
Species, Trees, Characters, and Concepts: Ongoing Issues, Diverse Ideologies, and a Time for Reflection and Change

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1. Introduction

Consider ideology in reference to species and their conceptualization and discovery. Ideology is a set of beliefs by which a group or society orders reality so as to render it intelligible; speculation that is imaginary or visionary.

An extensive library of writings exists on the topics of species, species concepts and the intersection of these with phylogenetics. Why then another paper on the topic? Following the dialogue on these topics in literature and in discussions of systematics, the discovery and descriptions of species, and arguments and actions of authors of master lists of species, it is clear that some specific areas relating to species warrants additional attention. Herein, I offer a condensed, episode relating to a series of topics that, in my opinion, are not generally understood by some working today with biodiversity or practicing systematics. It is hoped that the brief addresses to particular topics are perhaps more palatable to those not focused on these issues regarding species but, in my opinion need to be fully aware of their intentions and interpretations regarding the nature of species and the use of terms and concepts within a critical theoretical and philosophical context.

In the last two decades we have witnessed great advancements in our conceptual, theoretical and operational understanding of biological species, as well as varied views of species within each of these areas. All of these contributions are, of course, developed and clarified within the context of the standing theory of evolution, or descent with modification and speciation. Should this theory not apply to the origins of biodiversity then our advances with this complex issue must be reframed, discarded, and/or derived anew. Varied “conceptual views” of species have long been proposed or used in discussions and arguments of diversity and have been

reviewed [1-17] and whole volumes have been dedicated to the concepts and practices regarding species wherein various authors outlined their preferred concepts and critiqued other concepts [18-20].

Because of the nature of species being individuals, aspects of their discovery and interpretations of their evolution are complex and sometimes require considerable thought and reflection. Unlike those things that humans feel more comfortable with, sets, classes, etc. that have clear operational definitions - is or is not, black or white, species and interpretations of their evolution are much more complex. Species, unlike supraspecific taxa stand alone in many contexts and terms used in systematics. With a general lack a real interest in discussions relating to species, especially among systematists and taxonomists (as well as others in comparative biology) there remain critically important issues regarding the basic understanding of species. As such, in practice, when interpreting data and analyses relevant to the existence of species those not informed can make decisions about the question of "What is a species?" or the species diversity simply inappropriate. Likewise, regarding the above responsibilities of these research communities staying abreast of the general issues regarding "What is biodiversity?", the bottom line for studies by such investigators simply lead to many inappropriate outcomes. For example, misinterpretation or indifference to deciphering natural patterns related to species, leads to a sequence of events that I would think that the comparative biology (in the broadest of sense) would not want to see - inaccurate assessments of diversity, inappropriate evolutionary conclusions, misinterpretations as to the existence of character distributions or their evolution, inaccurate conclusions as to processes in ecology, speciation, biogeography, and lack of official protection and conservation of species. Lineages that are ignored cannot be included in comparative biology analyses - that being revealing natural patterns of descent with modification, appropriate comparisons, and seeking explanations/processes having lead to these patterns.

The issue of species simply boils down to many practitioners both inside and outside of the informed realm of the underlying theoretical and philosophical issues on species easily slipping into a more comfortable world of "black and white", that being a world of "science made easy", and a sense of self ease and tranquility regarding their own scientific reputation - view species as class constructs with simple definitions (includes most of the diversity of concepts, see below and [15-17]). If something in nature being studied does not fit their concept (actual black and white definition surrounding a concept), then it cannot be a species. Or, there is the unfortunate view of many involved in molecular biology that a species must have a "high enough" p distance to be valid, when the genes that we study today represent an infinitesimally small sampling of the genomes of the taxa. Or, despite the intentions of the discovery of naturally existing lineages, some actually believe that they can only be discovered and diagnosed on the basis of morphologically differentiation. For many, if morphological characters are not easily examined by eye, with a hand lens, or with a microscope, they do not exist unless differentiated enough genetically from other such things.

Adding to the confusion surrounding the topic and the artificial assessments and conclusions by some, many well-intentioned and informed practicing taxonomists/systematists still unfairly judge other's research on diversity and their recognition of species on their artificially

contrived basis of degree of difference or “value” of diagnostic morphological characters, as if anyone understands the genetic coding of any morphological characters used in a taxon-specific discipline. Sadly, even today the degree of morphological differentiation is considered as a surrogate to the degree of genetic divergence. Falsifying evidence of this long-standing hypothesis abounds, but as is argued in reference [21], paradigms are not usually shifted, changed, or evolve because to many scientists evaluating examples and data typically spend most of their time seeking examples to simply corroborate hypotheses. Hence, much of the “new synthesis” thinking remains, and with this is the traditional thinking of biological species.

Not all contributors to the recent advancements on species view species as real and individuals that are mutable and are lineages diversifying over time. Others, again for convenience and safety of their own scientific reputation, prefer to consider species as class-like constructs with safe definitions (not the same as diagnoses). Interestingly, this long held argument of proponents of concepts that in reality do not consider time as a component of the conceptualization and interpretations of species, a logic incompatible with the current paradigms, theories, and hypotheses underlying evolutionary biology still exist. With these definitions of varied class constructs, logically derived from all concepts except the Evolutionary Species Concept, species thought to participate in processes associated with evolution and used in reconstructions of evolutionary relationships are in fact immutable, thus precluding their existence in reference to any aspect of evolutionary biology.

Regardless of the valuable, important, and numerous advancements in the discipline that have ultimately lead to a critically important view of consilience among concepts with evolutionary biology, several issues and terminology remain unclear to many practitioners of the discipline. These are discussed below. This clarification and a call for a more informed systematic and taxonomic community investigating all of biodiversity will hopefully better inform and unify scientists within this broad field on species so they can be logically investigated within the current paradigm of evolutionary biology. The topics covered herein have been selected as ones that I interpret as a series of issues in this broad discipline wherein practitioners and users remain misinformed or have not dealt with or had the time to deal with the complexities of the issues surrounding species.

2. Taxonomy and systematics

Historically, these general areas of the study of biodiversity were considered to be or were referenced as separate but linked disciplines. Taxonomy has traditionally been viewed as the area of science related to the discovery, naming, and classifying species. Systematics was traditionally viewed as the study of relationships of species and supra-specific taxa. Under this organization these two disciplines remained inappropriately disconnected. Prior to the revolution of systematics by Hennig a sound method for reconstructing genealogical relationships did not exist and the field was dominated by the disciplines of Evolutionary Systematics and Numerical Taxonomy, both disciplines

lacking a logical means of providing natural biological classification reflective of ancestor-descendant relationships [22-25]. Hennig's methods provided a means with which one could reconstruct defensible hypotheses of relationships, as well as a time-dimensional discussion of species. Simpson and Wiley's works on species concepts provided the necessary connection between phylogeny reconstruction, character evaluation and interpretation of homologies, and species as lineages [1-4, 26].

Thus, today, these two once separate disciplines must be combined under the title Systematics. Neither of the formerly recognized disciplines can today work independently. The natural order is that phylogenetic interpretations of characters and their evolution, as well as phylogeny reconstruction leads to the discovery of new, previously unrecognized diversity. Phylogenies provide a framework for properly classifying diversity. This merger provides a more holistic view of a necessarily structured discipline focused on biodiversity. Below, I will use the term systematics to refer to this collective scientific study of biodiversity.

3. Life-long education, critical thinking, and biological species

As scientists our work should involve a process of continued education of specialized and many associated fields. Without continued life-long education, our practices and hypotheses, hence, scientific practices, become outdated and eventually irrelevant. Such "scientists" are anchored in the past but are frustrated and irritated as they watch the world change around them. Those who practice in the disciplines associated with the discovery and study of biological species have the responsibility to remain up to date on the theoretical underpinnings relevant to biological species, as well as the various operational mechanism used in the discovery of species, regardless of the types of characters used and their interpretations (see below under "Characters: their real function and why all types are important!" and "Concepts for Species as Lineages versus Operational Definitions"). Admittedly, there are volumes of publications relating to dialogues on species concepts but these are critical discussions for one to better understand the theoretical and philosophical underpinnings of the study of biodiversity as species in the natural sciences. They, along with an understanding of the difference between plesiomorphic and apomorphic characters (whether they be discrete characters, frequencies of characters as alleles/nucleotides), also need to have a phylogenetic perspective to evaluating diversity. In the science of biodiversity today, these are essential to understand and effectively participate in a more accurate depiction of the planet's biodiversity and its evolution. Only through the understanding of these topics (all reviewed in very good papers in the last 20 years) can one make an informed decision on species diversity and decide whether species are lineages and mutable (=participate in such basic process theories as anagenesis and cladogenesis and are individuals) or are simply artificial and immutable constructs that humanity has developed to simply organize nature (classes). These are the two basic propositions that one has to evaluate in the central argument to the species issue and one's ability to conduct science.

4. Participation in educational and experience-based dialogues on species?

In Mayden's discussion of species and species concepts several theoretical and philosophical issues were discussed in this area, as well as a number of practical, experienced-based observations regarding species and their investigation in a time-inclusive perspective [15]. My experience with biodiversity, species, and the lineage/phylogenetic perspective lead me to "paint myself into a corner" on the theoretical, philosophical and operational views on species in nature. This evaluation and discussion lead to the acceptance of species as individuals and the determination that other concepts were really not underlying concepts to be used to provide a theoretical underpinning for use in the organization of thought allowing for an accurate discovery of all types of diversity evolving as lineages. Thus, both theory and real-life experience surrounded my conclusions as to the discovery of the elements of the tree of life for informed study. Hull evaluated concepts and compared them with others discussing species and discussed the theory of monism and pluralism as associated with theories or perspectives on an issue [10]. He also addressed the issue of life experiences with biodiversity regarding multiple dimensions involving both and laboratory studies, both, in my opinion, being fundamental to understanding, discussing, and choice of underlying conceptualizations of species. Experience with naturally occurring entities and their variation in characters is no substitute for the theory and philosophy of species but both are necessary and sufficient to successful and meaningful study and dialogue pertaining to the discipline.

Scientists discovering and studying biodiversity and its evolution learn about the entities, known as species, through studies of theory and philosophy, as well as real-life experiences, on species and guidance from mentors and colleagues. A background on the readings of the theory and philosophy of species alone, and with no practical experience honed over time and with continued study is not enough, in my opinion, to prepare one to either discuss species as individuals or classes, appropriately viewing the reality of species, or judging the validity of any described species. As we all know, one does not become an expert in science overnight – it comes through study and mentoring. The theory and philosophy purported by some without these one of classes of experience is not enough to serve as an expert on this topic. The same is also appropriate for those restricting themselves to only phylogenetics or population genetics of entities hypothesized to be species (see section below entitled "The Nature of Biological Species: Assertions as to the Monophyly of Species?"). Likewise, the same applies to efforts in evaluation and hypotheses of homologies of character states or characters, regardless of the type of character system involved. Continued experience, studying literature and mentoring from one or more persons experienced in these areas of diversity cannot be substituted by the limits of theory and philosophy of a topic. This combination of experiences is essential in these and other areas of the natural world to fully understand process and diversity, as many more "things" in the natural world are actually individuals (like species; etc. individual organisms, populations, communities, ecosystems, planets, etc.) and cannot be defined; it is inappropriate to view them as simple class constructs artificially restricted by rigid definitions of membership. The repetitive study, examination, and tests of levels of tokogenetic versus phylogenetic relationships of biological diversity, of characters, and other

individual-type entities is a critical area of study in organismal biology that is uniquely occupied by specialists in systematics.

5. Concepts for species as lineages versus operational definitions

Wiley and Lieberman provide a very lucid summary for an important introductory discussion laying the foundation for understanding the issues and importance of topics surrounding species concepts [27]. As discussed by these authors two critical factors have been discussed for many years include:

1. Species-as-taxa are individuals and,
2. A species concept for the category species of the Linnaean classification is a kind concept – by intention.

This important distinction is likely the most common reason for many being confused in dialogues and writings about species. This has also led to the long-time debate on concepts, the delays in biodiversity discovery, and likely the extinction of biodiversity by neglect and ignorance in our interpretation of characters through time. The above distinction as to species-as-taxa and the species category is essential to understanding the central issues discussed by Mayden [15-17], de Queiroz [13-14, 28], Wiley and Mayden [29-31], Naomi [32], and Wiley and Lieberman (27). Without a clear understanding of this basic premise, future discussion and understanding will be difficult for the systematist and/or evolutionary biologist to integrate and be consistent with underlying principles of evolution given current paradigm as to descent.

In specific writings by Mayden [15-17] an explanation for the growing number or large number of historically developed concepts was related to 1) the lack of understanding or view of species as lineages versus classes and 2) concepts being developed based on the mentor-student lineages of researchers working with specific types of characters for specific taxa that ideologically think are the most important characters for the recognition of species – a legacy that should continually be evaluated by the researcher via life-long learning. All of the concepts, save the Evolutionary Species Concept, have arisen by this means. However, concepts underlying entities that are individuals must be developed under the premises through which they supposedly originated – or process-based concepts. As Wiley and Lieberman [27, pg. 29] correctly assert “Process-based concepts attempt to characterize species in a manner predicted by “covering laws” thought to explain processes occurring in nature.” One must examine each of the concepts individually to determine if they are concepts derived out of the currently held theory of descent with modification and related hypotheses and assertions. Thus, without an understanding of process-based concepts and kind concepts relevant to biological species, what constitutes a species across biological diversity derives from a historically “blinded,” non-lineage, definition-based view of species. Such concepts of naturally occurring entities make it impossible in comparisons, contrary to a lineage-based concept viewing species as individuals. What results from this limited insight into species and an underlying process-

based concept of what we are looking for will be discoveries or decisions based on limited thought as to lineages and time, and misunderstanding of the evolution of homologous characters. Hypothesized homologous character transitions are simply historical and heritable markers or tags to serve as evidence to formulate hypotheses as to independent lineages, entities comprised of organisms that maintain their identities from other such entities through time and over space and which have their own independent evolutionary fates and historical tendencies *visa-via* the Evolutionary Species Concept. Species are christened with proper names and are always testable hypotheses, not fact, as is the same for phylogenetic trees.

The important issues at risk here for evaluating and selecting definitions purporting to be equally viable for species are partially outlined below from Wiley and Lieberman (27, p. 28).

As kind concepts, they are defined by intention, each concept having properties that should provide necessary and sufficient conditions for "speciesness." ...

We might also expect some concepts to be nominal kinds, kinds that do not have direct connections with evolutionary theory but which are thought to be useful in some manner by those who invented them.

As kinds, we might expect that some species concepts are candidates for being natural kinds. Such concepts would "fall out" of evolutionary process theories (Quine, 1969). We might also expect some concepts to be nominal kinds, kinds that do not have direct connections with evolutionary theory but which are thought to be useful in some manner by those who invented them....

Wiley and Mayden (2000a – c) suggest that systematists form species concepts in a manner that reflects their ideas of how these concepts function in systematic and evolutionary theory. Some systematists form concepts that allow them to discover what they think are species. Others form concepts based on how they think species function in the evolutionary process. We suggest that this is nothing but the familiar debate on operationalism that surfaces from time to time in science (Wiley, 2002). Some systematists think that it is important to form "operational" concepts. (Wiley and Lieberman, 2011, 28)

As Wiley and Lieberman [27] further discuss, this issue is not one that should be easily dismissed. In my opinion (Mayden 15-17), without a clear understanding of these distinctions the “fog” that surrounds one may have about species and concepts, and their inappropriate applications, will plague the outcomes of a researcher and any clade of diversity studied by this researcher. I do not speak for Wiley or Lieberman with respect to my proposition of such a bewildered view of evolutionary diversity. However, this general issue was emphasized by these authors in a similar context [27, pgs. 28-29]:

It is exactly this distinction that led Frost and Kluge (1994), Mayden and Wood (1995), Mayden (1997), and de Querioz (1998) to suggest that a distinction can be drawn between what might be termed “general” concepts and “operational” concepts. General concepts provide an ontology from which “operational” concepts (= testable concepts) may be applied....

Process-based concepts attempt to characterize species in a manner predicted by “covering laws” thought to explain processes occurring in nature. Evolutionary theory (specifically that part of evolutionary theory concerned with the origin of species) provides such a “covering law,” which posits that there are two kinds of entities one might expect to find in nature that are of primary interest to systematists, species and monophyletic groups. Given that evolution appears to result in a hierarchy of entities, the monophyletic group seems to be a natural kind that falls out of the general theory of descent with modification, coupled with the general theory of speciation....

Because all particular examples of the kind “monophyletic group” have a beginner, a common ancestral species, this suggests that species are also a necessary kind. In other words, if “monophyletic group” is a natural kind, then that from which particular monophyletic groups are derived (“species”) might also have the status of being a natural kind (Wiley and Mayden, 2000a). The results form the basis for expecting, as Hennig (1966) suggested, that organisms have two sorts of relationships. Tokogenetic relationships are formed on the basis of reproduction and obtain among individual organisms. Phylogenetic relationships are formed by severing reproductive ties to the extent that two tokogenetic systems are formed out of what was once a single tokogenetic system (or, in the case of speciation via hybridization, two tokogenetic systems form a third through tokogenesis between the two systems). For sexual organisms, tokogenesis is nonhierarchical while phylogenesis is hierarchical (speciation via hybridization is the exception).

Given this insight into concepts, both process-based and operational (*sensu* Bridgeman's operationalism [33]), the recent syntheses on species by Mayden and de Queiroz lead to a singular conclusion as to a needed revision of the whole issue of "Species Concepts". Not all existing of species-as-taxa serve to facilitate our understanding of processes and patterns underlying the evolution of biological diversity. Only one, the Evolutionary Species Concept, is the appropriate process-based concept facilitating the discovery of species as individuals and natural kinds. Herein, I argue that the terminology associated with all other previously referenced "species concepts" (except the General Lineage Concept that is a synonym of the Evolutionary Species Concept) should be changed to their use as only definite criteria (*sensu* Wiley and Lieberman [27]). They serve as none other than simple criteria for the discovery of lineages or surrogates for the discovery of lineages, using any and all types of heritable characters, that are consistent with the processes of evolution under the process-based Evolutionary Species Concept. Thus, these historical concepts of species have new names as criteria, not concepts, and are referenced differently (Table 1).

| | |
|---|------------------------------------|
| Agamospecies Criterion | Internodal Criterion |
| Biological Criterion | Morphological Criterion |
| Cladistic Criterion | Non-dimensional Criterion |
| Cohesion Criterion | Phenetic Criterion |
| Composite Criterion | Phylogenetic Criterion |
| Ecological Criterion | Polythetic Criterion |
| Evolutionary Significant Unit Criterion | Recognition Criterion |
| Genealogical Concordance Criterion | Reproductive Competition Criterion |
| Genetic Criterion | Successional Criterion |
| Genotypic Criterion | Taxonomic Criterion |
| Hennigian Criterion | |

Table 1. Revision of terminology associated with a new process-based conceptual view of biological species. Above listed historical concepts of species (previously considered concepts equal to the Evolutionary Species Concept) represent definitions of class constructs and are herein consider definite criteria or criteria for short. See Mayden [15-17] and Wiley and Mayden [29-31] for further clarification of why these "concepts" are not equivalent or any are to the Evolutionary Species Concept as the underlying process-based concept of species.

A non-lineage perspective held by a researcher also leads to significant problems in accurately estimating biodiversity by not understanding the origins of characters in different populations or species. Very often two or more species are reduced to one or more simply by the non-dimensional interpretation of the existence of characters distributed across the species and intervening populations thought to be one of these species yet in an active and ongoing process of gene exchange through hybridization and intergradation (simple violation of the historical Biological Species "Concept"). Character interpretation even within populations of species or across the geographic landscape of one or more species must be evaluated from a phylogenetic

perspective, as illustrated in the simple example in Figure 1. In this instance one geographic grouping of organisms (Species II: population, set of populations?) is interpreted as a group of intergrades between Species I and III. In the world of species concepts without a dimensional component this may be a valid interpretation of the situation. However, as one can see in this example, the observation that Species II has both traits of Species I and II has a more parsimonious interpretation of possessing the unique combination of both plesiomorphic and apomorphic conditions relative to Species I and III. Species II would likely then be considered simply intergrades between the Subspecies I and III – thus a reduction of biodiversity from three likely valid species to only one!

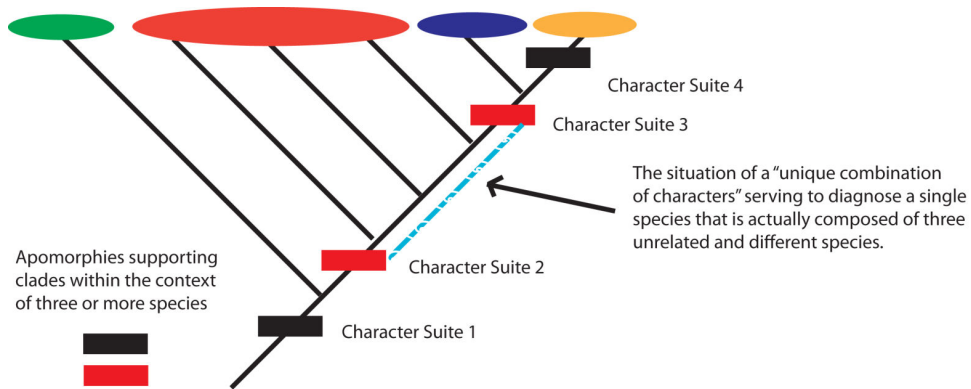


Figure 1. Hypothetical example of multiple geographic groupings of hypothesized taxa wherein the centrally located grouping, Species II, is polymorphic for the two character states found separately in Species I and II. A non-dimensional interpretation of this polymorphism would likely conclude the existence of continued gene flow and therefore the modification of diversity to only one species and two or more subspecies. The lineage perspective, however, provides a clear interpretation of Species II simply sharing one plesiomorphic allele with Species I and one apomorphic allele with Species III. No active process is necessary to invoke and the difference in biological diversity is 1 versus 3 species between these two approaches to interpreting the processes involved in possession of characters (alleles, morphology, etc.)."

6. Synonymy of the overall theoretical concept of biological species

With the great attention given to species and their conceptual framework over the last 20-30 years there has been tremendous progress in clarification and resolutions on the issue and the education of various communities of researchers and the general public. One of the most significant accomplishments, in my opinion, has been the realization that not all “concepts” of species have an equal status for use as guiding principles enabling one to discover biodiversity on planet Earth. Two basic ideas have been consistently repeated historically in theoretical or practical discussions of species in nature. Those that argue that species are of different kinds and as such require different concepts (pluralism; Hull [10]). Or, there are those researchers that argue that this is an incorrect and poorly formulated logic as to species, regarding the

result of natural selection, anagenesis, and cladogenesis or speciation (= individuals). In this second framework, the discipline should have an overarching, non-operation concept of species as lineages and a series of conceptual criteria for discovery of said species (monism). I argue the latter as these principles are consistent with what we currently understand or think we know about evolutionary biology. These two opinions have resulted in an enormous number of papers where researchers, philosophers, or both have simply not understood one another's arguments. This is exactly the same underlying issue that has plagued the debates over which characters and analyses are "best" or "should be used" in phylogeny construction. Most of the special issue in *Zootaxa* [38] on molecular and morphological characters involved authors that had a poor understanding or were ignorant of the underlying and generally sound methods of what they were criticizing. These two examples have, however, been to the benefit of science and lead to many important discussions that forced people to clearly articulate ideas and ideologies and evaluate principles and process-driven concepts. Unfortunately, however, those systematists, as well as reviewers and editors of papers, not up to date on these issues have simply delayed the discovery, authoritative decisions that have serious consequences. Among many other critical outcomes, there is the delay or denial of christening lineages of biodiversity with proper some names, some before they have gone extinct as their habitats are lost, there is species not being "authorized" for descriptions because of a prejudicial ideology of species as individuals and a process-based concept, there is squandered time for conservation interventions of endangered diagnosable entities due to ignorance and character bias, and there is a result in inappropriate or inaccurate process- and pattern-based studies of species, natural selection, and speciation.

Through these various discussions and debates, some researchers have focused on a higher-level understanding of the issues at hand and how to resolve ongoing incongruences of logic of some, conflation of many things about the vast writings on species and species concepts, the real underpinnings of the various species concepts, understanding process-based concepts and non-process-based concepts, etc. These recent papers were all done by experience professionals (field, laboratory, and theory) with real-life experiences with species and species issues, and were formulated in an effort to better present the history of this critical topic to all of the natural sciences in a more lucid, logical, and cohesive manner [1-4, 7, 11-17, 28-32, 27]. Common amongst these series of writings is that the issue is not a question of there being different types of species in nature that necessitate different concepts to realize their existence as natural biodiversity. Rather, they argue that species are the same theoretical entities and realized by a common overarching, process-based concept of these lineages, and that their discovery relies upon the other existing "concepts" or criteria for different defining qualities for recognition of these independent lineages consistent with the process-based concept.

As outlined by Mayden [15-17] and discussed by Wiley and Lieberman [27] the Evolutionary Species Concept is really a logical analog to the natural kind monophyletic group as neither of these are operational concepts. Critically important to this, however, is that *this is strength of a concept and not a weakness* [5, 29-31]. And, as Wiley and Lieberman [27]

discuss, “a concept can embody testable consequences without being operational sensu Gilmour [34].”

The writings of Mayden and those of de Queiroz parallel one another. However, as discussed in the detailed comparisons and review by Naomi [32] both have integrated frameworks of species concepts and consider operational methods of discovery. Each view is ultimately thought to lead to the same consequences as to the discovery and descriptions of species in nature. de Queiroz chose to develop a new title for his line of thinking of a species concept, the General Lineage Concept, to set it apart from the Evolutionary Species Concept. However, as aptly reviewed by Naomi (32, p. 1) the “existing and revised versions of the integrated framework of species concepts all are not new species concepts, but versions of the evolutionary species concept, because they treat the evolutionary (or lineage) species concept as the concept for species category. This was also concluded by Wiley and Lieberman [27]. As such, the General Lineage Concept is herein argued to be a synonym of the Evolutionary Species Concept.

7. Definition of the category species in the linnaean classification

An evolutionary species is an entity comprised of organisms that maintains its identity from other such entities through time and over space and which has its own independent evolutionary fate and historical tendencies (Wiley and Mayden [29]).

Synonymy: General Lineage Concept of de Queiroz [14]

8. What is a species? Reality, fiction, hypothesis, artifact, special creation?

It is my opinion that species are naturally occurring lineages that exist in nature irrespective of our abilities to find, study, or diagnose them. As such I am a realist. In concert with this, following the premises of scientific investigation, I consider discovered and named species that we place in the Linnaean Category Species to be testable hypotheses. Evolution operates at the level of the species lineage as this is the upper-most and most comprehensive level of tokogenetic relationships that exist prior to speciation. Species are individuals and are mutable and as such take on all types of apomorphic qualities. Their evolutionary relationships can be inferred, as well as any other historical or contemporary patterns and processes as tenants of evolutionary biology. Species are not artifacts or things of special creation that are immutable; if they are then they cannot be investigated or used in investigations of descent with modification that inherently involves anagenesis and speciation.

9. Characters: Their real function and why all types are important

Homo sapiens, as a species, are inherently compromised in doing an effective job at understanding and finding homologous characters and species as individuals. We, as a species, do not have access to or even know what the appropriate “markers” are to corroborate either a lineage or homologous characters independent of other such lineages/homologues.

Abundant discussion exists as to the question of “What is a character?” and several have provided discussions and overall definitions [3, 27]. The same is true for the question of homology of characters. In fact, without a doubt the two issues are often thought to be independent. This type of thinking about species readily leads a serious logic problem for species discovery and phylogeny reconstruction, and possibly conclusions resulting from related biodiversity investigations.

Simply put, characters are deciphered and hypothesized attributes of species unraveled to their most basic element and then sorted out as to hypotheses of various hierarchical levels of or independent instances of homology. No set type of characters is inherently better than any other, except where a hypothesized character is not heritable or is simply too variable to be evaluated given current algorithms or existing thinking on the topic. However, homoplasy can be very useful in phylogeny reconstruction to resolve nodes wherein homoplasy occurs. Actually, homoplasy is a contrived term for something that actually does not exist in nature. Homoplasy, in the systematic literature, derives simply from our inability to properly identify variation in homologues in our deciphering of character transformations.

In the world of molecular systematics, aligned genes, restriction sites, and frequencies of alleles of a gene are all analyzed. No data are excluded, even though variability exists in any of them. This variability is handled through specially designed algorithms that are formulated to deal with polymorphism of heritable traits. Morphological systematics, however, for the vast majority of studies is immune to these issues as users discard characters that they deem as too variable, in reality it is much more subjective and difficult to decipher the homology of characters, and nothing is known as to the genetic control (simple or complex) of any of the characters. All character types suffer from some sort of issue and they can be argued to be equally problematic. However, as a person that has used all of these types of characters, it is my opinion that hypotheses of homology are more difficult with morphological characters without very detailed ontogenetic evaluations or any additional investigation of any other type of morphological character.

In reality, characters are simply markers or tags that are left behind through anagenesis accompanying speciation. These tags or character transformations, when accurately interpreted in a phylogenetic context, must be evaluated in a context to ascertain its relative state of being either plesiomorphic or apomorphic. If anagenesis does not keep pace with speciation then no resolution of relationships of three or more taxa will be possible; although this depends entirely upon the character being examined as some not examined may have undergone anagenesis and kept pace with speciation. Phylogeny reconstruction is dependent upon the rate of anagenesis of any type of hypothesized heritable character either keeping pace with or

occurring faster than the development of independent lineages, or speciation. Thus, in summary, everyone should be careful in evaluations and critiques of characters used in phylogeny reconstruction and diagnoses of species. After all, today we use a variety of types of data, though mostly molecular and morphological data, for reconstructions or inferences of shared common ancestors. These synapomorphies, of varied types, provide evidence for the existence of a species that was an ancestor to two or more descendants. Yet, in the conservative world of those describing species, morphology rules and species are not, for example, diagnosed strictly using molecular apomorphies. This inconsistency in logic is unfortunate as species as lineages and individuals are not being recognized, conserved, and studied – simply because of a conservative character bias that has no underlying metaphysical justification.

10. Gene trees versus species trees?

Wiley [3] and Wiley and Lieberman [27] advocate that there is only one tree to explain the diversity of life, regardless of our abilities to discover it. In systematics, among at least phylogeneticists (not transformed cladists or many considering themselves cladists wherein phylogenetic hypotheses do not represent evolutionary trees), there has always been an underlying premise a reconstructed phylogeny represents a hypothesized tree of genealogical relationships for the taxa concerned. Such an inference of relationships is a hypothesis as to the best estimate of species (or species representing supraspecific taxa) relationships - based on synapomorphic, homologous characters employed in a phylogenetic analysis (model based or not). These inferred trees are hypotheses of speciation events (representing a diverse lineage by selected species or single species, subspecies, or other taxon used by the author(s)). It is a hypothesis of a genealogical tree, not a series of branching events that can be reconstructed on anything (nuts, bolts, cars, motorcycles, etc.). Why? Cladistic relationships, as advocated by some, for the above inanimate objects has no underlying reality in assessments of homology. While the objective of those that consider themselves cladists or transformed cladists (literature of the 1980s) is to avoid invoking any evolutionary bias in a reconstructed tree of relationships, this cannot be achieved because a simple use of any type of characters in a matrix invokes the evolutionary process of character homology. Otherwise, why not randomly distribute the character information across columns? Therefore, these arguments are pointless as not all nuts or bolts or cars or motorcycles originated in a unique common ancestor (of each type) wherein through time the character transformations may or may not have changed through time via anagenesis and that may or may not have been accompanied with speciation. When one purports to reconstruct a series of phylogenetic or cladistic relationships the underlying hypothesis of homology is an evolutionary process and cannot be avoided in any science-based study; thus, those wishing to divorce their study from any evolutionary-based assumptions are incorrect.

Prior to the generation and eventual landslide of genetic data in phylogeny reconstruction, species trees were discussed in the above context as descent and ancestor-descendant relationships supported only by homologous and derived characters. With advancements in capturing molecular data (allozymes, restriction sites, sequences) for hypothesized synapo-

morphic homologues things changed with respect to the idea of trees. References to such genealogical hypotheses involved either gene and/or species trees. Thus, one could discuss gene trees, species trees, or both. This plurality of discussion of trees arose when researchers discovered that different genealogical information (synapomorphies) used separately revealed different patterns of genealogical relationships [35]. This topic has recently been thoroughly covered in the compiled volume edited by Knowles and Kubatko [36]. Hence, these efforts, along with sophisticated algorithms to analyze the types of data resulted in the introduction of a new terminology and the idea of a group of species can actually have different gene trees. The differences amongst these gene trees result from lineage sorting issues, long-branch attraction, and other factors resulting in the evolution of individual genes. While this theory of gene trees is very convincing and is a real issue in systematics today, some solutions to these varied patterns of descent have been and are being developed as noted in Knowles and Kubatko [36].

The question then becomes “Exactly what is a species tree? The term species tree is widespread in the literature, usually in reference to a discussion of gene trees. However, there is limited coverage as to what exactly people hypothesize is a species tree. It could be envisioned to be a variety of things but rarely does one define their meaning of a species tree, a lapses exactly similar to those describing species but do not reference as to what concept they follow in discovering new diversity. The general thought of a species tree is that it is an estimate of all of the data combined, with some ad hoc explanations for some character transformations. However, the idea of gene trees versus species trees is usually in reference to molecular data sets and resulting phylogenies. Thus, while the issue of genes providing different hypotheses of descent of taxa examined is a valid and important issue, it is important to keep in mind the underlying theory of a species tree and not have the latter biased into only discussions relevant to genes.

Thus, what is a species tree? Is it a tree based on all gene sequences available or all molecular types of data? Is it a tree based on mitochondrial, plastid, or nuclear gene sequences? Is it a tree based on some combination or restriction of molecular data in the options above? Where do other types of characters, like morphological, behavioral, ecological, physiological, etc. fit into the discussions on species trees? Are they to be included or are species trees really those reconstructions based on morphological characters as some would argue (Mooi and Gill [37], and see series of papers relating to this issue in *Zootaxa*, Carvalho and Craig [38])?

I argue that when considering the idea of and discussion of a “species tree” one must keep in mind that such considerations should not be in reference to any particular type of data and this should be clearly addressed. As Wiley [3] and Wiley and Lieberman [27] advocate, and I concur with, there is only one tree of the genealogical history of life on earth, regardless of our ability to discover it. It is also an issue of a hypothesis-driven question and outcome. All reconstructions and inferences are biased in one way or another – from the obvious of weighting characters to a model based analysis (all analyses are based on some sort of underlying model, including simple parsimony) to one’s selection of characters or those characters that are available to the researcher (aspects of morphology, primers for and ability to generate gene sequences, behaviors, and a theoretically infinite number of character types).

Thus, a species tree is simply the one genealogical history of relationships of diversity of life. All of our analyses and attempts are simply estimates of this tree. However, the ways of combining or dividing characters and the types of characters employed are seemingly infinite and likelihood of converging on the species tree of life must always be considered. Trees are hypotheses subject to testing either through additional types of analyses, altering assumptions to even differing combinations of character transformations.

11. Which species tree is the best?

A common misconception amongst those practicing systematics or using systematic information (phylogenies) is that the latest published phylogeny of a group of taxa is the best and therefore represents the most probable set of relationships. This is a gross misconception. A phylogeny of taxa (species) is a hypothesis and multiple published phylogenies on a group of taxa may be equally probable/parsimonious hypotheses and stand alone as multiple hypotheses of relationships for the same taxa. It is not uncommon for the phylogenetic relationships of any group of taxa to change as more characters or taxa are added or taxa or characters are removed. This phenomenon is known as bias via taxon and character sampling [39-42]. It is predicted that with continued addition of samples of taxa or taxa alone as well as more character information on these taxa, the tree will stabilize as to relationships based on synapomorphies. Thus, for a particular group the phylogenetic relationships may change over time with new additions of hypothesized synapomorphies and/or addition or deletion of taxa. However, one must realize that, contrary to assertions of Mooi and Gill [37, 43], they are all competing hypotheses, just like alternative hypotheses of homology. They stand until appropriate statistical tests are used to evaluate their robustness. The future holds many uncertainties and possibly alternative interpretations of genealogical descent. After all, this is science and engages the process of refuting or corroborating hypotheses, not an exercise set out to prove a set of relationships engraved in stone.

12. The nature of biological species: Assertions as to the monophyly of species?

The term monophyly is not like many terms in the literature on evolutionary biology or derived from the new synthesis, wherein multiple interpretations or definitions exist. Monophyly was clearly defined by Hennig. So, why ask this question if it is a clearly defined term and many researchers use it in the literature, in descriptions, or in dialogue? Good question, and one that should not have to be discussed if practitioners in systematics and population genetics where, in fact, up to speed on their understanding of the theoretical and philosophical concepts surrounding species and supraspecific taxa, and the difference between these two frequently used or tossed-around terms.

So, what is the deal with the argument pertaining to monophyletic species? Is this the appropriate interpretation when one finds that not all geographic samples of a species form a lineage

independent of other such lineages? No! Unfortunately, this represents another instance of practitioners of the above listed fields misunderstanding and misusing the terminology and misunderstanding of concepts of monophyly, paraphyly, and polyphyly. To ask whether or not a species is monophyletic or argue that a species is monophyletic, paraphyly, and polyphyly is simply a *non sequitur*. The argument of one of the above three terms for a species is fallacious because of the disconnection between the initial premise and the resulting conclusion. By their very nature, species as entities, individuals, and lineages in nature or as taxa, one's preference in use, are natural. They are independent lineages that maintain their identity through time, even in face of factors that could compromise their identities, and are restricted in time and space. As Hennig [22-25] and Wiley and Mayden [29-31] have pointed out, the terms monophyly, paraphyly, and polyphyly do not relate at all to the entity species, but are correctly used in discussions relating to only supraspecific taxa of three or more species. The reinforcement of this misunderstanding and misuse of the term most likely stems from the definition and discussions relative to the "Phylogenetic Criterion (see Table 1)." This use of the term confuses issues – species discovery and naturalness of supraspecific taxa. It is a term for one of many frequently used criteria for discovering and diagnosing species in nature on the basis of apomorphic character(s) or the "monophyly" of all representatives of a hypothesized species. Monophyly and related terms refer to supraspecific taxa.

It is true that one may misinterpret variation and that multiple unrelated lineages as species (all but one undiscovered at the time) are recognized under one binominal. However, this will remain such until evidence supporting the contrary and corroborating such a hypothesis of greater diversity exists in the complex. "Problematic" instances that very likely point to such cases of diversity are those species that are diagnosed "on the basis of a combination of characters). How is this so? This type of diagnosis has the potential of using a mixture of plesiomorphic and apomorphic character states that in a unique combination diagnose two or more species but can also result in "cryptic diversity" that will remain to be discovered though a lineage-based interpretation of characters (Fig. 2; also see "Characters: their real function and why all types are important!").

Many researchers and philosophers may possess the theoretical and philosophical background relating to this topic but lack experience in the broad-based diversity and complexities of nature that biodiversity scientists, or systematists have to deal with in their studies. Likewise, those lacking the theoretical and philosophical understanding of species will likely error in their assessment of lineages representing species. The most appropriate solution to this dysfunctional situation is that the student and practitioner of systematics, biodiversity science, or whatever one may call the specialty of discovering and describing species and reconstructing relationships, must be educated in both areas and must learn through apprenticeships. This is how one learns the practice in most areas of the natural sciences. Only through such an experience that is part and parcel to a general education can one be more confident that they have the experience to evaluate a broad range of situations of diversity and generate informed hypotheses. It is analogous to what Hennig called reciprocal illumination. In varied systematic groups the specialists also know what characters tend to be highly variable and are less likely to be useful in corroborating a hypothesis of lineage independence. This only comes through

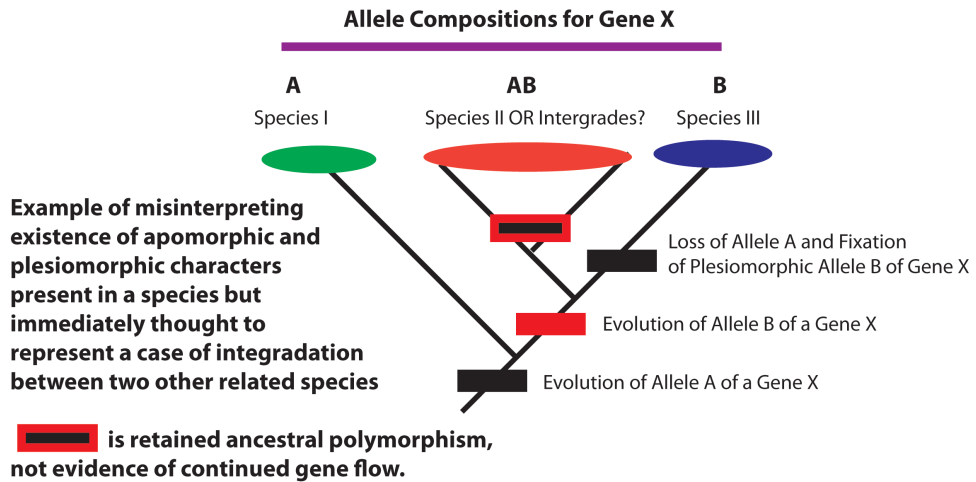


Figure 2. Hypothetical example of a known evolutionary history of a clade of organisms and the existence of multiple independently evolving and unrelated lineages diagnosed and interpreted as a single lineage on the basis of “a combination of characters.”

experience with diversity, not through theoretical and philosophical readings, discussions, or debates (although these are fundamental to some types of interpretations – see above). Everyone benefits from apprenticeships – both the student and mentor. Apprenticeships are critical to a developing professional and such experiences should be continuous throughout the process of life-long learning and practicing in the discipline of science.

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