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A hierarchy of species concepts: the denouement in the saga of the species problem

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ABSTRACT

At least 22 concepts of species are in use today and many of these are notably incompatible in their accounts of biological diversity. Much of the traditional turmoil embodied in the species problem ultimately derives from the packaging of inappropriate criteria for species into a single concept. This results from a traditional conflation of function of concepts with their applications, definitions with concepts, taxonomic categories with groups, and the ontological status of real species with teleological approaches to recover them. Analogous to classifications of supraspecific taxa, our forging inappropriate and ambiguous information relating to theoretical and operational discussions of species ultimately results in a trade-off between convenience, accuracy, precision, and the successful recovery of natural biological diversity. Hence, none of these expectations or intentions of species or classifications is attainable through composite, and possibly discordant, concepts of biological diversity or its descent.

Reviewing and evaluating the concepts of species for their theoretical and operational qualities illustrates that a monistic, primary concept of species, applicable to the various entities believed to be species, is essential. This evaluation reveals only one theoretical concept as appropriate for species, the Evolutionary Species Concept. This conceptualization functions as a primary concept and is essential in structuring our ideas and perceptions of real species in the natural world. The remaining concepts are secondary, forming a hierarchy of definitional guidelines subordinate to the primary concept, and are essential to the study of species in practice. Secondary concepts

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should be used as operational tools, where appropriate, across the variance in natural diversity to discover entities in accord with the primary concept. Without this theoretical and empirical structuring of concepts of species our mission to achieve reconciliation and understanding of pattern and process of the natural world will fail.

19.1 INTRODUCTION

> 'I believe that the analysis of the species problem would be considerably advanced, if we could penetrate through such empirical terms as phenotypic, morphological, genetic, phylogenetic, or biological, to the underlying philosophical concepts. A deep, and perhaps widening gulf has existed in recent decades between philosophy and empirical biology. It seems that the species problem is a topic where productive collaboration between the two fields is possible'.
>
> (Mayr, 1957)

Little has changed with regard to the species problem since Mayr composed this piece. Some researchers argue for a particular concept of diversity known as species, while others prefer a pluralistic approach (Mishler and Donoghue, 1982). Today, the controversy continues over the conceptualization of species. This volume reflects some of this diversity of thought across multiple taxonomic groups. This seemingly timeless debate has generated a heterogeneous proliferation of concepts, most hoping to capture the operational and/or theoretical qualities of a good concept. The search has been for a concept–definition that is biologically relevant and meaningful, one that is easily applied, and one that encompasses natural biodiversity. That is, a concept of real species assisting in and ensuring their recognition and our understanding of them in nature. This goal has not been achieved for several reasons.

The 20th century history of biological classification illustrates why this so-called silver bullet species concept, one that will attend to all our perceived needs, has not yet been achieved. In phylogenetic systematics (or cladistics) the Linnaean classification scheme represents a hierarchical system of categories coordinate with a phylogenetic tree of named taxa. Represented in the classification is the idea of monophyly of taxa, or sister group (genealogical) relationship. Classifications are information retrieval systems about genealogical relationships. In evolutionary systematics the classification is purported to represent sister group relationship and evolutionary distinctiveness. Paradoxically, while this may be viewed as an expedient method to group information in a retrieval system, under this method one can never be sure which criteria are optimized at any part of a classification. Thus, confusion is inherent in an ambiguous information retrieval system. The ultimate trade-off of combining too many desired functions into a convenient method is that it is not always possible to isolate any one function (e.g. genealogy versus distinctiveness).

Much of the turmoil embodied in the species problem ultimately derives from our packaging inappropriate criteria for species into a single concept. This results from a traditional conflation of function of concepts with their applications, definitions with concepts, taxonomic categories with groups, and ontological status of real species with teleological approaches to recover them. Analogous to classifications of supraspecific taxa, our forging inappropriate and ambiguous information relating to theoretical and operational discussions of species ultimately results in a trade-off between convenience, accuracy, precision, and the successful recovery of natural biological diversity. None of these expectations or intentions of species or classifications is attainable through composite, and possibly discordant, concepts of biological diversity or its descent.

With this in mind can one tease apart the theoretical concepts and operational definitions of species and develop a primary concept applicable to the various entities believed to be species? I think this is possible through a hierarchical view of species concepts and their definitions. Below, I review the various species concepts and propose a hierarchical classification for them. Each of these concepts is briefly evaluated relative to their consequential qualities thought to be important in a concept (Hull, 1997: Chapter 18). This evaluation reveals only one appropriate primary and theoretical concept of species. The remaining definitions are secondary concepts, forming a hierarchy of definitional guidelines subordinate to this primary concept. The secondary concepts are engaged only as operational tools, where appropriate, across the variance in natural diversity to discover entities in accord with the primary concept.

19.2 METHODOLOGY

Probably more is written about species than any other topic in evolutionary biology. There are many opinions and studies addressing this question. Hence, an exhaustive survey of these is impossible. Concepts are ideas or intuitions uniquely developed in the minds of every person. Definitions of these concepts are the only form with which one can compare them. Sometimes, these definitions may be poorly developed or misinterpreted, ultimately leading to miscommunication of ideas. Regardless, I have endeavoured to understand the arguments on the various species concepts (Table 19.1), and compare and evaluate them. In section 19.7 I have also made an effort to identify synonyms of concepts; these are listed by assigned standard abbreviations or full titles. Where concepts were formerly identified as synonymous, credit is provided; in part refers to the observation that portions of concepts are equivalent.

Table 19.1 Species concepts and standardized abbreviations

1. Agamospecies (ASC)	14. Morphological (MSC)
2. Biological (BSC)	15. Non-dimensional (NDSC)
3. Cohesion (CSC)	16. Phenetic (PhSC)
4. Cladistic (ClSC)	17. Phylogenetic (PSC)
5. Composite (CpSC)	1. Diagnosable Version (PSC_1)
6. Ecological (EcSC)	2. Monophyly Version (PSC_2)
7. Evolutionary Significant Unit (ESU)	3. Diagnosable and Monophyly
8. Evolutionary (ESC)	Version (PSC_3)
9. Genealogical Concordance (GCC)	18. Polythetic (PtSC)
10. Genetic (GSC)	19. Recognition (RSC)
11. Genotypic Cluster Definition (GCD)	20. Reproductive Competition (RCC)
12. Hennigian (HSC)	21. Successional (SSC)
13. Internodal (ISC)	22. Taxonomic (TSC)

19.3 IMPORTANT QUALITIES TO CONSIDER

Few concepts can be viewed as more fundamental to the natural sciences than that of the species. Species as individuals (Hull, 1976) represent a unique level of organization of the natural world; they are self-organizing entities or particulars. This level of universality is the upper-most limit to involve tokogenetic relationships and the lower-most level participating in phylogenetic relationships. They are purported to be the highest level of integration to participate in natural processes while being spatiotemporally constrained. Thus, they are essentially fundamental units of evolution. In plain English, this means that for all disciplines using any species in pure or applied research, education, management, conservation, etc., success at accomplishing identified missions or deriving informative answers to particular questions is inextricably tied to a basic assumption that the species involved are **real** by-products of natural processes and not misguided fabrications of our own invention.

One method to compare and contrast the various concepts of species is through three criteria that have traditionally been employed to evaluate scientific concepts. Hull (1997: Chapter 18) provides such a review for seven of the most frequently used concepts for their theoretical significance, generality (or universality), and applicability (or operationality). Following a review of definitions, metaphysical topics, and species concepts, I extend a similar evaluation to all 22 of the various concepts of species. The relationships of the concepts within and among the three criteria, together with the question of monism versus pluralism, reveals a hierarchy of species concepts that should finally put the species problem to rest.

19.4 CONCEPTS, DEFINITIONS, GROUPS, CATEGORIES AND NAMES: THE UNFORTUNATE CONFLATION OF TERMINOLOGY

Important in the discussion and resolution of the species problem is the correct usage and understanding of ideas and terms related to the species issue. Historically, discussions of species have involved the use of four critical terms: concept, definition, group and category. These terms have been central to the fundamental melange that both scientists and philosophers have encountered with the species problem.

Communication of ideas or concepts in science is of utmost importance and hinges upon statements or definitions developed by persons formulating or discussing the concepts. Critically important to exact communication of ideas embodied in concepts demands that we do not obfuscate the terms or words used in definitions or statements of the concepts. Here, we confront difficulties both in the logical treatment and the evaluation of definitions.

Concepts of biological systems serve as fundamental links between pattern and process in nature, are employed in every discipline, and help guide our perception of natural systems. They are formulated by individual persons through observation, study and synthesis (impressions and imagination) of both theory and empirical data. Concepts may be real or abstract. Real concepts are those representing easily agreed discrete objects. Abstract concepts are those representing hypothetical and transient phenomena. A concept may be relayed from one person to one or more other persons by adapting it into a statement or definition, either verbally, in writing, or graphically. Such a definition may or may not induce the same concept in the mind of the other persons, depending upon the appropriateness, precision, and accuracy of the words used in the definition and the level of understanding of the other person. With real concepts (e.g. round versus square) one may compare statements developed by different observers with discrete objects to see if they agree. With abstract concepts (evolution, natural selection, species as taxa) it is difficult to know for sure if statements represent the same transient or hypothetical things, and the respective definitions can only be compared using previously agreed definitions of words used in the statement. One may also observe the effectiveness of such a concept through direct examination.

The term 'group' refers to a collection of objects or things. In the intersection of natural sciences, taxonomy, and systematics the term taxon is often used synonymously with the term group. A group can be real and have objective reality if it corresponds to qualities that are real and exclusive to it, and if it consists of things that have material existence. They may be arranged hierarchically, either as non-reticulate or reticulate groups. They may be represented at various levels of universality from groups of things to more inclusive groups of things, etc. They may be of any size and arise on the basis of intrinsic attributes and/or extrinsic decisions. Organisms can be members of any number of groups so long as they possess the attributes of the said groups. Groups, however, are not like concepts. Groups develop from sense impressions of concepts and can be agreed upon and definite if the statements about them are unambiguous and decisive.

Groups and categories are distinctly different and there is no real connection between them. The tradition in codes of nomenclature artificially forces the use of taxonomic categories in a hierarchy for groups. A biological classification is a contrived system of categories used for the storage and retrieval of information about biological diversity, taxa, or groups. The concept 'category' is a class and has no separate existence from its use in organizing objects or thoughts; categories have no reality. Unlike groups, categories have no attributes; things or objects are not members of categories, but are parts of groups; and organisms are not members of any taxonomic category. For example, Cyprinidae is a proper name given to a group of fishes possessing certain attributes. By taxonomic convention the -idae ending denotes a traditional level of universality in the zoological hierarchy. The group Cyprinidae can be a part of many other groups (Cypriniformes, Ostariophysi, Teleostei), but is only a member of one taxonomic category, Family. Because categories have no reality the Family Cyprinidae is not a member of any other more-inclusive categories, but Cyprinidae is.

Multiple classifications may exist for the same group of organisms, depending upon criteria being optimized in the classification. The Linnaean hierarchy imparts information regarding relationship, descent from hypothesized immediate common ancestors. Supraspecific categories are more inclusive than the species category. Groups are assigned to categories; assignment is based on the definition of the category. Historically, categories of this hierarchy were defined on the basis of distinctiveness; that is, distinctiveness of the group assigned to Genus was less than distinctiveness at the Family, and so on.

In the modern-day hierarchical system a distinction between the supraspecific categories and the species category is a dichotomy between phylogenetic and tokogenetic processes and relationships (Hennig, 1966; Frost and Kluge, 1994; Wiley and Mayden, 1997). Supraspecific categories are defined only as monophyletic groups having phylogenetic relationships and historical cohesion. The categorical rank assigned to a group satisfying this criterion is only a by-product of its level of inclusiveness. Assignment of a group to a supraspecific category is definite because of its historical existence, and our discovery and recognition of this previous existence requires demonstration of monophyly. Demonstration that a group shared an immediate common ancestor is by way of synapomorphies, one or more features inherited from and evolved in the immediate common ancestor to all known descendants. Only the concepts of monophyly and historical cohesion apply to all groups assigned to supraspecific categories.

The species category shares some, but not other qualities with supraspecific categories. The groups assigned to this category are different. Like other categories, the category species is an artificial construct used for organization of information. Unlike groups assigned to supra-specific categories those assigned to the species category have tokogenetic relationships (sexuals) or are tokogenetic vectors (clones), and may or may not be definite. Because species being classified today are potential future ancestors of groups to be placed in supraspecific categories of tomorrow, their existence does not necessitate demonstration via synapomorphies. These groups (species) are the types of entities once existing in historical communities (as ancestors) that modern-day systematists endeavour to document today by way of synapomorphies. Unlike supraspecific categories, there is a real connection between the species category and the groups assigned to this category. While the species category is a class construct like supraspecific categories, it is ontologically distinct from the class construct supraspecific categories. The species category is unique and contains only those groups of things conforming to the concept of this category. Herein lies the nucleus of the species problem. What is the appropriate concept for species and the species category?

Names applied to categories should not be confused with the names applied to the groups included in the categories. For example, there is a categorical level of the hierarchy to which is assigned the arbitrary name genus. A group (or group of groups) may be referred to this level of the hierarchy and referred to as a genus (see discussion below on twin meanings of species). The group of organisms is given a proper name distinct from the category name. For example, there is a group of fishes named *Cyprinella* and this group is assigned to a level of the hierarchy, namely genus. Problems arise when one defines the named category (genus) and confuses this definition with or extends this definition to the group of particulars (*Cyprinella*) being placed into the category.

19.5 THE TWIN MEANINGS OF SPECIES

The term species has two different meanings that, when not clearly differentiated, will result in confusion and misunderstanding relevant to real species, species concepts, species category and speciation. The term species is used to represent both a taxonomic category and those naturally occurring particulars that we discover, describe, and order into our classification system. Confusion of these terms is most detrimental to elucidating and understanding the importance of species concepts because they each have a very different ontological status (Hull, 1976). While this may seem obtuse, irrelevant, or strictly metaphysical to the working biologist, naturalist, or general scientist, it is not. Much of the confusion over species concepts relates directly to the conflation of these critically different meanings.

The two species terms are aligned in two different philosophical categories, Class and Individual (not to be confused with the formal taxonomic category or single organism, respectively). The taxonomic category species is a class. A category is spatiotemporally unbounded, lacks cohesion, is not self replicating, does not participate in any natural processes, has members, and can be defined. Members of a class may be classes, or not. A class can exist anywhere in the universe, so long as there is a definition for membership. Members of a class also can exist anywhere, if the definition applies (Hull, 1976).

Those tokogenetic and cohesive entities discovered and described in nature, referred to species, that we place in the category species, are individuals (or things, particulars). Individuals are spatiotemporally bounded, have intrinsic cohesion, are self-replicating, participate in natural processes, have part–whole relationships, but cannot be defined. Individuals change over time and can only be described. Individuals exist throughout the universe. Because individuals have no definitions, they do not have members; rather, they exist as parts of wholes. Parts of individuals may be other individuals (*Homo sapiens*, organisms, organs, tissues, cells, mitochondria, etc.), also resulting from various natural processes.

Thus, the twin meanings of species refer to two, radically different and basic metaphysical categories, classes and individuals, that when confused generates elementary problems for understanding. As a class, the category species is temporally unbounded, has a definition, and only those things fitting this definition can be included. Species as taxa change with time, have no definitions, they can only be described, identified, pointed to, etc. In our discussions of 'What is a species?', we reference Linnaean category species, the class concept, and what we decide should and should not be included in this category through a definition. In discussions of species as they exist in nature we reference the individual with a unique origin and no definition. These are particulars. If an organism is found on Mars that looks, acts, and speaks like *Homo sapiens* on Earth, it is not *H. sapiens* unless it descended from *H. sapiens* on Earth.

19.6 SPECIES CONCEPTS VERSUS EMPIRICAL DATA

It is not uncommon to find in discussions of species and species concepts researchers confusing empirical data used in the operation of recognizing a species with a conceptualization or definition of species. Empirical data can include such things as anatomy, morphology, genetics (DNA, proteins), behaviour, etc., all possibly evaluated and analysed in a variety of ways and with a variety of methods. Our abilities to gather these data are artificially constrained by technological advances; that is, we can only collect data that current technology permits. These artificial constraints on our ability to perceive variation in nature should not be confused with our desires, objectives, or attempts to illuminate natural variation. For example, it is often said that a particular group of organisms represents a distinct species based on a morphological or genetic species concept. If empirical methods are confused with concepts of species the logical outcome will be confusion. That is, species that fit the definition of a morphological species concept may not fit the definition of a genetic species concept, and *vice versa*. Assuming that we are mainly interested in identifying natural diversity resulting from historical processes encoded in genomes, empirically driven concepts are untenable. Given that any research study is grossly limited in the type and amount of empirical data available from all that is technologically possible, universally applicable concepts of species should not be bound by or confused with empirical evidence.

19.7 THE SPECIES CONCEPTS

The taxonomic, systematic, and evolutionary literature reveals that at least 22 concepts have been developed to characterize diversity (Table 19.1). Developed by researchers to suit individual needs, some are operationally or empirically motivated, some are galvanized by theoretical necessity, while some are motivated by peculiarities of organisms studied. Not all concepts have been equally well characterized or explicitly defined. Some have been essentially bequeathed to academic descendants of particular fields (e.g. population genetics, taxonomy, entomology, mammalogy, etc.), together with an awareness of the requisite qualities of species and necessary operations to be employed by researchers embracing them. Only abbreviated discussions of the various concepts are presented below alphabetically. Included are synonyms, definitions, discussion, and a synopsis as to the suitability of the concept.

19.7.1 Agamospecies concept (ASC)

Synonyms
Microspecies, Paraspecies, Pseudospecies, Semispecies.

Discussion
This concept refers specifically to taxa that do not fit the biparental, sexually reproducing mode. It serves as a general umbrella concept for all taxa that are uniparental and reproduce via asexual reproduction; often these species are the result of interspecific or intergeneric hybridization. These species may produce gametes but there is often no fertilization, except via hybridization. Ghiselin (1984a: 213) refers to these species as 'heaps of leaves that have fallen off the tree that gave rise to them'. Agamospecies may be part of a species complex wherein there also exist bisexually reproducing species. In these cases the agamospecies may be facultative or obligate apomicts. Obligate apomicts are sometimes referred to as microspecies.

In reality the composite of individual organisms of the species may often be polyphyletic, resulting from multiple crosses between parental, bisexual species. These taxa are most often diagnosed by features related to either morphology or chromosomes. Often, these species have very restricted ranges. Some authors only recognize them as species if their range includes at least 20 km diameter (Weber, 1981).

Synopsis
Because of the limited application of the ASC to asexually reproducing species the ASC should serve as a primary concept.

19.7.2 Biological Species Concept (BSC)

> 'A biological species is an inclusive Mendelian population; it is integrated by the bonds of sexual reproduction and parentage'. (Dobzhansky, 1970: 354)
> '...groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups'. (Mayr, 1940)
> 'A species is a group of interbreeding natural populations that is reproductively isolated from other such groups'. (Mayr and Ashlock, 1991)

Synonyms
GSC, Isolation Species Concept (Paterson, 1993), Second Species Concept (Mayr, 1957), Speciationist Species Concept (Blackwelder, 1967),

Discussion
This concept has been reviewed by its strongest proponent, Mayr, in several publications and by several other authors (see Mayden and Wood, 1995). As recently espoused by Mayr and Ashlock (1991: 26–27) and Mayr (1997), species consist of reproductive communities wherein there is both an ecological and genetic unit. Individuals of a species seek and recognize one another for mating and thereby maintain an intercommunicating gene pool that, 'regardless of the individuals that constitute it, interacts as a unit with other species with which it shares its environment'. For Mayr (1997) 'each biological species is an assemblage of well balanced, harmonious genotypes and... indiscriminate interbreeding of individuals, no matter how different genetically, would lead to an immediate breakdown of these harmonious genotypes. As a result, there was a high selective premium for the acquisition of mechanisms, now called isolating mechanisms, that would favour breeding with conspecific individuals and inhibit mating with non-conspecifics. This consideration provides the true meaning of species. The species is a device for the protection of harmonious, well integrated genotypes. It is this insight on which the biological species concept

is based'. Central to this concept, and the sole criterion for the reality of a species, is thus the idea of reproductive isolation of species from other such species. 'A species is a protected gene pool' that is 'shielded by its own devices (isolating mechanisms) against unsettling gene flow from other gene pools' (Mayr and Ashlock, 1991). The word interbreeding in the definition above 'indicates a propensity; a spatially or chronologically isolated population, of course, is not interbreeding with other populations but may have the propensity to do so when the extrinsic isolation is terminated' (Mayr, 1997). Accordingly, speciation is the process of achieving reproductive isolation (Mayr, 1963: 502; 1970: 288).

The BSC specifically excludes uniparental species even though they are known to exist, and some have relegated diversity of this type to pseudospecies (Dobzhansky, 1970). The concept also is viewed as being an operational definition in that 'taxa of the species category can be delimited against each other by operationally defined criteria, for example, interbreeding versus non-interbreeding of populations' (Mayr and Ashlock, 1991: 27). This concept is relational because 'A is a species in relation to B and C because it is reproductively isolated from them'. Finally, it is a non-dimensional concept that 'has its primary significance with respect to sympatric and synchronic populations..., and these are precisely the situations where the application of the concept poses the fewest difficulties. The more distant two populations are in space and time, the more difficult it becomes to test their species status in relation to each other but the more biologically irrelevant this status becomes'.

At least ten elements of this concept are viewed by Mayden and Wood (1995) as counter-productive toward discovering and understanding biodiversity. The BSC has received substantial criticism in recent years for issues dealing with: (1) the absence of a lineage perspective; (2) its non-dimensionality; (3) erroneous operational qualities as a definition; (4) its exclusion of non-sexually reproducing organisms; (5) indiscriminate use of a reproductive isolation criterion; (6) confusion of isolating mechanisms with isolating effects; (7) implicit reliance upon group selection; (8) its relational nature; (9) its teleological overtones; and (10) its employment as a typological concept, no different from the frequently criticized morphological species concept.

Synopsis
The nature of the unfavourable attributes inherent in the BSC preclude it from being considered a primary species concept.

19.7.3 Cladistic Species Concept (ClSC)

> '...that set of organisms between two speciation events, or between one speciation event and one extinction event, or that are descended from a speciation event'. (Ridley, 1989)

Synonyms
ISC (in part; Kornet, 1993), CSC (in part; Kornet, 1993).

Discussion
Ridley (1989) proposed this minimalistic lineage concept of species wherein species are treated as individuals, not classes. As subtheories, discussion of this concept incorporates the BSC and EcSC (within cladistic framework) to provide a more complete theory for understanding species. Ridley is one of the few authors discussing species that makes a clear distinction between theoretical and practical concepts. A species is a lineage and speciation produces two or more lineages via splitting. By definition, species cannot be paraphyletic, even if individual organisms of one or more of the descendant species are genealogically more closely related to individuals of one or more other descendant species. Rather, ancestral species necessarily become extinct following a speciation event. This concept is free from operational constraints of necessary defining attributes, typical of concepts treating species as Classes.

Synopsis
In some ways, this concept of species could serve as primary concept for biological diversity. It is a lineage concept, treats species as individuals, and places no constraints on necessary attributes that a species must possess in order to be validated. In this sense it is similar to the CpSC, ESC, ISC, and some versions of the PSC. However, there are important differences that preclude all of these concepts, except the ESC, from being considered a primary theoretical concept. With respect to the ClSC, ancestral species, by definition, become extinct following a speciation event and hence cannot be considered paraphyletic with respect to the organisms of ancestral and descendant species. Descendant species, by definition, are monophyletic; ancestral species, by definition, go extinct following speciation. This concept is criticized by Wilkinson (1990) for lack of specificity with regard to speciation, an issue related to the enforced monophyly of species. Kornet and McAllister (1993) compare the ClSC and CpSC and argue that discussions concerning the monophyly of species are inappropriate, but that organisms forming species involved in a speciation event will, in all probability, be paraphyletic relative to one another. Thus, the ClSC is inappropriate as a primary concept.

19.7.4 Cohesion Species Concept (CSC)

> '...the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms'. (Templeton, 1989: 12)
> '...the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability'. (Templeton, 1989: 25)

Discussion

Templeton (1989) developed this concept following a review and short critique of the ESC, BSC and RSC. Of these concepts only the ESC did not exclude known biological diversity. The BSC and RSC were rejected because of substantial inadequacies for all living organisms. The argument emphasized was that both concepts underscore a certain level of sexual reproduction and, as such, fail in recovering naturally occurring diversity. This was considered highly significant given that a whole spectrum of known and valid diversity never, or only rarely, employs sexual reproduction or many have too high of levels of sexuality to be validated using either the RSC or BSC.

Borrowing positive aspects of all three concepts reviewed, especially the ESC, Templeton (1989) provides specific guidelines representing mechanisms of cohesion (1989: 13, table 2) to be used in understanding species. Cohesion of a species includes various aspects classified as either genetic or demographic exchangeability. As demonstrated, there is no clear break between sexual and asexual reproduction in terms of mechanisms and its ultimate outcome to a population. As such, this concept accepts all reproductive modes, and species are evaluated and validated on the basis of cohesion, not isolation.

Synopsis

Templeton (1989: 5) noted that the ESC 'is not a mechanistic definition', and favoured the CSC because it was developed with operational mechanistic qualities in mind. While this criticism is valid when one seeks an operational concept of species, because the CSC provides extensive operational details and guidelines for recognizing species it must be specifically excluded as a primary concept of species. However, the comprehensive operational nature of the CSC makes it an important practical surrogate (secondary) for a primary concept.

19.7.5 Composite Species Concept (CpSC)

> '... all organisms belonging to an originator internodon, and all organisms belonging to any of its descendant internodons, excluding further originator internodons and their descendant internodons'. (Kornet and McAllister, 1993: 78)

Synonyms

PSC (in part).

Discussion

This concept has its origin in the ISC as formalized by Kornet (1993). Fundamental problems with the ISC, recognized by Kornet and McAllister (1993), lead to the formulation of this concept. An internodon is defined by Kornet and McAllister (1993: 78) as 'a set of organisms such that, if it contains some organism x, it contains all organisms which have the INT relation with x, and no other organism'. While any internodon could technically be referred to as a species under the ISC, these authors view species as historical conglomerates formed of internodons that are permanently isolated and morphologically divergent. A species is a 'set of organisms belonging to several consecutive internodons in the phylogenetic succession, identified and grouped together by some procedure' (page: 66). Composite species begin with the evolution of an 'originator internodon' possessing 'a morphological property shown by the internodons' member organisms' (page: 67). They close with the extinction of the latest internodon that is a descendant of the originator, that is not an originator itself, and where another originator between it and its originator has not evolved. These species may endure permanent splits in the network wherein no morphological property shown by member organisms may be detectable or permanent reproductive isolation has not evolved. In other words, composite species are diagnosable or reproductively isolated entities that, using the terminology traditionally applicable to phylogenetic trees, may be either monophyletic or paraphyletic groups of internodons. When permanent rifts in networks are not accompanied with anagenesis of morphology or changes in reproductive abilities, then these rifts will not be permanent or detectable. That species are largely paraphyletic groups of internodons is viewed as an essential element of this concept because species must be mutually exclusive entities. If species, as groups of internodons, were required to be monophyletic then species would not be mutually exclusive, but nested sets. This concept also sanctions the recognition of successional species (page: 84–85) and 'superposed' species (page: 85), two or more species evolving within a single internode of a composite species and defined by at least one morphological fixation each.

Synopsis
These authors provide a lucid comparison of the appropriateness of the terms monophyly, paraphyly, and polyphyly which refer directly to groupings of things (species, internodons, or organisms), but not to species as Individuals. In a practical sense, this concept is essentially inseparable from PSC_1. Theoretically the CpSC and PSCs are very different. Kornet and McAllister (1993) recognize that under the CpSC species are like higher taxa; that is, historical entities that cannot interbreed, lacking interspecies cohesion. Treatment of species as classes, the recognition of successional or superposed species, and the intolerance for unisexuals precludes the CpSC as a primary concept. Like the PSC, it may be a useful operational surrogate assisting with discovering some species diversity.

19.7.6 Ecological Species Concept (EcSC)

> '... species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any

other lineage in its range and which evolves separately from all lineages outside its range' (Van Valen 1976: 233).

Synonyms
ESC (*sensu* Simpson; Stuessy, 1990; Minelli, 1993).

Discussion
This concept views species as ecological units forming lineages through time in a competitive environment. It is an operational definition wherein differences in ecology constitute different, independently evolving species. It is tolerant of both bisexual and unisexual species, species that evolve via hybridization, and the species that exchange genes, so long as ecological distinction is maintained in the lineage. The equivalence of the Evolutionary Species Concept (ESC) and EcSC (Stuessy, 1990; Minelli, 1993) is inaccurate. These concepts are distinct, in that the ESC does not necessitate or outline any ecological divergence between sympatric species. Only in the original ESC of Simpson (1961) was species referred to in an evolutionary and ecological context.

Synopsis
There is no doubt that the possession of divergent ecologies among sympatric lineages warrants their recognition as distinct species. While a tolerant lineage concept, as an operational concept it cannot serve as a primary concept.

19.7.7 Evolutionary Species Concept (ESC)

> '... a lineage (an ancestral–descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies'. (Simpson 1961: 153)
> '... a single lineage of ancestor–descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate'. (Wiley, 1978)
> '... an entity composed of organisms which maintains its identity from other such entities through time and over space, and which has its own independent evolutionary fate and historical tendencies'. (Wiley and Mayden, 1997)

Synonyms
ESU (in part; Mayden and Wood, 1995).

Discussion
This concept was championed originally by Simpson (1951, 1961) out of a general dissatisfaction with the non-dimensionality of the BSC. Wiley (1978, 1981) developed the concept further and argued for its general application to biological systems. Unlike other definitions reviewed herein,

the ESC largely was ignored, until recently. Frost and Hillis (1990), Frost and Kluge (1994), and Wiley and Mayden (1997) reviewed or further developed the concept. These authors argue that the ESC is the only available concept with the capacity to accommodate all known types of biologically equivalent diversity. Contrary to the perception of some (Minelli, 1993: 66–9) the ESC does not consider species as Classes or focus on species as ecological entities. The ESC is not equivalent to the EcSC. While Simpson (1961) advocated a lineage concept to species and ecological and evolutionary divergence, he also condoned the delineation of artifactual successional species. Thus, the logical corollaries of Simpson's ESC and Wiley's ESC are quite different.

The ESC is not an operational concept. However, it is a lineage concept that is non-relational. Thus, the attributes and patterns of species can be correctly interpreted with respect to their unique descent. The ESC accommodates uniparentals, species formed by hybridization, and ancestral species. It does not require knowledge of, nor specific changes in, a Specific Mate Recognition System (SMRS, see RSC, section 19.7.22). There is no threshold for particular attributes needed for the existence of a species. Finally, reproductive isolation, is considered a derived attribute from the plesiomorphic status of reproductive compatibility; reproductive success is thus largely uninformative.

Synopsis

The ESC is the most theoretically significant of the species concepts; it accommodates all 'types' of species known to date and thus has the greatest applicability. As such, the ESC can serve as a primary concept.

19.7.8 Evolutionary Significant Unit (ESU)

> '... a population (or group of populations) that 1) is substantially reproductively isolated from other conspecific population units, and 2) represents an important component in the evolutionary legacy of the species'. (Waples, 1991)

Synonyms

BSC (in part), ESC (in part; Mayden and Wood, 1995).

Discussion

The reliance upon criteria such as 'substantially reproductively isolated' and 'evolutionary legacy' incorporates attributes traditionally viewed as qualities of species from other concepts. It combines the isolation or mate recognition system of the non-dimensional BSC and RSC, and invokes the evolutionary lineage perspective of the ClSC, CSC, PSC, and ESC. These components are nothing more than the 'identities' of cohesive groups of organisms through time and over space, possessing their own independent evolutionary fate and historical tendencies advocated in the ESC. While the ESU has been proposed as a concept targeted at revealing 'distinct' populations within species (Waples, 1991, 1996), the distinction between 'distinct' populations and species as natural, evolutionary entities is not made clear.

Synopsis
This concept excludes known biodiversity, thereby unduly biasing our perception of process. Incorrect assumptions about diversity targeted for protection, brought about by misconceived formulations, only obstructs efforts to understand and preserve it. While basically a lineage concept, its emphasis on genetics and isolation preclude its use as primary concept (see Mayden and Wood, 1995).

19.7.9 Genealogical Concordance Concept (GCC)

> '... population subdivisions concordantly identified by multiple independent genetic traits should constitute the population units worthy of recognition as phylogenetic taxa'. (Avise and Ball, 1990: 52)

Synonyms
BSC (in part), ClSC (in part), PSC (in part).

Discussion
Faced with the impending abandonment of the BSC for the PSC, the GCC is asserted by Avise and Ball (1990: 46) to be from the 'better elements of the PSC and BSC'. They proposed that the general principles of the new concept 'derive most easily from the theories and observations in molecular evolution, but can also be applied to hereditary, morphological, behavioural and other phenotypic attributes traditionally studied by systematists' (page: 46). They noted three problems with the exclusive use of the PSC. These include: (1) the number of species depends upon resolving power of analytical tools available, (2) unless persistent extrinsic (geographic) or intrinsic RBs [reproductive barriers] are present different gene genealogies will usually disagree in the boundaries of 'species' under the PSC, and (3) shared ancestry in sexually reproducing organisms implies historical membership in a reproductive community.

The arguments generated by Avise and Ball (1990: 45) between the PSC and the BSC are deceptive; they build a strawman argument of the PSC and portray it inaccurately. For example, Cracraft (1983) never required monophyly of species, only that species be diagnosable. Furthermore, in no discussion by proponents of the PSC has it been restricted to uniparental species, or the possibility that eventually individual organisms will qualify as species under the PSC. Monophyly as part of the PSC was a criterion developed after Cracraft's hypothesis (de Queiroz and Donoghue, 1988; McKitrick and Zink, 1988) and well before the GCC. The GCC specifies at least two or more apomorphies of a species, while the PSC does not. The specification of at least two apomorphies is no less arbitrary than is the specification of one, three, or more. The PSC does not advocate that one can find apomorphies for almost every individual, any more than one would by employing the BSC. Thus, there is essentially no difference between the GCC and monophyly formulations of the PSC, criticized by these authors. Other problems associated with the GCC are those identified with PSC_1 or PSC_2. While the GCC is defined and titled as a genealogical characterization of species, the criteria used by Avise and Ball (1990) for species recognition actually range from monophyly to geographic concordance to genetic differences without relevance to genealogy.

Synopsis

Avise and Ball (1990) emphasize that a problem with the PSC is resolution with available tools. There is no question that this is a limitation, but this limitation extends to all operational definitions of species, including the GCC. Emphasis on **differences** relegates the GCC to a concept that ignores differences between primitive and derived attributes and uses diagnosability as an operational guideline. Genetic differences can exist with respect to plesiomorphies that provide no relevant information on genealogy, making this essentially a typological concept. The general philosophy promulgated in the GCC is largely inseparable from that of the BSC. Thus, the GCC adopts with it all of the misgivings of the BSC, making it inappropriate as a primary concept of species.

19.7.10 Genetic Species Concept (GSC)

> '... group of organisms so constituted and so situated in nature that a heredity character of any one of these organisms may be transmitted to a descendant of any other.' (Simpson, 1943)
>
> '... the largest and most inclusive reproductive community of sexual and cross-fertilizing individuals which share in a common gene pool'. (Dobzhansky, 1950)
>
> '... members of a species form a reproductive community. The individuals of a species of animals recognize each other as potential mates and seek each other for the purpose of reproduction... The species, finally, is a genetic unit consisting of a large, intercommunicating gene pool [and these] properties raise the species above the typological interpretation of a 'class of objects'. (Mayr, 1969: 23)

Synonyms
BSC (Grant, 1981), PhSC, MSC.

Discussion
This concept is similar to the morphological species concept except that the method used to delineate species is a measure of genetic differences, presumed to reflect reproductive isolation and evolutionary independence. As a phenetic concept genetic distances and similarities are used to identify different species. Genetic independence is assessed using methods varying from chromatography, to protein electrophoresis, to sequencing.

While apparently operational, one of the basic problems with the GSC is that for the vast majority of diversity there exists no genetic information. Because divergence for any particular gene may not be at a uniform rate, in all likelihood there will never exist a standard distance for species. This concept rests on the assumption that for every speciation event there will be particular changes in all genes. If the researcher examines 200 genes and they are all identical between two species they would be considered the same species. However, the next gene may show tremendous revolution between sister species as a result of the speciation event. One divergent gene out of 200 monoallelic genes will result in a trivial genetic distance. On a linear scale, such a divergence will be trivial to a species comparison where five of 20 genes are divergent. Yet, in this heuristic example both species pairs are existing as evolutionarily independent and genetically independent species.

Synopsis
The GSC is essentially a surrogate, operational concept developed out of the BSC. A particular degree of genetic divergence is assumed to warrant species recognition. However, this operational definition, lacks any guidance for researchers as to how much difference is enough? This is largely because divergence for particular genes or across multiple genes is impossible to predict either within or between taxonomic groups. Using this non-evolutionary concept researchers are also misled to believe that the lack of divergence in genes that are merely available because of technology negates the reality of divergence that may be present for any other characters. As such, the reality of species with divergent and heritable morphologies may be naively questioned if divergence at readily accessible genes or proteins is wanting. While this concept has served as a traditional method for identifying species it is fatally flawed as a primary concept. The general paucity of data, combined with the enormous genetic variability observed between sister species, the questionable validity of relying exclusively upon genetic divergence for species validation, and the deficiency of a phylogenetic perspective in interpreting variation precludes the GSC from serving as a primary concept.

19.7.11 Genotypic Cluster Definition (GCD)

'... clusters of monotypic or polytypic biological entities, identified using morphology or genetics, forming groups of individuals that have few or no intermediates when in contact'. (Mallet, 1995)

Synonyms
ASC, BSC, GSC, HSC, MSC, NDSC, PhSC, PtSC, PSC_1, SSC (in part), TSC.

Discussion
Mallet (1995) argues that a preferred alternative to the BSC is the GCD. While not stated directly, the GCD recognizes those clusters of monotypic or polytypic biological entities, identified using morphology or genetics, forming 'groups of individuals that have few or no intermediates when in contact'. This is a non-dimensional, polythetic, and phenetic concept of diversity serving largely as a surrogate of the BSC.

Synopsis
There are several evidential, philosophical, empirical and theoretical problems associated with this definition, precluding its use as a primary concept for species. Problems associated with the BSC, GSC, HSC, MSC, NDSC, PhSC, PtSC, SSC, and TSC hold true for this species concept.

19.7.12 Hennigian Species Concept (HSC)

'... involving tokogenetic relationships"; a (potential) reproductive community'. (Hennig, 1950: 45–46)
'... reproductively isolated natural populations or groups of natural populations [that] originate via the dissolution of the stem species in a speciation event and cease to exist either through extinction or speciation'. (Meier and Willmann, 1997)

Synonyms
BSC.

Discussion
This concept is a derivative of Hennig's (1950) earlier notion of species. It has been further developed by Willmann (1985a,b) and Meier and Willmann (1997). Importantly, however, the version advocated by these latter authors only incorporates some of Hennig's view of species. Their concept is an operational concept, and by their own admission, is 'identical to the biological species concept if absolute [reproductive] isolation is adopted as the criterion for contemporaneous populations, and the origin of the isolation of two sister species is used to delineate species boundaries

in time'. However, they do view this concept as different from the Mayr's BSC because 'he failed to provide a criterion that specifies how and when biospecies originate and cease to exist (if not by extinction)'. Intertwined in their discussion is the species concept issue and the significance of stem (ancestral) species. Logically following from this extreme version of the isolation concept (BSC) is that unisexuals are not species but are agamotaxa (*sensu* ASC), taxa not to be considered equivalent to bisexual species.

The HSC is rejected as an appropriate characterization of entities participating in speciation for many of the same reasons the BSC is rejected. The HSC should neither be employed for systematic questions nor issues of biodiversity. For some points, however, it is apparent that Meier and Willmann are more cognisant than Mayr of the fact that a concept of species is important to people other than just a 'cataloguer and curator of collections'. Thus, the HSC is characterized to be a dimensional concept to be used for allopatric or allochronic questions, and unlike the BSC, it acknowledges the importance of comparisons between sister taxa.

Synopsis

Regardless of any positive attributes over the BSC, the HSC is viewed as inappropriate for biological systems and developed out of a limited view of natural systems. Important problematic issues of this concept include the exclusion of some biological diversity, its relational nature, its heavy reliance upon operational criteria, its artificial advocation of isolation as a non-arbitrary demarcation of species, and its artificial contrivance of stem species.

19.7.13 Internodal Species Concept (ISC)

> '... individual organisms are conspecific in virtue of their common membership of a part of the genealogical network between two permanent splitting events or between a permanent split and an extinction event'. (Kornet, 1993: 28)

Synonyms

ClSC and HSC (in part; Kornet, 1993), PSC (in part).

Discussion

Formalized in philosophical and analytical detail by Kornet (1993), this concept identifies species solely on the basis of genealogical relationship. No criteria exist for conspecificity (e.g. morphological similarity, interbreeding) other than that species are mutually exclusive groups of organisms that derive from a permanent rift in genealogical connections. Permanence refers to separation of a lineage into two or more lineages that are never reunited by any level of interbreeding. This concept also precludes the origin of taxa via hybridization because such an event would terminate the independence of the lineages. While similar in some ways to the ClSC and HSC, Kornet and McAllister (1993: 64) advocate modified versions of each but admit that the concept has 'very limited practical value'.

Synopsis

The strict reliance upon permanent splits in genealogical networks, with no possibility for future exchange, and the non-acceptance of species of hybrid origin are unrealistic restrictions for a primary concept of species. Such a concept would eliminate many taxa that either maintain their independence through various mechanisms in spite of the fact that they freely interbreed with relatives or are divergent lineages of hybrid origin. This concept also confuses the phylogenetic lineages of species with the life spans of individual organisms in tokogenetic arrays, such that the death of one family unit would constitute a permanent split in the network and hence speciation. Thus, this 'concept does not approximate at all closely to our intuitions about the life span of species' (Kornet and McAllister, 1993: 64).

19.7.14 Morphological Species Concept (MSC)

> 'Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means'. (Cronquist, 1978: 15)
> 'Species may be defined as the easily recognized kinds of organisms, and in the case of macroscopic plants and animals their recognition should rest on simple gross observation such as any intelligent person can make with the aid only, let us say, of a good hand-lens'. (Shull, 1923: 221)
> 'The smallest natural populations permanently separated from each other by a distinct discontinuity in the series of biotypes'. (Du Rietz, 1930: 357)
> 'A species is a community, or a number of related communities, whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name'. (Regan, 1926: 75)

Synonyms

Classical Species Concept, Linnaean Species Concept, Morphospecies Concept, PhSC, TSC. (Sokal, 1973; Grant, 1981; Stuessy, 1990).

Discussion

This is probably considered the most sensible and commonly used method of species definition by taxonomists, general biologists, and laypersons alike. Because in the vast majority of situations involving allopatric populations little or no information is available regarding reproductive independence, morphological distinctiveness serves only as a surrogate to lineage independence. This concept also bridges a decided gap inherent in some other concepts between sexual and asexual species, so long as morphological distinctiveness is heritable and is representative of lineage independence. Given that humans are a vision-oriented species, it is readily appealing as an operational concept. Kornet (1993) considers morphology in its widest sense wherein 'similarity between organisms may thus be perceived in macromorphology as well as in gene-structure, and may range from shared "sets of independent characters" for classical taxonomists to shared "unique combinations of character states" for pattern cladists'. In this case, some may consider the MSC to be synonymous with the PSC_1.

The only real problem with a morphological concept involves instances of sibling or cryptic species, or the retention of plesiomorphic morphologies. Here, little or no morphological divergence has accompanied the acquisition of lineage independence and two or more different species may appear similar. In such cases a morphological concept of species will underestimate biological diversity. Another potential problem with this concept is the inherent tendency to require an arbitrary level of morphological divergence. By employing such a criterion the researcher assumes that all morphological traits, especially those traditionally employed in a taxon, evolve at a constant rate of divergence. This is an unjustified assumption and is falsified by the observation that even within a taxonomic group morphological divergence is largely random.

Synopsis
This is a non-dimensional concept that treats species as classes, defining them on the basis of particular essential morphological attributes. Possession of these essential attributes provides for membership in the species. As such it does not allow the researcher to treat species as historical entities forming lineages. As individuals, the definition of every species will necessarily change as the essential attributes of a species at t_1 will be different from t_2 through descent. While this concept has served as a traditional method for identifying species it is fatally flawed as a primary concept.

19.7.15 Non-dimensional Species Concept (NDSC)

Synonyms
BSC, GSC, MSC, Palaeontological Species Concept, SSC, TSC.

Discussion
Several traditional concepts of species qualify as NDSCs, the most popular being the BSC. Concepts of this type have limited spatial and no tem-

poral dimension of species in question. Thus, there is no evolutionary, phylogenetic, or lineage perspective with which one can view, perceive, or interpret descent of the taxa or their attributes (e.g. shared plesiomorphies or apomorphies, distances), including the ability or propensity to interbreed. Concepts of this nature may appear to be more operational than those incorporating temporal and geographic components. However, this convenience compromises both the accuracy and precision with which we are able to identify, quantify, and understand biodiversity. Finally, in this lack of accuracy we also lose our abilities to discover and understand the processes responsible for the evolution, functions, and maintenance of biodiversity.

Synopsis
Thus, while the non-dimensional species concept has been argued by some as a preferred operational concept of diversity, it has actually been a hindrance to the advancement of comparative and evolutionary biology. Concepts of this type should not be considered as primary concepts for species. Interestingly, in some areas of science (medicine) the non-dimensional concept has been perceived as grossly inferior to concepts incorporating spatial and temporal dimensions in discovering diversity (Paterson, 1993).

19.7.16 Phenetic Species Concept (PhSC)

> '... the species level is that at which distinct phenetic clusters can be observed'. (Sneath, 1976: 437)

Synonyms
BSC (in part), GCC (in part), GSC, GCD, MSC, NDSC, Palaeontological Species Concept, SSC, PtSC, TSC.

Discussion
This is a non-dimensional and strictly operational concept that may be likened to any concept where overall similarity is the primary criterion for the existence of species. Operationally, where variation in a set of characters is less within a group than between groups the entity is recognized as a distinct taxon. Species are treated as Classes under this concept; they do not exist as lineages and, if a species changes through descent, then the diagnosis will have to be revised.

Synopsis
While essentially the methodology employed by taxonomists, the barren theoretical nature of this concept precludes its use as a primary concept.

19.7.17 Phylogenetic Species Concept (PSC)

Currently at least three different concepts of species are identified as phylogenetic. These definitions represent an outgrowth of phylogenetic systematics and a general need among some researchers for an operational, lineage definition of species that is process-free. Some argue that with the growing popularity of phylogenetics it is critical to have a definition to identify the smallest units suitable for analysis (boundary between toko- and phylogenetic processes). For some, species is the smallest unit appropriate for analysis, and infraspecific units are inappropriate in this context (Nixon and Wheeler, 1990; Wheeler and Nixon, 1990). This same perspective holds that species diversity must be understood before a phylogenetic analysis is performed. Others defend the position that hierarchical patterns exist within species and phylogenetic methods are appropriate (de Queiroz and Donoghue, 1988, 1990; McKitrick and Zink, 1988).

Common to PSCs is an attempt to identify the smallest biological entities that are diagnosable and/or monophyletic. Species are thus the biological entities and unit product of natural selection and descent. Consequently, subspecies, fraught with ambiguities between convenience and naturalness, is not an appropriate evolutionary unit and has no ontological status (Cracraft, 1983; McKitrick and Zink, 1988; Warren, 1992). The different PSCs form three general Classes; one emphasizing monophyly, one emphasizing diagnosability, and one emphasizing both. Many similarities exist with the ISC, ClSC, CpSC and the PSC.

19.7.18 Diagnosable Version (PSC$_1$)

> '... a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind'. (Eldredge and Cracraft, 1980: 92)
>
> '... the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent'. (Cracraft, 1983: 170)
>
> '... simply the smallest detected samples of self perpetuating organisms that have unique sets of characters'. (Nelson and Platnick, 1981: 12)
>
> '... the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)'. (Nixon and Wheeler, 1990)
>
> '... the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states'. (Wheeler and Platnick, 1997)

Synonyms
ClSC (in part), CpSC (in part; Kornet and McAllister, 1993), GSD, ISC (in part; Nixon and Wheeler, 1990; Kornet, 1993), PhSC, PtSC, TSC.

Discussion
This Class of definitions emphasizes the *a priori* diagnosability of species, irrespective of a criterion of monophyly. There are two purported benefits of this perspective. First, process is not invoked before pattern is observed. Second, phylogenetic methodologies are argued to be applicable only to genealogical relationships of species and supraspecific taxa, not below the level of integration of species wherein tokogenetic relationships of infraspecific entities are the norm (*sensu* Wheeler and Nixon, 1990; Nixon and Wheeler, 1990). To conduct a phylogenetic analysis below the level of species would confuse the reticulate tokogenetic relationships with the usual non-reticulate phylogenetic relationships.

For proponents of this concept, monophyly, paraphyly, and polyphyly apply only at a level of organization above species. Species are delimited by the distributions of fixed, diagnostic characters across populations. Where variability exists in an attribute within the taxon this attribute is considered inappropriate for that level of analysis where only tokogenetic, not phylogenetic, relationships exist. However, the operation(s) necessary for the practical delineation of tokogenetic and phylogenetic relationships is not developed explicitly by those favouring this concept. Without knowing if you are dealing with one or more species *a priori*, one is not likely to know if phylogenetic methods are appropriate. Likewise, the difference is unclear between the theoretical inapplicability of phylogenetic methods in tokogenetic systems versus using the same methods for resolving relationships of species derived via hybrid origin. Both contain reticulate patterns of history.

19.7.19 Monophyly Version (PSC$_2$)

> '... a geographically constrained group of individuals with some unique apomorphous character, is the unit of evolutionary significance'. (Rosen, 1978: 176)

Synonyms
Apomorphy Species Concept (Wheeler and Platnick, 1997), ClSC (in part), ISC (in part; Kornet, 1993).

Discussion
For Rosen (1978, 1979) and de Queiroz and Donoghue (1988, 1990) species have reality if they are monophyletic and supported by autapomorphies. Any biological entity possessing a uniquely derived character, of any type,

magnitude, or quantity, qualifies as a species. Those not possessing autapomorphic attributes do not constitute a species, as traditionally viewed, but are referred to as metaspecies by some. The application of this concept necessitates a phylogenetic analysis. A lucid discussion is offered in papers by de Queiroz and Donoghue.

19.7.20 Diagnosable and Monophyly Version (PSC_3)

Synonyms
ClSC (in part), CpSC (in part; Kornet and McAllister, 1993), ISC (Nixon and Wheeler, 1990; Kornet, 1993), SSC.

Discussion
The PSC of McKitrick and Zink (1988) is a modification of the PSC provided by Cracraft (1983) but incorporates the criterion of monophyly for species. While a definition was not provided by McKitrick and Zink (1988), they identified a species as the smallest diagnosable cluster of individual organisms forming a monophyletic group within which there is a parental pattern of ancestry and descent. Because in this conceptualization all recognized monophyletic taxa are diagnosable, this definition, the methods for the discovery of species, and any associated practical and theoretical limitations are equivalent to aspects of the PSC_1 and PSC_2.

Synopsis
Several positive aspects of the phylogenetic concepts make them particularly attractive as operations in discovering biodiversity, and resolving some of the perceived problems with other concepts (Mayden and Wood, 1995). In all versions the PSC is an operational definition, whether one uses diagnosability or monophyly. The set of operations necessary to discover diversity associated with species are clearly outlined. The concepts incorporate the notion of lineage(s), making them appropriate for reconstructing descent and interpreting evolution of attributes. The ability to interbreed is viewed as a shared–primitive attribute and not of consequence in the recognition of species as taxa. These concepts also have the ability to recognize both biparental and uniparental species, and possess no implied modes of selection nor speciation. Finally, in the execution of these concepts there is no inherently arbitrary divergence or distinction between species or subspecies in a polytypic species (Cracraft, 1983; Warren, 1992); subspecies have no ontological status.

There are some problems with the use of these concepts and these are reviewed by Mayden and Wood (1995). However, while there are problems with the exclusive use of any of the Classes of the PSC, there are also important positive operational aspects to these concepts over some others. I concur with the conclusions of Warren (1992: 34) in that the PSC serves as an excellent operational surrogate to a concept of species not implicated with as many variables limiting our potential to discover biodiversity. Yet, none of the versions of the PSC should serve as a primary concept.

19.7.21 Polythetic Species Concept (PtSC)

Synonyms
BSC (in part), GCD, MSC, NDSC, PSC (in part), PtSC, SSC, TSC.

Discussion
This concept derives essentially from what philosophers call cluster concepts. That is, species are defined by the statistical covariance of characters deemed important. A given individual belongs to a particular species if it possesses enough of the important characters for the species. This statistical and practical definition treats species as classes, not individuals. Often, species are delimited by their possession of a unique combination of characters, and these are usually phenotypic. Most individuals of a species may possess attribute A, while those not possessing A will still have attributes B, C or D, all features also viewed as characteristic of the species. Treated as natural kinds, species are not viewed as lineages.

Synopsis
While this concept may serve as a very useful operational recipe for the delineation of species, especially in situations with complex patterns of variability of characters, it has no theoretical basis for being considered a primary concept. Because species are both individuals and lineages, their diagnoses will necessarily have to be modified over time as their diagnostic attributes become modified through descent.

19.7.22 Recognition Species Concept (RSC)

> 'A species is that most inclusive population of individual, biparental organisms which share a common fertilization system'. (Paterson, 1993: 105)

Synonyms
BSC (Mayr, 1988).

Discussion
This concept was introduced Paterson (collective writings in Paterson, 1993). It was developed from a dissatisfaction with the BSC, a definition considered inadequate and inaccurate of natural patterns or processes, and inhibiting progress towards related goals. For Paterson the biological limits to the field for gene recombination are determined by the mate

recognition system, more precisely, a specific mate recognition system (SMRS), a series of coadapted signals and releasing properties exchanged between partners through complementary systems. The system is functional across a broad array of conceivable signal-reception methods from elaborate behaviours, including chemicals and pheromones, to cellular recognition by gametes. This coadapted complex is maintained by strong stabilizing selection as long as the species inhabits its natural habitat; this changes when the natural habitat for the species (perhaps ancestral) is changed through geographic or temporal disjunctions. At this point the coadapted complex of signals exchanged between partners may become altered *via* directional selection in the new habitats occupied by the descendant groups of daughter populations (or species). Paterson (1993: 33) argues that 'a new SMRS, derived in this way, determines a new gene pool and, hence, a new species. According to the recognition concept, species are populations of individual organisms which share a common specific-mate recognition system. Species are, thus, incidental effects of adaptive evolution'.

The RSC does not invoke a major role for selection in the evolution of positive assortative mating, the development of isolating mechanisms, and does not require sympatry and evolutionary reinforcement to complete speciation. The fallacy that selection is responsible for producing adaptations that, by design, are responsible for the isolation of gene pools is obvious from the observation that in large part the documented cases of speciation are the direct result of total allopatry, a speciation model that does not involve secondary contact and/or reinforcement of isolating mechanisms (see Mayden and Wood, 1995). Thus, if isolating mechanisms are products of descent they are the result of chance rather than design.

The general question for the RSC is not what are the characters and mechanisms that have evolved in the recognition or reproductive systems of a species that prevents successful matings and resulting ontogenetic development between sympatric species? Rather, what are the characters and mechanisms that have evolved in species that ensure effective syngamy, development, and future generations within a population occupying its preferred or natural habitat? (Paterson, 1993: 33).

Synopsis

While there are important positive theoretical and applied aspects to this concept permitting the identification of species in a largely process-free environment, there are important problems with a universal application of the RSC. These include: (i) strict reliance upon and knowledge of the SMRS; (ii) lack of a lineage perspective; and (iii) exclusion of uniparental species and species with retained–primitive SMRSs. These are reviewed by Mayden and Wood (1985). Thus, the RSC should not be viewed as a primary concept of species.

19.7.23 Reproductive Competition Concept (RCC)

'... the most extensive units in the natural economy such that reproductive competition occurs among their parts'. (Ghiselin, 1974: 538)

Synonyms
BSC (in part; Ridley, 1989), Hypermodern species concept (Platnick, 1976).

Discussion
This is a non-dimensional and non-operational conceptualization of species. It is essentially limited to sexually reproducing species because of its focus on the intra- and interspecies competition for mates species. In its formalization, Ghiselin (1974, 1984a) likens species and evolutionary theory to firms, corporations, small businesses, craftsmen, etc. and economic theory.

Synopsis
The restriction of this concept to sexually reproducing organisms precludes its use as a primary concept of species. Should this restriction be eliminated, this concept could serve as a primary theoretical concept. However, competition for mates in reproduction is difficult to entertain for entities generally termed uniparentals.

19.7.24 Successional Species Concept (SSC)

Synonyms
Palaeospecies concept (Simpson, 1961), ESC (in part; Simpson, 1961), Chronospecies concept (George, 1956).

Discussion
This concept was devised as a surrogate for estimating divergence through time by researchers studying fossil taxa. Often these researchers have only fragmentary data both in specimens and through time to evaluate anagenesis and divergence.

In reality, the distinctions between successional species is an arbitrary delineation in time or strata based on divergent morphologies or gaps in morphologies or time. With anagenetic change within a lineage and only remnants surviving for study there is potentially an unlimited number of chronospecies throughout the history of what was once only a single self-integrating lineage behaving evolutionarily as a single species. The SSC is an operational concept, largely of convenience, to allow researchers of fossil taxa to communicate equivalent geological strata. Species identified using this concept should not be misconstrued as being biologically equivalent to species identified using most other concepts. This is not to say that there are not valid species that have been identified using this concept.

However, in general, palaeospecies are usually temporal forms of a single species' lineage. While Simpson's (1961) ESC did extend the non-dimensional BSC through time and provide much more of a lineage perspective to species, Simpson would argue for subdividing a single lineage into multiple chronospecies. The ESC of Wiley (1981) and Wiley and Mayden (1985, 1997), however, does not advocate chronospecies.

Synopsis
Because of the arbitrary and non-evolutionary nature of this concept it should not be considered a primary concept.

19.7.25 Taxonomic Species Concept (TSC)

> '... a species consists of all the specimens which are, or would be, considered by a particular taxonomist to be members of a single kind as shown by the evidence or the assumption that they are as alike as their offspring or their hereditary relatives within a few generations. When there is no evidence of the hereditary relationship, the taxonomist will rely on distinctions that have been found to be effective in segregating species among other [groups]'. (Blackwelder, 1967: 164)

Synonyms
ASC, GCD, MSC, PhSC (Sokal, 1973; Sneath, 1976), PSC (in part), PtSC.

Discussion
As described by Blackwelder (1967), 'these are the species of the taxonomist; they are not necessarily the species of the geneticist or the evolutionist'. This concept is probably used by most practising taxonomists as a working definition to segregate individual organisms in different taxa. It relies primarily on morphological attributes in the delineation of species because many other character bases have traditionally not been readily available to taxonomists. In practice, it is non-dimensional, treats species as classes, and lacks a lineage perspective.

Synopsis
The traditional character-based limitations for those in the field of taxonomy are less real in modern science. Many different types of characters are become increasingly more available and should be used in the delineation of taxa. However, given that humans are a vision-oriented species, the more convenient morphological attributes will probably remain the most used characters in deciphering taxonomic diversity. This truism, however, need not negate the existence of taxa identified using other types of characters (ecology, proteins, behaviour, sequences, etc.).

19.8 DISCUSSION

> 'An ideal species concept should meet the various intuitions that we have about species.... It is tempting to try to define a fully satisfying species concept which meets all the intuitions mentioned by somehow combining the definitions which address the different intuitive requirements. But part of the species problem originates in the fact that any attempt to combine [different] definitions into a more embracing concept, in which their criteria are given equal weight, is doomed to fail. This is because their criteria for conspecificity are incompatible; i.e., two organisms which are conspecific on the criterion of one concept are not necessarily so on that of another'. (Kornet, 1993: 29)
>
> 'To do justice to the intuition that species are historical entities, we required a species concept which defines species as entities with continuity in time between their origin and end'. (Kornet, 1993: 32)
>
> 'The species problem has often been approached with the presupposition that a single kind of entity exists in nature that corresponds to a species concept, just because the word 'species' exists in the language of biology. If this presupposition is dropped then the traditional species problem could be answered, at least in principle, by enumerating a heterogeneous list of the general characteristics that have been thought to bestow specific status to clusters of organisms'. (Wilkinson, 1990: 445)

In this discussion the following theories are taken as having reality in the natural world:

1. The notion of descent with modification is a unifying theory of natural sciences. Descent operates from kin-groups or populations to species as groups. Descent involves differential change in attributes or qualities originating through a variety of processes over time (generations) and space (geography).
2. Speciation results in the production of new species over time and space, a direct result of (1).
3. Classes have definitions, are spatiotemporally unrestricted, lack cohesion, and do not participate in natural processes.
4. Individuals lack definitions, are spatiotemporally restricted, have cohesion, and participate in processes.

There are at least five consequential factors that have fuelled the long-standing controversy over the species problem. These include: (i) a tradition of occupation; (ii) formalized rules of nomenclature; (iii) misunderstanding of terms; (iv) a persistent desire by humans for working definitions; and (v) the unique nature of those things that we hope to understand, i.e. species as taxa (or groups). Traditionally, the job of discovering and identifying diversity was left to the occupation of the taxonomist. For many of these researchers their responsibilities were viewed as finding different species and detailing attributes important for their identification (*sensu* TSC). In many ways this mode of operation relegates species as taxa to classes with essential features. While convenient for a user hoping to distinguish between the different things, this treatment ultimately leads to great difficulties with operationality and theory when species are known to participate in processes and evolve as either ancestors or descendants.

The formalized rules of nomenclature have reinforced the view of species as classes. The recognition of species requires not only their description and the designation of a type, but also its diagnostic features. For many, a diagnosis entails a listing of defining features, a prescription easily misunderstood as equivalent to essential traits. Thus, the operational necessity and emphasis on a diagnosis may be viewed as treating species taxa as classes. This, in concert with the traditional TSC, fosters great difficulties in the reconciliation of species as individuals.

This occupational and operational legacy has resulted in the confusion of the ontological categories classes and individuals (more recently Historical Groups). While some may view this aspect of the problem as purely metaphysical and without significant bearing on the issue, such a perspective is absolutely wrong and continually generates difficulties in resolving the controversy. As discussed herein, it is not merely an argument to distinguish between species as category and species as taxa. The delineation between classes and individuals is necessary, but not sufficient to resolve the problem. Species as taxa are individuals; species as category are classes. The former have no defining properties and can only be described; the latter can be defined through a series of desired properties for its members (species assigned to categories). Both diagnoses mandated by nomenclatural formalities and most species concepts treat species as taxa as if they are classes and immutable. In reality, they function only as operational guidelines or surrogate concepts for the discovery of those individual-like things that we think to be species. This exercise is of great necessity because the individual-type things are fuzzy and can only be diagnosed retrospectively. Most species concepts are functional constructs or definitions (class) employed link to our notion or concept of the species as taxon (individual).

19.8.1 Concepts and definitions of species and supraspecific categories

It is clear that the various categories used in biological classification are class concepts. In the way that we use these categories they are intimately linked to both theoretical and operational concepts. While there exists an infinite number of ways to organize groups of groups and assign them to supraspecific categories, the definition for Hennig (1950, 1966) and most others today is any historically formed group wherein the ancestor and all its descendants are included in a phylogenetic nexus, also known as monophyly. There is nothing operational about this definition; it is strictly a notion thought to be in harmony with the theory of descent with modification and our empirical observations of the end products of this process. Yet, most agree that while non-operational it is the appropriate theoretical concept for groups assigned to supraspecific categories. It is impossible to observe monophyly either historically or in real time because we do not witness the evolution of ancestors and their descendants, and the theoretical definition of monophyly provides no operational guidelines. Without direct observation, we are incompetent in our abilities to locate monophyly, unless we retain bridging principles through some type of operational concept. The concept that we now use as a suitable surrogate to monophyly is that of synapomorphy. That is, operationally we recognize supraspecific taxa or monophyletic groups through character analysis and the discovery of shared–derived characters inferred to have evolved in a common ancestor and retained or existing as homologues in immediate descendants. There are, however, other possible concepts of monophyly (e.g. percent similarity, ability to hybridize, etc.) that could be employed. These are rejected because of known inconsistencies between alternative concepts and empirical and theoretical observations of the real world. Families are no longer defined by a prescribed level of similarity greater than that expected of orders, but less than that of genera, because similarity does not always denote close relationship. Likewise, the ability to reproduce is an ancestral feature of lineages and is retained unless there is anagenesis of some attribute(s) closely linked to reproductive success.

Interestingly, the species problem can be seen to parallel the theoretical and operational issues traditionally associated with supraspecific taxa and categories. These separate problems are very similar if one is conscious of the ontological differences between species as taxa and species as category. Everyone has their own notion of what species as taxa really are. In many instances we use this concept to guide our perceptions, observations, and understanding about theoretical and empirical aspects of the natural world (diversity, character evolution, speciation, ecology, physiology, etc.). The class concept species as category used in the assignment of groups from nature thought to fit its definition. Is there, or should there be, a definition of species that is both theoretical and operational analogous to the relationship that exists for supraspecific taxa and categories? Should the concept of the species category be operational or should it be theoretical like the concept of monophyly for supraspecific groups? Either way, which concepts should be used? If operational, which of the available operations should be employed, if any? If theoretical, which theory should be used? Unlike the abundant discussions following from the long-standing issue of concepts and criteria for recognizing supraspecific taxa, there is limited discussion clearly focusing on these issues for species. To date, no progress has issued from the multitude of pages debating the species problem. It is my opinion that the difficulties associated with species in theory and species in practice derives directly from the conflation of these notions. Much to the disappointment of many, a coveted denouement in this long standing controversy will never follow until these questions are addressed with a sound metaphysical framework.

19.8.2 Evaluating concepts for important qualities

Hull (1997: Chapter 18) advocates a comparison of species concepts on three traditional criteria: theoretical significance, generality, and applicability (or operationality). I agree that this is an appropriately unbiased method of comparison. Herein, I regard applicability and operationality as separate criteria because a concept can be fully operational but not at all applicable to a problem, and *vice versa.* How do the various concepts fair in evaluations of these criteria?

(a) Theoretical significance

While difficult to measure across the various concepts, there are important theoretical differences between them. The most significant ingredient is the treatment of species as individuals rather than classes. Excluding the ESC, all concepts treat species as classes. Such concepts preclude sound interpretations of speciation, character evolution, etc. because species cannot be perceived as lineages. The deficiency of a lineage perspective eventually leads researchers to view all attributes and geographic locations of species as proximal and causal explanations. For example, if one of three taxa has an array of traits appearing intermediate between two other adjacent taxa, what explanation other than hybridization or introgression, could account for such a pattern? Phylogenetic intermediacy represents only one of several when species are viewed as lineages (Mayden and Wood, 1995).

(b) Generality

Several theoretical and empirical elements of species concepts, relative to species as taxa, may be considered under this criterion, including their tolerances of divergent lifestyles, modes of reproduction, modes of speciation, genetic exchange, distributional and character information, and finally, diagnoses. Not all concepts view evidentiary information pertinent to these elements equally. Informative comparisons of generality require some estimate of baseline diversity to be recovered, or things that we currently envisage as behaving like species. Tolerance limits for each concept must be compared with this baseline of diversity.

What is our working baseline of diversity? First, we know that species exist that encompass the entire gamut between sexual and asexual reproduction, with numerous intermediate conditions (Templeton, 1989). Numerous speciation modes have been hypothesized for organismic diversity, ranging from complete allopatry to complete sympatry (Wiley, 1981). Numerous examples exist wherein species exchange genetic information either in current communities or historical communities without condemnation of identities. In fact, some hypothesized historical genetic exchange between groups may be responsible for the evolutionary success of the involved groups, each going on to produce diverse clades (Mayden and Wood, 1995). Finally, the types of character information traditionally used to discover species is heterogeneously distributed across taxonomic groups. When viewed across all taxonomic groups all types of data from DNA and RNA sequences and similarity, to behaviour and ecology, protein variability, morphology, and other traits, are standard markers used to reveal species diversity.

Some concepts are basically intolerant of gene exchange between species and require sympatry before species can be validated (HSC, BSC, ISC, CpSC). Under the BSC, taxa in allopatry are sometimes considered semispecies. Because gene exchange is not tolerated, speciation via hybridization is also not a valid form of speciation under some concepts. Some of these concepts are also intolerant of uniparental reproduction. Some are intolerant of groups of individual organisms that may be paraphyletically related to one another relative to one or more descendants; that is, all surviving ancestral species (PSC, GCC, ClSC). Some usually only recognize species wherein there has been divergence at the morphological level (MSC, TSC, PhSC). Likewise, some demand divergence at the ecological (EcSC) or recognition system (RSC) level. One concept, the ESC demands only that speciation and evolution are natural processes involving lineages that maintain cohesion and have unique identities. The ESC has thus the greatest generality. All other concepts are less general and exclude real diversity.

(c) Operationality

This is one quality consistently argued in discussions of species, either implicitly or explicitly. That is, anyone should be able to follow a prescribed set of identifiable and repeatable operations and at the end of these operations be able to tell (with a certain level of confidence) if they have a species. The requirement of such an execution places limits on what is recognizable, defined by criteria of the operational concept. While this may be more convenient, convenience is not a criterion that should be optimized when attempting to discover and understand pattern and process in the natural world. Operationalism is a fundamental fault of any species concept adopting it. What is operational is determined strictly by the perceived reality of the viewer. If the viewer's senses perceive only a portion of reality and these are expressed in an operational definition of what reality consists of, then we will never know otherwise. If, however, the viewer is capable of perceiving or conceptualizing all of reality, then all of diversity can be discovered without placing limits on what can be recognized with an operational concept. For instance, it is a mistake for someone who is red–green colour blind to mandate a concept of species based on the operational criterion of colour. Anyone discussing species diversity of hummingbirds, flowering plants, or darters, with this person would continually be frustrated with what is reality.

Excluding the ESC, all of the other concepts are operational at some level. That is, with all of them one can conduct certain experiments and extract pertinent information about the criterion emphasized. Some are more operational than others but with this increasing operationality one necessarily sacrifices an ability to account for diversity. For example, the ASC, MSC, PhSC, SSC, or TSC are probably the most operational concepts guiding the discovery of species. These concepts, however, will necessarily exclude equally valid species that can and will be recognized using other concepts. The next most operational concepts would include ClSC, CpSC, EcSC, GCC, GCD, NDSC, versions of the PSC, and RSC. The BSC, HSC, and RCC are all minimally operational. The ESC is unique in not being an operational concept, a consequential quality for a primary concept. Nothing in the ESC, other than evolution produces species as lineages with identities and cohesion, is operational; this, however, is extremely difficult to apply without bridging principles.

(d) Applicability

Given that the various concepts were all formulated from research on patterns of diversity across a diversity of temporal and geographical situations using varied technologies, each attempting to unveil processes associated with descent, they are all applicable as concepts of species as taxa. However, applicability extends from those having lesser applicability and embracing only a subset of natural diversity, to those with greater applicability wherein the concept embraces most or all of diversity. The ESC has the greatest applicability because it is consistent with and embraces all known species diversity that has evolved through currently understood processes descent. All other concepts have lesser applicability because as class constructs they are capable only of embracing a lesser portion of natural diversity by excluding some forms of species (e.g. asexuals, ancestors, etc.).

19.9 HIERARCHY OF CONCEPTS: SPECIES IN THEORY AND PRACTICE

When Mayr (1957) discussed species concepts and definitions, he mentioned – but did not dwell on – a need for two different levels of concepts for species, these being primary and secondary concepts. 'All our reasoning in discussions of "the species" can be traced back to the stated three primary concepts. As concepts, of course, they cannot be observed directly, and we refer to certain observed phenomena in nature as "species", because they conform in their attributes to one of these concepts or to a mixture of several concepts. From these primary concepts, just discussed, we come thus to secondary concepts, based on particular aspects of species' (Mayr, 1957: 16).

As primary concepts, Mayr is referring to the typological, second and third species concepts discussed in that paper. From the discussion it is clear that he recognized that all species as taxa would fit one or a combination of these concepts, but that secondary concepts are those used to identify species and employ differences in morphology, genetics, behaviour, etc. to infer diversity consonant with primary concepts. It is unfortunate that more scientists from all disciplines had not read this passage in 1957 and bequeathed this philosophy to their academic descendants.

As fundamental links bridging observable patterns and inferred processes, concepts are employed in every discipline, assisting to guide our understanding, perception, and disclosure of natural systems. Given that descent with modification and speciation are undeniable processes of diversification and that individual species are the highest level of organization capable of participating in these processes, a monistic notion of species is not only natural but is logical. Descent and speciation are processes occurring in lineages. Individual organisms to populations, each with spatiotemporal cohesion, and only lineages with this type of integrity uniquely participate in speciation. A primary concept of species is fundamental to the whole of biological sciences, particularly for understanding species as taxa. Currently, the multiple concepts in operation are decidedly inconsistent with one another as to what constitutes diversity (also see Hull, 1997: Chapter 18) and most are inconsistent with the range of diversity acknowledged as species in different disciplines. Without a primary concept as a working hypothesis and to serve as a bridge between pattern and process, it is untenable that we can advance on many fronts. Heretofore, much of our effort has been expended struggling with the conceptualization of species. Many adopt only operational concepts that will produce contrived species diversity; unfortunately those searching for pattern and processes associated with this diversity may be deceived.

What then are the criteria we should be looking for in a primary concept? It should be consistent with current theoretical and empirical knowledge of diversification. It should be consistent with the ontological status of those entities participating in descent and other natural processes; that is, species as taxa must be referenced as individuals. Finally, it should be general enough to encapsulate all types of biological entities considered species as taxa by researchers working with supraspecific taxa. Only the ESC is suitable as primary concept, guiding our quest for species as taxa and our search for natural order. This concept is robust theoretically and is unique in its global generality. One drawback is that it is not operational. While this may be viewed as a possible shortcoming, it is not so for a primary concept. The ESC is maximally applicable because everything we currently understand about descent, speciation, and species are compatible with the intent of the ESC.

While the ESC is the most appropriate primary concept, it requires bridging concepts permitting us to recognize entities compatible with its intentions. To implement fully the ESC we must supplement it with more operational, accessory notions of biological diversity – secondary concepts. Secondary concepts include most of the other species concepts. While these concepts are varied in their operational nature, they are demonstrably less applicable than the ESC because of their dictatorial restrictions on the types of diversity that can be recognized, or even evolve. However, they serve as surrogates for the ESC and, together, further our understanding of descent, both anagenesis and cladogenesis, by recognizing any entity consistent with the primary concept. They represent the practical or applied definitions, guidelines, or tools, used by investigators to discover hypothesized real particulars, entities, individuals, or things that we accept as species. These secondary concepts can account for nearly all species diversity, with the possible exception of ancestral species, either surviving or extinct. Because the ISC and SSC are both capable of delineating diversity beyond real species, these definitions must be used with caution.

Together, the primary and secondary concepts form a hierarchical system displaying both their operational and theoretical inter-relationships (Figure 19.1). The primary concept is the ESC. Relationships among the secondary concepts may be envisioned in multiple forms; I have illustrated only one such system. The one criterion emphasized most throughout discussions of secondary concepts is sex. I have chosen to use this as a first level criterion among secondary concepts. Reproduction, similarity–dissimilarity, monophyly, diagnosability, apomorphy, and tolerances for gene exchange are other criteria used to further reveal relationships among secondary concepts (Figure 19.1). Some concepts (BSC, GSC, RCC) terminate at multiple locations in the hierarchy either because of different uses or ambiguities in the concepts. However, this is acceptable and one may view other concepts as having similar results.

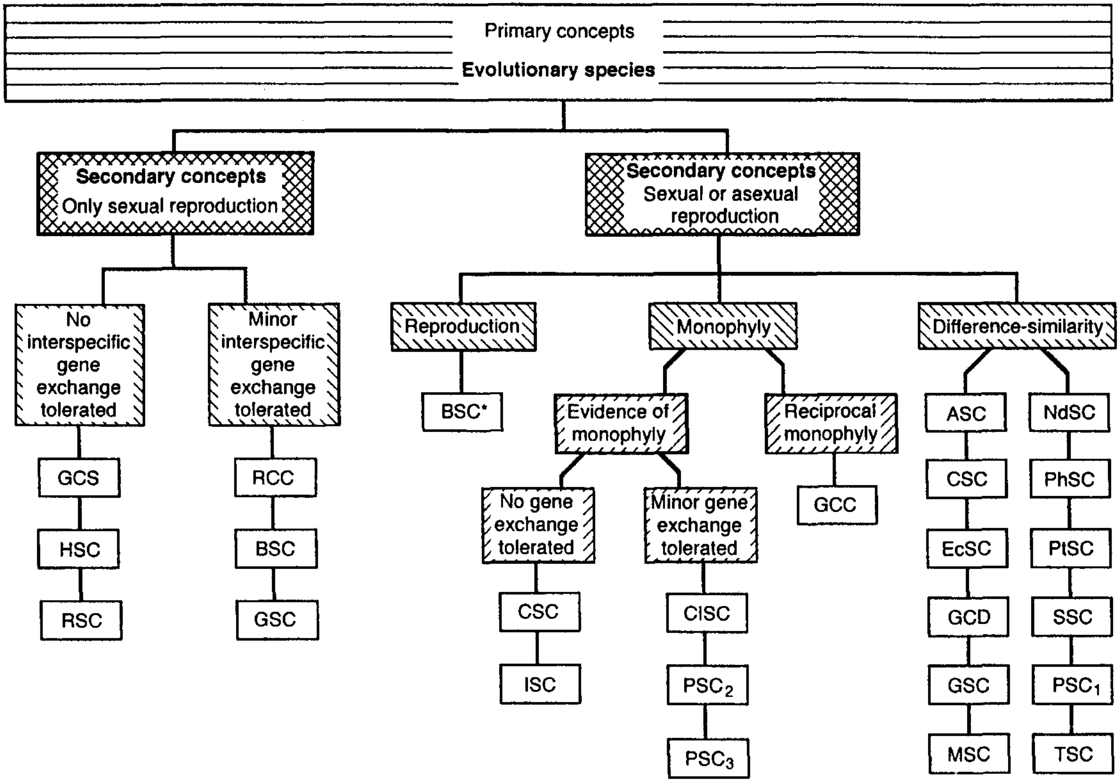

Figure 19.1 A hierarchy of primary and secondary species concepts. The non-operational Evolutionary Species Concept serves as the primary concept of species. The operational secondary concepts form a hierarchy below this primary concept based on their tolerances or requirements for modes of reproduction, gene exchange, monophyly, and diagnosability. Because some concepts represent hybrid versions of other concepts (mixed criteria) they may be depicted more than once in the hierarchy. Species concepts are listed alphabetically within any grouping. Asterisk denotes a version of BSC modified for asexual species. See Table 19.1 for concept abbreviations.

There are extraordinary advantages to accepting the premise of monistic primary and pluralistic secondary concepts of species. First, a primary concept of species that can be continually evaluated in light of new information ensures that all things behaving as species are potentially recoverable, given unavoidable constraints associated with available technology and extinction of taxa never observed. Second, with the possible exception of the ISC and SSC, all currently employed secondary concepts theoretically compatible with the primary concept can be mutually applicable in the discovery of species and the elucidation of pattern and process. While some concepts conflict in their intentions, they are all equally valid. When viewed together as guidelines in the detection of species they ensure that natural species diversity is neither unrecognized nor misunderstood. Thus, patterns observed in the natural world can be used by all disciplines to reveal natural processes in an uninhibited manner.

Our classification system for supraspecific taxa is analogous to the outlined system of primary and secondary concepts of species. Classifications are theories about the organization of biological diversity. What groups should be placed in the various supraspecific categories, and how and why should just these groups be recognized over other possible groups? One may choose to optimize various information in a classification, from overall similarity, ecological guilds, or modes of reproduction, to genealogical relationships, just to mention a few. In the current system the concept adopted for supraspecific categories is a particular genealogical relationship, specifically monophyly. Other criteria have been rejected as primary concepts because of ambiguity, inconsistencies or artificiality. Thus, we employ monophyly as a primary concept to bridge to natural groups in the classification of supraspecific taxa. Because we are unable to observe descent we adopt secondary concepts or definitions, particular homologies compatible with the intentions of the primary concept. Through character evaluation secondary concepts permit the organization of diversity into such groups. Inferences derived from phylogenetic systematics can either corroborate or falsify hypotheses of groups suspected to meet criteria outlined in our primary concept monophyly. That is, a secondary, operational concept, the discovery of synapomorphy, permits continual re-evaluation of monophyly of groups and our theory of descent represented through our classification. This is all done within the context of a theory that there is a history of descent, that characters are modified and inherited through this descent, and that pattern and process is recoverable. Here we have a primary conceptual basis for the type of supraspecific taxa that we wish to recognize in classifications. This concept is necessary and sufficient in our search for them. The concept of monophyly, like the ESC, is applicable but is in no way operational. Secondary concepts for both species and supraspecific categories are requisite in our discovery of species and supraspecific groupings, respectively.

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