Species Concepts and the Evolutionary Paradigm in Modern Nematology

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Abstract: Given the task of recovering and representing evolutionary history, nematode taxonomists can choose from among several species concepts. All species concepts have theoretical and (or) operational inconsistencies that can result in failure to accurately recover and represent species. This failure not only obfuscates nematode taxonomy but hinders other research programs in nematology that are dependent upon a phylogenetically correct taxonomy, such as biodiversity, biogeography, cospeciation, coevolution, and adaptation. Three types of systematic errors inherent in different species concepts and their potential effects on these research programs are presented. These errors include overestimating and underestimating the number of species (type I and II error, respectively) and misrepresenting their phylogenetic relationships (type III error). For research programs in nematology that utilize recovered evolutionary history, type II and III errors are the most serious. Linnean, biological, evolutionary, and phylogenetic species concepts are evaluated based on their sensitivity to systematic error. Linnean and biological species concepts are more prone to serious systematic error than evolutionary or phylogenetic concepts. As an alternative to the current paradigm, an amalgamation of evolutionary and phylogenetic species concepts is advocated, along with a set of discovery operations designed to minimize the risk of making systematic errors. Examples of these operations are applied to species and isolates of *Heterorhabditis.*

Key words: adaptation, biodiversity, biogeography, coevolution, comparative method, cospeciation, evolution, nematode, philosophy, species concepts, systematics, taxonomy.

Ever since Mayr (1942) codified a species concept in the taxonomic literature based on reproductive incompatibility (the Biological Species Concept, or BSC), nematologists have had to decide, consciously or not, whether to use it when describing and classifying nematodes. Subsequently, an extensive literature has been established and currently there are several well-articulated species concepts available to taxonomists (see Ereshefsky, 1992). However, the vast majority of species descriptions within the last decade make no mention of species concepts. Groups of nematodes are isolated and delimited as species, but a species *per se* is not defined at all. Thus, many taxonomic decisions are made by inference; it is never clear what parameters are in place during the discovery operations. We get the results (usually that one isolate is somehow different from others) but rarely are they accompanied by any explicit mention of methodology, or what the differences mean.[1] The extensive diversity of undescribed nematode species poses substantive challenges to the future of nematode taxonomy. Also, recent progress in systematic biology and the comparative method suggest that many research programs in nematology stand to benefit from a reevaluation of the philosophical and operational tenets of alternative species concepts.[2]

My intent here is not to address the merit

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[1] For an example of this problem as it exists in philosophy and evolutionary biology, see Dennett (1995), who views this as analogous to playing tennis with the net down: with no rules, no one can understand or play the game. Ultimately there is only confusion and nobody has any fun.

[2] This criticism is not unique to nematology and has been addressed in other fields including ornithology (Cracraft, 1983), herpetology (Frost and Hillis, 1990), and botany (McDade, 1995).

of species descriptions in nematology. Rather, my purpose is to show that species concepts are the crux of taxonomy and that a taxonomy based on irrational species concepts can subvert the goals of our taxonomic endeavors by misrepresenting evolutionary history and thereby significantly hindering efforts to recover other types of historical phenomena. To mitigate these problems, I advocate an alternative species concept for use in nematology, and a methodology for its application.

Before addressing the epistemological question of how we can logically recognize an entity as a species (the main thrust of this paper), I need to acknowledge a nontrivial ontological assumption, that speciation occurs by cladogenesis, and that the Nemata are a monophyletic group.[3] If this is true, then for nematode taxonomy to reflect evolutionary history all nematode species must by definition be monophyletic,[4] a requirement if species are to be given non-arbitrary recognition. For example, taxonomists use a variety of operations when naming nematodes, some theoretical and some pragmatic. But the central underlying premise is that the entities we call species are either i) species, ii) part of a species, or iii) a mixture of two or more species. This ontological dictum exhausts the taxonomic possibilities and lets us get on with the task of addressing epistemological problems. The epistemological questions I will explore involve the logical basis for recognizing a particular entity as a species.

SPECIES CONCEPTS AND THE PURPOSE OF TAXONOMY

To stimulate a more unified approach to systematic endeavors in nematology, Lorenzen (1983) posited: "Systematics has two objectives. Firstly, the clear ordering and registering of species diversity to facilitate practical work with the species. Secondly, the formulation of a scientific theory of the evolutionary relationships among species and groups of species; therefore, the resulting system should be based on phylogenetic arguments."

Few systematists will take issue with this statement. Evolutionary history has produced species that taxonomists hope to recover in order to facilitate practical work. It is also the taxonomist's objective to represent the evolutionary relationships among species. Without altering its intent or substance, Lorenzen's statement could be simplified to read, "The reason nematologists do systematics is to *recover* and *represent* evolutionary history." A clear understanding of these two objectives is critical because if species concepts differ in their ability to accomplish these goals, then it is possible to choose a concept of species least likely to fail in this regard. Other species concepts can be rejected as those more likely to confound or hinder taxonomic endeavors.

In the following sections I establish criteria and evaluate four prominent species concepts based on their ability to accomplish the two objectives of nematode taxonomy (Lorenzen, 1983). I will advocate an amalgamation of two concepts, explain the utility of this new approach in terms of its ability to reduce error, and provide a methodology for its implementation.

THE SPECIES PROBLEM

As long as the boundaries between populations and species have exhibited variation, systematists have at some point had to rationalize a way of distinguishing between the two. In the absence of any objective methodology within the Linnean paradigm, proponents of alternative species concepts have tried to establish objective solutions to the species problem (the problem of not being able to objectively identify just exactly what is or is not a species). Yet, in every case all current species concepts at some level fail to

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[3] Epistemology deals with the nature of knowledge, or "How do we know we have species?" Ontology deals with the nature of being, or in this case, "Do we have species?"

[4] By this I mean that all individuals that comprise a species must be more closely related to each other than to members of another species. It should be pointed out that there are problems with extending the term "monophyly" to subspecific entities (Platnick, 1977). However, this does not appear to be problematic as long as the phylogenetic patterns among comparable organisms (semaphoronts) within a species can be represented (but see Nixon and Wheeler, 1990).

satisfy the objectives of taxonomy. If reproductive incompatibility is a requirement of species, how can unisexual species or fossils be accounted for? If species are based solely on the similarities and differences between populations, exactly how similar or different must they be?

Realizing this problem, Myers (1952) pointed out that definitional species concepts will always fail because taxonomic statements about species are predictions of future events, and that the complex interactions within and among populations and species in the future are difficult to predict. Accordingly, I call these failed predictions "predictive systematic errors." This appreciation for the historical fate of species is the approach elaborated by O'Hara (1993) and reflected in Frost and Hillis (1990) and Frost and Kluge (1994). These papers provide the theoretical and systemic framework for the operational recommendations made in this paper. However, although a tempered respect for "predictive systematic errors" does not comprise a solution to the species problem, it does help us get over it (O'Hara, 1993).

PREDICTIVE SYSTEMATIC ERROR

As is made clear by "the species problem," when two populations are assigned to the rank of species, we are really saying two things: i) the two populations appear to be on independent evolutionary trajectories (sensu Wiley, 1978), and ii) they will continue to be independent in the future. Two populations that look like different species now might in the future converge into a single lineage again, and so may not have really been species in the first place. On the other hand, we may suppose that even though the two populations look like different species, because they could reticulate in the future they will; thus we conclude that they are the same species, when in actuality they are indeed on independent evolutionary trajectories and will remain so until they go extinct. This conflict introduces two types of error associated with determining the status of species (Frost and Hillis, 1990): type I error occurs when the taxonomist predicts

more species than actually exist, and type II error predicts fewer species than actually exist. These two errors affect the way in which we meet the first objective of taxonomy, that of accurately recovering species as products of evolutionary history. A third type of error occurs when a depiction of phylogenetic relationships among species is incongruent with recovered evolutionary history. This error is distinct in that it violates the representational aspect of taxonomy. A type III error misrepresents the actual historical relationships among species (Fig. 1).

The importance of a phylogenetically correct taxonomy is essential to emerging fields of nematology whose theoretical foundations rely on accurate estimates of species diversity and phylogenetic relationships. Prominent among these are studies of biodiversity, coevolution and cospeciation, adaptation, and biogeography. However, type I, II, and III errors vary as to their effect on these taxonomy-dependent research programs, and some errors can have more serious consequences than others. In the examples below I argue that, overall, type III errors are the most troublesome, followed by type II, and finally type I, in terms of their potential to arrive at misleading conclusions and negatively impact nematode research.

PREDICTIVE SYSTEMATIC ERROR AND
RESEARCH PROGRAMS IN NEMATOLOGY

Biodiversity: Predictive systematic errors can have a significant impact on studies of biodiversity and conservation biology. For example, Nixon and Wheeler (1992) detailed the importance of species concepts and phylogenetic correctness in terms of their influence on how areas, habitats, and species are designated for protection. In 1987 the U.S. Congress Office of Technology Assessment outlined several of these criteria. One example includes "families with few species or genera with only one species" (Office of Technology Assessment, 1987, as cited in Nixon and Wheeler, 1992). As pointed out by Nixon and Wheeler (1992), these criteria depend on two accurate determinations: i) phylogenetic diversity, or the
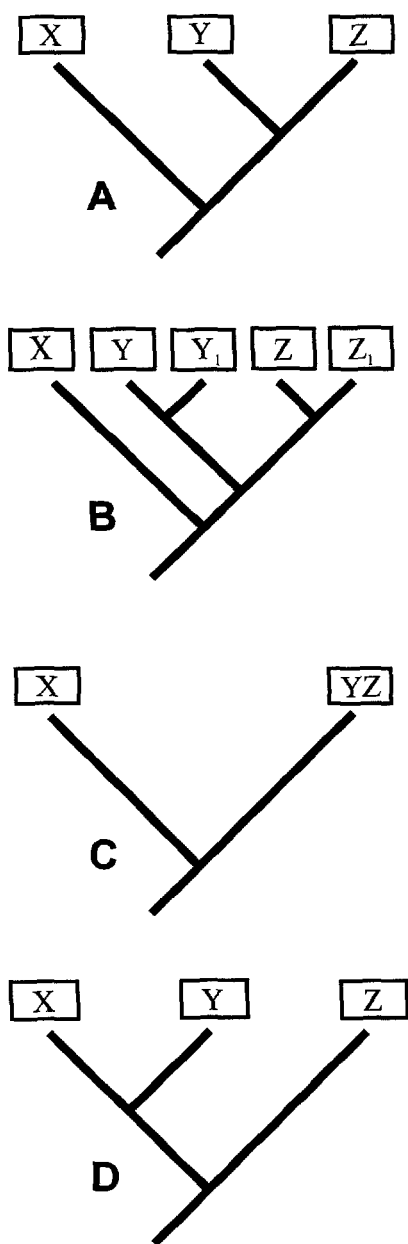
FIG. 1.   Three types of systematic error in the recovery and representation of evolutionary history. A) Phylogenetically correct tree, representing the best estimate of the actual evolutionary relationships among taxa X, Y, and Z. B) Type I error, where more species are delimited than actually exist. Y1 and Z1 are depicted as being separate species, when in fact they are simply members of Y and Z, respectively. C) Type II error, where fewer species are recognized than actually exist. Taxon Z is considered a member of species Y even though historically it represents a unique lineage. D) Type III error. Type III error misrepresents evolutionary history by positing that taxa X and Y are sister taxa, when in fact Y and Z are sister taxa.

actual number of species within clades; and ii) phylogenetic uniqueness, which is the diversity of a monophyletic group relative to its sister group. It is important to recognize the use of the word "clade" here because it infers that we know something about the phylogenetic relationships among the organisms with which we are working. Hierarchical arrangements without phylogeneticinformation are arbitrary (Farris, 1983) and thus useless to researchers interested in estimating how unique or diverse a group of nematodes are (Lynch, 1996; Wheeler, 1995).[5]

For an example of this distinction, we know that monotreme species are rare when compared to the number of species of mammals. But unless we know that these two groups are monophyletic, we cannot say that monotremes are phylogenetically unique relative to mammals. Similarly, in the Hoplolaiminae the genus *Helicotylenchus* with 172 species (Siddiqi, 1986) appears phylogenetically diverse when compared to the monospecific genus *Antarctylus*. But as the phylogenetic relationship between these two genera is unknown, it may be that *Antarctylus* is actually a member of another large, equally diverse clade. In the Heteroderinae, where phylogenetic relationships have been examined (Baldwin, 1992; Baldwin and Schouest, 1990), it can be argued that the two species of *Verutus* are the last surviving members of the genus that comprises the sister group to the rest of the Heteroderinae (104 species; Luc et al., 1988), and, thus, the *Verutus* lineage is phylogenetically unique (Fig. 2A).

In the example of the Heteroderinae, making type I and II errors could skew taxonomic clades to appear either more or less diverse than they really are (Figs. 2B,C). But a type III error could alter which clades are

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[5] I am convinced that species are real and not merely artificial human constructs (Ghiselin, 1974, 1987; Hull, 1978). However, taxonomic organization above the level of species *is* an artificial construct. The identification of phylogenetic diversity and phylogenetic uniqueness (sensu Nixon and Wheeler, 1992) is independent of nomenclatural hierarchy "above" the species level as long as the hierarchy is monophyletic (for examples of how nomenclature can reflect evolutionary relationships, see Eldredge and Cracraft, 1980; Hennig, 1966; Nelson and Platnick, 1981; Wiley, 1981).

Verutus
(2 species)　　All other Heteroderinae

A

Verutus
(5 species)　　All other Heteroderinae

B

Verutus
(1 species)　　All other Heteroderinae

C

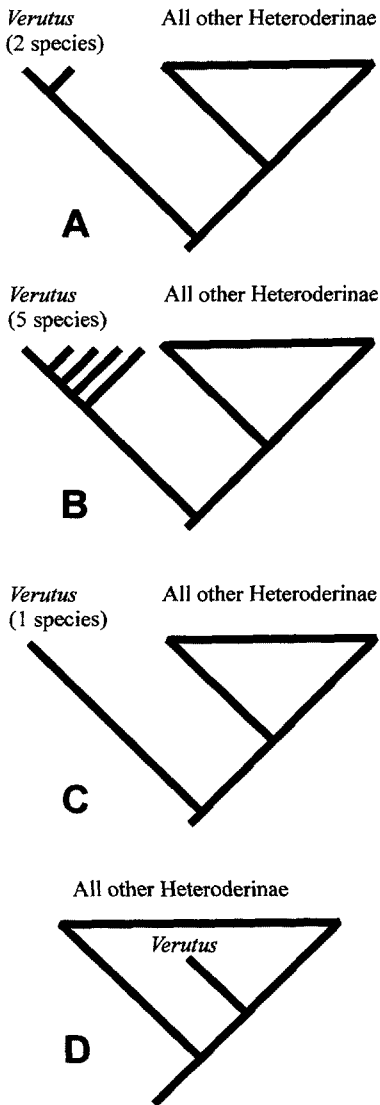All other Heteroderinae

Verutus

D

Fig. 2. Impact of predictive systematic errors on biodiversity estimates in a given geographic area and on the actual relationships among taxa. A) Best estimate of phylogenetic relationships for the Heteroderinae (Baldwin and Schouest, 1990; Baldwin 1992). According to this hypothesis it can be argued that the two species of *Verutus* represent the last surviving members of the genus comprising the sister group to the rest of the Heteroderinae, and are thus phylogenetically unique. B) Effect of type I error, where phylogenetic diversity relative to the rest of the Heteroderinae is artificially inflated. C) Effect of type II error, which underestimates the actual phylogenetic diversity within the genus *Verutus*. D) Effect of type III error, which incorrectly represents the relationship between *Verutus* and the rest of the Heteroderinae. Type III error prevents us from recognizing *Verutus* as being phylogenetically unique relative to the rest of the Heteroderinae.

unique and which are not, i.e. if populations of *Verutus* are represented as being more closely related to some other genus in the Heteroderinae (Fig. 2D).

Lambshead's (1993) estimate of 100 million species underscores the dearth of current species descriptions and systematic information for nematodes. In response, some researchers advocate the use of trophic groupings in lieu of recognizing species (Yeates et al., 1993). This approach has proven useful for basic studies of trophic interactions and food web structure. However, the use of trophic groups in soil community ecology has been criticized because groups of nematode species do not respond uniformly to environmental changes the way individual species do (Bernard, 1992).

Recognition of trophic groups instead of phylogenetic diversity can have even more serious consequences on biodiversity studies. Failure to recognize species and their evolutionary history can confuse the distinction between phylogenetically unique and phylogenetically diverse lineages. In response to global habitat destruction and elevated rates of extinction, efforts in conservation biology have shifted focus from protecting endangered species to saving threatened habitats and ecosystems. Consequently, indices of biodiversity are no longer simply considered the number of species per unit area but incorporate estimates of phylogenetic uniqueness as well (Forey et al., 1994; Nixon and Wheeler, 1992; Vane-Wright et al., 1991).

Consider two hypothetical ecosystems (A and B), each with the same number of nematode genera, species, and individuals per unit area (Figs. 3A,B). If the only difference between the two is that area A contains a population of the phylogenetically unique *Verutus,* and area B consists solely of other Heteroderinae, then area A is unique relative to B because it makes a larger contribution to global biodiversity (Wheeler, 1995). Nematode biodiversity promises to play an important role in our understanding of ecosystem function and monitoring, as well as identifying areas and habitats whose biological diversity and uniqueness merit protec-
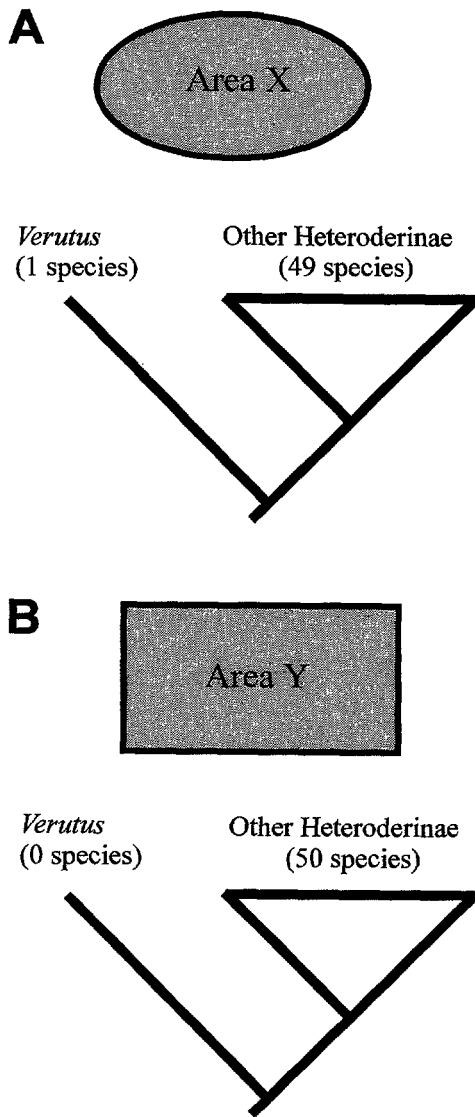
FIG. 3. Nematode biodiversity as a tool for identifying unique and (or) diverse areas. When the phylogenetic relationships among taxa in different areas are known, their relative contribution to overall biodiversity can be assessed. A) Hypothetical ecosystem (Area X) and the phylogenetic relationships among its taxa, including one species of the phylogenetically unique *Verutus* and 49 other species of Heteroderinae. B) Comparable ecosystem (Area Y) containing 50 species of Heteroderinae but without *Verutus*. Though both areas contain the same number of species, in terms of their biodiversity they are not equal. Area X has a phylogenetically unique species and, as such, makes a greater contribution to global biodiversity than Area Y.

tion. But the power of this approach requires the accurate recovery and representation of species and their historical relationships.

Biogeography and cospeciation: Studies of biogeography and cospeciation also are sensitive to systematic error, especially in light of the fact that the historical relationships between species and their hosts or geographic range comprise the theoretical basis underlying these studies (Brooks and McLennan, 1991; Harvey and Pagel, 1991; Nelson and Platnick, 1981).[6] Recent ex-

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[6] Although cospeciation (mutual phylogenetic association

amples in nematology include the coevolution of virulence and defense mechanisms (Herre, 1995; Huang et al., 1996), host-parasite biogeography (Hoberg et al., 1995), and host-symbiont cospeciation (Dubilier et al., 1995).

While adequate sampling of areas and species plays a large role in the accuracy of these studies, predictive systematic error can also have an effect on biogeographic and cospeciation analyses. For example, consider phylogenetic relationships within the genus *Tyleptus*, which show a cospeciation event (*T. variabilis* in India and *T. telyptus* in Africa) that is congruent with the breakup of Gondwanaland (Ferris et al., 1981) (Figs. 4A,B). If prior to analysis a type I error is made and *T. telyptus* is represented as two or more species, then the African clade appears to be more diverse in comparison to its Indian sister species (which now appears to be unique) when, in fact, it is not (Fig. 4C). This type I error is relatively innocuous because it does not alter the number or pattern of cospeciation events (all populations that can be elevated to species status occur in Africa). In this case, type I error merely inflates the number of post-cospeciation events (duplications), and its only consequential effect is the case where some biogeographers might interpret phyletic diversity as an indication of area of origin.

Using this same example, a type II error could have a more profound effect. Consider the outcome of failing to recognize either *T. variabilis* or *T. telyptus* as species (Fig. 4D). If this were to happen, then we would fail to recover a single cospeciation event in the genus that is congruent with the breakup of Gondwanaland, severely weakening the explanatory power of the vicariance model as applied to this data set. However, if either *T. projectus* (Americas) or *T. amalgans* (Puerto Rico) is not acknowledged, then

between host and parasite; Brooks and McLennan, 1991) and biogeography are different fields of study, their patterns in terms of historical congruence are the same. For this reason, type I, II, and III predictive systematic errors have equivalent effects on either of these research programs, and so while I provide an example of these errors on a biogeographic analysis, I do not provide a separate example for cospeciation.

there is little effect on the outcome in terms of historical congruence since the speciation event that led to these two lineages occurred on the same continent (Fig. 4E).

A type III error would have consequences similar to that of type II. For example, suppose that the real relationships among *T. striatus* (India and South America), *T. variabilis,* and *T. telyptus* were misrepresented such that *T. variabilis* (or *T. telyptus*) was the sister to *T. striatus* (Fig. 4F). This, too, would obscure any cospeciation event concomitant with the breakup of Gondwanaland, and we would have no evidence that speciation events in this genus were congruent with the breakup of Gondwanaland.

Species delimitation and studies of adaptation: Addressing adaptation research in nematology, Maggenti (1987) alluded to the fact that studies of adaptation are usually viewed with suspicion because of the speculatory nature of deducing past events from current evidence. Maggenti rightly asserted that these criticisms are unfounded (even in the absence of fossils and paleogeographic evidence) when these studies are based on the rich biological and morphological information innate to the nematodes themselves. For example, recent studies of a variety of adaptive scenarios in nematology have flourished, including temperature (Ferris et al., 1995; Gibson et al., 1995; Grewal et al., 1996; Schjetlein and Skorping, 1995; Wharton and Ramlov, 1995), laboratory culturing conditions (Stuart and Gaugler, 1996), environmental pollution (Millward and Grant, 1995), long-term dauer survival (Kagan and Clarke, 1995), behavior (Mori and Ohshima, 1995), olfaction (Colbert and Bargmann, 1995), and desiccation (Surrey and Wharton, 1995). However, explanations for hypothesized adaptations should be tested within a phylogenetic framework because some organismal features may simply be the result of nonadaptive processes (Brooks and McClennan, 1991; Gould and Lewontin, 1979; Harvey and Pagel, 1991).

For example, suppose we are interested in testing the hypothesis that the modified stylet of *Trichotylenchus*, with its slender, needle-like cone, is an adaptation for surface graz-
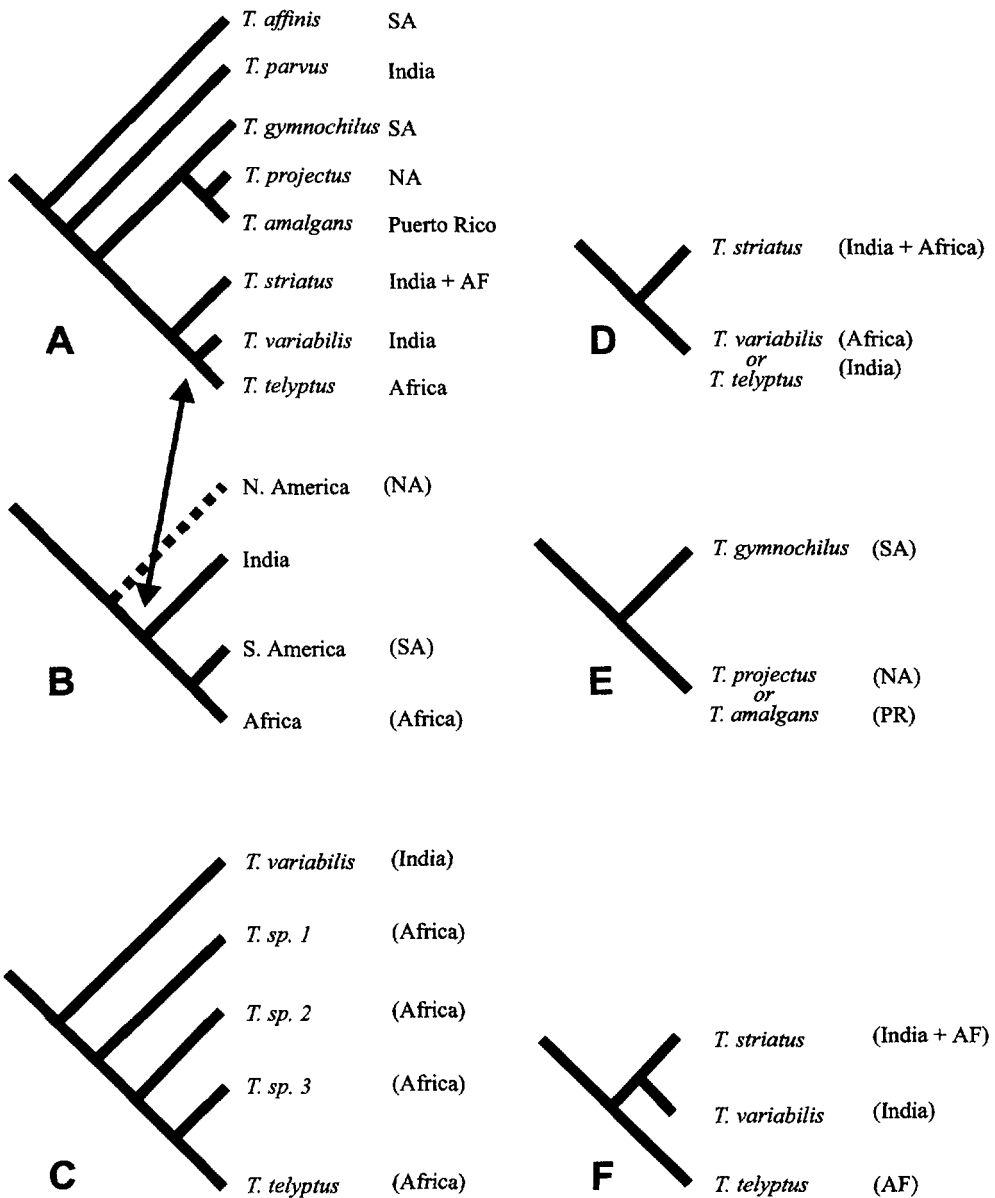
FIG. 4.   Sensitivity of studies of biogeography and cospeciation to predictive systematic errors. A) Best estimate of the actual phylogenetic relationships in the genus *Tyleptus* (Ferris et al., 1981). B) Depiction of the breakup of Gondwanaland. The speciation event in Fig. A congruent with the breakup of Gondwanaland is identified by the double-headed arrow. C) Depiction of a type I error made concerning the actual number of species of *T. telyptus.* The number or pattern of congruent speciation events is not altered; the number of duplications, or post-coevolutionary events, is artificially inflated. D) Effect of type II error and its failure to recognize either *T. variabilis* or *T. telyptus* as a species, resulting in the inability to identify the actual cospeciation event. E) Similar type II error, but with different taxa. The failure to recognize *T. projectus* or *T. amalgans* affects the number of duplication events but has no effect on the ability to correctly identify the cospeciation event. F) Effect of type III error. The representation of *T. striatus* and *T. variabilis* as sister species results in failure to identify the cospeciation event, undermining the hypothesis that speciation in the clade is congruent with the breakup of Gondwanaland.

ing. Presumably, this stylet morphology confers the advantage of easily penetrating cells along the root periphery (Fortuner and Luc, 1987). This seems reasonable. But the possibility remains that *Trichotylenchus* spp. have this morphology not as an adaptation for surface grazing, but because their ancestors evolved it for some other purpose which is now well suited for surface grazing. Is this truly an adaptation attributable to surface grazing, or an ad hoc explanation?

If a needle-like cone confers a net fitness advantage, then we would predict that individuals with a less slender, blunter cone would not be able to feed as effectively and leave fewer offspring. Assuming all other variables can be accounted for, this hypothesis can be tested experimentally by comparing the fitness of individuals with thick, blunt cones vs. those with slender, needle-like cones. But as Brooks and McLennan (1991) pointed out, this approach can explain only the maintenance of this trait and cannot address the questions of when, and under what environmental constraints, a slender, needle-like cone arose. Thus, in addition to bionomic information (such as host morphology and feeding behavior), testing hypotheses of the origin of an adaptation requires phylogenetic information as well. In this case, the genus *Trichotylenchus* shares a similar cone morphology with *Tylenchorhynchus* and *Merlinius*. A phylogeny showing the relationships among these genera and the rest of the Tylenchina would reveal whether the evolution of a slender cone is novel to *Trichotylenchus*, and under what environmental constraints it may have arisen.

Predictive systematic error can play an important role in our ability to accurately identify an adaptation. This is not evident in the example above, where the trait in question is fixed within an entire genus, because as long as each genus is monophyletic, phylogenetic relationships among species within the genus are irrelevant in identifying the origin of the adaptation. But when the trait in question varies among species within a genus, then the number of species and their relationships become important.
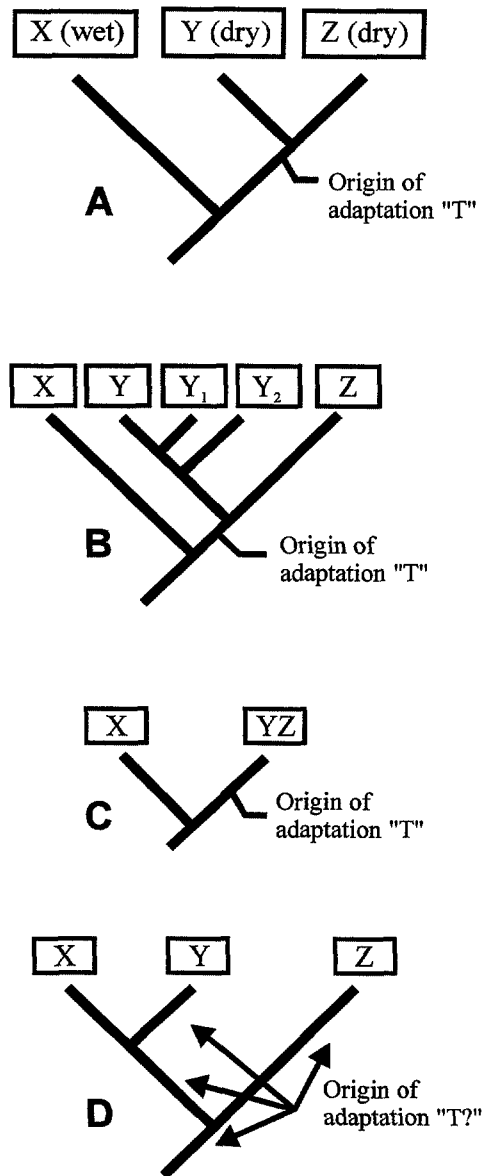

FIG. 5. Effect of predictive systematic errors on the accurate imputation of an adaptation. A) Best estimate of the actual phylogenetic relationships among hypothetical taxa X, Y, and Z. Trait T arose once and can be identified as originating in a seasonally dry environment. B, C) Effects of type I and II errors, respectively. These errors have a negligible effect on recovering an adaptation because they do not hinder accurate identification of the origin of "T." D) Effect of type III error. By incorrectly representing species X and Y as sister taxa, it is impossible to determine whether "T" arose once and was subsequently lost in species X, or if it evolved independently in species Y and Z.

For example, suppose we are interested in desiccation survival and want to investigate the hypothesis that elevated levels of trehalose found in a particular species of nematode is an adaptation for cryptobiotic anhydrobiosis. Consider three species (X, Y, and Z, Fig. 5A) where two species (species Y and Z) have evolved trait T (the elevated presence of trehalose) and we want to test the hypothesis that trait T arose as an adaptation to living in a dry environment (species X is found in a wet habitat, species Y and Z occur in a seasonally dry environment). When this trait is mapped onto our best estimate of the phylogenetically correct tree, the most parsimonious explanation suggests that it arose only once, and in a dry environment, indicating correlative evidence to support our adaptive explanation.

Type I and II systematic errors have a negligible impact on testing hypotheses of adaptation (Figs. 5B,C). Overestimating or underestimating the actual number of species does not alter our ability to identify the origin of the trait in question. However, type III errors can have a profound effect (Fig. 5D). If species Y is represented as being more closely related to species X than it is to species Z, then trait T either arose once and was then lost in species X, or it evolved independently in species Y and Z. In other words, we now have no way of knowing whether or not elevated levels of trehalose in species Y arose as an adaptation for desiccation survival—it may simply be a legacy of sharing a common ancestor with species Z.

Summary of errors and their effects on other research programs: In light of the above examples, type III predictive systematic errors are the most costly in terms of their effects on other research programs. In biodiversity studies, the degree to which predictive systematic errors are misleading depends on which species or group of species the error is made. However, for coevolution, biogeography, and adaptation, misrepresenting the relationships between species is much more damaging than underestimating or overestimating them. In these studies, type I and II errors can lead to inconclusive or speculative results, but type III errors lead to seem-

ingly well-supported, but erroneous results. To summarize, type III is the most risky, followed by type II, with type I error the least harmful to these research programs.

SPECIES CONCEPTS AND PREDICTIVE SYSTEMATIC ERROR

Numerous species concepts have been proposed and advocated for general use in species delimitation. Of these, the Linnean, biological, evolutionary, and phylogenetic species concepts figure most prominently in the substantial literature on the subject. I will briefly introduce each of these concepts and discuss their weaknesses in terms of their susceptibility to predictive systematic errors during the process of species delimitation.

Linnean Species Concept: The Linnean, or typological morphospecies concept, delimits species as groups of organisms that have the most overall similarity (Mayr, 1963). It recognizes all characters, whether primitive or derived, homologous or analogous, and in any combination, as the basis of species delimitation. An extension of this, the Phenetic Species Concept (Sneath and Sokal, 1973) originally allowed for overall similarity to form the basis of phylogenetic relationships, as well.

A review of the taxonomic literature over the last two decades suggests that, in practice, most nematode taxonomists are operating within the Linnean system. Interestingly, it is also the approach most prone to type I, II, and III errors. Under the Linnean paradigm, at the species level it becomes difficult to determine just how different or similar populations must be to call them species. This situation can result in type I and II errors. Type I errors arise when variation within populations is undersampled, giving the appearance that each population is a different species. On the other hand, type II errors arise when there are cryptic species that, based on overall similarity, may look alike but have unique evolutionary histories, and the resulting taxonomy fails to reflect this diversity. Type III error occurs as a result of inferring phylogeny from phenetic similarity.

Biological species concept (BSC) (Mayr, 1942): The BSC recognizes species as groups of interbreeding natural populations that are reproductively isolated. Though the BSC is also prevalent in the nematological literature, it, too, is capable of all three types of predictive systematic errors. As an example of type I error, each obligate unisexual *Meloidogyne* individual must be considered a separate species, since each is reproductively incompatible with any other nematode.[7] Likewise, two amphimictic populations can be on two independent phylogenetic trajectories yet, because they have maintained their reproductive compatibility, would still be regarded as a single species, resulting in type II error. Finally, adherence to the BSC can cause type III error in the case where two populations can evolve reproductive incompatibility while a sister population to these two remains reproductively compatible to one of the two. This results in two of the three populations being named as species even though one of the populations is actually more closely related to another "species" than it is to its "biological" species (Figs. 6A,B). In addition to these theoretical errors, there are operational considerations as well. For instance, as demonstrated with the example of type I errors, we cannot apply the BSC to unisexual lineages or nematodes that are difficult to breed or maintain in culture (e.g. parasitic nematodes with complex life cycles, unknown hosts, hosts that are difficult to maintain, etc.).

Evolutionary Species Concept (ESC) (Simpson, 1961; Wiley, 1978): According to the ESC, a species is defined (Wiley, 1978) as ". . . a single lineage of ancestral-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." In contrast with Linnean and biological spe-
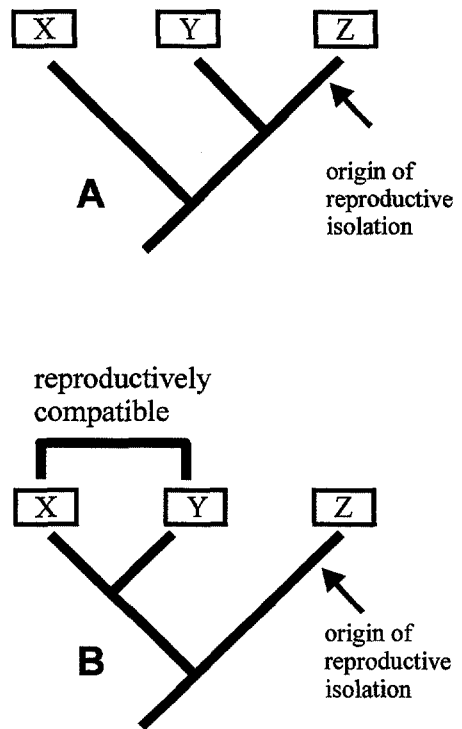

FIG. 6. Systematic errors inherent in the Biological Species Concept (BSC). Type I error fails to account for unisexual nematodes, while type II error fails to recognize sister populations that are on independent phylogenetic trajectories yet maintain reproductive compatibility. Type III error occurs when reproductive compatibility is considered an indication of phylogenetic relatedness. A) Phylogenetically correct tree, showing anagenetic evolution leading to reproductive isolation in population Z. B) Type III error. Populations X and Y are considered more closely related to each other than to population Z, confounding the actual historical relationships among these taxa.

cies concepts, the ESC is the first to realize the necessity of evolutionary history in making rational statements about species by requiring that lineages and fates of lineages be identified. However, the fates of these lineages must be predicted; therefore, the ESC is susceptible to type III error because paraphyletic species (like those prone to type III error under the BSC in the example above) can be recognized on the possibility that in the future they will combine. Similarly, the ESC can commit type I error by recognizing many seemingly unique lineages as species that in the future may permanently coalesce. These two errors are a potentially serious problem but can be accounted for in part by

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[7] Reproductive compatibility is always a primitive, or plesiomorphic, character. However, sister group relationships can be established only by shared derived characters (synapomorphies) and diagnosed as species by uniquely derived characters (autapomorphies; Hennig, 1966). Thus, while they are interesting, plesiomorphic characters are useless in identifying species or taxonomic groups.

requiring evidence of lineage exclusivity (discussed below in the section, "A proposed set of operations to identify species"). The most limiting aspect of the ESC is that it fails to account for lineages of hybridogenic origin because the hybrid species' lineage does not arise from a single ancestral lineage. It does, however, account for unisexual lineages since in this case phylogenetic and tokogenetic (ancestor-descendant) arrays are essentially the same thing.

Phylogenetic Species Concept (PSC) (Cracraft, 1983, 1989; Nelson and Platnick, 1981; Nixon and Wheeler, 1990; Rosen, 1978, 1979): According to this species concept, species are the smallest units reflecting phylogenetic history that are analyzable by cladistic methods. This species concept is immune to type II or type III errors but is susceptible to type I error. For example, each hybridization or polyploidy event can produce "diagnostic clusters" of individuals. Thus, this species concept would recognize each of these non-unique groups as distinct species, possibly to the point where each time a hybrid were to reproduce it would result in the formation of a new (but non-unique) species.

NEMATODE SPECIES: STATE OF THE ART

There have been several attempts within nematology to address the problem of species. One thoughtful consideration was that of Inglis (1971) who drew heavily upon Mayr (1942, 1963) in describing some of the problems associated with species definitions delimited by morphological differences between populations, and interbreeding-based concepts such as the BSC (species defined as populations of potentially interbreeding groups of individuals). Inglis (1971) pointed out the subjective nature of identifying species according to the Linnean system, primarily that of delimiting the boundaries between individual variants, and similarities shared by populations. Inglis (1971) also acknowledged the pragmatic difficulties associated with identifying biological species in the Nemata (i.e., the determination of whether populations, especially parasitic populations, are reproductively compatible)

but was unable to offer any recommendations other than the "hope" that "species . . . primarily recognized on morphological evidence . . . will reflect genetic unity and so supply secondary interbreeding data." Inglis (1971), therefore, had the optimistic expectation that, by using the discovery operations of the Linnean definition of species, taxonomists would somehow be able to recover the more philosophically objective "biological" species.

Gibson (1983, 1992) posited that, for technical reasons (that of performing adequate hybridization experiments), application of the BSC was unsuitable, at least for parasitic nematodes. Gibson (1983) acknowledged the hope ". . . that the morphological species is congruent with the biological species . . ." but did not share the optimism of Inglis (1971) that this is a reasonable expectation. Gibson (1983) further criticized the Linnean species concept as applied to parasitic nematodes, citing examples of host-induced and environmentally induced morphological variation.

Also rejecting the subjectivity of the Linnean paradigm, Coomans (1979) and Sturhan (1983) seemed comfortable with the BSC as applied to sexual nematodes. However, as the BSC fails to account for unisexual nematodes, they advocated that Simpson's (1961) ESC be applied to these cases. This definition allows for unique populations of unisexual nematodes to be incorporated into a species concept. Thus, Coomans (1979) and Sturhan (1983) appeared to advocate a pluralistic approach to species concepts—that the BSC can satisfactorily account for most nematode species and that the ESC covers the rest (see also Mishler and Donoghue, 1982).

Ferris (1983) provided an insightful criticism of the use of the BSC in nematology, and a progressive investigation of species concepts. As alternatives to the status quo, Ferris (1983) mentioned an updated version of the ESC (Wiley, 1978) and the PSC of Nelson and Platnick (1981). These two methods rely on phylogenetic information in order to identify species as evolutionary lineages but differ as to their discovery op-

erations (deciding which data are important and how those data are interpreted) and how they deal with the products of hybridization and polyploidy.

Maggenti (1983) and Luc et al. (1987) embrace the BSC of Mayr (1981). In defense of the BSC, Maggenti (1983) cited Ghiselin's (1974) revised version of the BSC, which emphasized processes (such as reproductive competition) as opposed to the products of evolution (reproductive isolation). However, Frost and Kluge (1994) pointed out that this version of the BSC was philosophically indistinguishable from Wiley's (1978) version of the ESC.

Finally, although Andrassy (1976) made a noteworthy attempt to integrate evolutionary theory and taxonomy, a serious discussion of species (the fundamental units of these two research programs) was absent.

EPISTEMOLOGY, ONTOLOGY, ESSENTIALISM, AND OPERATIONS: HOW SPECIES CONCEPTS DIFFER

At this point it may still be unclear as to how these species concepts differ operationally. The differences are more apparent when we look at the paradigm that forms the basis of their discovery operations. For example, Cain (1958) asserted that Platonic and Aristotelian essentialism formed the philosophical basis of the Linnean species concept because species are identified based on the overall similarity exhibited by individuals within a population. Thus, morphological variation within a population is viewed as unimportant noise. Characters that are important in determining whether a population is a separate species are those characters that are invariant among the individuals in a population. This establishes a criterion that comprises the "essence" of a species, and it is this disregard for variation within species that inadvertently results in individual variants being described as separate species (Mayr, 1963).

Mayr (1963) criticized the Linnean system because of its essentialist (typological) underpinnings but failed to see the essentialism of the BSC: If species are reproductively isolated populations independent of phylogenetic relationships, then reproductive isolation is their "species-ness": a non-evolutionary, essential property of species (Frost and Hillis, 1990;[8] Hennig, 1975). The operational problem facing these two species concepts is that, because they are non-evolutionary, they can represent relationships among species that are incongruent with phylogeny.

The PSC requires that relationships among species be consistent with evolutionary history. However, abuse of its discovery operations can also lead to unintentional essentialism. For example, there may not be a single independent character that can distinguish one population from all others. However, it is possible that several characters in combination can. The problem here is that, while the characters themselves may be heritable, combinations of independent characters are not. Characters that are not heritable are non-evolutionary in the same way that reproductive isolation and overall similarity are.

The reason these three species concepts get trapped in essentialism is because they take an epistemological approach to defining species. That is, the question they are trying to address is "how do we know we have species?" As a result, all of their discovery operations are aimed at recovering "real" species from arbitrary sets of individuals and populations. The ESC is able to escape the problem of essentialism because, unlike the three other species concepts discussed, it takes an ontological approach and is more concerned with whether or not there are species to be recovered in the first place. The ESC asks "do we have species?" Therefore, its discovery operations will always result in the identification of unique

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[8] Frost and Hillis (1990) pointed out that, while it may be tempting to think that reproductive compatibility is a good indicator of phylogenetic relationships, there is ample evidence that suggests otherwise, citing a study on ranid frogs, which reveals that some distantly related frogs show higher degrees of gametic compatibility than more closely related species (Hillis, 1988).

phylogenetic lineages. Thus, the most powerful approach involves using the discovery operations of the PSC to recover the "largest integrating lineages" of the ESC (Frost and Kluge, 1994). However, an amalgamation of these two species concepts requires an amended set of discovery operations in order to identify all the unique evolutionary trajectories without grossly overestimating them. This involves rejecting the notion that combinations of characters are useful in estimating phylogenetic relationships and delimiting species. It also requires that each species possess characters that suggest they are a unique, exclusive lineage and that they will remain that way until they become extinct. Taxonomic statements based on these types of characters are *predictive*, and I contrast these with *speculative* taxonomic statements. The latter are statements of future events that do not require prospective evidence.

HISTORICAL FATE: PREDICTION OR SPECULATION?

As mentioned by previous students of species concepts who understood the temporally transient nature of species (Hull, 1983; Myers, 1952; O'Hara, 1993; Popper, 1960), the species problem is actually a problem of identification and temporal representation, not definition. Since evolutionary science cannot predict the paths of all future events (Jacob, 1982; Medawar, 1984), all definitional species concepts will fail us at some level. But no matter what species concept we use, definitions of species boundaries are dependent upon expectations of future events. In this sense, describing species is analogous to forecasting the weather. For a species description to be a prediction rather than speculation, its discovery operations must include subjecting evidence to a process that produces accurate, replicable results.

A PROPOSED SET OF OPERATIONS TO DELIMIT SPECIES

As an alternative to the prevailing methods for delimiting nematode species, I recommend abandoning the use of phenetic and biological species concepts and adopting an amalgamation of the PSC and ESC (Frost and Kluge, 1994): To discover species, look for the smallest diagnosable units in order to recover unique independent phylogenetic trajectories. However, to avoid the caveats of over-reductionism and to avoid recognizing more species than actually exist, I advocate that a species not be a speculative statement, made solely on the basis of a definable "difference," but rather predictive, based on evidence that suggests the two prospective species are on independent trajectories and not simply doomed to intractable reticulation in the future.

Again, it is impossible to predict the future, and all guesses at the future will fail with some degree of frequency. Of all the species ever described, or that will be described, many will still be recognized as lineages in the future. The rest will be affected by one or more of the three types of systematic error, or remain in limbo because we do not or cannot have all the information required to know either way. But to hedge our bets, we can require that the recognition of unique lineages demonstrates the anagenetic evolution of an autapomorphy, a uniquely derived character fixed among all comparable individuals (semaphoronts). Simply put, sister species must each have an autapomorphic character.

Though the requirement that species have an autapomorphy appears to be the Autapomorphic Species Concept (ASC) that de Queiroz and Donoghue (1988, 1990) ascribed to the PSC, it differs significantly in that it does not recognize "metaspecies," the taxonomic distinction given to an entity that does not have an autapomorphy but whose sister taxon does. As pointed out by Nixon and Wheeler (1990), the use of metaspecies is the recognition of entities that lack autapomorphies but are not assignable to species. I find such recognition to be incompatible with the ontological dictum stated in the introductory paragraph of this paper, which requires that entities are either a species, part of a species, or a combination of two or more species. As an alternative to

this method of delimiting species, Nixon and Wheeler (1990) suggested that species be diagnosed by their unique combinations of character states. But again, this is incompatible with being able to depict species historically because their non-heritable nature renders them ahistorical (recall that, although characters are heritable, combinations of independent characters are not).

One final difference between this species concept and other phylogenetic species concepts is that I do not wish to confound the discovery operations involved in recovering species with the properties (*sine qua non*) of the lineages I hope to recover. The only lineages we can apprehend are those with one or more autapomorphies. But this does not mean that *only* these lineages are evolutionary units. Other lineages may exist, but this is the only way I know of comprehending them. This can be contrasted with the concept of Nixon and Wheeler (1992), who confused what lineages are with how we can recover them when they suggest that *only* lineages that have autapomorphies are species.

Consider the following example of populations X, Y, and Z, where Y and Z are united by synapomorphy λ, and X and Y have evolved autapomorphies α and β, respectively, while Z has remained unchanged (Fig. 7A). All three populations are distinguishable; populations Y and Z are distinguished from X by λ, and Z can be distinguished from Y because it lacks an autapomorphy (population Z is defined as "not Y"). De Quieroz and Donoghue (1990) delimit Z as a "metaspecies" because it is neither X nor Y. Some taxonomists would consider this lack of an autapomorphy as a diagnostic character and describe it as a new species. However, since its only diagnostic character is the absence of an autapomorphy, then we have run into the unnerving problem of having a population (Z) which is at the same time an ancestor to Y and a descendant (Z), a logical absurdity. The absence of evidence should not be confused as being evidence of absence. In this case, one population has evolved a new character, while the other remains static. Even though the new population can be diagnosed as
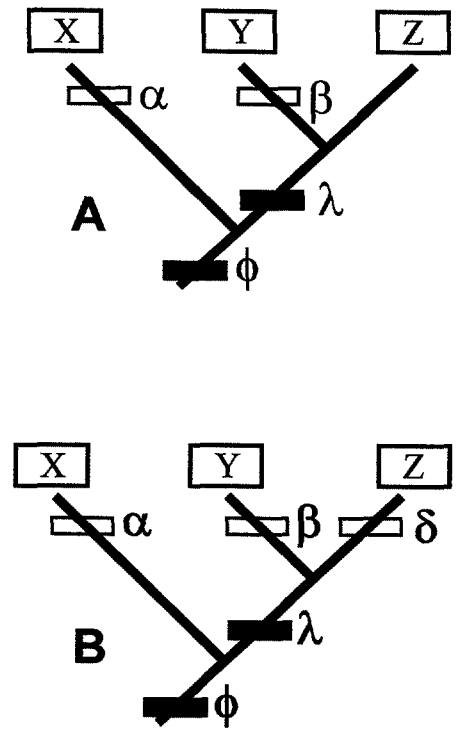

FIG. 7. Evidence sufficient to indicate the origin of two unique lineages requires the anagenetic evolution of an autapomorphy for each sister taxon. A) Phylogenetic relationships for taxa X, Y, and Z, where X has evolved the autapomorphy α and Y has evolved the autapomorphic character β. All three taxa are diagnosable (X = ϕ + α; Y = ϕ + λ + β; Z = ϕ + λ). Though all taxa can be identified, it does not follow that each is a separate species. Taxon Z is defined only as "not Y," and to recognize it as a sister species to taxon Y requires that it be the ancestor to Y and Z and descendant Z at the same time, a logical absurdity. Also, although the independent characters ϕ, λ, α, and β may be heritable, combinations of them are not and, as such, are not suitable to infer phylogenetic relationships or lineage exclusivity. B) Identical scenario as Fig. 7A except that taxon Z has evolved autapomorphy δ. Each smallest diagnosable evolving unit with an autapomorphy displays sufficient evidence that it is on an independent phylogenetic trajectory and can be delimited as a species. These operations guard against making all three types of predictive systematic errors in order to most accurately recover and represent species.

"different," this does not imply that the old population has also evolved anagenetically. Clearly, it is not evidence of the initiation of two new lineages, the definition of cladogenic speciation. The same is true if we are dealing with any number of autapomorphies or combinations thereof. Simply being different is not sufficient evidence to suggest that speciation has occurred.

For example, suppose that even though taxon Z does not have an autapomorphy, certain of its characters in combination can be used to diagnose it as different from taxa X and Y. Z, therefore, deserves species status $(X = \phi + \alpha; Y = \lambda + \beta + \phi; Z = \phi + \lambda)$. This is essentially the recommendation of Nixon and Wheeler (1990). But the problem here is that, even though these characters may be heritable, combinations of them are not. Thus, this method of delimiting species is also incompatible with representing them historically. In both of these cases there is no evidence that these two lineages are behaving as if they are exclusive, so there is no reason to believe that these two populations will not reticulate. Thus, describing populations Y and Z as separate species requires a speculative statement, and the probability of making a type I error is high.

Now consider that populations Y and Z both have evolved autapomorphies (Fig. 7B). The autapomorphy β provides evidence that all Ys share a single common ancestor, that they are monophyletic, and that they appear to be evolving exclusive of lineage Z. The autapomorphy δ does the same for all Zs. This can be seen as evidence sufficient to predict that these two smallest diagnosable units are on independent phylogenetic trajectories and, as such, are species. The set of all Ys and all Zs is a complete set, diagnosed by autapomorphy λ. This obviates the existence of "metaspecies" as well as all three types of predictive systematic error, and results in a delimitation and representation of species within a historical context. It is important to note, however, that this operation does require an objective discovery method for apomorphic characters (e.g. Hennig, 1966).

AN EXAMPLE: *HETERORHABDITIS*

Currently there are nine described species of *Heterorhabditis*, and, although reproductive compatibility has been studied among some species and isolates (Dix et al., 1992), all species descriptions have been based on the diagnosis of phenetic differ-

ences between isolates. Using ribosomal DNA sequences, a gene tree has been established and phylogenetic relationships among populations within the genus have been inferred for eight of these species.[9] Although it is shown that the genus is indeed monophyletic, current taxonomic relationships among isolates of *H. bacteriophora* appear to be paraphyletic. An example of these relationships is shown in Fig. 8, a simplified phylogenetic tree of the genus containing two described heterorhabditid species (*Heterorhabditis bacteriophora* [Brecon strain, Brecon Australia], *H. argentinensis* [Rafaela, Argentina]), and three isolates of *H. bacteriophora* that are assumed to represent different populations (HP88 [Utah, USA], ACOWS [Nebraska, USA], and NC-1, [North Carolina, USA]). The outgroup taxa, *Pellioditis typica*, *Rhabditis (Caenorhabditis) elegans*, and *Steinernema carpocapsae*, also are included.

Application of the Linnean species concept obscures evolutionary history by suggesting that *H. bacteriophora* isolates HP88 and NC-1 are the same species, even though the HP88 population is more closely related to *H. argentinensis* (Fig. 8A). In this case, application of the Linnean approach results in type II and type III errors. Likewise, applying the BSC results in type II and III errors by suggesting that the reproductively compatible NC-1 and HP88 isolates are the same species, even though HP88 is more closely related to its reproductively isolated sister taxon, the Brecon strain of *H. bacteriophora* (Fig. 8B) (Dix et al., 1992; Joyce et al., 1994).

To reconcile these problems, I propose following Frost and Kluge (1994) in using the discovery operations of the PSC in order to recover the unique phylogenetic lineages of the ESC, with the addition of an operational requirement that sister lineages delimited as species must demonstrate autapo-
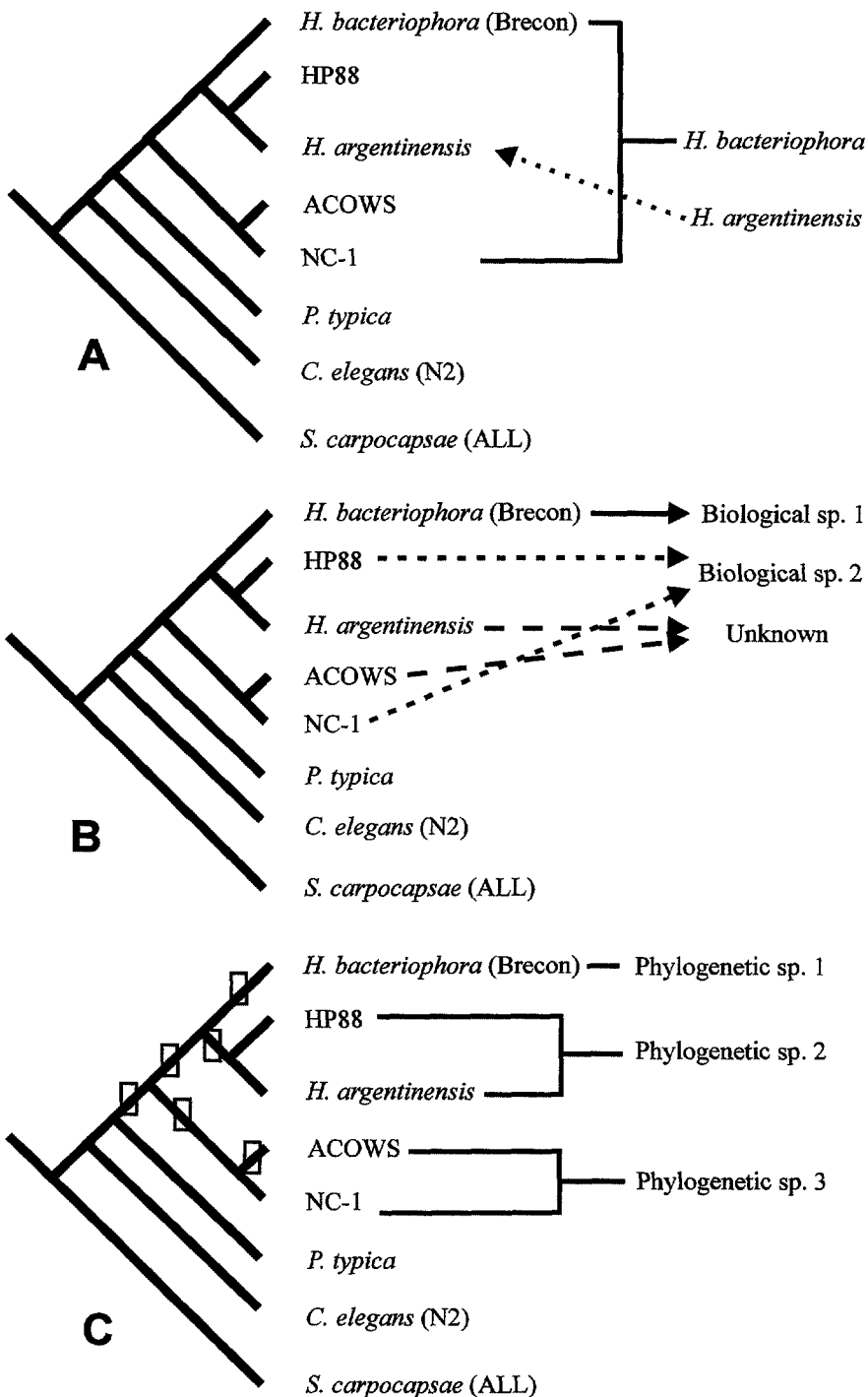
FIG. 8. Delimitation of different populations of *Heterorhabditis* as species by different species concepts, based on a ribosomal gene phylogeny. Isolates assumed to represent disparate populations are NC-1, from North Carolina; HP88, from Utah; and ACOWS, from Nebraska. A) Two species recognized by the Linnean paradigm, *H. argentinensis* and *H. bacteriophora*. Inclusion of *H. argentinensis* within *H. bacteriophora* reveals a paraphyletic assemblage. B) Depiction of two species currently delimited by the Biological Species Concept, *H. bacteriophora* (Brecon strain) and NC-1+ HP88. Breeding studies have not yet been conducted for *H. argentinensis* or ACOWS. C) Species delimited by an amalgamation of the Phylogenetic Species Concept and the Evolutionary Species Concept, requiring sister taxa to anagenetically evolve an autapomorphy (bars on the tree represent autapomorphic and synapomorphic nucleotide characters). Of the three hypotheses (Figs. 8A–C), Fig. 8C is the only taxonomic arrangement congruent with recovered evolutionary history.

morphies. This species concept recognizes three species within the *H. bacteriophora* complex: i) *H. bacteriophora* (Brecon), ii) HP88 + *H. argentinensis,* and iii) ACOWS + NC-1, as each of these lineages has evolved at least one defining autapomorphy (Fig. 8C). ACOWS has evolved an autapomorphy that distinguishes it from NC-1, but NC-1 retains the ancestral condition (an autapomorphy has not been detected). As mentioned earlier, because it can be defined as different, some might delimit NC-1 as a separate species. However, this implies that ACOWS is both ancestor and descendant at the same time, and that population NC-1 is defined only on the basis that it is not ACOWS (negative evidence). Both proposals are inconsistent with the ontological dictum of species and their delimitation based on heritable, independent characters. Thus, I can reject the hypothesis that the two isolates represent two distinct species.

One caveat of this example is the failure to include characters from other heterorhabditid nematodes. The inclusion of these characters could reveal non-unique autapomorphies within the *H. bacteriophora* complex. Also, it is inferred that variation within and among isolates are representative of the populations from which they were collected, but it is important to note that this does not necessarily follow. If it can be shown that the autapomorphies alluded to in Fig. 8C are representative of populations and are fixed within their respective lineages (accomplished via a satisfactory sampling regimen), we have sufficient evidence to predict that the three lineages (NC-1 + ACOWS, HP88 + *H. argentinensis, H. bacteriophora* [Brecon strain]) represent three unique phylogenetic trajectories and should be considered separate species. In doing so, it is possible that I make a type I error, certainly if in the future any two or more of these three lineages reticulate into a single lineage. But at least I can show that for now they appear to be behaving like species, and predict, rather than speculate, that persistent reticulation does not appear likely. More importantly, I am less inclined to make type II or type III errors.

DISCUSSION

Much of nematode taxonomy is based on species concepts that can produce serious predictive systematic errors. But just because they can, does not mean that they do. On the contrary, while a reevaluation of nematode species using these methods may result in a few subspecies being elevated to species, or a complex of species being recognized as populations, it is unlikely that what we designate a species will change much. The importance of this approach is apparent in what rank we give populations of nematodes. But even more important is the resulting classification that is consistent with recovered evolutionary history. This is not a trivial undertaking, but the payoff in terms of explanatory power afforded our resulting taxonomy is certainly worth it.

Dobzhansky (1973) stated that "nothing in biology makes sense except in the light of evolution," suggesting that an understanding of evolutionary history is requisite to making sense of the patterns biologists observe and seek to explain. This can be extended to nematologists in all fields, whether investigating interactions between hosts and parasites, or incorporating the genetic variability of populations of plant parasites into cropping systems. No matter what the application, the benefits of looking at problems from a historical, phylogenetic perspective can yield great profits in terms of understanding, from testing old hypotheses to providing new explanations from old data sets.

I have argued that species concepts are fallible but important if we are to have confidence that our taxonomy forms a reliable foundation for evolution-based research. According to the objectives of taxonomy, the best species concept for use in nematology is an amalgamation of the ESC and the PSC. To make this concept functional I advocate a set of operations to delimit species in a way that maximizes the historical utility of our taxonomic statements while avoiding the overreductionism concomitant with teasing out evolutionary lineages from populations. The methodology and philosophical basis of

this set of operations are explicit, and the results (taxonomic statements) are testable, falsifiable hypotheses, making it a scientific endeavor, not art (Popper, 1972). Fundamental to any description of species is the underlying concept used to delimit them, and I encourage nematologists of all persuasions to make explicit their methods of delimitation.

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