

SPECIES CONCEPTS

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Introduction and Scope of this Summary

Since this Species Concepts presentation in October, I have attempted to distill a few key ideas of what was enthusiastically debated and presented, and incorporated more detail that time precluded being said then. As with the evolution of lineages, time has not stood still since the afternoon these ideas about species were discussed. The stance is even more partisan. As my argument on the species debate has consolidated even more so on the Evolutionary Species Concept (ESC); and I have not shied away from these developments in these few pages. I have not followed the flow of the seminar precisely, but rather tried to present a summary and overview of the species problem, the solutions, and the way forward. Obviously, much more remains to be discussed, and refined! In particular, there is no substitute for reading the key literature, of which there's indeed a great deal. Kluge (1990), Frost *et al.* (1992) are key and illuminating summaries that one benefits from reading closely, and then reading again and again. Above all, nothing beats applying species theory to real specimens and populations.

This seminar tackled a very broad topic covering many complicated issues; in which the source of their understanding lies largely in the realm of metaphysics. The importance of the "Species Problem" has been repeatedly raised both informally and formally within BFA. Attention to the multifaceted issues as to what the species category is, and how species are characterized has waxed and waned for decades. The temperature of the debate is currently at an apex; for the arguments have increased in content and thus scope (and volume too!) since the mid 1980s. The audience and contributors has grown and diversified to include many new protagonists. This is for the following major reasons:

1. *Philosophy of Science and Philosophy of Biology*. The spread of an historical philosophy through biology. This began in the 1960s in biogeography, and especially in the development of phylogenetic systematics - using the methodologies and philosophies of cladistics, inaugurated by German entomologist, Willi Hennig (see below). The species problem is a topical issue in the philosophy of science, feeding a cottage industry of debates. An important aspect and parallel development has been dissatisfaction with the Neo-Darwinian synthesis, which is centred on the BSC (Biological Species Concept) as the multidisciplinary definition of the species category;

2. *BSC and the Neo-Darwinian Synthesis of Evolutionary Biology*. Criticisms of the Neo-Darwinian synthesis of evolutionary biology have been many and diverse. An important axiom of the synthesis has been its apparent dependence on the Biological Species Concept (BSC) which emphasizes that species are reproductive communities. This idea dovetailed rather nicely with the theories and practices of population genetics and classical community ecology. So much so that Brooks & McLennan (1999) distinguish the heyday of this period (1960s to 1970s) as forming an 'eclipse of history' from biology. The idea that species might have a time dimension (as lineages

namely) did not get much attention, if any. So certain very useful ideas about species proposed by evolutionary biologists soon after World War II, notably G. G. Simpson, have had to await wider appreciation only in the 1990s.

Dissatisfaction with the BSC has been widespread and growing since the early 1980s. The BSC was never popular with botanists and microbiologists. It seems that something resembling a morpho-species concept has persisted and persists in the latter disciplines since the 19th century. One should not forget that Mayr and Dobzhansky and colleagues pushed biological understanding forward a great deal. Notably, the Synthesis finally grappled with typological thinking that can be traced back to the Ancient Greeks. The forgers of the Synthesis recognized that populations vary; and population-thinking spread through and structured taxonomic theory. This rediscovery of what Mayr came to term population-thinking vindicated Darwin's philosophy nearly a century after the *Origin of Species* was published.

3. *The "Cladistics Wars" in Systematics.* By the end of the 1970s, the school of cladistics (phylogenetic systematics) had won out over that of phenetics, as the superior scientific methodology to classify biodiversity. The ideal of the phenetists had been to classify organisms using comparisons of their overall similarity. Cladistics, founded by German entomologist Willi Hennig, argues that classifications must reflect true phylogeny. The third school, evolutionary taxonomy, took a more ambivalent view being a mixture of phenetics and phylogenetic approximation (apparently). Each of these different philosophies have coined their own species concepts. As detailed below, the Phylogenetic Species Concepts (PSC) are a direct result of tree-thinking (*sensu* O'Hara 1997 - the term for the philosophy underpinning phylogenetic systematics). Criticisms of the synthesis have dovetailed with the spread of an historical philosophy through biology. Its most pertinent aspect has seen the advocacy and adoption of ideas emphasizing the temporal dimension of the lineages that form species. In hindsight, and as detailed below, the Evolutionary Species Concept (ESC) introduced by palaeontologist G. G. Simpson in the mid 20th century was proposed decades before a critical mass of biologists acknowledged that history matters a very great deal in biology. Brooks & McLennan (1999) term this period that saw (and in fact is seeing) cladistics and tree-thinking spread through systematics as "Eclipse of the Eclipse" - breaking down the hegemony in which the NeoDarwinian Synthesis fathered an "Eclipse of History" in biology.

4. *Biodiversity Crisis.* Concern over species extinctions has injected an urgency and wider appreciation by society of the importance of systematics and taxonomy. Conservation biology has come to realise how critical sound taxonomy is to far reaching decisions over the future of biota. Biologists have to know what they are working with; and this especially applies to biodiversity prospectors and biotechnologists - if they want to know where exactly they discovered that new biocontrol agent or wonder drug. It especially matters what species concept we use to identify such organisms. Not only billions of dollars are potentially at stake but humans' futures. As Cracraft (2000) has emphasized, the exigencies on accurate and precise taxonomies of organismal biodiversity have never been greater.

5. *A Unified Nomenclature for Linnaean Taxonomy.* The burgeoning attention to biodiversity (extending across the three Domains of Life) has brought unprecedented demands for a unified codes of taxonomic nomenclature. Up to now, botany, microbiology and zoology have named species and higher taxa independently according to the own rules and quirks of their respective codes. Since the 1980s, there have been calls to unify these three codes of taxonomic nomenclature (Hawkesworth 1994). While welcomed as a logical step forward to a unified biology, it has also generated great angst in some quarters of biology. A unified code will obviously hinge on a universal concept of the species category. We need a species concept that accounts precisely and accurately for the organismal diversity across all three Domains - vertebrates, plants, microbes, all of the invertebrates, and fossils too.

6. *Phylocode.* A development even more radical than that of a unified taxonomic nomenclature is grounded in dissatisfaction with deficiencies of the Linnaean system of taxonomy in characterizing biodiversity accurately; there have been recommendations for its complete replacement (De Queiroz & Gautier 1994; Ereshefsky, 2001; Pennisi, 2001). The deficiencies of the Linnaean system are more serious than many realize, and the system has been patched and stretched as to be unrecognizable from the ideal Linnaean system that its protagonists believe they are defending. There are recent and credible suggestions in the form of a Phylocode to provide a phylogenetic taxonomy that maps phylogenetic patterns accurately with respective unique phyla (Cantino *et al.* 1999). The battle lines have been drawn in this debate, whose underlying aim is for an optimal replacement for the Linnaean system. Here again, a universal species concept is a prerequisite for the Phylocode.

Philosophical Foundations

Species are individuals, not classes. This means that an organism is a part and not a member of a species. This metaphysical foundation of the species category leads to some interesting and perplexing caveats. Notably, the identity of a species lineage persists even though there is a turnover or flux of organisms through time; and episodes of hybridization similarly do not alter its identity. An organism is a more familiar example of an individual. An organism, such as any dung beetle (call him Horace) maintains his identity from the formation of the zygote to adulthood. Horace looks very different through his life history, as egg, grub, and adult. The key to the persistence of Horace's individuality are the unbroken cell lineages through the insect's life. Likewise, a species persists because its populational lineage does. Yes, history really matters in biology.

Species comprise lineages that have formed from the more-making activities of constituent organisms. Analogously to an organism, each lineage has a life history; such that cell lineages in an organism are analogous to the populational lineages (comprised of organisms) that make up species. A species originates as a neospecies: budding off from an ancestral lineage and either goes extinct or persists. Only diagrammatic renditions of these and related ideas can describe these properties of the species category adequately (see Harrison 1998; De Queiroz 1998, 1999). Some people might term a neospecies (or budding lineage) a subspecies, or incipient species. The most ardent proponent of the subspecies concept, Ernst Mayr (1982 - see Frost *et al.* 1992), admits that subspecies are merely a means of sorting museum specimens in storage. The subspecies concept

has also reappeared in the guise of the phylogroup (Avice & Wollenberg 1997), but the same problems, and more, apply to this typological concept (Klicka, & Zink. 1999).

Most alarmingly, infatuations with notions of incipient evolution and prospective reproductive isolation runs counter to the fundamental goal of systematics, namely to discover and describe patterns of evolutionary history. The resultant taxonomies are maps or descriptions of these elucidated patterns. Attempting to predict the future properties of living entities lies in the realm of astrology etc. In this vein, it is noteworthy to recall that the BSC purported ability to predict reproductive isolation is maintained as its key scientific strength! In a similar vein, little, if I recall correctly, was said about subspecies during the seminar. Well, until someone comes up with a scientific definition of the concept, the subspecies concept will continue to be abused and ridiculed. Frost *et al.* (1992) neatly disposed of any scientific credibility of the subspecies concept. I am amazed that some taxonomists still employ it.

Species cannot be defined, but their existence can be discovered - evidence permitting. Again, this distinction is critical and prescribes how biologists can operate in characterizing species. The reason for it lies in the historically derived properties of species and monophyletic phyla being individuals. (This axiom was revisited several times during the seminar, notably in response to questions from AG and JT.) It is no mere affair of semantics. Elucidation of real species requires a taxonomist use all the evidence he or she has to hand. This can be genetic, behavioural, coevolutionary data (e.g. mutualisms and specific parasites) to compare whether or not sampled populations represent one or more species.

“All true classification is genealogical; that community of descent is the hidden bond which naturalists have been unconsciously seeking, and not some unknown plan of creation, or enunciation of general propositions, and the mere putting together and separating of objects more or less alike” (Darwin, 1859:420)

The Consilient Solution to the Species Debate

The answer to what is long-agonized-over problem “What is the universal concept of the species category?”, I term the “Consilient Solution”. The Consilient Solution not only provides biology with a universal species concept, but even more importantly empowers biologists to discover and characterize species. The ‘consilient’ label refers to how the same solution as been converged on from different starting points through independent processes of discovery about the properties of the species category and species. These solutions are not only complementary but mutually reinforcing (Cotterill *in press* a,b). Perhaps even more significantly, several of these papers have tackled very different parts of biodiversity (nematodes and vertebrates, for example). The essence of the Consilient Solution to the species problem distinguishes and agrees on the following points:

1. Species, whether comprised of asexual or sexual organisms, are segments of populational lineages, whose existence forms a trajectory through space and time;
2. There are theoretical (primary or non-operational) and operational (secondary or practicable) species concepts, This point appears to have been first emphasized by Mayr (1957) and then ignored (especially by Mayr himself) until resurrected by Mayden (1997);

3. Only one species concept comes anywhere near approximating all the heterogeneous properties of the species category. This is Simpson's (1951) Evolutionary Species Concept (ESC) - amended by Wiley (1978).
4. All other species concepts are secondary to the ESC, and we can employ them to evaluate lineages, and so discover evolutionary species. The methodology is to test whether or not two or more extant populations represent a single populational lineage;
5. The theoretical supremacy of the ESC has been consistently arrived at by several authors: including Brothers (1985), Brooks & McLennan (1991, 2000 *in press*), Frost & Kluge (1994), Wiley & Mayden (1995), Mayden (1997), Adams (1998), and Wiley & Mayden (2000). The recognition that species are lineages has been formalized by De Queiroz (1998, 1999), and his conclusions mirror those of Mayden (1997);
6. In fact, De Queiroz (1998, 1999) went further by emphasizing that operational species concepts are better termed species criteria, as each has a complementary function in distinguishing between different properties of lineages. For example, the PSC picks out divergence; the RSC (Recognition Species Criteria) cohesion; and the Genealogical Species Concept (GSC) (Avice & Ball, 1990) genetic coalescence.

Use of the ESC is spreading in herpetology and ichthyology. It has penetrated ornithological taxonomy more successfully than many would believe. Contemplation of the well known arguments over the PSC versus BSC (e.g. Zink 1996) reveal that what is at stake is a non historical versus historical philosophy of biology, and the avian species characterized by the PSC are actually evolutionary species. R. M. Zink (*in litt.*) recently admitted as such...“that the PSC is the operational analogue of the ESC”. All these “new” phylogenetic species of birds are merely evolutionary species!

On a different tack, the ESC is equally applicable to asexual populations. In addition, the Ecological Species Concept (EcSC, Van Valen 1976) can identify discrete lineages that have persisted through ecological selective pressures (Ereshefsky 2001).

It is interesting that mammalogy is one of the last bastions of the BSC, where it seems that the trend has been to try and ignore the debate and historically grounded revolution in microtaxonomy that began in herpetology and ornithology in the 1980s! The forthcoming 3rd edition of *Mammals of the World* is adopting “a more phylogenetic viewpoint” (D. E. Wilson pers. comm.), and a draft of the chapter on Chiroptera now recognizes an additional 110+ species to those acknowledged to exist (using the BSC) by Karl Koopman in 1993. Groves (2001) also acknowledged that the PSC is the operational analogue of the ESC, but remarkably persisted to employ trinomials for a revision of the world's extant primates! The ESC (with PSC and RSC as operational criteria) has proved essential to decipher the real species diversity of Afrotropical bovids and bats (Cotterill 2001a,b; 2002, *in press* a,b). So it appears that expurgation of the BSC from mammalian taxonomy has begun. The most positive attribute of this revolution is the replacement of a non-historically based taxonomy with that grounded intrinsically in the philosophies and methods of historical biology.

Compared against the ontological scope of the ESC, other species concepts fail to accommodate the species category in all its entirety; and some of these are of little use in any secondary role in

helping a taxonomist discover and characterize a species. Their failures hinge on being unable to conceptualize historically derived properties of lineages. It may strike many biologists as remarkable news that one notorious failure is the BSC. Being prospective, it does not consider any historical aspect of lineages; and any test it purportedly enables of reproductive isolation are far more ably conceptualized and framed by the RSC (better employed as the Recognition Species Criterion, or Cohesion Criterion). The latter frames comparisons of characters of organisms to evaluate whether a lineage has evolved a distinct SMRS. Contrary to what many authors (e.g. Mayden 1997; Ereshefsky 2001) have concluded, the RSC differs fundamentally from the BSC. The BSC is prospective; the RSC is retrospective. An SMRS and with it reproductive isolation are historically derived products - incidental products of evolution for successful syngamy in sexually reproducing organisms.

"Rather than getting over the species problem, we need to get over the inclination to obliterate history by changing the names of historical entities whenever reticulation or, as is more often the case, limited exchange or donation of parts has been detected or inferred."
(Zink & McKittrick 1995: 711)

Practical Examples

Two examples were used to try and interface this theoretical stance with real biodiversity. Both used recent research on African bats and bovids. A CVA - Canonical Variates Analysis (or Discriminant Function Analysis) for *Damaliscus* (tsessebes) specimens plotted the results of analysis of 12 variables in terms of 2 CVA's (Cotterill *in press a*). The point of this example was contrary to the time-honoured phenetic analysis of overall similarity. Rather, the use of these multivariate statistical methods is to test whether or not these populations of antelopes are significantly different. The discovery that they do indeed differ, suggests beyond reasonable doubt that we are dealing with two divergent lineages. In clear-cut cases, one character may be sufficient to distinguish two divergent populational lineages. This methodology is basically employing the rationale of the PSC to discover species. Here, the PSC has discerned an evolutionary species, in this case the Bangweulu Tsessebe, in terms of its dichopatry (see Cracraft, 1984) and morphological distinctiveness (Cotterill, *in press a*).

Species Concepts and Errors in Classification

Type I, II, and III errors. I am not going to try and summarize and explain the attached figures, as they are based on detailed discussion by Adams (1998), who provides a far better argument than I feel capable of mustering. The explication and avoidance of these errors places a priority on accurate and precise taxonomies. Here again, one's choice of species concept is critical. Note how the superspecies concept (a massaging of the BSC - which has been very popular with many vertebrate taxonomists) fails miserably to correctly classify these duikers. Incidentally, a phylogeny for selected *Cephalophus* was published a couple of months back (by Jansen Van Vuuren & Robinson 2001) and came to my attention only after presenting this seminar.

Here, precision (degree of detail) pertains to whether the real species are characterized; while accuracy (correctness) refers to whether or not one classifies species correctly with respect to their evolutionary relationships, and thus phylogenetic uniqueness. The scientific costs of errors in

characterizing species centre on describing too many or too few (Type I and II errors, respectively). A now entrenched criticism of the BSC is that it misses species, and invariably lumps lineages into non historical groups (see Frost *et al.* 1992; Zink & McKittrick 1995 among others). Incorrect taxonomies also arise through inaccurate constructs (and depictions) of phylogenetic uniqueness. Type III errors afflict many taxonomies, especially of vertebrates. Mammalogy is rife with these problems, as depicted in lumping Hook's Duiker (*Cephalophus hooki*) as a subspecies of the Black-fronted Duiker (*C. nigrifrons*). These failures to characterize phylogenetic uniqueness precisely are insidious in being harder to detect. Here, I use accuracy to denote characterization of the actual number of species that have evolved in a clade; while precision refers to whether or not one classifies them correctly. An example of a Type III error is the failure of the superspecies concept to discern the phylogenetic uniqueness of the duikers in the illustrated example. Note how Peters' Duiker, *Cephalophus callipyrus*, was erroneously lumped into a superspecies alongside a suite of red duikers. Contrary to popular belief, the superspecies concept (whether trying to employ the vague concepts of semispecies, allospecies, or megasubspecies) does not overcome inadequacies of the BSC. In fact, it compounds inaccuracies, because it confers a false sense of "taxonomic security".

So to emphasize, it is not sufficient to just avoid Type I and II errors, such that you diagnose the correct number of species. A correct phylogeny, therefore avoiding a Type III error, is equally critical. So the point to remember is that phylogenetic uniqueness really does matter, and only one species concept (the ESC), among the many suggested, comes anywhere near coping with temporal dimensions of species lineages. Only the ESC comes anywhere near characterizing the real diversity of the duikers depicted in Fig 4a.

Uncertainties and Conclusions

The more I have read and interacted with working biologists, the more convinced I have become that the most commonly used species concept employed routinely in biology (on a day to day basis) is some variant of an idea of a morpho-species. Too few consider the theoretical underpinnings and goals of what taxonomy is trying to classify; and equally fail to appreciate how the historically properties of organismal biodiversity constrain the options for species characterization.

Debates over what species are, and how biologists go about characterizing them seem set to rage on and on. My personal conclusion is that little new has been added to the philosophical and theoretical aspects of the debate since the early 1990s, albeit earlier ideas have been refined and interfaced. This rehashing of decades-old ideas, and especially progress in their refinement and consolidation, has been masked by considerable hyperbole and woolly thinking about the ontology of biodiversity and epistemology of biology. Latterly, the Consilient Solution has revealed that we actually have had a universal species concept since the mid 20th century. It is only very recently that our understanding of the ESC has been refined sufficiently so we can now use it practicably. It is far more challenging and important to get on with the practical issues of charting the biosphere. The central theoretical and operational problems about species characterization have been solved over the past decade; biologists now need to get to grips with biodiversity and actually describe a lot more species. Only then can theory be tested with real data. Perhaps, we might then have to face up to the problems that really are no evolutionary species of microbes, slime molds and protozoa.

Beyond the species debate, there is a far more disquieting and challenging problem for comparative biology. This is the demands to define and objectively articulate what characters are. An important aspect of the character debate dates back at least to arguments about the concept of homology in the early 19th century, if not earlier. In part, cladistics smoothed brows furrowed from trying to understand the concept of homology (and also homoplasy); now the problem has swung back with a vengeance in developmental biology, with agonies in trying to understand and refine the character concept, and a swelling debate over the ideas of homologous genes, biochemicals, and subcellular structures. Very rapid progress in genomics and molecular biology catalyse this debate, and have injected thornier problems into the sphere of consideration. The idea of the character is central to what and how comparative biologists compare and understand parts of organisms, and is integral to the study of their form and function. Characters are the currency of taxonomy, and the study of organismal biodiversity (Wagner, 2001). Elucidation of the “Character problem” is likely to influence how we go about phylogenetic systematics and species discovery more and more in the years ahead.

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