Contemporary Debates in Philosophy of Biology

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CHAPTER FIVE

Species Are Real Biological Entities

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Species concepts are central ideas to most areas of biology and are certainly not just the property of systematists. Biological systems are all characterized by variation and are thus complex. Species concepts must take account of this variation and complexity. The term "species" derives from classical Greek logic, which dictates that they are absolutely distinct from other species with no overlap. This *typological* approach also characterizes many more modern concepts of species, but cannot take account adequately of biological variation. Most biologists accept a broadly biological species concept where species is that level in divergent evolution when two lineages are genetically divergent and intergrading, or interbreeding, between them is rare or non-existent. Interbreeding in the field, crossability, is the important criterion for determining species status, but this cannot be absolute. Problems of geographical variation and non-sexual reproduction greatly complicate the problems, but that is the nature of biological systems. Ranks of classification above, or indeed below, the species level are much more subjective than the species itself and depend on the views of particular sytematists and the characters that they use. Ranks above the species are purely relational within particular groups of organisms and lack the biological reality of species.

[T]he Swiss sometimes find it difficult to say exactly where the Jungfrau and neighbouring Monch mountains start and stop, but this does not lead them to doubt the reality of these two mountains because their limits are unclear.

M.H.V. van Regenmortel, "Viral Species" (1997)

1 Introduction

A fundamental feature of biological systems that differentiates them most obviously from physical ones is the all-pervading presence of variability. Variation is characteristic of living organisms at all levels of organization. As the late Ernst Mayr

pointed out forcibly many times during his long life, and most recently in 2004, any philosophy of biology must be able to accommodate both genetic and evolutionary variation. The earliest biologists in Europe naturally followed the classical Greek philosophers, most particularly Plato and Aristotle, in their systems of logical division and the consequent absolute separation of different resulting categories. One of Mayr's greatest contributions was repeatedly to make quite clear the need for population thinking in systematics and evolutionary biology (e.g., Mayr, 1942, 1963, 1982, 2004). Animals and plants in nature exist as populations of individual organisms. These organisms show statistical patterns of variation in their various characteristics, both within and between populations. Since the eighteenth century, the so-called "species problem" has been essentially an argument about and between different philosophies of biology.

No topic in evolutionary and systematic biology has been more contentious and controversial than the nature and meaning of *species*. In the words of Ernst Mayr (1982), "There is probably no other concept in biology that has remained so consistently controversial as the species concept" (p. 251). One of the aspects of the species problem that has made it, on the one hand so intractable, but, on the other, so rewarding is that it is not only a very practical problem for all taxonomists and biologists, but also a deeply philosophical and theoretical one (Hey, 2006). In addition to arguments about different philosophical approaches, much of the controversy has centered on the confusion between, on the one hand, the philosophical concepts of species and, on the other, the practical recognition of species taxa themselves. The frequent confusion of these two different aspects of the species problem continues to cause much argument and controversy among biologists and philosophers. So much so that the expanding interest in these problems over the past 10 or 20 years has led to the publication of many relevant books and review articles, notably in Claridge, Dawah, and Wilson (1997c), Ereshefsky (1992), Foottit and Adler (2009), Paterson (1993), Wheeler and Meier (2000), and R. Wilson (1999). Species are widely regarded by biologists as the primary units of biodiversity and conservation (E. Wilson, 1992, 2005), so it is obviously practically important, so far as possible, that we agree on their nature. Perhaps surprisingly, most biologists and philosophers, often with very different attitudes to species concepts and definitions, have broadly agreed that species taxa represent attempts to recognize real biological entities in the field, the units of diversity and conservation of E.O. Wilson. This view, which might be seen as the traditional one, has been attacked strongly in recent years particularly by Mishler (1999) and Mishler and Theriot (2000a, 2000b, 2000c), but also by Ereshefsky (1999). On the other hand, it has been defended by me and my colleagues (Claridge, 2009; Claridge, Dawah, & Wilson, 1997a, 1997b), and, from a quite different standpoint, by de Queiroz (1998, 1999, 2005). In this paper, I again defend the traditional view. To do this, it will be helpful to review briefly the history of the application and development of species concepts in biology. This review section is largely based on a recent paper of mine on insect species (Claridge, 2009).

2 Early Species Concepts–Linnaeus

The term *species* is a very old one and derives from the writings of classical Greek philosophers, most notably Aristotle (see Cain, 1958). It was natural for scholars and

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naturalists of the seventeenth and eighteenth centuries to adopt the systems of Aristotelian logic in attempting to classify and make sense of the natural world. This was taken at the time as the only possible system of reasoning, despite the fact that such logic requires that all entities classified must be absolute and clearly separated from other comparable entities with no overlap between them. Technical terms from Aristotelian logic that were used in attempts to classify living organisms included *definition*, *genus*, *differentia*, and *species*. Here the *genus* referred to the general kind, while *species* referred to the particular kind within the genus, as qualified by the *differentia*. Carl von Linné (1707–1778), better known to us as Linnaeus and the founder of the binomial system of nomenclature that we still use for living organisms, clearly documented his principles and practice in producing classifications of both animals and plants (Cain, 1958, for a full account). Indeed, the binomial system itself is a result of the use of the Aristotelian system. Authors previous to Linnaeus, and Linnaeus himself in his early works, had given multinomial names to organisms; the genus being one word, but qualified by a descriptive phrase, the *differentia*, to describe and delineate particular species. Linnaeus, from the tenth edition of the *Systema Naturae* in 1758, probably primarily because of the pressures to describe such large quantities of new material, reduced the differentia for animal species to a single word—the specific name—and so established the binomial that has been used for plants and animals since then and continues to this day, despite a spate of criticism.

To Linnaeus, species were simply the lowest category of particular kinds in his classifications, though he did also in practice often recognize *varieties* within species! Not only did Linnaeus publish classifications and descriptions of many animals and plants, but he also wrote books in which he detailed his methods and philosophy (e.g., Linnaeus, 1737/1938). It is clear that Linnaeus, as a practicing taxonomist, frequently found it difficult to adhere to his strict philosophical principles, and his works were sometimes an uneasy compromise between philosophy and pragmatism (Cain, 1958). In a detailed study of the many writings of Linnaeus, Ramsbottom (1938) showed that in developing a practical concept of species, he recognized three main criteria. Species were: (1) distinct and monotypic; (2) immutable and created as such; and (3) true breeding. Criteria (1) and (2) here are to be expected in pre-evolutionary philosophy, but (3) may be a little more surprising and clearly results from practical field experience. The idea that species had a single norm of morphological variation and were clearly each distinct from, and did not overlap with, other species within the same genus was widely accepted following the broadly typological thinking of the times (Mayr, 2004) deriving directly from Aristotelian logic.

Linnaeus was, of course, working in very exciting times when European explorers were travelling widely in regions of the world previously unknown to them and bringing back large collections of plants and animals for study. For obvious reasons these samples consisted of dead and often poorly preserved material. Thus, in order to describe new species and to classify them, early taxonomists had little recourse but to use only morphological characters. The total immutability of species was widely accepted in the eighteenth and early nineteenth centuries, but it is now clear that even Linnaeus later in his life developed some complicated theories of speciation by hybridization (Cain, 1993).

Before the enormous influx of largely tropical material into European museums, most early taxonomists, including Linnaeus, were field naturalists themselves and familiar

with the organisms on which they worked as living entities. They certainly knew that the species they described from local fauna and flora using morphological characteristics to differentiate them were also biologically distinct and differed in obvious features of their natural history, in addition to the differences observed in their museum specimens. The swamping of museums by large collections from overseas inevitably led to the almost exclusive use of morphological differences both to describe and to recognize species. This obviously still remains so today for most groups of animals, and particularly for species-rich groups such as insects. The morphological species or morphospecies has evolved from these early classifications solely for reasons of convenience. Interestingly, today such "morphospecies" ideas are now being developed further by the use of molecular characters for recognizing species (see Blaxter, 2004; Tautz, Arctander, Minelli, Thomas, & Vogler, 2003). It is important to emphasize that the morphospecies is not a philosophical concept, but simply a practical methodology used to differentiate species taxa. No doubt Linnaeus himself would have been very unhappy that his philosophy should be reduced to such a purely practical matter! Following the lead of Linnaeus and his many followers, taxonomists were forced more and more to use the practical morphospecies for what they largely knew only as dead museum specimens. The amount of difference required to recognize and separate species became inevitably more and more subjective, as illustrated by different variants of the well-known quote, "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, p. 75).

Unfortunately, as taxonomy and systematics were, through force of circumstance, based more and more only on morphological differences between dead museum specimens, so two quite different traditions of studying the natural world diverged, with what we might call the morphologists on the one side and the naturalists on the other. Naturalists, even in the late eighteenth century, were well aware that species had some real biological basis in the field. For example, Gilbert White (1789) first showed that several morphologically very similar species of song birds in Britain of the genus *Phylloscopus*, the warblers, were very clearly separated in the field by their quite distinctive male songs, now known to function as important elements of their specific mate recognition systems. This interest in breeding barriers and species as reproductive communities was an essential element of the naturalist tradition. Later in the nineteenth-century English-speaking world, most notable as part of the naturalist tradition were Charles Darwin and Alfred Russell Wallace. It was from this tradition that they independently developed the theory of evolution by natural selection and accumulated overwhelming evidence for descent with modification. After the general acceptance of evolution, species were then recognized as the end terms of different lines of descent. The controversies around evolution meant that the nature of species was not regarded at that time as a high-priority subject. Darwin himself certainly normally regarded species as more or less arbitrary stages in the process of evolutionary divergence.

3 Biological Species Concepts

In addition to developing the idea of species as morphologically discrete entities, Linnaeus had the rather more vague idea of species as breeding units that generally

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breed true (Ramsbottom, 1938). However, it was not until the late nineteenth and early twentieth centuries—largely through the writings of the British entomologists Karl Jordan (Mayr, 1955) and Sir Edward Poulton—that these ideas were clarified and became central to species philosophy. Probably the most important contributor to this way of thinking was Poulton. First in 1904, in his Presidential Address to the Entomological Society of London, and later expanded in a volume of essays on various aspects of evolutionary biology (Poulton, 1908), Poulton made the most important advance toward what has since become known as the *biological species concept*. He emphasized the importance of interbreeding in the field as the most critical species criterion. This was what later Mayr (1942, 1963) termed *crossability* and contrasted strongly with *interfertility* or simple ability to hybridize. Poulton was one of the first authors to make this clear differentiation and thus effectively to develop the modern biological species, for which generally he receives insufficient credit (Claridge, 1960; Mallet, 1995; Mayr, 2004).

During the early and mid-twentieth century the revolution in evolutionary thinking, often known as the evolutionary synthesis (Mayr & Provine, 1980), was developed by the attempted unification of systematics, genetics, and evolution, exemplified by the publication of major seminal volumes, including *Genetics and the Origin of Species* (Dobzhansky, 1937) and *Systematics and the Origin of Species* (Mayr, 1942). The so-called "biological species concept" was central to these ideas and was formulated by Mayr (1942): "[A] species consists of a group of populations which replace each other geographically or ecologically and of which the neighbouring ones intergrade or interbreed wherever they are in contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers" (p. 120). More useful from a practical point of view, and certainly the most widely cited since the original publication, is his shorter definition: "[S]pecies are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (p. 120). Reproductive isolation in nature, as also for Poulton, was the key factor in identifying and maintaining species as discrete entities. Such reproductive isolation was maintained by what Dobzhansky (1937) termed *isolating mechanisms*, which were any attributes of species populations that reduced the likelihood of interbreeding between them. Clearly such a category is a very broad one, including not only all sorts of post-mating genetic incompatibilities as well as behavioral and ecological differences that act before mating and fusion of gametes, but also totally extrinsic geographical barriers. The latter are clearly not properties of the organisms and are not now generally classified with the intrinsic factors. To Dobzhansky, speciation was the origin of reproductive isolating mechanisms and, thus, of reproductive isolation. Dobzhansky's system of classification of isolating mechanisms was followed and modified by many authors during the twentieth century, including particularly Mayr (1942, 1963, 1982) and Cain (1954).

A major set of criticisms of the biological species concept has been developed over some years by Hugh Paterson (see Paterson, 1985, 1993). One of his main concerns is with the concept of species isolating mechanisms and with the implication that they have evolved as adaptations under natural selection to achieve and maintain reproductive isolation. Clearly Paterson must be correct, at least for all so-called "post-mating mechanisms," which logically cannot be due to such adaptation (see also Claridge,

1988; Mallet, 1995). Avise (1994) and, more recently, Coyne and Orr (2004) have suggested the neutral term *isolating barrier* to replace *isolating mechanism*. This is a useful suggestion, but does not deal with Paterson's further criticisms. Maybe there is no need anyway now for a term to include such a diversity of phenomena?

Paterson (1985) regards species as groups of organisms with common fertilization systems: "We can, therefore, regard species as that most inclusive population of individual biparental organisms which share a common fertilization system" (p. 25). He recognized an important subset of the fertilization system that he termed the *specific mate recognition system* (SMRS), "which is involved in signaling between mating partners and their cells." Thus, the often complicated reciprocal signals and signaling systems of mating and courtship (well-documented and reviewed by ethologists including Brown, 1975; Eibl-Eibesfeldt, 1970; and Tinbergen, 1951) have ensuring specific mate recognition as one essential function. In such behavior sequences successive signals release in turn successive responses via tuned receptors in the opposite sex. These sequences are usually, but not exclusively, initiated by males. Unless appropriate responses are received at each stage and the signals are recognized as appropriate, exchange will be terminated and ultimate exchange of gametes will not occur. The exchanges of signals between partners may be broken off at any stage. Thus, to Paterson, species are defined by their unique SMRSs, and the evolution of new species, speciation, is the origin of new SMRSs. He has argued at length over the years that his concept of species is quite distinct from the biological species *sensu* Mayr. He terms the latter the *isolation concept*, because it is defined by reproductive isolation from other species, and terms his own system the *recognition concept*. Lambert and Spencer (1995) and Vrba (1995) have strongly supported this line of argument, but others have doubted the clear demarcation between isolation and recognition concepts (Claridge, 1988, 1995a; Claridge et al., 1997a; Coyne & Orr, 2004; Coyne, Orr, & Futuyama, 1988; Mayr, 2000a, 2000b, 2000c).

Thus, in practice a broadened biological species concept would recognize that different species are characterized by distinct SMRSs which result in the levels of reproductive isolation between sympatric species observed in the field. However, species taxa are only rarely recognized by direct studies of the SMRS, which are themselves equally rarely understood with any certainty, but they are the final arbiters for determining biological species boundaries (Claridge, 1988, 1995a, 2009; Claridge et al., 1997a, 1997b). Normally, biological species are recognized by markers that are thought to indicate the existence of reproductive isolation. In the past, these were usually morphological markers, so that, after the evolutionary synthesis of the mid-twentieth century, taxonomists hypothesized that the differences they recognized and used to separate morphospecies were also indicators of biological species boundaries. More recently, morphological markers have been supplemented by a wide range of others, including cytological, behavioral, and biochemical ones. In particular, increasing use is now made of molecular markers involving characters derived from the amino-acid sequences of specific pieces of DNA (Avise, 1994). Indeed, it has even been suggested that all species taxa should be diagnosed by such molecular differentiation (e.g., Blaxter, 2004; Tautz et al., 2003). However, the enormous diversity of markers currently available to taxonomists simply indicate levels of reproductive isolation. Levels of gene flow between populations, and therefore levels of reproductive isolation, are now routinely estimated by molecular divergence.

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A particular feature of the biological species concept is that reproductive isolation may occur between species populations without any obvious accompanied morphological differentiation. This phenomenon of real biological species existing in nature without obvious differentiation to the human observer has been recognized since early in the twentieth century and was well discussed by Mayr (1942). Such species are usually known as *sibling* or *cryptic* species and have been clearly demonstrated in many groups of living organisms, most particularly insects (Claridge, 1960, 1988, 2009; Claridge et al., 1997b; Mayr, 1942; Thorpe, 1940).

During the primacy of the biological species in the middle years of the twentieth century, a large body of opinion among museum taxonomists was nevertheless opposed to it (e.g., Sokal & Crovello, 1970) and preferred either some overtly morphological species approach or a purely phenetic one. Such views have always been strongly supported by botanists on the grounds that interspecific hybridization is so common in plants that reproductive isolation is not a useful criterion (Gornall, 1997; but see Mayr, 1992). However, entomologists have also often led the criticism of the biological species.

There are two important problems in the practical use of biological species that are acknowledged by all of its proponents. These concern the status of (1) asexual and parthenogenetic forms and (2) geographically or spatially isolated (allopatric) populations:

1   *Agamospecies*: The biological species in its various manifestations can only be applied to biparental sexually reproducing organisms in which a distinctive SMRS leads to reproductive isolation. Neither asexual nor obligate parthenogenetic organisms have a functional mate recognition system that leads to the fusion of gametes, so that the biological species cannot strictly apply to them. These organisms exist as clones which may differ in morphology, biochemistry, cytology, behavior, ecology, etc. (Foottit, 1997), and which, contrary to some opinion, may show considerable genetic variation (Loxdale & Lushai, 2003). Although distinctive and diagnosable clones are often described as species, they cannot truly be biological species. They have, however, been given the useful name agamospecies (Cain, 1954). Such agamospecies often differ between themselves in important features of behavior, such as feeding preferences and ecology (de Bach, 1969). They are thus practical categories like the morphological species. Many groups of living organisms, including most micro-organisms, can only be agamospecies, but of course such organisms show obvious patterns of variation and are clearly subject to evolution.

2   *Allopatric forms*: A practical problem with applying the biological species is that reproductive isolation in the field can be determined only for sympatric populations, where alone there are possibilities of testing the effectiveness of SMRSs in the field. Geographical variation and the status of allopatric populations have long been of major interest to both taxonomists and evolutionary biologists. Degrees of observable differentiation between allopatric populations vary from almost nothing to large differences, at least comparable with those observed between distinct sympatric species of the same taxonomic group, but the criterion of gene flow and reproductive isolation in the field cannot be conclusively tested. Experimental crossings of allopatric forms under laboratory and experimental conditions yield results of only limited value.

The polytypic nature of biological species has for long been recognized, and a series of taxonomic categories, from superspecies to subspecies, has been developed to describe such essentially continuous geographical variation (Cain, 1954; Mayr, 1942). This continuum, on the one hand, has provided vital data for the development of theories of allopatric, or geographical, speciation (Cain 1954; Mayr, 1942); but, on the other, it has led many workers also to regard the species as no more than a rather arbitrary stage in the divergence of local populations. For example, Alfred Russell Wallace (1865), when confronted with the bewildering range of geographical variation and polymorphism in the swallowtail butterflies of South East Asia, in a widely cited quote, stated:

> Species are merely those strongly marked races or local forms which, when in contact, do not intermix, and when inhabiting distinct areas are generally believed to . . . be incapable of producing a fertile hybrid offspring. . . . [I]t will be evident that we have no means whatever of distinguishing so-called "true species" from the several modes of variation . . . into which they so often pass by an insensible gradation. (p. 12)

Interestingly Wallace (1889), in a wider discussion, later supported a much more biological type of species concept. Wallace, as of course also Darwin, was impressed with variation within and between natural populations as the basic material for evolution by natural selection. Equally today the allocation of allopatric populations within the superspecies/subspecies continuum is largely subjective. Drawing a line through any continuum must indeed be to some extent arbitrary. This is undoubtedly a practical weakness of the biological species, but I would argue equally that it is a weakness of all discrete species concepts.

These obvious complications, together with a frequent desire to eliminate the priority given to one set of organismal characters—the SMRS and resulting reproductive isolation—over all others, have persuaded many systematists to abandon the biological species concept in favor of what we might term a *general phylogenetic species concept* (Claridge et al., 1997a).

Before moving on to consider phylogenetic concepts in more detail, it is appropriate to discuss the interesting ideas of Mallet (1995) on his "genotypic cluster criterion" or concept of species. Mallet is a geneticist who has worked on widely distributed species and populations of tropical butterflies, like those studied earlier by Alfred Russell Wallace (see above). One of his concerns is that the biological species is absolute and does not allow for interspecific hybridization and intergrading, a subject which he himself has recently extensively reviewed (Mallet, 2005; 2008). However, since intergradation is the basis of the polytypic biological species espoused by Mayr, Cain, and others, this criticism cannot be a real problem. Even in sympatric interactions, re-productive isolation does not need to be absolute in order to maintain species integrity. Indeed, the acceptance of the reality of evolution demands that species cannot always be completely reproductively isolated. Intermediates and intergradation must be expected. Thus, all realistic species concepts must allow for such intergradation, and the broadly conceived biological species certainly does this.

Another interesting contribution, along similar lines to that of Mallet (1995), is the *genomic integrity species* definition of Sperling (2003). Here, species are "populations

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that maintain their genomic integrity when they contact each other, even if they occasionally exchange genes" (p. 432). Clearly, biological species in the broad sense that I follow here must be both distinct genotypic clusters and maintain their genomic integrity, as argued by Mallet and Sperling, respectively. These various attempts to formulate more inclusive and realistic species concepts appear to me, then, to be quite compatible with, and indeed very similar to, the broadly based biological species concept advocated here.

4 Phylogenetic Species Concepts

A revolution in the philosophy and practice of systematics took place in the English-speaking world after the publication of Hennig's *Phylogenetic Systematics* in translation in 1966. Few systematists today do not use some variant of the cladistic methodologies pioneered by Hennig. Coincident with this widespread acceptance of cladistic methods for constructing phylogenetic hypotheses and making robust classifications came increased published dissatisfaction with, and rejection of, the biological species concept by some systematists (e.g., most authors in Wheeler & Meier, 2000). Oddly enough, Hennig himself thought of species as reproductive communities, so his species concept was broadly similar to the biological species of Mayr (1942)! Of course, Hennig was interested primarily in extending species back in time as diagnosable clades and lineages. In this he was developing what Simpson (1951) had begun as a broader evolutionary species concept based on phylogenetic lineages, which has since been taken up by many others (e.g., Cain, 1954; Wiley, 1978; Mayden, 1997; Wiley & Mayden, 2000a, 2000b, 2000c; and see Hey, 2006). Most recently, de Queiroz (1998, 1999, 2005) has developed what he terms the *metapopulation lineage concept* based on similar reasoning.

Cladists have certainly not spoken with one voice on the nature of species. Hennig (1966) saw species as that unique level in the taxonomic hierarchy at and above which cladistic methods could be applied to determine phylogenies and below which they could not. Within species, interbreeding relationships dominate, and these Hennig differentiated from phylogenetic relationships as *tokogenetic* ones, a term that has not been widely adopted in the general literature. Many more recent cladists have followed this view of species. For example, Nixon and Wheeler (1990; Wheeler & Nixon, 1990) clearly stated that species are uniquely different from higher-level taxa, in that they lack resolvable internal phylogenetic structure. On the other hand, other cladists, including Nelson (1989) and Mishler and Brandon (1987), clearly state that the species represents just one rank in the taxonomic hierarchy and is of no more or less significance than any others, such as genus, family, order, etc. Mishler (1999) and Mishler and Theriot (2000a, 2000b, 2000c) developed this line of argument in further detail. For example, Mishler (1999) concluded: "[W]e have no and are unlikely to have any criterion for distinguishing species from other ranks in the Linnean hierarchy, which is not to say that particular species taxa are unreal. They are real, but only in the sense that taxa at all levels are real Species are not special" (p. 309). In criticism of this view, Wheeler (1999, p. 136) commented that species "exist in nature is one aspect of species about which I can agree with Mayr (1963)," and most taxonomists also seem broadly to agree with this long-established view.

Many authors have attempted to formulate an expressly phylogenetic species concept. In a valuable volume devoted to a debate about species concepts and phylogenetic theory, proponents of three different such phylogenetic concepts, including what was termed the *Hennigian species concept* (Meier & Willmann, 2000) and two quite different versions confusingly each termed the *phylogenetic concept* (Mishler & Theriot, 2000a, on the one hand, and Wheeler & Platnick, 2000, on the other), presented their arguments and many disagreements, not only with the biological species concept and the evolutionary concept (supported by Wiley & Mayden, 2000a), but also with each other. In the same volume, Mayr (2000a) took a lone stand to defend his view of the biological species concept. Clearly, there are fundamental disagreements between the three sets of authors claiming to base a species concept on phylogenetic and cladistic theory. However, despite these disagreements, there is some practical consensus, and perhaps the most widely cited definition of the phylogenetic concept is that of Cracraft (1983, 1997), who stated that the species is the "smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft, 1983, p. 170). Some critics have suggested that this definition applies only to individuals and not to populations, a view fiercely refuted by Cracraft (1997). Nixon and Wheeler (1990) also emphasized this when they defined phylogenetic species as "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals" (p. 218). Thus, to me it seems that the essence of the dominant phylogenetic concept in its various forms involves the recognition of diagnosable clades. The major question then has to be just exactly what is diagnosable? How different do two populations or lineages have to be to be diagnosably and recognizably distinct? These judgments must surely be subjective, particularly since what is distinct to one taxonomist may well not be to another.

Leaving aside the latter difficulty, it is clear that any of the markers discussed above as useful for delimiting biological species, including molecular and behavioral ones, may also be used to characterize phylogenetic species, though in most groups such characters have tended to be exclusively morphological. My colleagues and I (Claridge et al., 1997a) concluded that the purely practical differences between a phylogenetic concept and a broadly biological one for determining the limits of species taxa were not very great, a view which I still hold. To me, the great disadvantage of the phylogenetic concept is the difficulty in agreeing on what precisely is a diagnosable difference and that therefore such species can only be the subjective judgments of particular systematists. A major advantage of the biological concept is that it does attempt, however difficult that may be, to identify real reproductively isolated and therefore independently evolving populations, even though isolation may not always be complete. Clearly, the phylogenetic concept can be applied to asexual or parthenogenetic lineages which are effectively agamospecies (Cain, 1954), though the subjective judgment is still central. For the phylogentic species, the problems of differentiating allopatric populations are no different to those involved in differentiating sympatric ones. Thus, diagnosably distinct allopatric populations will be regarded as separate species. The result will almost always be that more allopatric populations will be recognized as distinct species than will be the case with an application of the polytypic biological concept. For example, the well known analysis of the Birds of Paradise (*Aves*, *Paradisaeidae*) by Cracraft (1992), using his phylogenetic

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concept, established more than twice as many species (90) than had previous applications of the biological species to the same data set! However, that judgment will always be essentially subjective under both concepts, though various authors, from Mayr (1942) to Sperling (2003), have attempted to provide more objective criteria for assessing the species status of totally allopatric populations. Though there are fundamental differences of philosophy and theory between the biological and phylogenetic concepts, I see little difference generally in practice when applied to species taxa by competent taxonomists.

Despite the apparent advantages of the phyologenetic concept in breadth of application, in my view it has at least one major practical disadvantage compared to biological concepts, and that is the improbability that its application will reveal the existence of complexes of sibling species and thus a full picture of biological diversity. The philosophy of the phylogenetic species gives no incentive or reason to search for further divisions once diagnosably distinct forms have been established. On the other hand, the emphasis of the biological species on reproductive isolation and specific mate recognition means that sibling species will be revealed by its diligent application. Among most groups of living organisms, sibling species are now widely known and are of great biological significance (see contributions in Claridge et al., 1997c).

5 Species Concepts and Speciation

Theories of speciation, the evolutionary diversification of species, have often been closely tied to the development of particular species concepts, so that a brief review is needed here. Most modern authors will agree that in recognizing and describing species, taxonomists are providing a framework for understanding the diversity of living organisms and their evolutionary relationships. However, the philosophical interactions between different species concepts and particular theories of speciation are longstanding and still not fully resolved. It seems obvious that a system for describing observed diversity should be independent of the various possible modes by which that diversity may have evolved (but see Bush, 1994, 1995; Claridge, 1995b).

Probably the most widely accepted mode of animal speciation is that of *geographical* or *allopatric* speciation (Cain, 1954; Mayr, 1942, 1963). The essence of such theories is that an ancestral population is subsequently divided into at least two daughter populations, isolated in space, where they diverge and develop genetic isolation prior to any subsequent meeting and sympatry. The most extreme view of this is that the daughter species must have diverged to the extent that they do not interbreed on meeting: that is, they have developed completely separate specific mate recognition systems, in the terminology of Paterson (1985, 1993), perhaps the strongest current supporter of this view. Contrary to this theory of speciation involving complete allopatry, many authors–most notably, Wallace (1889) and Dobzhansky (1940)–developed theories of the reinforcement of species-isolating mechanisms in sympatry by natural selection, after the partial divergence of incipient allopatric species. This is still a controversial theory, which has been well-reviewed recently (Coyne & Orr, 2004).

Quite distinct from the various theories of allopatric speciation are those of sympatric speciation, where no period of allopatry is necessary for two species to diverge from one previous one, normally by powerful disruptive selection. Though

not strongly supported in the early years of speciation theory, such ideas have always been advanced by some entomologists and others working with large groups of sympatric specialist feeders, including parasites and herbivores (Bush, 1975, 1993, 1994; Walsh, 1864; Wood, 1993). Here, descendant species diverge within the range of the ancestral species and therefore all stages of such divergent populations may be expected to exist in the field together. These ideas have become more and more acceptable to mainstream evolutionary biologists in recent years (Coyne & Orr, 2004), to the extent that even Ernst Mayr, the strongest opponent of such theories since his 1942 book, in his final work accepted that sympatric speciation is probable at least in some parasitic organisms (Mayr, 2004). In fact, there appears to be a developing consensus that there may be a continuum from pure allopatric to pure sympatric speciation, where intense natural selection may outweigh the swamping effects of gene flow by hybridization (e.g., Feder et al., 2005).

Whatever the final consensus on speciation, there surely can be little doubt that the nature of our species concept should not depend on the mode of speciation. Thus, in principle I agree with most cladists at least on the particular point that we should describe the patterns of diversity that we see in nature, so far as possible, independently of the theories concerning the evolution of such patterns (Wheeler & Nixon, 1990). However, I cannot agree with Wheeler and Nixon (1990) that "the responsibility for species concepts lies *solely* with systematists" (p. 79). Aside from the essential arrogance of such a statement, an evolutionary view of species inevitably must involve at least genetics and evolutionary biology, in addition to systematics. If we accept the generality of evolution and species as the results of evolutionary divergence, then it follows that the species concept itself must be an evolutionary one. As noted above, Simpson (1951) first attempted to fuse the then biological species, the agamospecies and the paleospecies, into a unitary all-embracing evolutionary concept. Cain (1954) developed further and clarified these ideas, as later, particularly following the general acceptance of cladistic methodologies, did Wiley and Mayden (Mayden, 1997, 1999; Wiley, 1978; Wiley & Mayden, 2000a). Such theories, like those of de Queiroz (2005), provide a reasonably satisfactory philosophical fusion of the variety of species concepts that account for the diversity of living organisms and their relationships over time, but do not help much in the practical recognition and identification of species taxa.

6 Conclusions

The species problem has always confused two almost completely separate phenomena—species concepts and species taxa—as emphasized frequently over a period of more than 60 years by Ernst Mayr. Species taxa are recognized and described by taxonomists according to their own preferred species concepts. Taxonomists may also be influenced in their choice of concept by the particular groups of organisms on which they work. I follow Mayr (2004) in the view that many species concepts are in reality recipes for recognizing particular species taxa and not themselves significant and distinct concepts. However, the question that is being posed in this volume by Mishler (next paper) concerns the idea that species do not represent any biological reality distinct from that of other levels in the taxonomic hierarchy, such as genera,

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families, orders, etc. Clearly from what I have said earlier in this paper, unlike Mishler, I certainly do think that species are of unique and real biological significance. Higher-level categories are to me clearly subjective, depending on the views of any particular taxonomist, despite the added objectivity of cladistic methodologies. I agree with Dobzhansky when, as long ago as 1935 (translated in 1937), he said the species is "that stage of the evolutionary process at which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding" (p. 312). Later, he put this more succinctly in describing a species as "the most inclusive Mendelian population" (Dobzhansky, 1951, p. 263), as did Carson in his widely cited title for a paper, "The Species as a Field for Gene Recombination" (1957). This view is very close to that advocated more recently by Paterson (1985), who regarded species as "that most inclusive population of individual biparental organisms which share a common fertilization system" (p. 25). Clearly, any such evolutionary view of species must recognize that the process of speciation is a continuous one, so that drawing real lines between species as they evolve will be very difficult and intermediate stages must be expected.

The quotation that I have given at the beginning of this paper from a little cited, but very significant, contribution by the virologist van Regenmortel (1997) concerning the Jungfrau and Monch mountains in Switzerland to my mind provides an excellent analogy for understanding the species problem. Here, he introduced the notion of the species as a *polythetic class*, after Beckner (1959), to replace the classical idea of universal classes. Such polythetic classes are "defined by a combination of characters, each of which may occur also outside the given class and may be absent in any member of the class. . . . Contrary to the situation with universal classes, no single property is either necessary or sufficient for membership in a polythetic class" (van Regenmortel, 1997, p. 21). There can be few practicing taxonomists who have not had this type of problem when confronted by large assemblages of apparently related species. A further very relevant and clearly related philosophical concept that van Regenmortel also introduced in the same publication was that of *fuzzy logic* and *fuzzy sets* (after Kosko, 1994, and Zadeh, 1965). This philosophy contrasts strongly with the rigid Aristotelian systems of thinking about classification that Ernst Mayr called typological. Such typological approaches still, often unwittingly, underlie some species thinking. Because intermediates or hybrids between otherwise distinct populations may occur in the field, it does not mean in principle that we cannot and should not recognize distinct species within the continuum of variation. The reality of species as distinct from higher taxonomic categories is not invalidated by such fuzzyness, as, for example, Ereshefsky (1999) has argued. This brings me back full circle to my introductory comments on the all-pervading nature of variation in biological systems and the need for us to recognize it in discussions on species.

Postscript: Counterpoint

Mishler argues from the narrow viewpoint of his own preferred species concept, which is one of several phylogenetic concepts and the most strictly cladistic of them all. He follows his previous definition (Mishler & Theriot, 2000a) where: "A species is

the least inclusive taxon recognized in a formal phylogenetic classification" (p. 46). To me, this is not very helpful and certainly not very precise. Of course, it begs the question of just what is a formal phylogenetic classification; there would certainly be much controversy over that even within the cladistics community. On several occasions, Mishler mentions the biological species as being too simple, and he appears to misunderstand the criterion of interbreeding, which is certainly not just simply the "ability to interbreed." If nothing else, I hope that my discussion above has demonstrated the enormous complexity of the modern biological view of species and particularly the nature of an interbreeding criterion. Contrary to Mishler's comments, the biological view of species is certainly not absolutist or typological: above all, it allows for the natural variation in biological systems, and particularly in populations. Mayr was the first author clearly to differentiate what he called typological concepts in contrast to populational or biological ones. Mishler, uniquely I think, sees a similarity between the biological species and creationism through a common inheritance from classical and Christian thinking, which he believes "is so ingrained in Western thought . . . that most evolutionary biologists and ecologists have serious trouble letting go of it." I object to this view, which clearly implies that all who accept the biological view of species are unable to think critically about these matters! The biological species has been the basis and focus over more than 50 years for most recent discussions on evolution in general, and in particular on speciation— the origin of new species. Ernst Mayr (1942) certainly did more than any other recent author to develop and establish these ideas. Mishler contrasts what he terms the "simplistic Mayrian view" with "Darwin's richer conception" of species. In fact, in *The Origin of Species* Darwin clearly regarded species as more or less arbitrary stages in the process of divergent evolution. I find it difficult to think of this as a richer conception of species than the "Mayrian" view! Of course, few will argue that during the process of speciation and divergence between two populations, the exact point when species status is achieved may be an arbitrary one. In the 1850s, Darwin was so concerned to establish both the fact of evolution and the process of adaptation by natural selection that, unsurprisingly, he did not concern himself with the detailed nature of species and the process of speciation. However, many of his contemporaries, including Wallace and Poulton, certainly predated Mayr with biological species thinking, as discussed above. It is interesting that Darwin himself, in his taxonomic studies, spent much time thinking in detail and worrying about the limits of species in the particular group that he was studying, most notably the barnacles (*Crustacea*, *Cirripedia*). This hardly fits with his view of species as completely arbitrary constructs.

I certainly do agree with Mishler that the particular groups of organisms studied influence greatly the attitudes of different biologists to species concepts. It is obviously a very different problem trying to understand the diversity of, for example, bacteria, on the one hand, and birds, on the other. The nature of reproduction and breeding systems in different groups is clearly critical and may in part account for some of my differences, as an entomologist, with those of Mishler, a bryologist.

After a brief statement of his preferred species concept, much of Mishler's paper here is concerned with what appears to me to be an important discussion, but one peripheral to our present argument, on the nature of ranking in classification and his perception of the advantages of a rank-free classification! Of course, it is true

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that particular ranks, such as family, order, etc., in different groups of living organisms are not, and probably cannot be, truly comparable. Mishler suggests that users of classifications assume "that taxa placed at the same rank must be comparable in some way." However, even the most naïve ecologist is unlikely really to expect that, for example, orders of bacteria, flowering plants, and insects are strictly comparable entities! These rankings are surely simply relational within any major group. To me this provides a powerful argument as to just why species are real biological entities and why other higher- or, indeed, lower-ranked groups within a classification are not.

In conclusion, I find it hard to believe that establishing a totally novel rank-free classification and a totally new system of biological nomenclature, the so-called "PhyloCode," can possibly be helpful in the current biodiversity crisis. We need broadly applicable species concepts and the existing Linnean system of nomenclature, certainly for species names. In my view, revolutionary new systems designed to replace the current system of taxonomy and nomenclature can only cause unnecessary diversions from the real and urgent problem of documenting biological diversity.

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