On biological species, species concepts and individuation in the natural world

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Abstract

I am a realist and argue that biological species exist in nature. I also argue that the validity of findings of the many disciplines within the natural sciences employing biological species in their endeavours of inquiry are unequivocally linked to the accuracy of the species used in experiments. Few scientists today see the fundamental importance of taxonomic and systematic studies in both addressing accuracy of diversity and the delineation of species diversity for other areas of science. The basic controversial issues in the debate revolve around opinions regarding the nature of species as either Individuals or Classes, confusion of Species as a taxonomic category and as entities in nature, the varied practitioners studying diversity, a general lack of a Lineage perspective and a gross chauvinistic perspective on the types of data worthy of exposing and delineating diversity. I argue that species in nature are Individuals and form Lineages. As Individuals, they cannot be defined but can only be diagnosed in time. The category Species is a Class with a definition. The difficulties realised by scientists studying biodiversity in ‘defining’ a species hinges upon the fact that as natural entities they cannot be defined. Recognizing and understanding the origins of characters in species is further complicated if one views species in nature as Classes and lacks an appreciation for the Lineage and the origin and retention of traits through time. This forms an interesting paradox that many scientists have fallen victim to wherein species are viewed as Classes (hence definable, but immutable) yet are used to understand the process of descent that involves lineages and Individuals! The pre-Darwinian Class perspective of species, combined with a common chauvinistic perspective on characters ultimately delays progress and places a ‘glass ceiling’ on species diversity for planet Earth. One resolution to the species and species concept issue is to view the concepts in a hierarchical manner of primary (theoretical) and secondary (operational) concepts. Interestingly, the issue of Individuals versus Classes for naturally occurring entities is much more widespread and exists in many other scientific fields. Thus, a hierarchical perspective of having a primary, nonoperational concept for natural entities and multiple operational concepts serving as ‘tools’ for discovering natural things consistent with the primary concept is a heuristic methodology that is applicable to the advancement of many areas of science.

Keywords biodiversity, classes, conservation, species, species as individuals, systematics of fishes
Introduction

The nature of biological species has seduced scientists from many disciplines for centuries and has resulted in an overwhelming amount of literature and debate. Given this intense focus, it would necessarily follow that the topic of species must be something of major significance in science. This is exemplified by the continued number of papers addressing this complex, yet fundamental, issue and the occurrence of three recent volumes specifically targeting the topic (Howard and Berlocher 1998; Wilson 1999; Wheeler and Meier 2000). As commonly perceived units of biodiversity participating in natural processes and the focus of many research paradigms, their characterization is fundamental to the natural sciences. Although scientific debate continues over what constitutes a species and different conceptualizations of species, two fundamental observations hold true. First, it is true that species, as biological diversity, are essential elements of scientific investigations for multiple disciplines, are studied at varied levels of scale and for an infinite number of questions. Species are the basic currency of biodiversity worldwide. Second, diversity is disappearing worldwide at unprecedented rates, and international, national or state protection is largely administered to biological entities that are referred to as species. Unfortunately, the consternation surrounding the issue of species and species concepts has driven many practising scientists studying biodiversity, population genetics, ecology and systematics away from the topic and in search of the comfort of 'safe' or less controversial issues in their disciplines. In fact, it is not uncommon to talk with these scientists, educators, researchers and even policy makers and discover that they either have no interest in the topic, have not followed the debate, do not think that the topic pertains to their science, or are simply confused by much of the philosophical jargon that is traditionally tossed about by those scientists and philosophers of science participating in the exchange. This, of course, is detrimental to advancing multiple fields of the natural sciences because biological units (species) being used in investigations may not reflect legitimate by-products of descent, thus calling to question the results of such studies.

The disjunction in both the scientific and nonscientific communities between theoretical and empirical discussions, literature and research regarding species is particularly disconcerting. Why? Because in these instances data, empirical observations and discussions are interpreted or conducted within a theoretical, philosophical, or metaphysical vacuum. The interpretation of raw data, and their presumed patterns or relationships is done by individuals processing a particular worldview rooted in some preconceived theoretical framework that is traceable to

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their academic heritage, experience and breadth of knowledge of any field. However, this framework is not clearly stated and obvious to a reader, thus preventing critiques, debates and advancement of research hypotheses. Scientific debate is good; from these exchanges come advancement, though it may come at a cost. In the case of biological species, the extended healthy debate over what constitutes a species, comes with a cost to both biodiversity and individual scientists. Without resolution, biological diversity unaccounted for by particular species concepts may go unnoticed and eventually go extinct. For the individual scientist, the cost is time-necessary to stay abreast of this fundamental species issue. As such, value judgements, and as we will see below, aesthetics are also a part of the equation in dealing with the issue of biological species.

As myself and others have outlined in previous papers, the difficulty in resolving the many issues surrounding biological species can be fundamentally linked to the nature of their 'existence', as Individuals, and the inherent difficulty in dealing with things that are Individuals. Although in the natural sciences, the discussion of biological species has received considerable negative attention that has been derisively summarized as 'a bunch of scientists and philosophers arguing over how many angels can dance on the head of a pin', the underlying reasons for the controversy in this issue is not unique to the topic of biological species, but extends beyond this topic, and is significant to numerous scientific disciplines including biodiversity. As I discuss in this essay, understanding the nature of being an Individual is critically important in structuring our thought, analyses and interpretation of empirical data. The same issues surrounding Individuality of biological species are common in other disciplines of the natural, social and physical sciences but, interestingly, have not been the focus of such debate. It is possible that dialogues in these other disciplines do not have the historical inertia as the biological species issue or the scientists may be less aware of the important philosophical issues related to Individuality underlying their science. However, as promulgated herein, understanding Individuals and incorporating this understanding into disciplines beyond biological diversity will unquestionably provide for both a better education of prepared scientists to advance their fields and, for those in biodiversity-related fields, will improve our success in acquiring important empirical data and properly interpreting these data in our quest to account for, understand and conserve our natural world.

**What are species?**

If different biological professionals and higher education students majoring in the sciences of the post-Darwinian age were polled on this question, it is likely that it would result in fewer answers than one might expect. Without a doubt, the vast majority of the introductory biology textbooks used in secondary schools, colleges and universities provide limited discussion on the topic and are likely focused on biological species being reproductively isolated from other species – the traditional Biological Species Concept (BSC). Logically, in the disciplines closest to the species question there will be a much greater diversity of opinions on what a species is. Aside from systematists and some philosophers of science, very few will be familiar with the many alternative conceptualizations of species. However, very few, even those close to the subject, will answer this question: 'They are scientific hypotheses regarding the existence of a unique and distinct biological and evolutionary entity. They are hypotheses presented on the basis of evidence that lead skilled researchers in systematics and taxonomy to propose that some populations are unique and form independent lineages relative to other populations traditionally grouped with them.' Thus, people describing species are conducting scientific research and presenting hypotheses about unique and distinct biological entities that are the result of and participate in the evolutionary process as distinct lineages.

As part of the scientific process, however, and as hypotheses they need to be testable, and just like other hypotheses generated in the natural sciences, they can never be proven. Yes, hypotheses of this nature can be tested, although some may argue otherwise. When someone presents a hypothesis of a new species, it is done in the context of the species concept that the researcher adheres to at the time of the description. What is the concept that the author adheres to? How often does the author provide the readers with the species concept that she/he is working under? Does the process of falsification of a given
hypothesis have to be done in the context of the given species concept? Or can it be done within the context of any species concept? Then what is the hypothesis to be tested? Is it the species concept that is being tested, that the concept appropriately recognizes species? Or is it the species itself? It is clear that there is very little in the literature dealing with this question, but it should be a question in the minds of scientists conducting systematic, taxonomic and biodiversity research. The answer to this question (discussed below), I think, provides very significant insight into resolving the species question. However, one of the major points is that species descriptions represent testable hypotheses, just the same as what is presented in other areas of the natural sciences.

For some scientists, genera, families, orders and other supraspecific taxonomic groups of the Linnaean hierarchy are thought of as ‘real’ things existing in nature. In other words, there are such things that can be identified with generic, familial or ordinal characters; should one find something possessing one of these traits, then one has discovered one of these supraspecific taxa (Winston 1999). Education and practice of this type of system was largely conducted through close mentoring relationships wherein ideas as to ‘what species, genera, families, etc. are’ is learned ostensibly by the student interacting with the mentor. Traditionally, prior to phylogenetic systematics and the criterion of monophyly, earlier systematists argued for new genera or families because the taxa differed from other such taxa by a certain magnitude for characters, usually morphological. In this framework, genera were less different from one another than were families and so on; some even argue that some taxonomic groups should include a given number of species. Thus, taxonomists largely classified on the basis of differences and the magnitude of these differences. Today, the systematic community argues that supraspecific taxa do not exist in nature; they are manifestations of the historic past through ancestor–descendant relationships and are given proper names that we, as systematists, superimpose on a phylogenetic tree to identify monophyletic groups – nothing more and nothing less. These names serve as convenient communication devices to relay information regarding groups of species at different hierarchical levels.

Are species like this? After all, all monophyletic groups (supraspecific taxa) begin as an individual species. Are the things that we identify with a binomial constructs based in a human need to classify, much the same as with supraspecific taxa? Are there such things as species characters that we are or should be using to look for species? As such, if we can have the sense of a species character does it empower us in the process of discovering biological diversity? Answers to these questions will depend upon the person, the time in which the question is asked, and even the group of organisms that a person works with, if any. While some of these questions are addressed below under different sections, it is worthy of some discourse here.

For most modern systematists, species are not like supraspecific taxa. Supraspecific taxa in the domain of phylogenetic systematics are monophyletic groups. Monophyletic groups are natural groups and contain the hypothesized or real common ancestor and all of its descendants (species). Monophyletic groups only have historical cohesion as a result of descending from a common ancestor; the group as a whole does not participate in any natural processes as a whole. There are no ‘species characters’ that one can use to find species. A particular species differs from a particular supraspecific taxon in that species participate in the natural processes of selection, descent, modification, etc. all processes that a supraspecific taxon cannot. That is, particular supraspecific taxon cannot, as a whole, participate in selection, descent and modification. Because supraspecific taxa, by definition, consist of two or more species with a unique common ancestor, following the first speciation event any type of cohesion (other than historic) is lost. Species are thought to be entities in nature that arise via speciation events; the exact nature of these events is still largely unknown. Species are not thought of as entities that are artificial groupings with no common history of descent, as would be the case if they were created and grouped on the basis of defining characters. As descendants of a process of character modification, any number of attributes in the lineage can change and the lineage (species) will defy definition. It is impossible to predict the type and degree of character modification that will result from a speciation event. Thus, ‘species characters’ naturally do not exist any more than do characters for genera, families, orders, etc.

The comment is often made that ‘sure, species may be elements of evolution but evolution operates on smaller groupings like populations and metapopulations.’ Thus, for many there is a concern over whether species are the units of evolution or are the smaller groups of individuals organisms the units of evolution? From my perspective, the answer to this question is yes and yes. All of these groupings of
individual organisms make up entities that participate in evolutionary processes, and the exact make up of these entities can and will vary over time. However, biological species are perceived as the highest level of organization wherein tokogenetic relationships between individuals are maintained for cohesion and identity (Wiley and Mayden 2000a,b,c). Species are also perceived as those things that maintain themselves as independent lineages and have cohesion, and change over time through modifications during descent. If this is not the case, then the whole underlying principles of evolution are problematic. A species undergoing a speciation event changes from one Individual with tokogenetic relationships to two Individuals having phylogenetic relationships. This leads to questions regarding the differing population structures that may exist within a species. How does one know to identify something as a species and christen it with a proper name as an independent entity of evolution? Where is the natural cut-off between things that are clearly populations or metapopulations and things that are species? These questions are as difficult to address operationally as questions regarding the process of speciation and how it happens—because they are one and the same. The difficulty for humans to clearly answer this question relates to the fact that, as a species, we have a tendency to assign values to things, view many things from an aesthetic perspective, and desire clear boundaries. However, if we strip these unquantifiable assessments from our decisions, then we are left with a basic underlying principle of descent with modification, that is, species are lineages that maintain their independence from other lineages and participate in natural processes. Only when we impose or incorporate values and aesthetics does the question arise—what types of characters should be used to identify species and what degree of difference is needed for an entity to qualify as a species?

One remaining point that often escapes the thought process of many is that particular species have historically participated in the speciation process that lead to the production of two or more species (sister species), and, as such all natural, monophyletic supraspecific taxa begin as a single species, no different than species that neotological scientists research today in divergent disciplines. Hence, ancestral species are those taxa that gave rise to other taxa through speciation, and the autapomorphic traits that they possessed, be they morphological, molecular, behavioural or ecological, are the synapomorphies of the supraspecific taxon that they form the root (Wiley 1981). Given this twist, is it not odd that phylogenies are reconstructed routinely using various types of data and that monophyletic groups (or common ancestral species) are defended on differing numbers of synapomorphies or probabilities, but recognition of valid, extant descendent species as fundamental units of biodiversity is held to a different criterion? This paradox, the nature of species as Individuals (not Classes1), and the nature of humans gravitating towards chauvinistic behaviours and aesthetic priorities in character choices for species forms the body of the following dialog on species.

Some basics and known caveats

Any discussion on biological species should be prefaced with a brief discussion of a number of points that are basic to the issue and admonitions of the current state of this discipline. Herein, I outline some key issues that readers must keep in mind about our current state of knowledge, the real emphasis on progress in understanding species, requisite information needed to fully achieve our quest for species, why so many different conceptualizations of species are in existence today, and the existence of personal and social bias in this scientific process.

While the conception of species has changed, from historic time scientists have recognized biological species as fundamental elements in the natural sciences. Even prior to the Darwinian revolution, when descent with modification replaced previous theories explicating the diversity of life, researchers identified species as entities participating in processes and having essential attributes. Theories and concepts are fundamental links between pattern and process in the natural world, and are employed by everyone, not just scientists, to aid in our understanding and interpretation of the world around us. They derive from our metaphysical world view, provide a framework influencing our observations and the kinds of observations made, and serve as fundamental bridges between observations to interpretations and conclusions. Today, most scientists work

1The term Class is capitalized and in italics to denote my reference to specific types of groupings of entities discussed by scientists and philosophers of science (Ghiselin 1966, 1974, 1989, 1997; Hull 1976) and is explained in detail below. A particular species is an Individual in the Class construct of the Linnaean Hierarchical System Category Species. Likewise, a single helium atom is an Individual in the Class Helium that we visualize in the periodic table.
within the metaphysical paradigm of descent with modification, not pre-Darwinian paradigms invoking the creation of diversity without diverging lineages underlying the speciation and diversity observed today. Thus, diversity results from some degree of selective process, divergence, lineages through time and speciation.

Directly related to this notion and addressed to some degree below is the fact that a dialogue on biological species almost always involves theoretical and operational issues, and these issues are often conflated. Discussions on concepts of species often really focus on the operational issues of the recognition of such entities and argue for particular views making the identification process more clearly operational. Thus, by focusing on such discussions, species will be those things that favoured concepts will recognize in the operational process (sexually isolated, morphologically distinct, etc.). Operational concerns, like 'Is this a reasonable way to diagnose species?' or 'Is 10% divergence (or some other artificially derived number) for a particular gene indicative of a valid species?' or 'Exactly how much reproductive isolation is prerequisite for speciation?' have their place in discussions of practice. However, the theory and metaphysics that should bear on and underlie questions such as these and the general science of evolution, diversification, or biodiversity are often given lesser concern, are disregarded, or may be supplanted by some apprehension for discrete limits in defining species. Complete focus on operational concerns, without reference to theory, leads to a process that is not scientific.

With the acceptance of descent with modification, the scientific community adopts a number of underlying premises for theoretical concepts. These include: (i) selection and other factors that operate on lineages, (ii) lineages change over time via anagenesis, (iii) modifications during descent occur with any number of types of attributes, (iv) heritable modifications are passed on to descendants in lineages, and (v) lineages, at some time, cease to exist as single entities via speciation (or extinction). These are basic underlying postulates in their simplest terms, of comparative evolutionary and systematic biology. If the whole process of descent with modification via lineages does not hold true then much of our search for diversity, establishing evolutionary relationships of this diversity, and understanding the evolutionary mechanisms behind diversification are nonsense. With respect to anagenesis, the changes that occur in lineages over time are the very attributes used in systematic biology to recover patterns of ancestor-descendant relationships, or common ancestral species. As unique homologous modifications, they are the clues used to detect the unique history of descent. They are modifications that occurred in previously existing species. The types of characters or traits used in systematic biology to recover evolutionary histories are extremely varied, including such traditional attributes associated with morphology to behaviour or ecology, to many genetic markers including protein, DNA and RNA sequences, cytology, and 2' and 3' structures of molecules. Given the numerous comparative systematic studies that have been conducted on varied organisms, using various types of characters, and at various taxonomic levels, two things have become abundantly clear. First, not all types of traits (morphology, genetics, behaviour, etc.) change at a constant rate within and between taxa. Second, not all types of traits change at the same rate within and between taxa. Logically, these two empirical observations should make one take notice that not only does this endanger any notions of a 'clock hypothesis' for particular characters, but that different types of traits are important in resolving the tree of life and in identifying species, either as ancestors or descendants!

The species concept issue has been a continuing saga of controversy for many reasons, all equally justifiable to researchers proposing them, and has resulted in many, many publications focusing on the topic. As a result of years of controversy and antagonism surrounding this debate, there have been over 20 different conceptualizations about biological species, what constitutes a biological species, and what does not (Mayden 1997, 1999; see Table 1). All, but the Evolutionary Species Concept (ESC) (Mayden and Wood 1995; Mayden 1997, 1999; Wiley and Mayden 2000a,b,c; Coleman and Wiley 2001; Stauffer and McKay 2001), are highly operational and serve as convenient, operational definitions of things known as Classes or Natural Kinds 3, that is, nearly each concept provides the researcher with a clearly outlined criterion for when something is or is not a valid biological species. In the BSC, the taxa need to be sexually reproducing sister species (derived from a unique

3Natural Kinds are special types of Classes that include as their members entities that participate in natural governing processes and theories. A helium atom is in the Natural Kind Helium and is subject to the laws of atomic theory; Earth is in the Natural Kind Planets and is subjected to the laws of planetary theory.
common ancestor) in sympatry and reproductively isolated from one another. Do asexual species have any ontological status? How would asexual species be recognized? Given that the vast majority of speciation is allopatric and sister species do not occur together (Lynch 1989; Grady and LeGrande 1992; Chesser and Zink 1994), how can the species recognized under this concept that live in allopatry be tested? This concept, if employed by its operational guidelines, would account for only a trivial amount of Earth’s biodiversity. In one version of the Phylogenetic Species Concept (PSC), species are only those things that possess autapomorphic traits (Table 1). What about ancestral species? Ancestral species, by definition, do not possess any autapomorphic traits; these species can be discovered through thorough analyses but only possess the synapomorphic traits of the clade. They will be involved in a polytomy with other members of the clade to which they gave rise, and will lack any uniquely derived traits. In the Genetic Species Concept, species are only those things that differ from one another by a set genetic distance. Who determines the genes or proteins to be examined? Or, better yet, who gets to determine the magic distance at which species diverge? Finally, in the Ecological Species Concept species are those things that have divergent ecologies; thus, can no two species in sympatry or allopatry possess the same ecologies? Given that the vast majority of speciation occurs in allopatry would one expect all speciation events to be accompanied by ecological changes? I suspect not, given that close relatives and potential ‘competitors’ would live in allopatry. Many ecologies of species living in allopatry will likely be very similar, if not the same, because the species are derived from unique shared common ancestors. Given the tremendous number of constraints of the BSC, this concept would also only account for a trivial amount of diversity, and is likely the worst concept that any area of biology should adopt.

Table 1 Various species concepts, abbreviations used in text and authors promulgating individual concepts.

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<th>Species Concept</th>
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<td>Agamospecies concept (ASC)</td>
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<td>Biological Species Concept (BSC)</td>
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<td>Cladistic Species Concept (ClSC)</td>
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<td>Cohesion Species Concept (CSC)</td>
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<td>Composite Species Concept (CpCS)</td>
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<td>Ecological Species Concept (EcSC)</td>
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<td>Evolutionary Significant Unit (ESU)</td>
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<td>Evolutionary Species Concept (ESC)</td>
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<td>Genealogical Concordance Concept (GCC)</td>
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<td>Genotypic Cluster Definition (GCD)</td>
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<td>Hennigian Species Concept (HSC)</td>
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<td>Internodal Species Concept (ISC)</td>
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<td>Morphological Species Concept (MSC)</td>
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<td>Nondimensional Species Concept (NdSC)</td>
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<td>Phenetic Species Concept (PhSC)</td>
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<td>Phylogenetic Species Concepts (PSC):</td>
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<td>Composited Species Concept (CpSC)</td>
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<td>Diagnosable/Monophyly Version (PSC3)</td>
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<td>Recognition Species Concept (RSC)</td>
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<td>Reproductive Competition Concept (RCC)</td>
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<td>Successional Species Concept (SSC)</td>
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<td>Taxonomic Species Concept (TSC)</td>
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Concepts and abbreviations are from Mayden (1997). Superscripts correspond to authors employing or describing the concept. All concepts are reviewed in Mayden (1997).

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be determined. First, it is the nature of species being Individuals (discussed below) and, as such, they will always have fuzzy boundaries on them. Second, scientists have diverse academic backgrounds and they adopt perceptions of reality and judgements reflective of their backgrounds. If scientists have a more ecological or genetic background in their academic history, then they are more likely to be swayed by or employ concepts emphasizing these qualities. If one is a morphological taxonomist or systematist, then there will likely be more emphasis placed on these types of traits validating the existence of a species, even in the face of dramatic genetic differences between morphologically similar ‘forms’. Sociologically, current-day practitioners of natural sciences related to the recovery of biodiversity are heavily swayed by the advertised potential to discover species as part of biological diversity using molecular tools. Although the methods being employed in molecular studies to unearth natural variation can be more informative in some cases, it is equally likely that they will either not provide information in other cases or the information generated is of questionable validity to ask evolutionary and biodiversity questions because of questions of homology (Stauffer and McKaye 2001). Yes, molecular methods and studies do indeed have problems in data recovery and analysis to the same degree as traditional morphological studies or those studies using protein gel electrophoresis!

Another area of critical importance that has silently permeated the ‘species concept issue’ has been the rules of nomenclature. These rules seek stability, advocate a type concept, minimize emphasis on variability, and are fine for a world where nothing changes over time (e.g. lineages) and the entities in the world are Classes or Natural Kinds (see below). To be fair, as we will see below, the world does consist of a number of Natural Kinds or Class constructs and nomenclature rules work quite well for these things; however, species are not these things. At the level of species and below entities are changing over time, differ in space, and do not fit the general ideas promulgated in the nomenclatorial documents. Thus, researchers need to be cognizant of this paradox and realise that the rules do exist for naming but should not reflect our metaphysical view of the world today.

Finally, no candid discussion of species concepts should go without addressing some admonitions of the field and those working in the field. First, clearly there remain many types of biological ‘entities’ that we really don’t know what to call – especially in the world of unisexual, asexual, or parasaexual organisms. Those working with sexually reproducing organisms have conducted the vast majority of the ‘species’ work, and most of the targeted groups are vertebrates. Sociologically, this is where most researchers feel most comfortable in their investigations; lineage cohesion, formation, maintenance and splitting in a world without sex is perplexing and somewhat abstract, and can actually lead to some very interesting and bizarre discourse as to biological diversity. Thus, we really don’t have it all covered in this saga and many more papers will develop on this subject. This must be realised in our continuing studies of the ‘Species Quest’, and those searching to succeed in completing our understanding must be cognizant of the fundamental significance of metaphysics, theory and philosophy of science, and the appropriateness and limitations of empirical evidence. Likewise, as also outlined below, researchers must also be aware of the inherent bias of our traditional attempts to discover and understand species because of human-induced value systems and aesthetic considerations.

What are individuals and what is individuation?

The Individual, in a philosophical sense, has been discussed in considerable detail by philosophers and系统atists Ghiselin (1966, 1974, 1989, 1997), Hull (1976), Frost and Kluge (1994), Mayden (1999), Wiley (1981), Coleman and Wiley (2001) and Stauffer and McKaye (2001), to mention only a few. As outlined in Fig. 1(A), Individuals are entities with restricted spatio-temporal frameworks and have both cohesion and continuity. They are capable of self-replication, are particulars with a unique beginning and ending, and are parts of a whole. Individuals can change over time and space, so they may only be diagnosed and described, but not defined. They can lose some of their parts or gain additional parts and still remain the same Individual, depending upon what is and how much is lost or gained. They participate in natural processes as evidenced by their cohesion and continuity over time and under various selective or non-selective regimes. Because Individuals cannot be defined, the desired clear-cut boundaries are inherently impossible, and they are often referred to as ‘fuzzy’. If an entity is an Individual, because of these boundary issues, one will often see multiple pragmatic or operational definitions for the entity. It is also true that there will be disagreement among those posing definitions for the entity. Not every
researcher will focus on the same attributes of the Individual in their definitions because each will see different things to qualify, quantify and describe, and will likely have their definitions influenced by their own values and aesthetic priorities.

In the example of an Individual (Fig. 1A), I illustrate a single lineage undergoing lineage-splitting via speciation, divergence via anagenesis, and the termination of an Individual via extinction. Prior to the speciation event a single lineage maintained cohesion and continuity since its unique origin. During the speciation event, two new Individuals were derived (or the ancestral lineage could survive and one new species is derived) with each having independence, cohesion, a new beginning, and an eventual end. Each lineage is constrained by the properties that it inherits from its ancestral lineage and those resulting from the speciation event, plus any unique traits that evolve after the speciation event. All of these attributes will, at some time, eventually serve as historical constraints in development, ecology, physiology, genetics, etc. This process of generating new Individuals, as well as the process through which we identify Individuals, I refer to as Individuation.

Biological species are Individuals and the process of their formation is speciation, a type of Individuation. Individuals are entities in the natural world that we hope to discover, investigate, use in our experimental studies, use to test hypotheses or theories, use for developing predictions, and they are the fundamental observations in the foundation of theories of the natural world. As species, they are subject to selective pressures and anagenesis. Thus, one might expect that if Individuals are subject to natural forces and can change in time and space, lack clear boundaries, and cannot be defined, then they are likely to be difficult to delineate and will come with some level of scientific uncertainty. Depending upon the particular criterion that a researcher may focus on to delineate an Individual (morphology, genetics, etc.), the boundaries may differ from one researcher to another and from one criterion (character) to another. Yes, the same Individual may have different hypothesized boundaries because of different rates of change in or differential emphasis on each of the criteria. In fact, unless all criteria for delineating an Individual are all changing in the Individual at exactly the same rate temporally and spatially, then there will appear to be inconsistency in the delineation of

![Figure 1](image-url)
the Individual. This inconsistency only exists, however, if one lacks an appreciation for the qualities of the Individual and the need to evaluate cases such as this with a temporal perspective. Even with differing rates of change in time and space, if the Individual is viewed from a historical perspective (phylogenetic systematics), one can make sense of the differing boundaries based on the different criteria for existence. Some examples of Individuals are provided in Table 2. The organism Rick Mayden is an Individual and it can be diagnosed at various stages of its life transformation. However, if different researchers each decide on the delineation of Rick Mayden and develop this at different times in his ontogeny, with or without different criteria, then there will be differing and conflicting definitions of Rick Mayden.

\textbf{Table 2} Examples of Individuals and Classes.

<table>
<thead>
<tr>
<th>Individual</th>
<th>Class or Natural Kind</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydrogen</td>
<td>Hydrogen</td>
</tr>
<tr>
<td>Mesenchyme cell</td>
<td>Cell</td>
</tr>
<tr>
<td>Rick Mayden</td>
<td>Organism</td>
</tr>
<tr>
<td>Species (in nature)</td>
<td>Linnaean species category</td>
</tr>
<tr>
<td>Monophyletic group</td>
<td>Linnaean supra-specific category</td>
</tr>
<tr>
<td>Horseshoe Lake, IL, USA</td>
<td>Ecosystem</td>
</tr>
<tr>
<td>Earth</td>
<td>Planet</td>
</tr>
<tr>
<td>Milky Way</td>
<td>Galaxy</td>
</tr>
</tbody>
</table>

Individuals on the left can be placed in the Class or Natural Kinds on the right. See Fig. 1 for the basic comparisons of qualities of Individuals and Classes.

Alternatives to individuals?

If species are not Individuals, then what are they? Some prefer to think of species as Class constructs, either as artificial Classes or as Natural Kinds (Kitts and Kitts 1979; Kitcher 1984, 1987, 1989). First, the term Class should not be confused with the taxonomic category of the Linnaean hierarchy termed Class (nonitalic Class refers to the taxonomic category). Classes and Natural Kinds (Fig. 1B) are unbounded spatiotemporal constructs with members, and membership is determined by the definition of the Class. They are not self-replicating. Any entity that fits the definition belongs to the Class regardless of its historic origin or location in time and space. Classes do not participate in processes as a whole, they do not change in time and space, and hence, they have very clear and infallible definitions. Thus, members of a Class can have origins in different locations on Earth or anywhere in the Milky Way Galaxy and they are immutable (prerequisite to staying in the Class), but the Class itself never has a beginning or end and does not participate in any process. Some examples of Classes are provided in Table 2. If the organism Rick Mayden is a Class, then the ontogeny of Rick Mayden requires an infinite number of definitions for the infinite number of stages of his life transformation. The same is true of individual species; if species are Classes, then each requires an infinite number of definitions to accommodate an infinite number of molecular, morphological, physiological, behavioural, etc. changes occurring in the descent of each lineage. If species are Classes, they are immutable and only require one definition; consequently, descent with modification cannot exist if species are Classes.

\textbf{Individuals versus classes: what's the big deal?}

One of the most important issues facing the natural sciences today and delaying important progress toward understanding, and compromising our scientific progress in developing appropriate and interrelated fields in biodiversity, evolution, ecology, systematics, and conservation biology, is a continuing tradition of scientists thinking of and treating species in nature as Classes or Class constructs, that is, many natural scientists continue to think about and treat species like essentialists, fictionists, phenomenologists, or nominalists— not realists. Entities like biological species exist in the real world and can be discovered in nature and used to investigate natural processes. They are not ‘phenomena’ or ‘artificial constructs’ that we recognize and arrange in some order perceived in the mind of a particular scientist.

This is an extremely important issue to consider because it creates an interesting paradox: scientists seek definitions of every particular species as if they are immutable, even given our currently accepted metaphysical worldview regarding the origin of the diversity of life. The paradox is simple. How can one view or treat particular species in nature as Classes or Natural Kinds and yet aspire to investigate real processes associated with their origins and their continued existence?

The history of scientific thought and the scientific process has been clearly marked with prominent metaphysical and paradigm shifts (Kuhn 1962). Theories and concepts are formulated and embodied in a particular metaphysical worldview of the time of their development. Ideas, hypotheses, causative
explanations, and even observations of reality all derive from the metaphysical paradigm or theory in existence at that time. Every discipline can identify metaphysical shifts in their timeline that occurred for a variety of reasons, including the acquisition of new knowledge, mergers of disciplines, improved instrumentation, new primary theories exposed to strong scrutiny and rejected, etc. For example, one may examine the history of our inquiry of the cosmos and identify a series of important metaphysical shifts extending from the Ptolemaic (Earth-centred) Model of the Heavens, to the Copernican Heliocentric (Sun-centred) Cosmos, to the Descartes Model embodying a mechanical philosophy, to the Keplerian view of elliptical motion. In all of these changes, a new worldview came about that altered how people interpreted the world around them, impacted how data are interpreted, and provided constraints on how information is processed by individual scientists and nonscientists.

Probably, one of the most significant of the metaphysical shifts that has ever occurred in the sciences involved the explanation for the origin of biological diversity. The change in the scientific worldview as to the origin of biological diversity from that of immutable entities formed by a Creator to entities existing because of evolutionary descent through natural selection and modification was clearly a significant metaphysical shift in the natural sciences. From the Darwinian paradigm of lineages existing through time and consisting of ancestral and descendent species evolved the ideas of speciation, multiple types of selection and speciation, and many other areas of evolutionary biology. Consistent with all of these endeavors of evolutionary biology are the notions of lineages, descent, stasis, anagenesis, and heritable attributes, to mention just a few.

Paradoxically, none of these notions are even tenable, and the theory of evolution is completely implausible, unless one views species as Individuals and not Classes or Natural Kinds. As the former, species are natural entities, lineages, to be discovered, but they lack definitions and can only be diagnosed retrospectively (Frost and Kluge 1994). They are inherently difficult to define, but as lineages they can be characterized or diagnosed on the basis of any heritable attributes that provide evidence of lineage independence. Likewise, as Individuals, they change over time and it is impossible to predict what attributes will be changing in their descent (e.g. morphology, genetics, behaviour, etc.). Thus, in order to discover these natural by-products of descent researchers must search for evidence of lineage independence. Practitioners of science requiring particular definitions or a degree of differentiation for particular qualities (outlined in various species concepts) be met before a species is considered valid view and will treat biological species as immutable Classes or Natural Kinds, a metaphysical worldview held prior to the Darwinian revolution. All of the current concepts of species except for the ESC treat biological species as Classes or Natural Kinds (Mayden 1997, 1999). Thus, it is a difficult position to be in as a contemporary evolutionary biologist, systematist, geneticist, or any other type of biologist advocating descent with modification and at the same time possess a metaphysical world view of species as immutable kinds as was thought prior to the Darwinian revolution.

Only the ESC is acceptable as a guide to discovering diversity referable to biological species as Individuals; all other concepts require a predetermined type of divergence or process. The search for clearly definable products of nature meeting predetermined standards inherent in operational concepts or definitions formulated because of pragmatic concerns or arguments clearly identifies a scientific culture satisfied with species as Classes or Natural Kinds. Such concepts lack the breadth of temporal and spatial concepts to interpret the origins of attributes possessed by species, deny the existence of some species diversity diagnosable on the basis of other types of traits, require the existence of some special qualities before lineages are recognisable, and among a number of other malformations, preclude the study of evolutionary processes (Mayden 1997, 1999; Wiley and Mayden 2000a,b,c). These concepts not only provide definitions or operational tools for discovering only certain types of diversity consistent with the concepts in favour at a particular point in time, but they likewise serve to fulfil predetermined statements of value and/or aesthetic priorities for particular kinds of species and traits acceptable to recognize such diversity. When presented with the logical outcomes of viewing and treating biological species as Class constructs in our current Darwinian worldview of descent with modification that has structured so much of scientific thought, it is untenable to accept any of the standard concepts of species save the unique nonoperational ESC.

The dichotomy of these two approaches to viewing and treating species is identified in Fig. 1 (B) wherein species as Classes have no temporal component, do not change, and lack any (including historical)
cohesion. However, species as *Individuals* possess these attributes. In a final example illustrating the gross differences between these two philosophies, we will look at a heuristic example of diversity. A researcher discovers two populations or metapopulations of a taxon that she/he believes represents a unique evolutionary lineage and describes it as a new species (Fig. 2, Phase I). Later, the same researcher examines genetic variation in this new species and discovers that it possesses alleles A and B in both metapopulations (Fig. 2, Phase I). A second researcher examines closely related species in adjacent northern and southern regions of the new species and finds that the southern species possesses only allele B and the northern species possesses allele A (Fig. 2, Phase 2). At this time, based on no phylogenetic or historical perspective to interpret these patterns of character variation, the second researcher argues for large-scale introgression between the northern and southern species and that the new taxon described by the first researcher is nothing more than populations of intergrades, thus falsifying the hypothesis of a unique independent lineage (Fig. 2, Phase 2). Without a historical or phylogenetic perspective to interpret the origins of the character data the second researcher, without possibly knowing, has just treated these populations/species as *Class* constructs, not *Individuals*. Interestingly, this
standard Class-like interpretation of character variation or character validity does not view species as entities possessing traits because of descent from common ancestors participating in natural selective processes wherein features may be gained, lost, or modified through time. When viewed from this extremely limited historical perspective the levels of natural biological diversity will both be less than what actually exists and will decline with increasing revisionary studies conducted outside of a phylogenetic framework. Alternatively, the first researcher examines the character variation in a phylogenetic context (Fig. 2, Phases II and III). Through this process, the researcher discovers that the occurrence of both alleles A and B in the centrally located new species owe their origins not to active or historical introgression, but to the retention of the plesiomorphic allele B in the new species and the southern species and the origin of a new allele A in the common ancestor to the new species and the northern species. The lack of allele B in the northern species is simply a matter of fixation of allele A in this population. This interpretation is only possible because it is rooted in a researchers perception of species and lineages as Individuals evolving through time and participating in natural processes of descent, including speciation. Thus, practitioners of biological diversity, at any level, must have an appreciation for and understanding of the knowledge of phylogenetic systematics and species (and other elements of diversity below species) being Individuals. Otherwise, inappropriate decisions by untrained ‘specialists’ will occur.

Why then are Individuals so important to clearly identify?

Nature produces Individuals that participate in processes. We use these Individuals to pose questions, hypotheses and theories, from which we make observations, generate new hypotheses, and refute or corroborate existing hypotheses. The intermediate between questions and investigation phase and the phase wherein we develop conclusions, test theories and hypotheses, and generate new hypotheses is the biological species. Thus, how we Individuate things in our natural world will have major implications on our science! In this sense, the quote by E.O. Wilson (1992) in The Diversity of Life is, particularly apropos: ‘the species concept is crucial to the study of biodiversity . . . Not to have a natural unit such as the species would be to abandon a large part of biology into free fall, all the way from the ecosystem down to the organism’. The need to emphasize that species as Individuals are lineages and can be identified using a variety of data types and analyses and falsified as scientific hypotheses cannot be emphasized enough. This basic understanding is lost, however, in much of the discussion of species concepts and is also ignored by many having tired of the controversy. Rather, they prefer to recognize taxa on the basis of what they think is best. In many cases, this method probably serves well in identifying biodiversity for the experts on particular taxonomic groups. However, as evolution proceeds at different rates and on different scales and characters, others may have important information to refine our ideas of diversity.

The bottom line is that viewing and treating species in nature as Classes destroys one’s ability to work harmoniously within the theory of descent with modification. It prohibits one from understanding the lineage, temporal, and spatial explanations for the origins of characters or attributes possessed by species. Under this paradigm many errors accounting for biological diversity will occur. In fact, in the recent book Biodiversity: A biology of numbers and distance (1996) chapters by Gaston (1996a, b) and Mallet (1996) both miss the significance of species as Individuals and damn the controversy over species by essentially calling for strictly phenetic methods by completely untrained personnel to delineate diversity. Both of these authors also miss the point of species as lineages delineated by multiple types of characters under differing rates of evolutionary change. Such attitudes of species as Natural Kinds will most emphatically have a severe negative effect on any scientific discipline related to biodiversity.

Finally, treating species as Classes also has long-term effects on the perception of biological diversity in natural systems. Naturally, most ecologists, behaviouralists, fisheries biologists, physiologists, etc. are not particularly skilled at the nature of species or even biological diversity. Their knowledge of the nature of species may be basically limited to the Linnaean category species, which is a Natural Kind or a Class construct into which we place species in nature thought to participate in natural laws governing such entities. This limited perspective can have a major effect on how science is done in these disciplines. As an example, in many ecological studies, species and organisms are typically grouped into functional groups like scrapers, shredders, filter feeders, etc. as examples of feeding groups. As such they create groupings of Individuals into Class constructs and discuss the generalities of the Classes in...
ecosystem dynamics, food webs, energy flow, etc. In order to be a member of one of these particular Classes, each species must have the required attributes set forth in the definition. The general conclusion to many of these types of studies has been that it does not really matter which particular species of the Class ‘filter feeder’ or ‘predator’ are present in a system, there simply need to be filter feeders, predators, scrapers, or whatever in communities. This type of reasoning is extremely damaging to ecosystems and communities because the investigator is not cognizant of the inherent uniqueness of different lineages that evolved at different times and places, as would be implicit with the education of species as lineages. Treating species as Classes that fit into ecological or other guild Classes completely removes any temporal and spatial, as well as historical, components from these interpretations. Sadly, such logic may eventually determine or be used to argue that only a few species worldwide are really needed to serve as functional communities!

Thus, although those continuing to acknowledge the dialogue of species as Individuals may be viewed as eccentric, and the philosophical dialogue as inapplicable to science, they lack an appreciation for how the differences between Individuals and Classes will have significant underlying implications to inquiries in science and other disciplines. In my opinion, once armed with this knowledge, advancing the many fields of the sciences will come naturally through empirical studies, analyses and interpretations.

The hierarchy of concepts of species

A hierarchical view of concepts of species provides a functional and productive means of avoiding the paradoxical notion of treating species as Classes while aspiring to discover and understand natural processes involved in evolutionary history, patterns of speciation, or the tree of life. As previously proposed (Mayden 1997, 1999), the only sound method to account for the diversity of life is through the guidance of the ESC as a primary concept. As the only concept not precluding the existence of some independent lineages thought to be species because of operational, pragmatic, value-driven, or aesthetic concerns for particular types of traits or divergence levels in these traits, it is the only concept currently available to serve as an over-arching idea as to the notion of biological species. This concept is free of the baggage encountered in all other concepts requiring particular kinds or qualities of essence being present. Hence, Individual-like entities are acceptable or permissible under this concept as biological species regardless of the types of changes in characters or homologues or inferred processes (mate recognition system, reproductively isolated) that have occurred to substantiate the central hypothesis of lineage independence.

The only problem with employing a nonoperational concept is that it is difficult for anyone to find anything to fit the concept without prior knowledge or guidelines or tools to use in the discovery phase. As one solution to this seemingly intractable dilemma of trying to discover entities that lack definition, I proposed that most other hypothesized concepts of species are consistent with the primary concept and outline minimal standards for species recognition, and that these be considered as surrogate concepts to the ESC. Using these concepts as our ‘toolbox to biodiversity’, researchers can use these various concepts, where appropriate, to discover lineages consistent with the primary ESC. In this framework, researchers using any of the secondary concepts can identify species diversity based on criteria of homologous divergence in morphology, ecology, behaviour, genetics, or any other quality supporting the hypothesis of lineage independence. This argument was adopted and supported by Stauffer and McKaye (2001).

Advocating this position, I acknowledge that I am a monist with respect to a concept of species, that is the ESC. However, I am a pluralist with respect to advocating multiple concepts of how to identify entities in nature that are consistent with my preference for the primary species concept. To some, my position may seem reasonable, but to others, maintaining both a monistic and pluralistic view may seem unacceptable. However, let us examine a simple real-world example illustrating the continuity and harmony of my position with the species concept issue. In this case, it involves the widely accepted concept of monophyly and surrogate concepts used to aid in identifying monophyletic groups.

A parallelism of monophyly and the evolutionary species concept

Throughout modern systematic literature, the term monophyly has significance to not only systematists but to many other scientists from varied disciplines, probably second only to the term synapomorphy. Today, the recognition of supraspecific taxa requires that the grouping be monophyletic, that is the group
must include the unique common ancestor and all of its descendants. Other groups, those either not including a unique common ancestor or excluding some of the descendants of a unique ancestor, are not recognized because they are artificial constructs that are completely misleading to anyone looking to biological classifications for insight into evolutionary history of the tree of life. Interestingly, as discussed above, species are the initiators of all supraspecific monophyletic groups and all monophyletic supraspecific taxa are special types of Individuals (Wiley 1981). Likewise, all nonmonophyletic taxa (para and polyphyletic groups) are artificial constructs and can be referred to as artificial Classes, but not Natural Kinds. Although monophyletic groups are often referred to as clades, these latter groups are often referred to as grades or grade groups (artificial constructs).

Interestingly, although the term and concept of monophyly receives worldwide acceptance as an appropriate concept for supraspecific taxa, there is no one thing operational or pragmatic about this definition. Given the definition of monophyly as a describing a theoretical entity (much like biological species), one would be hard pressed to go out, use the definition, and return with a monophyletic group. Why? Because it is a theoretical concept characterizing a special type of by-product of nature, a special type of Individual referred to as a Historical Group (Wiley 1981). It is a type of Individual that originates as a biological species and participates in natural processes that result in additional Individuals, none of which can be defined in the traditional sense, only diagnosed. What are the diagnostic traits of a monophyletic group? They are the same traits that were diagnostic of the unique common ancestral species (Individual) to the monophyletic group. Lacking an ability to discover monophyletic groups, scientists must bridge over to surrogate concepts that are consistent with the over-arching concept of monophyly, just as with the ESC and the alternative pragmatic, operational concepts of species.

But, as with the conundrum of biological species, what operational, purely pragmatic concept do we choose to identify monophyletic groups? Theoretically, there are many ways to discover monophyletic groups, or groups of species thought to be derived from a unique common ancestor. One may argue that overall similarity is a good criterion, that genetic or morphological dissimilarity and discontinuity are good criteria, that taxa engaging in sexual reproduction following distinct mating rituals of some sort can distinguish groups, or that only things with distinct colour groupings can form monophyletic groups. We may use any or all of these criteria for monophyly and will find that some diversity may be excluded by each of these concepts or that these concepts lack logically sound justifications for identifying monophyletic groups. In fact, in the history of systematics different criteria have been used to justify groups recognized in the Linnaean Hierarchy (even phenetic similarity) and today the concept most often employed is that of synapomorphy, that is, monophyletic groups are supraspecific taxa containing Individuals thought of as species that can be identified and grouped on the basis of at least one shared-derived character that they inherited via their unique common ancestor. This is a character that evolved in the common ancestor to the group and passed on to the descendants of the group (or parts of the whole) as homologous characters. The most commonly employed scientific method for identifying synapomorphies is the process of outgroup comparison (Wiley 1981). Thus, systematic biology searched and tried various ways to logically discover meaningful methods to identify monophyletic groups consistent with the theory of descent with modification. We do not want to preclude groupings because of bias against particular types of characters or degrees of differentiation as long as groups being recognized are consistent with the idea that natural lineages and groups of lineages exist as a historical process. The recognition of this natural order versus artificial constructs developed not from scientific principles or processes but by simple value judgements and aesthetic desires, is beneficial to the scientific community. Today, the synapomorphy concept is most widely accepted as a criterion for recognition. This is not to say that other criteria may not work or will not be discovered in the future. In fact, if one knows that all traits being examined for a particular group of organisms evolved at a constant rate (anagenesis), or if one knows the particular model of character evolution in the evolutionary history of a group, then overall phenetic/genetic similarity or probabilities assigned to nodes in likelihood analyses, respectively, would work equally well for identifying monophyletic or natural groups. Unfortunately, assumptions on rate changes of characters and models of character evolution are dangerous because they are not known or predictable.

Thus, it is clear from this parallel situation that the biological community identifies the significance of a hierarchical structuring to identifying monophyletic
groups wherein criteria like synapomorphy serve as acceptable surrogate means for discovering clades. In the same vein, the hierarchical arrangement of concepts of species identifies the ESC as the primary concept and almost all other concepts as operational surrogates for discovering and hypothesizing the existence of species in nature. Some concepts, however, are not acceptable for identifying species (Successional Species Concept) and some others should be used with caution to avoid recognizing artificial constructs (Mayden 1997, 1999). In my opinion, the most useful surrogate concept for the ESC is the PSC (all versions, Table 1), although caution must be employed even with this concept. It is clear that none of the PSC concepts will allow one to discover ancestral species and if one employs only the diagnosable version one may recognize artificial groupings.

**Data chauvinism, aesthetics and evidence for the existence of a species**

Following from and directly related to theoretical and philosophical issues of species (or monophyletic groups) is the question of what constitutes the ‘best’ methodologies and empirical data for identifying species? This particular topic is one that is rarely discussed within the realm of species concepts because of the inherent nature of species being *Individuals* and their lacking definitions. Given that species descriptions are hypotheses presented to the scientific community regarding a unique and independent lineage in our biodiversity what type of data and methodology does one need to propose such hypotheses? Species concepts themselves are hypotheses regarding the nature of species as being reproductively isolated, morphologically distinct, genetically distinct, having phenetic similarity, etc. Basically, what is it that a practicing scientist in systematics and taxonomy charged with discovering and documenting the diversity of life looking for? In my opinion we should be looking for *Individuals* consistent with the first order principles of the Darwinian paradigm of descent with modification wherein tokogenetic relationships exist within a lineage and the lineage maintains cohesion and independence from other such lineages – evolutionary species. As such, these lineages are subject to selection, anagenesis and speciation and many other evolutionary mechanisms that operate within lineages but not between them.

What then is subject to falsification in this scientific process? This depends upon the frame of reference. Clearly, the hypothesis of a particular species being described by a researcher is a testable hypothesis that can be falsified. However, the various species concepts themselves should be and can be the subject of testing and falsification. For example, systematists traditionally reject the hypothesis of the chronological or successional species concepts as valid hypotheses for recognition of independent lineages. This concept, while functional for biostatigraphers, knowingly recognizes different ‘species’ transforming within a single lineage. Thus, other concepts used to recognize valid species as independent lineages participating in evolutionary processes should also be subject to falsification. As discussed in earlier papers (Mayden and Wood 1995; Mayden 1997, 1999; Wiley and Mayden 2000a,b,c) the great diversity of species recognized today should be used to test the validity of the different concepts as to their ability to account for the diversity of independent lineages. All of the secondary concepts would fail such a test because of their emphasis on particular pragmatic necessities for recognition above and beyond the basic premise of an independent lineage. Some species diversity, hence biodiversity, will necessarily be excluded from recognition as valid evolutionary entities that should be recognized for various reasons.

What about hypothesized species? How does one test the validity of a species as an independent lineage? Simply, evaluate the characters being used to denote it as an independent lineage, as well as other traits appropriate for testing lineage independence, *within the proper methodological framework*. If one cannot falsify the hypothesis presented by the original author(s) that the biological entity represents an independent lineage, then one cannot reject the species status. Further study, however, may provide additional evidence for lineage independence that would corroborate the original hypothesis (but, see caveats below).

Does a particular concept of species permit one to falsify the hypothesis of a distinct species formulated under a different hypothesized conceptualization of species? Emphatically, no, hypotheses of species stand alone independent of particular hypotheses outlined as species concepts. It has been clearly demonstrated that except for the ESC, all current species concepts may be rejected as sole hypotheses of species in nature if subjected to falsification by all currently accepted species described from nature. A researcher employing one concept of species will propose new species thought to represent *independent lineages* based on that concept. Other researchers
identify independent lineages based on other concepts. If there is conflict between these hypotheses it will likely be because of the a priori requisites of the species concepts and not because of inadequate evidence for proposing lineage independence. It is here that the area of species concepts and species recognition departs from science and moves into the non-scientific realm involving value judgements and aesthetic assessments. Using the hierarchical method of primary and secondary concepts, however, species recognized under one concept are just as valid as those recognized under other concepts, as long as they are consistent with the ESC. Under this model, species as lineages are the hypotheses to be tested, regardless of the concept that one employs.

Descriptions of species should be well-formulated hypotheses of independent lineages that are hypothesized to exist into the future until such time that they become extinct. No particular person has a crystal ball that can predict the future of an entity that is clearly an independent lineage today. It may be that such a lineage may merge with another lineage through introgressive hybridization in the distant future. It may also maintain its independence even in the face of differing levels of hybridization. Thus, it is impossible for a researcher, armed with multiple technologies, to decide between these situations and value assessments as to whether one lineage is a species or that another is not inappropriate in the scientific realm.

What kinds of evidence should be used to individuate species as lineages? It is also here that values and aesthetics are inadvertently involved in proposing and testing scientific hypotheses. All types of heritable characters capable of identifying distinct, evolutionarily independent lineages are appropriate for hypothesis generation and testing. Obviously, this has not always been accepted and will not likely be completely accepted in the future. Why? Because as humans, we have a tendency toward assigning personal values or aesthetic priorities. Characters used to identify lineages and their use in determining appropriate level of recognition of naturally occurring entities are neither immune to our imposition of these priorities that have little to do with the discovery process of science. Preference is given towards characters that recognize species on the basis of morphological divergence, traits that are more easily observable and leave little doubt in the minds of those capable of seeing these characters. Behavioural characters have traditionally been taboo in systematics and taxonomy for recognition of both biodiversity and their phylogenetic relationships (Stauffer et al. 2002). Why? Because, for many years, dogma held that these character types were very labile and not reliable. Interestingly, the advent of many new methods for either enhancing our observational skills (microscopes vs. hand lenses) or providing new information pertinent to the lineage independence question (proteins, DNA) has led to mixed methods for diversity questions. Unquestionably, cryptic biodiversity does exist, as species that look essentially identical for us but maintain independent lineages. However, alternative attributes and techniques (behaviours, mating systems, ultrastructure, pheromones, molecular techniques, etc.) are capable of sorting out independent lineages identifiable as species. Oddly enough, some of these lineages enjoy much attention in the scientific arena because of the evolutionary peculiarity that they appear identical to us but are not the same to each other! In other cases, however, independent lineages are identified based on alternative traits to morphology but are not recognized as species, largely because of the dominance of morphological attributes for diagnosing or keying out species. Many recent molecular studies have revealed many new evolutionary lineages that are consistent with the primary objective of discovering species diversity. However, few of these are ever recognized, an exception being the work by Highton et al. (1989) molecular study of salamanders of eastern North America. The inconsistency in recognition of biological diversity clearly identifiable as independent lineages and equally justifiable as those based on morphological traits lacks scientific rigor and derives from values and aesthetic assessments imposed by each scientist.

Rank order in taxonomic systems, based on degree of differentiation, while largely eliminated from systematic biology in the recognition of superspecific taxa is commonly employed in studies investigating species diversity. As with the inappropriate use of value and aesthetic assessments described above, researchers frequently argue over the validity of species based on the degree of differentiation that a species may possess for a trait or the type of trait being used in recovering diversity. While these arguments do not pertain to evidence for lineage independence and do not falsify initial hypotheses of species, these are used to determine whether lineages should be considered variants, races, subspecies, evolutionarily significant units (ESUs) or species. Essentially, the more divergent a lineage is, mostly based on morphological evidence, the higher the ranking. Why?
Because researchers feel more comfortable in recognizing lineages that are more divergent and are lead into a false sense of security and comfort that these lineages are more likely to survive the test of time. These lineages are assigned higher value in evolutionary biology and general public opinion because they are given proper nouns, receive recognition as elements of selection and speciation, and even have higher priority in listing and protection when endangered. Lineages recognized solely on the basis of molecular, biochemical, physiological, or behavioural traits have little or no chance of being recognized in the current philosophy because researchers do not find these types of lineages as aesthetically pleasing to their sense of being or existing in nature as \textit{real}. These same lineages, if recognized, are usually not named or are given lesser rank than are taxa that are recognisable on the basis of other types of data, typically morphological. However, even within morphological analyses lineages identifiable on the basis of some types of characters are ultimately deemed less valuable or less aesthetically pleasing than those based on other types of characters. In fishes, lineages that differ only in complete differences in the number of anal fin rays counts are less likely to be recognized than those differing in colour patterns and anal fin ray counts. Both of these sets of evidence may provide exactly the same information supporting lineage independence; the only difference is an arbitrary assessment of value and aesthetic palatability by the scientist or the panel of experts evaluating what constitutes recognisable diversity.

Are some types of data better in the scientific expedition of discovering diversity? No, as long as the evidence is heritable and provides biologically meaningful information for lineage independence. As discussed above, the disciplines of taxonomy and systematics have a history of favouring morphological types of characters and certain degrees of differentiation. One may argue that this is inherently linked to two things, use in identification and the need for diagnoses in species descriptions. True, morphological differentiation at significant scales does make it easier to identify diversity. It is a more convenient tool for identifying species given the inherent limitations of the senses of perception of humans. However, is this the operational criterion, the value component, or the aesthetic assessment that we should be using in delineating species as elements of our biodiversity. I would think not. Again, evidence for lineage independence, cohesion and continuity derived via whatever biologically meaningful methods or tools should all be considered on an equal playing field. There are at least four caveats to this statement. First, any comparisons or tests of hypotheses of lineage independence of species must be cast in a phylogenetic perspective wherein researchers are cognizant of the existence of both plesiomorphic and apomorphic traits existing in lineages. Thus, the existence of plesiomorphic traits in a lineage is not necessarily indicative of a lineage not maintaining its independence from close or distant relatives. Second, any comparisons of species validity must be between sister species derived from a unique common ancestor. Comparisons between distantly related species regarding lineage independence is meaningless given that lineage independence results from speciation events producing sister species. Third, comparisons must be cognizant of known differing rates of evolution or anagenesis of within and between different types of characters that occur both within and between lineages. Fourth, species as \textit{Individuals} can maintain their lineage independence, cohesion and continuity even in the face of observed cases of sexual transgressions across species ‘boundaries’ (Wiley 1981; Dowling \textit{et al.} 1989; Warren 1992).

Regarding character superiority and rates of evolution, today many biologists and laypersons alike tend to view molecular studies and data as having more strength than other types of studies involving behaviour, physiology, ecology, and even morphology in ‘testing’ species hypotheses. This prejudice relates directly to an ignorance of the inherent and routine problems one encounters with generating and interpreting molecular data, a problem often not realised in such studies or the intended audiences. For example, it is commonly believed that when two entities share the same feature they are said to be the same; two species with the same mobility of an allele at a particular locus are thought to be the same, or the occurrence of the identical allele provides ‘evidence’ of sameness of the two or more taxa. This mode of interpretation permeates all types of data but is especially prominent in studies involving molecular data. Little thought is given to the well-corroborated evidence that different types of traits (and genes being sequenced) evolve at different rates over time, and that even within the evolution of a gene, the rate of divergence can vary. This is shown in Fig. 3 where genes A and B exemplify the common view of gene evolution by individuals holding that \textit{similarity equals sameness}. Both of these genes have a constant rate of change over time, but gene A is evolving at a
rate higher than gene B. However, in this example genes C–F have differential rates of evolution depending upon the time period when examined. Within an evolutionary perspective this means that one cannot rely upon a general ‘molecular clock’ to predict or define the ‘amount of divergence necessary’ before a biological entity is considered a species! Thus, it is natural that different species will have differing levels of genetic differentiation (fixed genetic differences, differences in morphological divergence, differing genetic differences). There is no magic amount of divergence that should be used to declare species validity!

This view of character divergence and rate of evolution is also illustrated in Fig. 4 where hypothetical speciation events are identified along the time scale. Here, the arrows indicate the timing of speciation events corresponding to the phylogenetic hypothesis. Each of these events also have particular rates of change in genes A–D associated with them before, at and after each speciation event. In this example, only genes C and D would meet the general assumptions of a molecular clock or a generalized criterion for genetic divergence necessary for speciation. For these two genes, the untrained biologist is faced with one gene providing more evidence of divergence (gene C) than the gene evolving at a slower rate (gene D). The other two genes are evolving at variable rates over time. The pattern of evolution in all of these genes offers explanatory evidence as to why in some groups of organisms a particular gene evolves at a slower or faster rate than in other groups. Thus, a strict reliance upon particular levels of divergence in particular types of characters, whether morphological or molecular, is very problematic in identifying biological diversity.

**Implications of species concepts on the diversity of fishes**

Quite clearly, the above essay on species as *Individuals*, the hierarchy of concepts under the ESC, and the logical unbiased interpretation of all types of data to identify and test for lineage independence, cohesion and continuity will have major, long-lasting implications to the diversity of fishes and other groups. The arguments for this ideology are already well developed but have not been implemented. There is some hesitance in the community to employ non-traditional tools to validate the existence of independent lineages of diversity. To some degree, this is logical in the sense that describing species on the basis of molecular (or other) characters alone may preclude the identification of species using traditional characters. This is a practical concern that I am confident many have considered. However, we must also consider the impact of not recognizing any type of diversity that clearly is consistent with the logic for describing species based on acceptable morphological characters. That is, if our objectives are to discover natural patterns of biological diversity and use this information to understand natural processes responsible for its evolution, what good is it for us to only recognize some types of diversity, but not others.
when they all can be justified equally well? Interpretations of pattern and process will necessarily be fatally flawed. Our understanding of these processes and resulting patterns will be completely contingent upon priors.

The impact of not recognizing independent lineages of diversity is probably most noticeable in conservation biology with the recent increase in the destruction of ecosystems and extinction of species. Recognizing species as Individuals and thinking of them as lineages related to other lineages is critical to conservation efforts (Mayden and Wood 1995; Roe and Lydeard 1998). Conservation strategies for the recovery of species must be soundly based and, in my opinion, must incorporate phylogenetic information as to the sister-group relationships of species (Mayden and Wood 1995). Using sister-group relationships, one can identify sister species that can be used as surrogates for extensive investigations inquiring as to the nature of the imperilment of an endangered species. When species are endangered it is customary to do certain things. These include: (i) protection of the species, but not necessarily its habitat or ecosystem, so that no one can sample or harass the species; (ii) a type of ongoing status survey of the species; and (iii) inaction to see what happens, all the while hoping that the species status will improve. This is a very passive approach to a problem of unprecedented proportions relative to ecosystems and species diversity. Alternatively, if one views the problem with species being Individuals behaving as lineages and sharing common ancestors with other closely related species, then we may use this information in the development of a more proactive and profitable conservation strategy. Sister species can and will be used as surrogate species for detailed investigations and through phylogenetic methods involving character-state reconstruction, we may predict with a high level of confidence what the underlying ecological, physiological, behavioural, etc. ‘weaknesses’ are for an endangered species in a particular habitat. This is conservation through phylogenetic surrogacy. Agencies and researchers need to acknowledge natural diversity recognisable as independent lineages on the basis of multiple types of data. They must acknowledge and incorporate a lineage and phylogenetic perspective in their recovery plans to better serve their objectives.

**A glass ceiling on species diversity**

Undoubtedly, many reading this essay will cringe from the thought of recognizing all independent lineages as biological species. Who knows how much diversity this may result in, as we perfect our methods of better understanding biological diversity. However, under the ESC as outlined most recently by Wiley and Mayden (2000a) species are characterized as follows: an evolutionary species is an entity composed of organisms that maintains its identity from other such entities through time and over space and that has its own independent evolutionary fate and historical tendencies. This concept is further amplified in this paper to cover all types of questions regarding varied kinds of entities and how they are interpreted. But, one thing must be clearly understood. This is a lineage concept of ancestor-descendant populations, metapopulations, or other groupings; it is not a concept that should be abused by those that may critique the lineage idea wherein ‘anything’ could be diagnosed as a lineage using the right techniques. Such arguments are biologically meaningless and only cloud the important issue of striving to recover natural patterns of descent.

Yes, it is very likely that the number of species that will be recognized by employing the ESC will increase relative to the numbers of taxa that have been recognized using other concepts, especially the BSC. In a real example resulting from phylogenetic studies and species diversity, Cracraft (1992) found that the number of species of birds-of-paradise increases from 40 under the BSC to 90 using the best surrogate concept for the ESC, the PSC. Why is this? Because other concepts severely restrict the types of biological diversity that is allowed to be recognized. Ironically, probably the most widely know concept, the BSC, represents one of the biggest impediments to not only recognizing diversity but also conserving diversity. This concept, often referred to as the polytypic species concept, resulted in a tremendous amplification of taxa referred to as races or subspecies in the 1960s. As members of the same species, populations of these ‘polytypic species’ in allopatry were often transported and mixed with other populations of the same or different subspecies. This is often a problem in fishes, particularly those of importance to fisheries and anglers. The result of many of these efforts to maintain populations in different areas by mixing different ‘subspecies’ has resulted in the loss of what are now known as divergent lineages, especially in western North American trout (Miller et al. 1989; Behnke 1992). In fact, some ‘subspecies’ or ‘races’ of trout were actually found in the same lakes and in sympatry, and some have gone extinct as a result of introgressive hybridization with introduced...
taxa. The implication that, of all the independent descendent lineages that exist in nature, only some can be recognized as species, justified on the basis of value judgements, aesthetic priorities, or even confidence of eventual lineage mixing of two 'subspecies' in 'potential contact', is not in the realm of science. This logic can and will have detrimental effects on many, many disciplines working with biological diversity, not to mention the diversity itself.

Today there is a glass ceiling on species diversity driven largely by nonscientific values, aesthetic assessments and preferences, and operational issues. While predictions as to the number of species differ widely between authors, ultimately the recognition of diversity rests in the information that is permitted to be published. If we, as practising scientists, knowingly exclude biological diversity, proposed and published to represent valid evolutionary species, on the basis of unpublished opinions that may or not have any scientific rigor and validity, we depart from science. Rejection of species hypotheses must be based on well-formulated studies that demonstrate falsification of the lineage hypothesis and must be unbiased with respect to the nature of the characters (as long as the characters are heritable and homology can be ascertained) and free of a propensity of value and aesthetic bias. Historically, some publications, books and checklists driven by committees or panels knowingly exclude hypothesized species diversity, or decide what are the valid species and which ones should be relegated to 'subspecies' or not recognized at all (Robins et al. 1980, 1991). Although some may argue that this is done with good intentions for accounting for only the 'good' or 'valid' species or to 'simplify' complex systems, such decisions should not be made without presenting adequate data to the scientific community to demonstrate alternative views. At least for North American fishes this trend is beginning to change with an improved understanding and appreciation for the diversity of species concepts. This has recently been demonstrated by Warren et al. (2000) wherein criteria for species inclusion were clearly outlined.

Today we live in a world of incredible technological abilities and the number of species recognized should not be constrained to those that can only fit in an atlas or those that are morphologically divergent for preferred character types within particular higher taxa. Experts of different taxonomic groups ultimately determine the diversity of species within any one group, but this should be done with peer review. As experts, we provide fundamental knowledge that other disciplines rely on for their own investigations into a vast array of data- and theory-driven inquiries of the physical and natural worlds. We hold the responsibility of providing sound scientifically based estimates of biological diversity referable to species and we must make this information readily available to the world. We must aspire to provide these unbiased estimates of evolutionary lineages regardless of differences of opinion regarding nonscientific issues, and we must successfully achieve these goals that our disciplines have pledged to the scientific and nonscientific communities. In doing so, systematics and taxonomy as scientific endeavors will continue to maintain its fundamental significance and its deserved respect in these communities.

**Returning to the hierarchy of concepts**

As outlined above and in previous papers (Mayden 1997, 1999) the Evolutionary Species Concept serves as a logical and fundamental over-arching conceptualization of what scientists hope to discover in nature behaving as species. As such, this concept with its lack of operational necessities can be argued to serve as a primary concept of diversity. Also as discussed, however, it is impossible to use this concept to go out and operationally discover or recover entities consistent with the ESC. As in the analogous situation between monophyly and synapomorphy described above, we must implement means by which species can be discovered, described, and diagnosed as hypotheses of lineage independence, cohesiveness and continuity subject to falsification. Clearly, the synapomorphy serves as a functional guide or part of our phylogenetic 'tool box' best suited to identify monophyletic groups, given our current understanding of phylogeny reconstruction. From this, it logically follows that the numerous secondary species concepts in actuality do not have the same ontological status as the ESC and are subservient to it, serving as functional guides or part of our lineage or species 'tool box' best suited to identify natural lineages thought to represent species, given our current understanding of the patterns and processes of descent with modification. Thus, in reference to this fundamental difference between the ESC and secondary concepts, I do not consider them to represent fundamental concepts but simply guidelines. As such, I recommend that these alternative concepts
be referred to as methods, guidelines, or prescriptions for the different types of diversity that our current and ancestral academic ancestors have developed for detecting species, derived out of differences in taxonomic groups, and preferences for different types of criteria. None of these guidelines, however, should be acknowledged as scientific if they knowingly permit the recognition of false taxa (Successional Species Concept) or if they or their applications are laden with nonscientific value- or aesthetic-based arguments (Table 1).

**Individuals above and below the scale of species**

The idea of Individuality has focused largely of late on the species issue and has brought considerable debate to the topic that has lead not only to multiple conceptualizations but also questions as to the scientific rigor of the scientific discovery process in systematics and taxonomy with species. While only briefly addressed herein, the issue of Individuality, Individualism and Individuals is not restricted to the species. In fact, entities fitting the characterization of the philosophical term Individual dominate many other disciplines of sciences. Characteristically, one can easily identify such issues, among many other means, by looking for those things in disciplines that have an inordinate number of definitions and are controversial. The fact that entities thought to be naturally occurring by-products of some natural process have multiple definitions is a clear indication of the fact that the boundaries of these entities are not clear but are 'fuzzy' (Fig. 1). Why are they fuzzy? For the same reasons that species boundaries are fuzzy, they change over time, they do participate in natural processes governing these bodies and, probably most importantly, as Individuals they cannot be defined – they can only be described or diagnosed. Where are these nonspecies examples? Only to list a few in an order of scale, things such as galaxies, stars, planets, biomes, ecosystems, communities, wetlands, populations, organisms, organs, organelles, molecules and atoms are all Classes that contain Individuals and will necessarily invite controversy when boundaries are to be made (similar to the taxonomic category Species as a Class containing Individuals known as species). Taking the planet Earth as an example, where is the boundary of Earth such that investigators wishing to better understand processes can limit their collection of data? Is it the geological surface, the geological and aquatic surfaces, the edge of the stratosphere or beyond? For ecosystems, communities and, in particular, wetlands where does one begin and end? Depending upon the multiple definitions of a wetland the boundaries can vary by several meters. Given that there are multiple definitions as to the boundaries of ecosystems, communities and wetlands, how can scientists conduct scientific study without knowing the exact boundary of their experimental plan? These issues extend to our solar system and the classification of planets. What about Pluto? Is it a planet or not? Current controversy exists over whether or not Pluto is a planet, a trans-Neptunian object, a minor, major, or principle planet, a comet, or an asteroid (McCaughrean et al. 2001; Osorio 2001). Thus, planetary definitions vary widely depending upon the scientist, the types of features being considered, the nature of one's academic background, etc. Stars represent my last example of Individuality beyond species. Stars, like all of the other examples listed above have their own unique ontogenies that are predictable in many ways because our knowledge of the physical laws governing the Individuals put into the Natural Kind called Stars is based essentially on their initial mass. Individual stars are classified into Natural Kinds referred to as Red Supergiants, Red Giants, Blue Giants, White Dwarfs and Main Sequence (Fig. 5). Although all stars did not evolve from a 'mother' star, and not all of the stars of any one group were derived from a common star of the group, the famous Hertzprung–Russell classification derives from a number of qualities of the individual stars such as temperature, absolute magnitude, and spectral type given off by the star during its ontogeny. Although discrete boundaries between star types is arguably inconclusive, the evolutionary ontogeny of a star is predictable. Those stars of the Main Sequence all have their initial mass roughly equivalent to 16 suns but they differ substantially in their luminosity, temperature, spectral type and absolute magnitude. Each of these stars will evolve with time and some may depart the Main Sequence and be classified as Red Supergiants, Giants, or White Dwarfs. Along the way, however, the star is still the same Individual governed by natural physical laws but with boundaries that are less than clear for classification purposes!

Thus, the issue of Individuality is a much more dominant occurrence in the natural world than some may believe. While entities referable to Individuals as by-products of and governed by natural processes may be perceived as being difficult to understand, the benefit of making that extra effort to incorporate
this philosophy in to a scientific process results in promising results that will further our understanding and resolution of the formation and preservation of our natural world.

Acknowledgements

Many people, either in person or through literature, have been most influential in assisting me to formulate my ideas on species. I wish to thank those of you who have discussed these ideas with me at various times. In the development of the ideas expressed in this paper, I specifically wish to thank Darrel Frost, Anna George, Michael Ghiselin, David Hull, Bernard Kuhajda, Nick Lang, Michelle Mayden, David Neely, Steve Powers, Richard Richards, Kevin Roe, Andrew Simons, E.O. Wiley, Rob Wood and Quentin Wheeler. I also thank the National Science Foundation (USA) for supporting my systematic studies of fishes that have made my conceptual papers on species, speciation, systematics and evolution possible. Finally, I thank the organizers of the symposium on which this special issue is based and the American Society of Ichthyologists and Herpetologists for developing the outstanding symposium opportunity to discuss one of the most important issues in contemporary biology.

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