtles) is equally related to every archosaur. Monophyletic groups form “clades” – branches on the Tree of Life.

Just as a monophyletic group can be collapsed, it can be expanded as well. A tip that forms an exclusive group can become multiple tips if there are multiple exclusive groups inside it. Since the original tip was an exclusive group, doing this does not disturb the rest of the tree in any way. For example, in Figure 3a two groups of turtles are placed on the tree. These two groups do not exhaustively cover all turtles. Since turtles form an exclusive group, every non-turtle is equidistantly related to every turtle, whether a snapping turtle or a sea turtle – just as is true of the groups depicted in Figure 3a.

If a non-exclusive group such as the traditional Pisces (fish - including tuna and sharks) is placed on the tip of a tree as in Figure 3b, it will lead to mistaken inferences about evolutionary history. This is because the branch leading to this group cannot represent real historical lineages since there is no lineage that leads to both tuna and sharks without also leading to birds and a host of other groups. Placing “fish” at the tip implies that all non-fish, like turtles, are equally related to every fish. But this is not true; for example, turtles are more closely related to tuna than they are to sharks. Just as “fish” is a paraphyletic group, “reptiles” (including crocodiles and turtles but not birds) is too, so we cannot put reptiles at the tip of a tree. If we did, we would be misled if we attempted to use the resulting “tree” to infer anything about the history of the groups in question such as determining the dates of nodes, the history of character changes or biogeographical changes, or simply determining genealogical relations among subgroups.

Figure 3. The tree on the left properly combines the birds and the crocodiles into the archosaurs while splitting the turtles into two (non-exhaustive) groups. The tree on the right attempts to place the paraphyletic groups "reptiles" and "fish" onto tips, but is an incorrect tree.



Importantly, the tree in Figure 3b is not incorrect because of its branching order; rather, there is no correct tree with those tips. Including a non-exclusive group as a tip must lead to a false tree. For these reasons (and others) it has become an widely (but not universally) accepted principle of systematics that taxa (the groups of organisms which we seek to formally name in our classification system) must be monophyletic. When traditional groups such as Reptilia and Pisces are discovered to be paraphyletic, they are readily abandoned as taxa.[3] Of course this is not to say that there is no reason to consider Reptilia and Pisces as "real groups" or to stop using their names in all contexts. Rather, these groups are not taxa – they are not part of the single all-purpose classification system that is used to store and communicate information in an efficient manner. An oceanographer may be interested in studying the whales, plankton, and various fishes and

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[3] Some classifications force taxa to be monophyletic by definition. In cases like this, if Reptilia is used, it will include the birds so that birds are reptiles, just as primates are mammals. Here, I use "reptile" and "fish" in the more traditional sense.

other organisms that inhabit a certain geographical location, just as an economist might be interested in studying the group of humans that have graduated from the University of Wisconsin-Madison. The fact that the organisms in these groups share interesting properties should in no way lead us to demand that they are taxa in our biological classification system. Similarly, Reptilia and Pisces can be interesting as objects of study and can be defined as groups of organisms without leading to the conclusion that they must be taxa.

It is important to note that there is nothing essential about the use of phylogenetic trees for phylogenetic inferences – they are simply extremely perspicuous aids to help us represent history. A paraphyletic group cannot be put at the tip of a tree, but that doesn't mean that there is something defective about trees – rather, historical inferences that we might attempt to make using paraphyletic groups will be misleading. Trees simply display an easy way of seeing this. The problem is not that they don't work with trees – rather, the problem is that they do not have a unique genealogical history that is not shared by any other groups.

Furthermore, it is easy to that even if we allowed paraphyletic groups to be taxa in our classification system, they still could not serve as taxa in the sense of being able to serve as the tip of a phylogenetic tree and therefore being able to play a role in a variety of historical inferences. No particular view about classification is being assumed when it is pointed out that reptiles do not share any evolutionary history that is not also shared by birds – this is simply a fact about evolutionary history. Ignoring this fact leads to serious errors.

In spite of this view that taxa must be monophyletic, a number of non-monophyletic taxa continue to be used in systematics; these are some of the “species” recognized by species concepts such as the Biological Species Concept, which group organisms together in ways that are incompatible with genealogical history.

3. The Biological Species Concept

One of the earliest and most influential statements of what is now called the Biological Species Concept (BSC) is the definition given by Mayr in 1942 – “Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups” (Mayr, 1942: 120). Many recent discussions simply drop the “actually or potentially” from the definition, including some by Mayr himself (Mayr 2000). However, Mayr and other friends of the BSC who do this do not intend to alter the original concept. This is clear when Mayr says “interbreeding indicates a propensity” (Mayr 2000: 17); he sees “potentially interbreeding” as redundant, not incorrect. The concept demands that different species possess intrinsic isolating barriers defined as “those biological features of organisms that impede the exchange of genes with members of other populations” (Coyne and Orr 2004: 29). Extrinsic barriers such as mountains and rivers or just simple separation in time or space may prevent actual interbreeding, but these are not the kinds of barriers that make for separate species.

The BSC has survived for decades and remains popular among biologists despite the many criticisms that have been levied against it. However, rather than being a natural fit with evolutionary theory, the BSC in fact conflicts with much of current evolutionary thought. The BSC and its focus on reproductive isolation is a product of the Modern

Synthesis forged in the 1930's and 40's and does not cohere with more recent advances in phylogenetics that began in the 1960's (Baum, 1992). Many phylogenetic systematists have criticized the BSC because it distorts evolutionary history. For example, Rosen (1978), Cracraft (1983), Donoghue (1985), and Mishler (1985), all present versions of the same problem for the BSC – that reproductively isolated groups might be non-monophyletic and as such should not be viewed as taxa. Defenses against this charge have been attempted (Coyne & Orr, 2004; Harrison, 1998), but I will argue that they are unsuccessful. In addition, the criticism of the BSC discussed in this literature pinpoints only one way in which the BSC distorts history. The underlying problem can be used to generate additional and more serious objections. These objections to the BSC also straightforwardly apply to other species concepts that are not explicitly concerned with evolutionary history – for example, the Ecological Species Concept of Van Valen (1976), the Phenetic Species Concept of Sneath and Sokal (1973), the Cohesion Species Concept of Templeton (1989), and the Genetic Species Concept of Mallet (1995). Since representing evolutionary history is of primary importance in evolutionary biology, these problems show that the BSC, along with these other species concepts, are unacceptable.

4. How the BSC distorts history

I will discuss three ways in which the BSC can distort evolutionary history. The first case, which has been widely noted in the literature, is that species picked out by the BSC can be paraphyletic – i.e., they can be composed of some, but not all, of the descendants of some ancestral population.[4] For consistency with the literature, I follow the convention of calling the groups picked out by the BSC “biospecies” even though if I am right, they are often not actually species at all.

The other two ways in which the BSC distorts history rely on the fact that the genealogical history of biospecies is often in conflict with the genealogy of the organisms in these biospecies. This fact will be much easier to understand once we have a more solid grip on the first problem. I will therefore postpone discussion of the other two problems until after we have discussed the first in some depth.

The first problem, which I call “the paraphyly problem”, is that biospecies do not always form exclusive groups. Since they are not exclusive groups, placing them on the tips of trees misrepresents history and leads to incorrect inferences. In fact, this error is more than possible; it often occurs in nature when the BSC is used. For example, start with two or more separate populations of the same biospecies. One of the populations then splits and one of the resulting lineages becomes reproductively isolated from all the others. The population tree (a tree that has populations at its tips) that results is displayed in Figure 4. Although A1 and A2 are historically separated groups, we imagine that there is no intrinsic reproductive isolation between A1 and A2 so they are members of the same biospecies, whereas evolution in the lineage leading to B has resulted in current members of B being unable to reproduce with either A1 or A2. B is reproductively isolated from the A’s, so the BSC entails that B and A are distinct species. Yet, the population A2 is genealogically more closely related to B than it is to A1. Thus A

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[4] It is also possible for a biospecies to be a polyphyletic group. But the difference between paraphyletic and polyphyletic groups depends on classifying ancestral groups which is usually ignored by defenders of the BSC. What is essential to the problem is only that the group is not monophyletic.

(=A1+A2), a biospecies, is not an exclusive group. A is a paraphyletic group since the most recent common ancestor of A1 and A2 is also an ancestor of B.

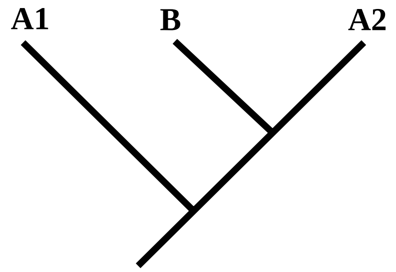

Figure 4. A phylogenetic tree of three populations. Populations A1 and A2 are reproductively compatible with each other, but both are isolated from B.

A real example of this type is supplied by two different groups of moths in the genus *Greya* (Figure 5). In the first case, *Greya solenobiella* is paraphyletic; in the second case, *Greya piperella* is. Harrison (1998) lists several other likely cases from the literature. In fact, when we consider current models of the evolution of mechanisms that induce reproductive isolation, it seems that not only is this kind of paraphyly possible, but that it likely occurs very often. A paraphyletic biospecies often forms when we have founder events such as a splinter group invading an island or when a parasite shifts to a new host within only one local region. Similarly, if an entire population evolves into a reproductively isolated group without splitting, as long as it was more closely related to one of the populations of its ancestral species than to any other, we again have a paraphyletic biospecies (formed from the remaining organisms of the old species).

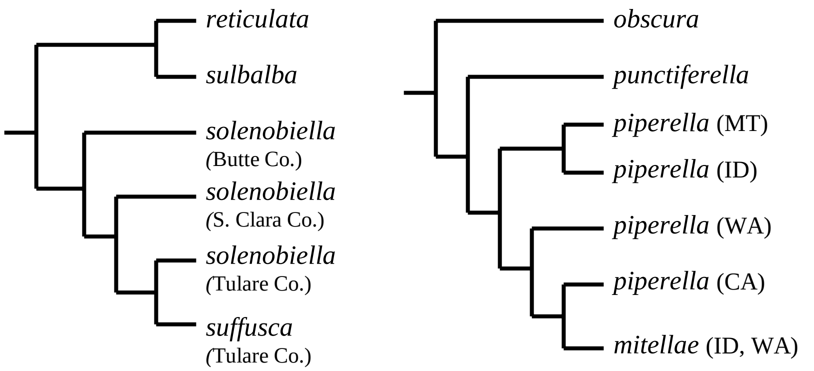

Figure 5. Two groups of moths each from the genus *Greya* (Prodoxidae). Geographical locations are indicated in parentheses. The data is from Brown et. al (1994).

Before discussing this case, it is worth considering one common reply, which claims that it is impossible for a species to be either monophyletic or paraphyletic because these terms apply only to groups of species. The idea is that these terms apply to collections of "atoms", but not to the atoms themselves. This claim has often been made, even by those who are not attempting to defend the BSC (for example, Wiley 1981, and Nixon & Wheeler 1990). My reply is that this point does not address the objection, but is merely a semantic point. Even if we accept the premise that these authors are relying on that species and higher taxa are simply different sorts of entities, the objection is that the BSC allows populations of one species to be more closely related to another species than to other populations in the same species. This has the consequence that species cannot be the tips of phylogenetic trees. If correct, this is a difficulty that even those who wish to restrict the terms “monophyly” and “paraphyly” to groups of species must recognize.

Abandoning the BSC because of scenarios like the moth examples above has been called “fear of paraphyly” (Harrison, 1998). The paraphyly problem stems from the fact that historical splits between groups can take place without the evolution of reproductive isolation between these groups. When the problem is put this way, it is easy to see that many other species concepts also fall prey to it. The phenomenon will occur equally, when “speciation” involves a population switching to a new ecological niche, diverging in morphology or genetic composition, or ceasing to show phenotypic cohesion with other populations.

Authors who notice the above problem tend to develop some version of what they call a “Phylogenetic Species Concept” (PSC). Cracraft (1983) was perhaps the first to use this term. His version of the concept groups species by unique patterns of shared characters and Rosen (1978), Eldredge & Cracraft (1980) and Nixon & Wheeler (1990), among others, present versions of the same idea. A recent explication of this concept defines species as “the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states” (Wheeler and Platnick 2000: 58).

Although these authors criticize other species concepts for being inconsistent with phylogenetic theory, ironically, their “phylogenetic” concept is also unsuitable for phylogenetics. Baum and Donoghue (1995) divide versions of concepts that have been named PSCs into two groups – those that are based on characters and those based on history. Those based on history such as Baum and Shaw (1995) will not suffer the problems that I will allude to. However, the above version of the PSC that mentions diagnosable characters falls in the first group defined by characters and as such suffers the same fate as the BSC for the reasons indicated above. Just as reproductive compatibility can be the ancestral state of a group of populations, a particular character or cluster of characters may be present in an ancestral group. Then populations diverge and one of the new populations loses some or even all of these particular characters. Now two distantly related populations share the combination of traits that is said to suffice for conspecificity and so this character-based species concept also leads to paraphyletic taxa.

When we group organisms by any single property other than genealogical history, it is possible to form paraphyletic groups. It is worth noting that the recent philosophical literature on species has seen the rise of a number of defenses of pluralism about the properties that define species. For example, both Boyd (1999) and Wilson (1999) defend versions of what they call a “Homeostatic Property Cluster” view of species, while Pigliucci (2003) and Pigliucci & Kaplan (2006) claim that species is a “family resemblance” concept. In both cases, the thought is that no one property such as reproductive compatibility or a shared ecological niche is necessary for conspecificity. Since shared genealogy is explicitly declared to not be necessary either, some species grouped by these concepts will fail to form exclusive groups and therefore cannot function as phylogenetic taxa. The further criticisms of the BSC that I will enumerate apply to these other species concepts as well.

5. Responses to the paraphyly problem

In responding to the paraphyly problem, defenders of any of the above species concepts have only two options available: they can deny that it occurs or deny that it is a problem. The first response denies that this kind of paraphyly occurs or perhaps just insists that it occurs only very rarely. But there is nothing special about the *Greya* moths case described above. Consider the literature survey done by Funk & Omland (2003) of 584 animal phylogeny studies published in 14 journals between 1990 and 2002. Of the 2,319 species where paraphyly could have possibly been detected (it can be detected if at least two individuals from the same nominal species are selected), paraphyly or polyphyly was detected in 23% of the cases. And it has been suggested that the numbers would be even higher if plant studies had been taken into account (Crisp & Chandler, 1996; Rieseberg & Brouillet, 1994). While not every traditional species used in these studies was constructed using the BSC, many certainly were. It is implausible to claim that most of these published results are mistaken. Coyne and Orr (2004) attempt to minimize the impact of these numbers, but in the end, they admit that the BSC has misrepresented real history in actual cases.

To some systematists, this represents a fatal blow to the concept, but not to all. Perhaps we should not abandon the BSC too quickly; after all, it would appear that no single concept could do everything we might want. Coyne and Orr develop this reply and then attack other species concepts, arguing that the positive aspects of the BSC outweigh what they see as a relatively small problem. But Coyne and Orr then switch gears and mount the other kind of defense – namely, claiming that paraphyly might not even be a problem at all. They approvingly cite Harrison as saying, “If we accept that species are defined by isolation and/or cohesion and do not start with the assumption that they must be exclusive groups and the units of phylogeny, then including paraphyletic assemblages as species does not misrepresent history" (Harrison, 1998: 25).

An important claim being made here is that "evolutionary history" represents the history of <u>species</u> over time; again, species are being treated as atoms that have no internal histories. These atomistic species would by definition be acceptable as tips of phylogenetic trees and the splits leading to different species would, by necessity, be speciations. In fact, a phylogeny, and therefore a phylogenetic tree, is often defined just this way: "A phylogenetic tree is a representation of the historical course of speciation. … It is the business of phylogenetic systematists to attempt to recover the history of speciation…" (Wiley, 1981: 2). Of course these kinds of definitions can lead to the conclusion that no species concept could possibly misrepresent the phylogeny, but with more careful wording, the idea is simply that the evolutionary history that matters is the history of reproductive isolation. This is what the BSC species tree is said to allow biologists to capture.

However, defining evolutionary history in terms of speciation events in this way is based on a fallacy. Coyne and Orr do provide a number of reasons to think that reproductive isolation is a very interesting property that we might want to study. However, nothing whatever follows about phylogenetic history. Wiley appears to reason that since we want to uncover the history of reproductive isolation, a phylogenetic tree must be a representation of this history. There are two related fallacies in this area. The first is the obviously invalid argument that because reproductive isolation is important, it must be a defining characteristic of species. But the following argument is also invalid:

1) Species are defined by the Biological Species Concept

Therefore, 2) Phylogenetic history is the history of reproductive isolation

I will call this kind of reasoning the BSC fallacy. Other species concepts generate parallel fallacies. I will argue that it is a fallacy by arguing that phylogenetic history should be understood in a way that is completely independent of any particular theory of speciation.

I will continue to refer to the “phylogenetic tree” as the representation that tracks cladogenetic splits – splits in the actual genealogical connections among organisms that constrain the transmission of genes and phenotypic traits. This may be contrasted with the “species tree”, which tracks the history of speciation as defined by some specified species concept. In the case of the BSC species tree, it will track the history of reproductive isolation. It is often assumed that these two trees are the same (or at least consistent), but as we will now see, that assumption is incorrect.

6. The second kind of misrepresentation

Recall that the first kind of misrepresentation of evolutionary history, the paraphyly problem, occurs when reproductive isolation evolves between one phylogenetically distinct population and all the other populations in a formerly unitary biospecies. In those cases, the BSC does misrepresent history in some respect, but the misrepresentation could be considered relatively unimportant as this does not lead to any mistaken inferences about the relationships between species, but only about the history of populations. However, the problem becomes more severe when the species trees don't just fail to inform us of important details, but positively mislead us about interspecific relationships. This happens if there are further speciation events within the paraphyletic biospecies. This is the second kind of misrepresentation: the species tree implies a clear relationship when either there is no such relationship or there is in fact a different relationship. I have divided this second kind of distortion into two cases:

> 2a) The No Tree problem. We want to ask about the historical relatedness of three or more biospecies A, B, and C, but when examined carefully, this question appears nonsensical. The use of an inappropriate species concept has lead to the construction of a tree when none exists.
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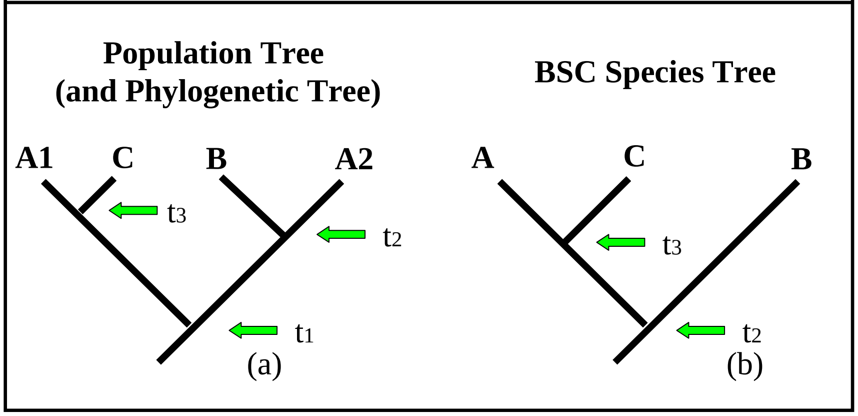
> 2b) The Wrong Tree problem. We want to ask about the relatedness of three or more biospecies and the answer appears to be that A and B form a clade, but the species tree shows something entirely different. Here there is a true tree, but an inappropriate species concept leads to the wrong tree.

To see this new problem, let's add a detail to the population tree in Figure 4. Imagine another speciation event occurs later in one of the A lineages. Perhaps A1 has its own splinter group – call it C. As before, the earliest split, at time t_1, occurs when the lineages leading to B and A2 split from the lineages leading to A1 and C. However, no intrinsic isolating mechanisms have evolved so the BSC species tree does not recognize the split. Then, at t_2, B splits from A2 and becomes isolated from both A1 and A2. Now the new event which was not on pictured in Figure 4 occurs – at time t_3, C splits away from A1 and becomes reproductively isolated. This history yields the trees depicted in Figure 6.

Figure 6. The following trees result when the (A1,(B,A2)) tree of Figure 4 is expanded to account for another split – this time in the A1 lineage. As before, A1 and A2 are reproductively compatible. Thus there are four separate populations, but only three biospecies.



Population Tree (and Phylogenetic Tree)

BSC Species Tree

The problem with this species tree is that it implies an unambiguous relationship between the three species: A is closer to C than it is to B. In terms of biospecies and their ancestor/descendant relationships (as determined solely on the basis of speciations), this is correct and unambiguous. A and C do share a more recent common ancestor than either does with B since A and C were reproductively compatible more recently in the past (before t_3 rather than t_2). The problem is that in phylogenetic terms, it is incorrect to assert that A is more closely related to C than it is to B – A does not have a unique genealogical history. The population tree captures this important phylogenetic distinction, but the BSC species tree does not. The species as a reproductively compatible whole has a history, but individual populations within it have different reproductive histories. It would be better to say that A1 is closer to C while A2 is closer to B. Asking, “Is A more closely related to B or to C?” is asking a question with a false presupposition; it assumes that A has a unique history. But it does not. It is like asking whether animals that can fly are more closely related to crocodiles or to primates. There is no answer – <u>some</u> flying animals (like birds) are closer to crocodiles while <u>other</u> flying animals (like bats) are closer to primates. It is a mistake to ask about the genealogy of flying animals (bird+bats) because they lack a unique genealogical history. Similarly, it is a mistake to ask about the genealogy of biospecies A, and therefore it cannot be placed on a phylogenetic tree, and so cannot be a taxon. This is the type of misrepresentation I have called “The No Tree problem”.

Misrepresentation (2b), “The Wrong Tree problem”, occurs when the species tree implies that a group has one history when in fact it has a different history. Imagine that rather than having one of the A populations in Figure 4 split, reproductive isolation simply evolved between A1 and A2 without any more splits.[5] Here the history is just as in Figure 6, except that at t_3 there is no cladogenetic split, only the evolution of reproductive isolation between already existing lineages. Since it is unclear what is required for either of these populations to be the same species as before, let's simply give them both new names. A1 has evolved into C while A2 has evolved into D. Now we have the three species, C (from A1), B, and D (from A2) shown in Figure 7. Alternatively, we could have the split at t_3 as before and imagine that A1 has simply gone extinct. The tree would be identical.

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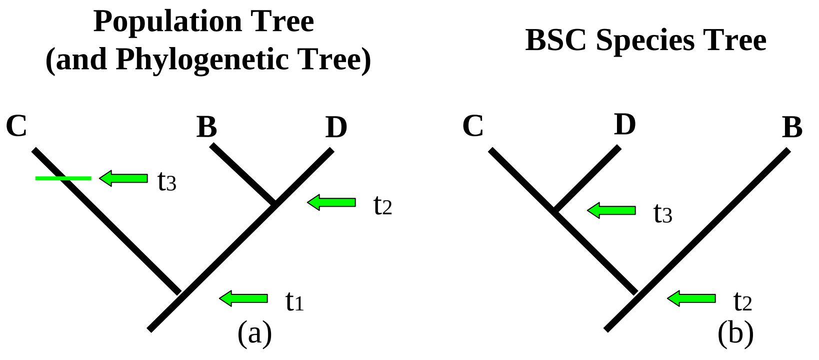
[5] If there are further lineage splits, the problem will still arise as soon as all of the lineages become isolated from each other.

In either of these cases, if we apply phylogenetic methods we will construct a tree with D and B forming a clade while C is more distantly related. Everything here seems correct – in fact, you might suspect that the earlier problem of a paraphyletic species has simply disappeared. Not so. If we take the Wiley/Harrison line that evolutionary history is the history of speciation, then the evolutionary tree (which matches the species tree) will have C and D forming a clade – they share a more recent common ancestor. Thus the phylogenetic tree (stemming from the history of the populations, the organisms, or the genes) and the species tree come apart as in Figure 7.

Figure 7. The following trees result when the (A1,(B,A2)) tree of Figure 4 is expanded to account for the evolution of reproductive isolation between A1 and A2. A1 has now become C whereas A2 has become D.



In summary, if one population out of several becomes isolated, you get a paraphyletic species. But then if another becomes isolated, you get a species tree that is either phylogenetically misleading or just simply wrong. Furthermore, the misleading case will eventually convert to an incorrect case unless the populations that make up the paraphyletic biospecies merge into a single population before any one of them acquires intrinsic reproductive isolation from any other. Thus if the BSC <u>Species tree</u> is what we are trying to infer when we apply phylogenetic methods, it is likely that we will often arrive at the wrong tree (since phylogenetic signal will track the phylogenetic tree) without having any way of detecting that we are making this error.

The talk of attempts to infer the species tree may make the problem seem as though it is merely epistemological. But it is not. In cases such as those in Figure 7, the BSC Species tree is simply the wrong tree as it is not consistent with the Phylogenetic tree. The obvious response is just to reiterate the Wiley/Harrison line that evolutionary history is the species history (and that the BSC is the correct species concept) and that to assume otherwise is blatantly question-begging. In the last section, I will attempt to draw out the consequences of taking this line seriously – consequences which I think are so severe that they cannot be accepted even by the most staunch defenders of the BSC.

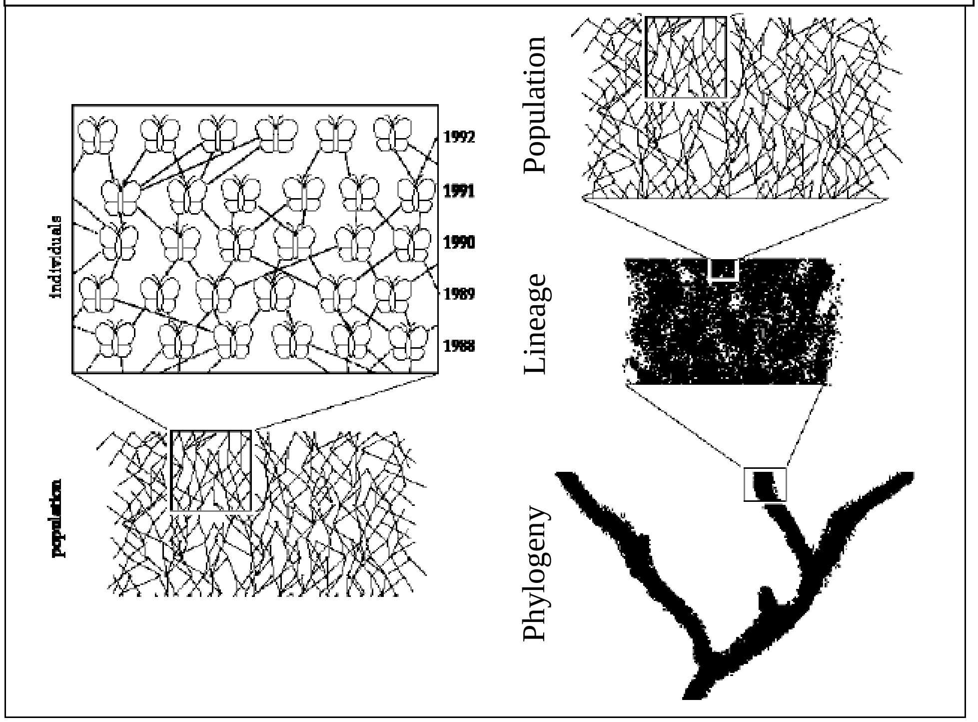
7. Species and the Tree of Life

A few authors have noticed versions of the above problems with non-genealogical species concepts. Bremer & Wanntorp (1979) present a case of a mismatch between geographic isolation and reproductive isolation, but their discussion seems to have been largely ignored in the biological literature (but see Mishler and Donoghue 1982). In the philosophical literature, LaPorte (2005) provides similar examples showing that the BSC and the Phylogenetic Species Concept (the PSC of Cracraft 1983) can lead to different species trees. However, he then draws the wrong conclusion from this observation. Starting from the premise that there is no objective solution to the species problem, he concludes that the trees given by the BSC and the PSC are equally valid and that, therefore, there is no objective Tree of Life. As he points out, this same conclusion follows for many other species concepts.

The basic idea is simple. As argued above, different species concepts lead to incompatible groupings into species. Then different speciation concepts can lead to different orders of branching of the various “species” under consideration (as in Figure 7). But LaPorte is assuming a type of pluralism *about classification* which dictates that each of the groups picked out by the BSC or by the PSC really are species. Each species concept leads to a particular species tree and since these can be different, there are different Trees of Life. He then argues that since there is no reason to prefer a phylogenetic species concept to a biological one or an ecological one, then there can be no reason to prefer the species tree represent the history of speciation according to a phylogenetic species concept over a history of speciation represented by the Biological Species concept.

On this point, LaPorte is correct – If evolutionary trees simply represent the history of speciation, then different species concepts yield different trees. However, it is a mistake to think that this is the same as concluding that the trees are equally correct. There is an objectively correct tree - a phylogenetic tree, not a species tree - because there is an objectively correct history of life. Imagine a full record of every organism and all of their ancestor/descendant relationships connected in one huge network as partially depicted in Figure 8. We can “zoom out” on a portion of the full network of individuals to look at a population which is merely a part of a larger lineage which is merely a “zoomed in” portion of a large-scale phylogeny. When we zoom in very carefully at particular portions of the phylogeny, the relationship of individuals is reticulate and does not appear tree-like. At the “nodes”, or lineage splits, there is no instantaneous separation of one lineage into two, but rather, the borders are fuzzy. However, if we are looking at a current time slice of the phylogeny, the genealogical pattern between the tips is clear. This is not surprising in the least – taking a very careful look at the borders of a material object in space – say a table – will produce equally vague results. Here, we are attempting to find the precise temporal borders of a lineage which is surely vague in precisely the same way.

Figure 8. Picturing a phylogeny as a summary of broad scale patterns in the full network of the genealogical connections of individual organisms. (Adapted from Maddison and Maddison 1992).



Although the full phylogeny is far too complex a structure to perfectly represent in a small picture on a piece of paper, we can attempt to summarize this full Tree (or at least those parts of it that have a tree-like structure) by placing groups of organisms into taxa and then displaying the genealogical relationships among those taxa. But the objectivity of this organismal genealogical network leaves open the question of whether organisms can be grouped in such a way that the species tree properly represents the phylogenetic tree. LaPorte assumes that the Tree of Life tracks just the history of speciation and as such, it is dependent on an arbitrary choice of species concept. However, the Tree of Life is metaphysically prior to, and independent of, any particular species concept that we choose.

We don't create the Tree of Life; we attempt to discover it. The fact that two different species concepts lead to two different trees simply shows that at least one of these trees is wrong and therefore that at least one of these species concepts is wrong (or at least not suited for phylogenetics). LaPorte's conclusion that there is no objective phylogenetic tree is a reductio of his premise that one species concept is as good as another. I have argued that there is something that counts here, namely, that many species concepts, like the BSC, misrepresent history. While different species concepts may pick out groups that are biologically interesting, this is no argument that these interesting groups are *species*. If we aim to have a phylogenetic system of classification where taxa are branches on the Tree of Life, species must be monophyletic groups.

The history of reproductive isolation, ecological divergence, or morphological divergence is certainly interesting, but for studies of evolutionary history, these divergences are only useful in so far as they are reliable guides to what I have called the phylogenetic tree. In fact, even if one is interested specifically in the evolution of reproductive isolation between lineages (or one of the other traits associated with various species concepts), it is essential to first obtain the correct phylogenetic tree as a basis for understanding when and in what lineages various isolating traits evolved. It is a non sequitur to conclude that the BSC is correct based on the assumption that the evolution of reproductive isolation is an important problem. And even assuming that reproductive isolation does define species, this has no bearing on phylogenetic history since speciation events do not define evolutionary history. This is the fundamental problem with the BSC fallacy. Even if we do accept that we want to study the history of reproductive isolation, we should still use phylogenetic trees (not BSC species trees) to help us recover this history.

As noted at the end of the previous section, given the popularity of defining phylogenetic trees as species trees, an obvious response is that I am simply begging the question by calling something else the "phylogenetic tree". Rather, on this view, the phylogenetic tree is the species tree and there is no other tree that one needs to consider. However, not only does this approach lead to the epistemological problem that our methods of inference will tend to reconstruct a tree other than the species tree, but it also leads to bizarre ontological claims. For example, phylogenetic evidence indicates that humans and chimps are more closely related to each other than either is to gorillas. But what exactly does this mean?

The "species tree" view would have it mean that the species *Homo sapiens* and the species *Pan troglodytes* share an ancestral species that is not an ancestor of *Gorilla gorilla*. But it is perfectly natural to also say that any particular human (like myself), shares a more recent common ancestor with any particular chimp than with any gorilla. This may seem like a simple translation (or at least a consequence) of the claim about species relationships, but it is not. The claim about species relationships (for the BSC) properly translates to the idea that reproductive isolation mechanisms preventing the interbreeding of the ancestors of chimps and humans appeared more recently than did reproductive isolation mechanisms preventing the interbreeding of the ancestors of humans with ancestors of gorillas. On the other hand, the claim about organism relationships is a straightforward claim about their genealogy. A human is more closely related to a chimp than to a gorilla if the most recent common ancestor of the human and chimp is more recent than the most recent common ancestor of the human and the gorilla.

In cases of disagreement like that depicted in Figure 7 (which is likely to be quite a large number of cases) these two answers will be different. The following is a description of evolutionary history which is an epistemic possibility consistent with much of the evidence we have about the relationships between humans, chimps, and gorillas. In the past, ancestors of humans, chimps, and gorillas all were part of a single population. Now imagine that the branch leading to gorillas split off from the branch that subsequently splits and leads to both chimps and humans. Next, chimps develop some intrinsic mechanism which isolates them from both humans and gorillas. Lastly, isolation mechanisms develop preventing the interbreeding of humans and gorillas. For all we know, this is how it happened. Our best phylogenetic information leads us to think that we are more closely related to chimps – but this inference is based on facts such as that the genes found in humans appear to share common ancestry with chimp genes more recently than with gorilla genes. This is as it would be if the above narrative were in fact the true history. However, the above story is captured by the “Wrong Tree” problem as in Figure 7 with chimps being group B, gorillas group C, and humans group D. As can be seen from Figure 7, if the above story is correct, the correct BSC species tree has humans and gorillas more closely related to each other than humans and chimps. If the great apes were such a case then, as a species, humans would be more closely related to gorillas, but I (and all other humans individually) would be more closely related to a chimps. This is unacceptable. Phylogenetic trees should be based on the genealogical relationships of organisms not on the order of speciation events (if species are defined in non-genealogical terms). Genealogy is what our methods track and is what common sense tells us is the intended meaning of statements about the evolutionary relationships between species. While there might be some interesting biological relations that track the order of speciation events, surely the very concept of genealogy implies some connection with the passing on of heritable traits. In cases where all of the organisms in A are more closely related to those in B than those in C, what could it mean to say that species A is "genealogically" closer to C?

My position does not to deny that species have genealogical relationships to each other. Nor does it invalidate talk about the history of speciation. Rather, it holds that what we want is a species concept for which the answer to both kinds of questions is the same as answers to questions about the genealogical history of organisms.[6] The acceptance of species concepts such as the BSC allow the formation of non-exclusive groups of organisms as taxa. I have argued that if we allow species to be non-exclusive groups of organisms, we cannot prevent clades of species (such as humans + gorillas in

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[6] Here it would be possible to talk about the genealogical history of a species “reducing to” the genealogical history of organisms, but on some ways of understanding reduction, this actually implies that species do not have a history of their own. I do not want to assert that, and clarification of the proper meaning of “reduction” in this context is not needed to make the essential point that species histories and organism histories should be consistent.

the above story) from being non-exclusive groups either. Not only is there an obvious theoretical tension in demanding monophyly for all taxa except those at the species rank, but if we delimit species in non-historical ways, we cannot prevent these non-historical connections from “bubbling up” and infecting superspecific taxa.

Species are the units of our classification system. Given that theories in systematics demand that classification be based on phylogenetic history, species must be units of phylogeny as well. Even if we want to allow non-monophyletic groups as taxa in our classification system, we still need phylogenetic units. Species play this role in phylogenetic theory. It is in this role that they are placed at the tips of phylogenetic trees and serve as units in historical inferences. We typically treat phylogenies as a record of speciation and treat clades as clades of species. But as we have seen, in order to do this, our species concept must respect phylogenetic history. The BSC, along with the other non-phylogenetic concepts that I have mentioned, fails to do so.

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