The Species Delimitation Uncertainty Principle

Byron J. Adams[1]

Abstract: If, as Einstein said, "it is the theory which decides what we can observe," then "the species problem" could be solved by simply improving our theoretical definition of what a species is. However, because delimiting species entails predicting the historical fate of evolutionary lineages, species appear to behave according to the Heisenberg Uncertainty Principle, which states that the most philosophically satisfying definitions of species are the least operational, and as species concepts are modified to become more operational they tend to lose their philosophical integrity. Can species be delimited operationally without losing their philosophical rigor? To mitigate the contingent properties of species that tend to make them difficult for us to delimit, I advocate a set of operations that takes into account the prospective nature of delimiting species. Given the fundamental role of species in studies of evolution and biodiversity, I also suggest that species delimitation proceed within the context of explicit hypothesis testing, like other scientific endeavors. The real challenge is not so much the inherent fallibility of predicting the future but rather adequately sampling and interpreting the evidence available to us in the present.

Key words: evolution, nematode, phylogeny, speciation, species concepts, species delimitation, systematics, taxonomy.

In the sharp formulation of the law of causality —"if we know the present exactly, we can calculate the future" —it is not the conclusion that is wrong but the premise. —Werner Heisenberg, in his uncertainty principle paper, 1927.

As biologists, we typically have the mistaken impression that the "species problem," or problem of demarcating the boundaries between species and populations, and "higher" taxonomic categories, was first tackled by Aristotle, Linnaeus, or Mayr. To the contrary, early literature pushes the date back much further. In the King James Version of the book of Genesis (Genesis 2:19–20) we read, "And out of the ground the LORD God formed every beast of the field, and every fowl of the air; and brought them unto Adam to see what he would call them:" One interpretation of this passage suggests that God did not know what to make of biodiversity, and sought taxonomic consultation with Adam. The passage continues, "and whatsoever Adam called every living creature, that was the name thereof." This passage provides a glimpse of the origin of authoritarianism in taxonomy, a practice that continues to dominate the field in modern times. Finally, we read, "And Adam gave names to all cattle, and to the fowl of the air,

and to every beast of the field; but for Adam there was not found an help meet for him." The latter passage introduces another legacy of taxonomy, that of inadequate resources and competent technical staff to accomplish the monumental task of recovering and representing biodiversity.

Treating biblical passages, or religious scripture of any sort, as a primary source of scientific literature is not unencumbered by technical and(or) philosophical difficulties (Galilei and Drake, 1974; Langford, 1971). It does, however, serve as yet another example of how long humans have wrestled with taxonomy, and with the problem of species in particular. What is it about the species problem that makes it so persistent? To be sure, species have weird attributes (such as contingent emergent properties and historical connections) that present methodological problems to the process of scientific discovery (Frost and Kluge, 1994; Ghiselin, 1997). Compounding the problem is the fact that infallible species delimitation entails predicting future events (Myers, 1952; O'Hara, 1993). Does this mean the algorithmic process of scientific discovery and progress is precluded from addressing the species problem? Is the species problem intractable? In this paper, I argue that the process of scientific discovery—and the resolution of the species problem, like other difficult problems of scientific inquiry—will continue to approach resolution.

Why the Species Problem Persists

One reason the species problem persists doggedly is that we confuse what species are with how we can find them (Christoffersen 1995; Frost and Kluge 1994). In part, this can be attributed to the semantic baggage associated with the word "species." For example, were I to survey a room full of nematologists from around the

world and ask them what comes to mind when they think of the word "species," I would field a smattering of answers ranging from morphological or ecological distinction to "reproductively isolated populations" or even "cladistically resolvable clusters of entities." With rare exceptions, all of the responses are intrinsically connected to the operational criteria we use to determine species boundaries. The signals we send and receive when bandying the word "species" are entrenched in operational methodology, or how we find species, and have little to do with what species *really* are at all. Talking about species as if they are real, but without any common connotation to the current vernacular, is, in my opinion, the single greatest obstacle to making progress toward solving "the species problem."[1] We try to communicate the reality of an entity we call a species but instead end up wallowing in a jumbled mess of methods for determining species boundaries.

At the heart of the problem is the fact that when we use the word "species" we imply two activities—one of them ontological, the other epistemological. Ontology deals with the nature of being and, in this case, asks, "Is there such a thing as species?" Epistemology deals with the nature of knowledge and asks, "How do we know we have species?" When we talk about species, the ontological activity we are engaged in involves a theoretical definition of what species are.[2] The epistemological aspect deals with how best to go about finding the entities (species) our ontology tells us exist.

Improving Our Notion of What We are Looking for Can Facilitate Better Ways to Find It

Albert Einstein, describing the nature of scientific progress, confided to a friend that ". . . it is the theory which decides what we can observe" (Heisenberg, 1971). By this, I think Einstein meant that it isn't until you can define what it is you are looking for that you can begin to come up with ways of observing it. Seen from this perspective, it is hardly surprising the "species problem" continues to be so pernicious. If we don't know what we are looking for, how much confidence can we have that we will find it?

In 1687 Isaac Newton published an elegant equation that described the metaphysical reality of gravity (Newton 1687; Newton et al., 1729). By "metaphysical" I mean the fundamental reality that exists independent of human observation[3] (i.e., apples fall from trees whether or not people are around to observe them).

Newton's ontological equation accurately described the reality of gravity. Armed with an ontological definition of what gravity is, Newton adapted his epistemological approach to accommodate old data and proposed methods of collecting and analyzing new data and phenomena. This allowed him to explain a wide range of previously unrelated peculiarities, such as the elliptical orbits of comets, ocean tides and their variations, the precession of equinoxes, and the motion of the Moon as perturbed by the gravity of the Sun. It even led to the prediction and subsequent discovery of the previously unforeseen planet Neptune.[4] The discovery of Neptune in 1846 was sensational in astronomy because, for the first time, a planet had been discovered based on predictive reasoning. Newton's ontological definition was incorporated into an elegant series of epistemological equations aimed at predicting where the planet should be. Lo and behold, there it was. Refined theory led to improvements in epistemological methodology that subsequently led to new discovery.

In 1907, two years after publishing his Special Theory of Relativity, Einstein noticed that Newton's expressions for gravitational force depend on mass and distance, but make no mention of time. Without accounting for time, Newton's expressions predict a physical effect that travels faster than light (in fact, it travels at infinite speed). Since the notion was inconsistent with his Special Theory of Relativity, Einstein concluded that Newton's gravitational equations were not strictly correct. Einstein plugged time into the equation and improved upon Newton's notion of gravity.

Einstein discussed his idea with George Hale, who reasoned that if Einstein's theories were correct, during a solar eclipse one should be able to see light emitted from stars known to be behind the sun. According to Einstein, the gravitational pull of the Sun should bend the light of stars that lie behind the Sun around the Sun, making them visible to observers on Earth. Later, in 1919, after the formulation of Hale's epistemological methods, the predicted phenomena were observed (Coles, 1999). The take-home message? The ontological improvement of Einstein's contribution spawned testable hypotheses that led to numerous discoveries that were observable only once epistemological methods were developed. Some of these include the discovery of the gravitational lens (Walsh et al., 1979) and the

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[1] A related problem, but one that lies outside the scope of this paper, is the failure to distinguish between species as a taxonomic category and species as individuals. For a discussion of how this confusion thwarts efforts to deal with the species problem, see Hull (1976).

[2] I am convinced that species are real and not merely figments of our imaginations. Justification for this premise involves treating species as individuals, and not as subjective classes. The ontological reality of species is a major premise of the ideas in this paper, and the reader is encouraged to explore the literature on this subject (Ghiselin, 1974, 1987, 1997; Hull 1978).

[3] My use of the term "metaphysical" should not be confused with its uncomplimentary connotation as a surrogate for the supernatural or paranormal.

[4] Forty years after the discovery of Uranus Alexis Bouvard observed its anomalous orbit and concluded that either Newton's equations were incorrect or there was another unknown body exerting a force on Uranus. In 1845 John Couch Adams used Newton's equations to compute the position the unknown body must be in to produce the observed effect on Uranus. He sent his results to the director of Cambridge Observatory, James Challis, asking him to look for the unknown planet in the foreseen location. Challis ignored him. Two months later, Urbain-Jean-Joseph Le Verrier came up with the same idea and sent his results to Johann Gottfried Galle at the Observatory of Berlin. After only one hour of searching, Galle found the new planet very close to the exact location pointed out by Le Verrier. Adams was scooped. Nevertheless, in 1861, Adams was appointed director of Cambridge Observatory, the position previously held by the man who ignored him (Moore, 1988).

Bose-Einstein condensate (Anderson et al., 1995; Bradley et al., 1995; Davis et al., 1995).[5]

THE PROCESS OF SCIENTIFIC DISCOVERY AND THE SPECIES DELIMITATION UNCERTAINTY PRINCIPLE

If the process of scientific discovery proceeds in biology as it has in physics (i.e., the "normal science" of Kuhn, 1962), shouldn't we be able to solve the "species problem" by simply honing and redefining species ontology and epistemology? David Hull, a philosopher of science and prominent contributor to the literature of species concepts, argues that this can never be the case (Hull 1997). Good theories, argues Hull, like gravity, must be both theoretically (ontologically) sound and universal (applicable to all entities). However, with species concepts, Hull argues that ". . . if a species concept is theoretically significant, it is hard to apply, and if it is easily applicable, too often it is theoretically trivial. Attempts to make them more operational result in their being theoretically less significant." The

inverse relationship between theoretically significant and universally applicable species concepts (as described by Hull) is acutely reminiscent of another phenomenon in the field of physics, the Heisenberg uncertainty principle.

In 1927, Werner Heisenberg noted that the speed and position of an electron could not be simultaneously known with certainty. Simply stated, the more you know about a particle's energy, the less you know about the time of the energy (and vice versa). The same uncertainty applies to momenta (speed) and coordinates (position) (Wheeler and Zurek, 1983). To me, this seems analogous to the arguments of Hull (1997), to whom I will (perhaps unfairly) attribute the "Hull uncertainty principle": Attempts to make species concepts operational come at the expense of theoretical rigor (and vice versa). The same uncertainty applies to the general applicability of the species concept and the specificity of its discovery operations (Fig. 1).

Examples of the inverse relationship between theoretical significance and applicability of species concepts abound (i.e., Mayden, 1997, 1999). For example, consider the Evolutionary Species Concept of Wiley & Mayden (Wiley and Mayden, 2000): "An evolutionary species is an entity composed of organisms that maintains its identity from other such entities through time and over space, and which has its own independent

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[5] Aptly, the Newtonian notion of gravity that allowed Le Verrier to predict the existence and location of Neptune also led him to the conclusion that the orbit of Mercury was influenced by another planet even closer to the Sun. He named the planet Vulcan and calculated its distance from the Sun as 13 million miles, zipping around the Sun in less than an Earth day. Unfortunately, Vulcan doesn't exist. No one has ever seen it, despite Le Verrier's explicit calculations as to where and when to look. Unknown to him, Mercury's peculiar orbit can be explained by Einstein's improvements to Newtonian gravity.
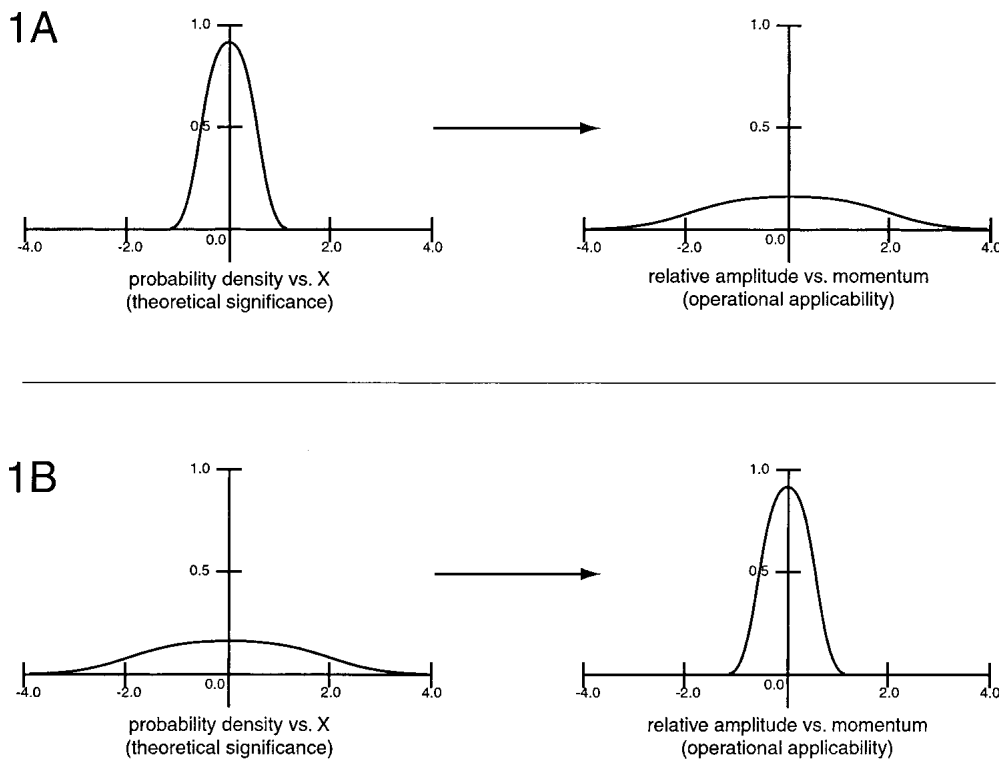

FIG. 1.   Actual probability density plots for determining electron speed and position and, by analogy, theoretical rigor and applicability of species concepts. A) When the probability of accurately estimating the position (X) of an electron is high, the probability of accurately estimating its speed (momentum) is low. Similarly, species concepts that are theoretically robust tend to sacrifice their general operational applicability. B) When the probability of accurately estimating the position of an electron is sacrificed, the probability of accurately estimating its speed is high. Similarly, it appears that theoretical rigor must be sacrificed for discovery operations of species concepts to be explicit and applicable.

evolutionary fate and historical tendencies." This species concept has universal application but is explicitly non-operational.

Contrast the ESC of Wiley & Mayden (2000) to the concept of Wilhelmi (1940): "Species of helminths may be defined tentatively as a group of organisms, the lipid free antigen of which, when diluted to 1:4000 or more, yields a positive precipitin test within 1 h with a rabbit antiserum produced by injecting 40 mg of dry weight liquid free antigenic material and withdrawn ten to 12 days after the last of four intravenous injections administered every third day." Wilhelmi's application is restricted in the scope of taxa to which it can be applied, but it is explicitly operational.

The literature on species concepts is replete with other examples that illustrate and support Hull's idea that, as the theoretical significance of a species concept increases, its applicability decreases (and vice versa). Does this mean that all our efforts to operationally delimit species are doomed to being theoretically trivial?

I believe Hull is right, that we are not likely to develop a single unifying species concept that is both generally applicable and theoretically significant (Hull, 1997; Mayden, 1997, 1999). However, on closer inspection, treating Hull's uncertainty principle in this way is unfair because it conflates ontology and epistemology by lumping theory and application into the same activity (Christoffersen, 1995; Frost and Kluge, 1994; Mayden, 1997, 1999). To do so forces two very different aspects of species into the same equation, but without acknowledging their fundamental differences. This is like saying Newton's simple equation for gravity, without any modification, must simultaneously define what gravity is *and* be able to predict when a particular apple is going to fall on my head. *That's not fair.*

Species Ontology: What is a Species Really?

A species is an entity composed of organisms. It is an individual (in the philosophical sense), not a class. Supraspecific taxonomic categories like genera and phyla are generally treated as classes and are delimited according to the subjective whims of taxonomists.[6] Species, on the other hand, are self-delimiting and exist independent of our observations. They are not merely groups of organisms lumped or split to suit our fancy (Ghiselin, 1974, 1987, 1997; Hull, 1976, 1978).

Species are spatiotemporally limited and are internally cohesive. They maintain their independence from other entities over time and space. That is, relationships

among species are phylogenetic (characterized by splitting). Relationships among species are not tokogenetic (reticulate, as expected among sexually outcrossing members of a population). A species has a unique origin and a unique historical fate. The same species does not arise multiple times, nor does it share its fate with any other entities (Simpson, 1961; Wiley 1978). Thus, *infallibly* delimiting species infers that we know something about the future fate of lineages.

Species Epistemology: How Can We Find Species?

Given our idea of what species are, how can we best find them? Since species delimitation involves predicting the future, it is logical to require evidence that putative species have been evolving independently in the past. As with other sciences, such as geology and physics, the only logical way to proceed is within the law of uniformitarianism. The same processes that we observe now are sufficient to account for the historical relationships among species. If two entities appear to be behaving like species now, then they have probably been evolving independently in the past, and, if allowed to persist on their current trajectory, they will continue to do so in the future. Unique, derived characters that are fixed within a lineage provide the historical evidence of independent evolution sufficient to predict their future trajectory. The purpose of considering the future fate of lineages is to protect against recognizing two or more species where there is historical evidence for the existence of only one. The results of our guesses at the future are based on the best evidence available to us in the present and constitute testable hypotheses (Adams, 1998).

To better illustrate species ontology and epistemology, Figure 2 depicts species as lineages (space-time worms of Baum, 1998). The lineages are comprised of self-replicating organisms and populations. Species X originated sometime between time 1 and time 2, and persisted until sometime between time 3 and time 4 when it went extinct. Species X had a unique origin and historical fate. It arose only once and did not share its fate with any other entity (as we would expect were it to combine with another lineage and *then* go extinct). Similarly, species Y and Z originated sometime between time 2 and time 3, and persist until the present time.

Species Y and Z appear to have unique origins, but we cannot tell what their ultimate fate is until they are extinct. They may behave like two species now, but, if in the future they ultimately coalesce, then they never really were separate species but simply temporarily isolated populations that gave the appearance of having split into two lineages. Taxonomically, the misleading appearance would have to be rectified.[7] Relationships

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[6] Supraspecific categories are not necessarily subjective and can be made to have their own systematic ontogenies (such as the recognition of monophyletic sister taxa). That is, they too can be spatiotemporally limited (but not necessarily internally cohesive). This is rarely the case in the current Linnean system, but unnecessarily so (Christoffersen, 1995; de Queiroz and Gauthier, 1990; Nixon and Carpenter, 2000). Still, even if higher taxa are spatiotemporal, monophyletic portions of a phylogenetic tree, decisions as to where to make divisions are open and more arbitrary than delimiting species.

[7] Ontologically, an isolated, integrated lineage constitutes a species regardless of its fate. Requiring historical evidence of independence is a methodologi-
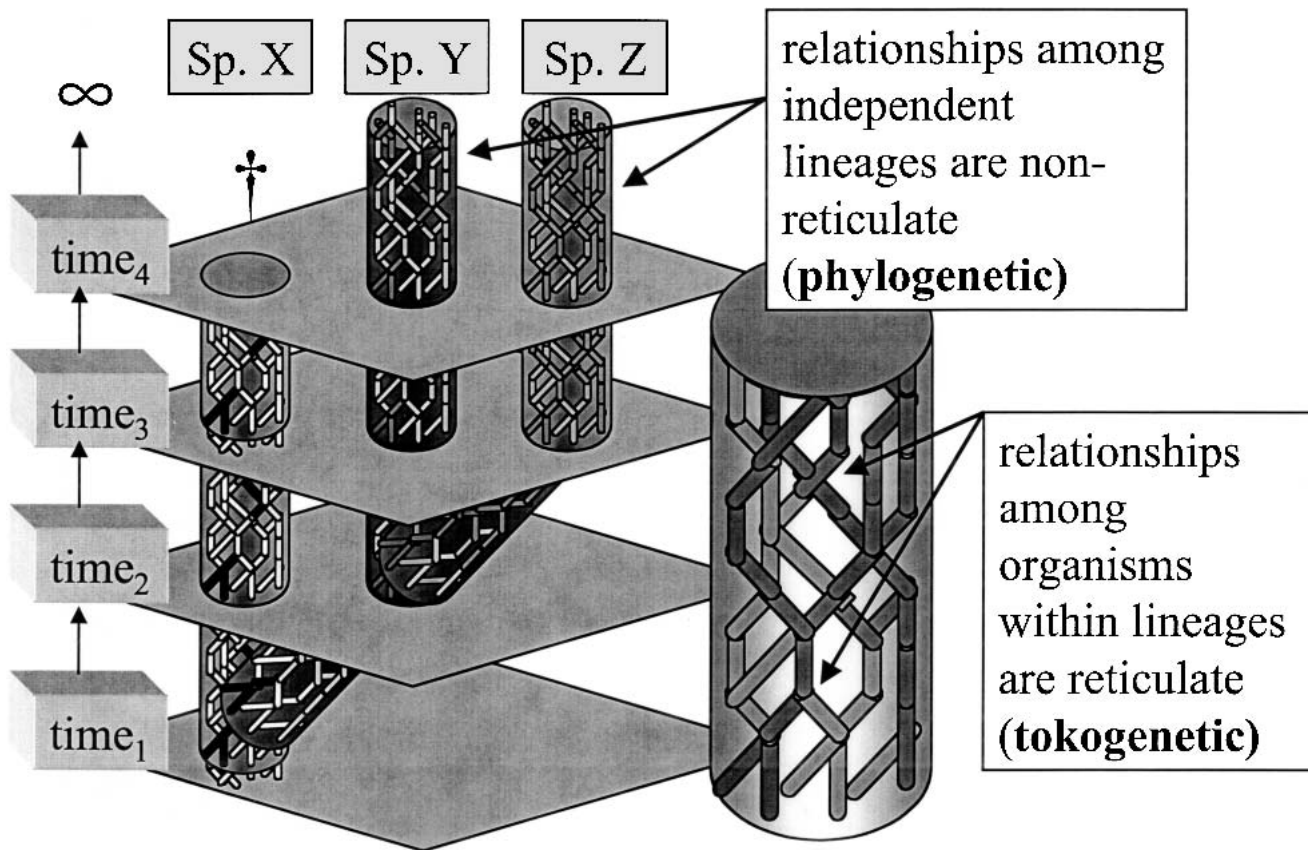
FIG. 2. Species depicted as lineages that extend through space and time. Species X arose sometime between $time_1$, and $time_2$, and persisted until sometime between $time_3$, and $time_4$, when it went extinct. Species Y and Z arose sometime between $time_2$ and $time_3$, and persist into the present. Relationships among species are characterized by lineage splitting (cladogenesis). Relationships among individual organisms within their respective lineage is characterized by reticulate outcrossing (tokogeny). All three species have a unique origin (they arose only once). Species X has a unique fate (it does not share its extinction with any other lineage). Species Y and Z are extant and appear to be evolving independently, but to infer that they will not share a common historical fate (coalescence) requires predicting the future.

among cohesive, independent lineages (such as those depicted in Fig. 2) are non-reticulate, characterized by splitting.[8] However, relationships among the individual organisms that comprise independent lineages *are* reticulate (tokogenetic, like those of outcrossing members of a sexual population[9]).

Ontologically, the species depicted in Figure 2 can be considered real entities (they exist independent of human observation) because they behave like individuals, and not like classes. For example, species X, Y, and Z are spatiotemporally bounded, with historical connections among their parts (individual organisms, populations, and metapopulations). The historical (genealogical) connections, bounded spatially and temporally,

create exclusive intrinsic cohesion that is maintained independent of other such entities. If these entities had no metaphysical reality, like categories, they would be spatiotemporally unbounded and lack cohesion. If species are real, then they are self-delimiting in nature, and it is our task to come up with ways of discovering them.[10]

Epistemologically, the best way of discovering metaphysically real species is to look for exclusive lineages of organisms. Evidence of historical lineage exclusivity can be used to predict that a particular lineage under investigation in the present will remain exclusive in the future. For example, in Figure 2 species Y and Z begin to diverge between time 2 and time 3, and may even be diagnosably different. However, we cannot say with any confidence that they are evolving independently until characters unique to each lineage have evolved and become fixed within their respective lineages. *Thus, it is not until some time after they have been evolving independently*

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cal construct aimed at reducing systematic error (in this case, distinguishing between temporarily isolated populations and independent lineages). Predicting the fate of lineages is not a metaphysical construct but an epistemological one.

[8] Some have argued for a distinction between cladogenesis and "budding" models of speciation (i.e., Mayr 1954). However, theoretical arguments aside, there is little empirical evidence in support of the latter model (Lynch, 1989, 1999).

[9] The distinction between phylogeny and tokogeny among self-replicating individual organisms is irrelevant for unisexual organisms because their phylogenetic and tokogenetic branching patterns are indistinguishable.

[10] But see Baum (1998) who, by tinkering with the individuation criterion, explores an alternative metaphysical reality of individuals, and consequently species epistemology.
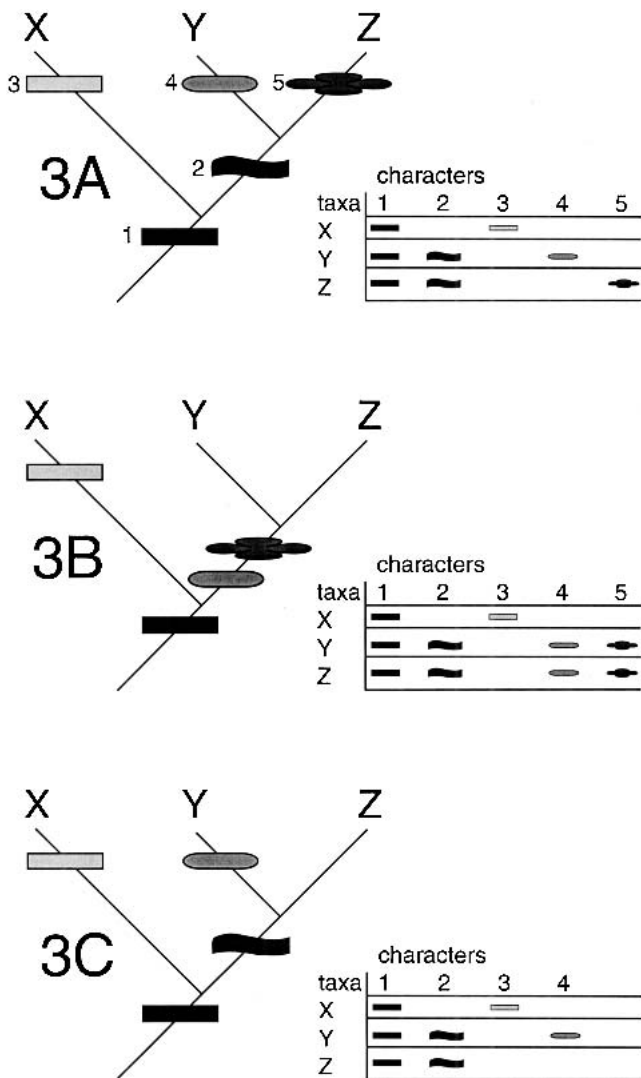
Fig. 3. Species delimitation based on the distribution of unique, derived characters (autapomorphies) among sampled populations. A) Each lineage (X, Y, and Z) possesses a unique, derived character that is fixed among all populations sampled and not shared with any other lineage (autapomorphy). That each lineage has evolved a character not shared with any other suggests that they are evolving independently of one another, and can be delimited as species. B) Variation exists that can distinguish taxa Y and Z from taxon X, but taxa Y and Z cannot be differentiated from each other. Although variation exists within taxa X and Y, it is not partitioned exclusively within their respective lineage. C) Sufficient variation exists to diagnose taxa X, Y, and Z, but there is insufficient evidence of historical lineage exclusivity for taxa Y and Z, as Z can be described only as a privative group.

that we can have sufficient evidence to make predictions about their future independence.

For example, consider Figure 3. If there are two species, by their ontological definition we must expect their lineages to be evolving independently of one another. Evidence of this can be demonstrated only by each species having a character that is common to all members within its lineage but not found among any other taxon (an autapomorphy) (Fig. 3A). Characters that are not unique may provide evidence of common ancestry but cannot be distinguished from evidence of

reticulation, or that the lineages are not evolving independently.

If taxa Y and Z represent only one species, then we expect characters to be distributed among them as depicted in Figures 3B and 3C. In Figure 3B, no variation exists among the sampled populations. In Figure 3C, diagnostic variation exists, but the evidence of lineage exclusivity is not robust enough (ontologically or epistemologically) to protect against making systematic errors (Adams, 1998). While this condition fulfills the requirements of some definitions of the phylogenetic species concept (Wheeler, 1999) or "metaspecies" (de Queiroz and Donoghue, 1988, 1990), there are at least two fundamental flaws with this thinking. First of all, taxon Z is a privative character, a character of which its essence is absence. Because taxon Z is defined only as "not Y," it cannot be subdivided. This is a problematic property of taxon Z because no species can be delimited based on the absence of nothing (Lynch and Renjifo, 1990; Plato [320 BC] and Skemp, 1952). Secondly, if taxon Z is a species, then it cannot be differentiated from its direct ancestor. The individual lineage Z is at the same time an ancestor and its own descendent. This too is a logically absurd statement. Evidence of historical lineage independence (species) is provided by the evolution of a unique, derived character.

Can two species be delimited by a single nucleotide (or any single, multistate character)? Figure 4A depicts the anagenetic evolution of a single multistate character—in this case a single homologous nucleotide position. Fixed variation exists at this position, and the variation is partitioned independently within its respective lineage. "T" and "C" appear to be autapomorphies. However, without an independent cladogram, crystal ball, or time machine, we cannot be certain. For example, "G" may have evolved to a "T" in the common ancestor of taxa Y and Z (Fig. 4B). Alternatively, if this happened, and this is the only fixed, variable character in the data set, then we cannot unambiguously say that both lineages have evolved an autapomorphy. Maybe it did. But we must consider the alternatives depicted in Figures 4B-C and their similarity to the structure and caveats of the scenario depicted in Figure 3C. The alternative scenarios depicted in Figures 3 and 4 demonstrate that *no single character, regardless of its number of states, can be used to delimit two species without a priori knowledge of evolutionary history.*

CONCLUSION

Do I contend that *only* lineages that have autapomorphies are species? No. Other lineages may exist. Other methods may recover entities that *really are* species, possibly lineages that are unrecoverable using the operations I describe (Mayden, 1999). However, the epistemological approach I advocate is the only one I know of that is compatible with species ontology sensu stricto. It
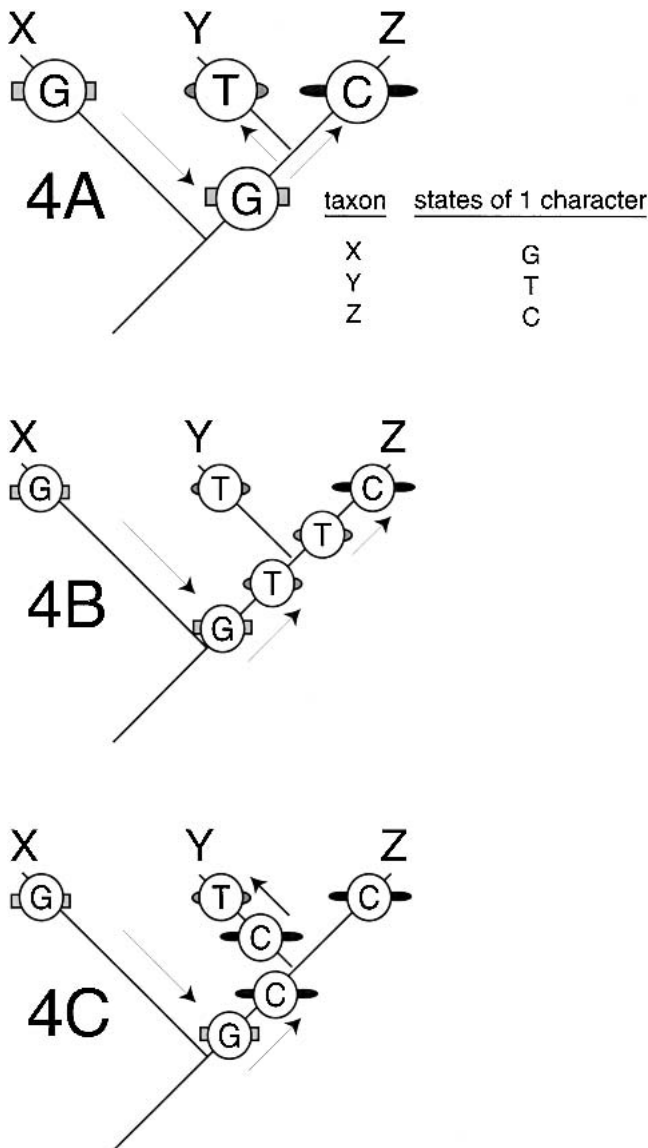
FIG. 4. Alternative hypotheses of the transformation or a single, multistate, homologous nucleotide position. A) Misleading indication of independence. G evolves to T in taxon Y, and C in taxon Z. The lineages appear to be evolving independently of one another, but this particular reconstruction ignores two alternative transformations and can be inferred only from external evidence (i.e., an independent cladogram). B) An alternative to Figure 4A. G evolves to T prior to the divergence of taxa Y and Z. Subsequently, T evolves to C. C) G evolves to C prior to the divergence to taxa Y and Z. Subsequently, C evolves to T. Figure 4B–C depicts either Y or Z as privative groups lacking historical evidence of evolutionary independence. Thus, no single nucleotide character, in the absence of external evidence, can delimit two species.

is consistent with recovered evolutionary history and incorporates the prospective nature of species delimitation as a way of guarding against making systematic errors (predicting too many or too few species).

The four critical discovery operations are: (i) identification of heritable characters, (ii) identification of fixed characters among populations, (iii) polarization of characters (outgroup comparison), and (iv) identification of evidence of historical lineage exclusivity (autapomorphies).

Because species delimitation usually proceeds in an authoritarian, ahistorical context, it is often depicted as an "art" and not science. This need not be the case. The "art" of species delimitation enters the realm of science when: (i) species are considered testable hypotheses, (ii) we figure out what things we are looking for (species ontology) prior to coming up with ways of trying to find them (species epistemology), (iii) we determine which data are important and how they will be analyzed based on methods compatible with recommendation 2 (Sites and Crandall 1997), and (iv) we accept the fact that sometimes we will fail to accurately predict the future (correctly delimit species) and get on with our lives (return to recommendation 1).

Is the "species" problem compounded by the "population" problem? Amalgamations of theoretically robust and operationally explicit species definitions have been promoted as steps toward mitigating the species problem (Adams, 1998; see also Christoffersen, 1995; Frost and Kluge, 1994). Accordingly, "fixed" autapomorphies are indicative of lineage exclusivity and, therefore, of species. But by what metric are autapomorphies determined to be "fixed"? Without non-arbitrary boundaries to my use of the term "population," whatever I decide to say represents an adequately sampled taxon can mean just about anything. That is, without constraining the term population, I can say anything I want about whether or not a taxon is a species. As currently applied to the species problem, the term "population" is laden with debilitating assumptions sufficiently powerful to render our uses tautologies, obviating the objectivity and even necessity of analysis (Lynch, pers. comm.). For example, not unlike the species problem, I can define, very explicitly, a concept of "population" such that the entities I have sampled conveniently constitute one. Given the fundamental role population structure plays in species delimitation, efforts, both conceptual and practical, will benefit from a careful reexamination of the term "population" and its definitions.

As punctuated at the outset by Heisenberg's axiom, species delimitation is constrained in some ways by our ability to adequately understand the present (population structure, sampling error, methodological and technical constraints). Worse, even if we could know the present exactly, the peculiar attributes of species (contingent properties, historical connections) make predicting their future interactions even less likely. Acknowledging our limited ability to understand the present *and* predict the future doesn't solve the species problem, but it does allow us to face it in more meaningful and productive ways. Species are real entities but, beyond their distinction as individuals of common descent, they may share little else. The "solution" to the species problem remains to continually refine a best

theoretical definition of species and then supply an explicit list of discovery operations that can find them.

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