

Species concepts and species reality: salvaging a Linnaean rank

M. S. Y. LEE

Department of Environmental Biology, The University of Adelaide and Department of Palaeontology, The South Australian Museum, North Terrace, Adelaide SA 5000, Australia

Keywords:

gene flow;
Linnaean hierarchy;
reproductive isolation;
species category;
species concepts.

Abstract

The validity of the species category (rank) as a distinct level of biological organization has been questioned. Phenetic, cohesion and monophyletic species concepts do not delimit species-level taxa that are qualitatively distinct from lower or higher taxa: all organisms throughout the tree of life exhibit varying degrees of similarity, cohesion, and monophyly. In contrast, interbreeding concepts delimit species-level taxa characterized by a phenomenon (regular gene flow) not found in higher taxa, making the species category a distinct level of biological organization. Only interbreeding concepts delimit species-level taxa that are all comparable according to a biologically meaningful criterion and qualitatively distinct from entities assigned to other taxonomic categories. Consistent application of interbreeding concepts can result in counterintuitive taxonomies – e.g. many wide polytypic species in plants and narrow cryptic species in animals. However, far from being problematic, such differences are biologically illuminating – reflecting differing barriers to gene flow in different clades. Empirical problems with interbreeding concepts exist, but many of these also apply to other species concepts, whereas others are not as severe as some have argued. A monistic view of species using interbreeding concepts will encounter strong historical inertia, but can save the species category from redundancy with other categories, and thus justify continued recognition of the species category.

The reality of the species category

Species have long been assumed to represent important and irreducible (basal) phylogenetic entities, and thus to play a unique role in evolution. This view can be traced back at least as far as Darwin (1859), who equated evolution with 'the origin of species'. Many subsequent books had titles directly asserting the importance of the species category (rank) in evolutionary processes (e.g. Dobzhansky, 1937; Cain, 1954; Mayr, 1963; Ereshefsky, 1992). However, there has been a long history of dissent,

the alternative view being that the species category does not represent a level of biological integration worthy of special recognition. This view can also be traced back to Darwin (1859), who despite the title of his most famous work, stated that the species category did not differ in any fundamental way from lower ranks such as varieties, and higher taxa such as genera (e.g. see Ereshefsky, 2001; Hey, 2001). This view continues to attract significant support, with many recent calls for the abandonment of the species rank as a taxonomic category altogether (e.g. Pleijel, 1999; Ereshefsky, 2000; Mishler, 2000; Pleijel & Rouse, 1999, 2000).

There have been very cogent arguments for the abolition of higher taxon categories such as the genus, order and class (e.g. Hennig, 1969; Griffiths, 1976; de Queiroz, 1988, 1997; Gauthier *et al.*, 1988; de Queiroz & Gauthier, 1992; Ereshefsky, 1997, 2001; Lee, 2001; Bryant & Cantino, 2002; but see Nixon & Carpenter, 2000; Benton, 2000). All genera, for instance, do not

Correspondence: Michael S. Y. Lee, Department of Environmental Biology, The University of Adelaide and Department of Palaeontology, The South Australian Museum, North Terrace, Adelaide SA 5000, Australia North Terrace, Adelaide SA 5000, Australia.
Tel.: 61-8-8207-7568; fax: 61-8-8207-7222;
e-mail: Lee.Mike@saugov.sa.gov.au

possess unique genus-level properties such as a common age of origin, or a particular level of morphological divergence or species richness. The current codes of nomenclature (Sneath, 1992; Ride *et al.*, 1999; Greuter *et al.*, 2000) completely lack criteria for recognizing the genus category, i.e. objectively deciding that a particular assemblage of species represents an entity at the genus rank rather than some other rank (e.g. family, tribe). Rather, such ranking decisions are based on arbitrary and very loose conventions (e.g. the 'acceptable' amount of divergence permitted in a genus), resulting in endless and unresolvable debates over whether to split or lump particular genera. Thus the genus category (rank) does not have any special properties and is not a level of biological integration worthy of special recognition. The same problems afflict other higher taxon categories, such as families, orders, classes, phyla or divisions, and kingdoms. These supraspecific categories, therefore, do not represent quantifiable, objective (i.e. 'real') levels of biological organization. In contrast, there are strong arguments that the only real supraspecific taxa are clades (monophyletic lineages) of varying inclusiveness, united by shared ancestry. Under this argument, the only supraspecific category (rank) that should be formally recognized is the clade (e.g. Hennig, 1969; de Queiroz, 1988, 1997; Ereshefsky, 2001; Hey, 2001).

The species category must also be subject to similar scrutiny as its Linnaean counterparts. For the species category to warrant special recognition, it must represent a distinct level of biological organization that can be distinguished from lower levels (e.g. organisms, demes, populations) and higher levels (e.g. clades or 'higher taxa'). Taxa assigned to the species rank will then share some particular property, making them comparable entities according to that criterion. Conversely, if the species category cannot be clearly distinguished from other levels of biological organization, then its validity is questionable, as is the equivalence of species taxa (e.g. Ereshefsky, 2000; Mishler, 2000). If species have no special properties and are merely (for instance) extended populations or small clades, there is no reason for recognizing the species category in addition to other categories such as populations and clades. Moreover, it would be impossible to objectively determine that a given taxon belongs to the species category, rather than to the population or clade category. Although much has been written on the numerous proposed species concepts, the implications of these concepts for the distinctness (and thus reality) of the species category have been largely overlooked. Here this problem is explored in relation to the most widely known species concepts (e.g. those discussed in Wheeler & Meier, 2000; Ereshefsky, 2001; Hey, 2001). The concepts are grouped according to the primary criterion they use to classify taxa as species (i.e. to assign them to the species rank). The problem is framed initially in relation to sexual species; the implication for the reality of asexual 'species' will be clear and

is explicitly discussed later, along with the implications for species pluralism and monism. Finally, it should be emphasized that the following discussion does not deal with the ontology of any particular taxon (which might be called a species); rather, it deals with the ontology of the species category as a whole (Hey, 2001). Individual low-level taxa (e.g. populations, small clades) might be real, but their grouping into a single category (the species rank) might not be warranted. By analogy, different individual objects might each be valid entities, but a grouping (category) containing a heterogeneous assemblage of such entities might not be meaningful.

Similarity concepts

The phenetic species concept, at its most extreme (Sokal & Crovello, 1970; see below for more refined versions), uses phenetic resemblance as the sole species criterion, asserting that organisms should be grouped into species based on overall similarity. It is rarely if ever used today, and has been criticised strongly on numerous grounds. A very naive application of it could classify different sexes and ontogenetic stages as different species; there is no objective measure of total similarity; and different similarity indices and clustering algorithms can yield different phenograms based on the same data matrix (see review in Ereshefsky, 2001).

Let us assume (generously) that an enlightened phenetic analysis, perhaps of DNA characters, always yields the same phenogram (regardless of ontogeny, dimorphism, similarity metric or clustering algorithm), and further assume that this phenogram accurately reflects phylogenetic relationships. There will be a nested hierarchy of organisms, with small clusters of very similar organisms/populations within successively larger clusters containing more diverse arrays of organisms/populations. There remains the problem of deciding what level of clustering corresponds to the category (rank) of species. There is no rigorous criterion to determine which clusters should be recognized as species, and which should be recognized as lower (intraspecific) and higher (supraspecific) taxa. Using obvious 'breaks' (long branches) as species boundaries will not work: although there will be discontinuities (some tight clusters and major gaps between such clusters), these will occur at multiple levels throughout the phenogram. The only criteria are arbitrary and hazy conventions about just how much divergence one should allow within a species. Asserting that clusters at a certain level of divergence (e.g. 10–20%) correspond to the 'species category' might provide a more objective ranking criterion. However, this will not be practical since consideration of different sets of traits, and use of different similarity metrics, will result in different similarity scores for the same organisms.

This lack of a rigid criterion for defining just how much phenetic divergence corresponds to the species category means that the statement 'organism X belongs in species

Y' is untestable. If one subsequently discovers that organism X is very different (and distantly related) to the type of species Y, there is no objective criterion preventing one from greatly expanding the boundary of species Y so that it now contains organism X. Conversely, even if one discovers that organism X is almost identical (and closely related) to the type of species Y, there is no objective criterion preventing one from shrinking the boundary of species Y so that it now excludes organism X. At an absurd extreme, under a very broad phenetic concept, most of life could be considered the same species, whereas under a very restricted concept every organism could be considered a separate species (e.g. see Mayr, 2000b). Furthermore, if certain clusters are arbitrarily assigned to the 'species' category, they will not have any properties distinct from those of less inclusive ('intraspecific') and more inclusive ('supraspecific') clusters. Thus, under phenetic species concepts, there is no objective criterion for recognizing the species category, and accordingly the 'species' recognized lack properties distinguishing them from other (intraspecific and supraspecific) entities. The entities above the organismal level recognized under this system, including 'species', are all merely phenetic clusters of varying sizes.

Some recent species concepts utilizing similarity address some of the problems of the original phenetic concept, especially the problem whereby different sexes or ontogenetic stages might be assigned to different species. They also provide a (potentially) clear ranking criterion by which to recognize the species category. Species are 'the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states' (Wheeler & Platnick, 2000 p.58; see also Cracraft, 1983). If subsequent work reveals diagnosable subgroups within a putative species, then the species should be split. However, with increasingly fine genetic probes using nonrecombining DNA and hypervariable loci such as microsatellites, very fine-grained diagnosis of populations (and indeed, identification of individual organisms) is possible. There will be no clear level below which all organisms and populations are undiagnosable, and above which all taxa are distinct. This erodes the utility of the rule that the species level corresponds to the smallest groups of organisms or populations exhibiting a 'unique combination of character states' (Wheeler & Platnick, 2000).

Cohesion concepts

The ecological (Van Valen, 1976), cohesion (Templeton, 1989), evolutionary (Simpson, 1961; Wiley & Mayden, 2000) and genotypic cluster (Mallet, 1995) species concepts, although differing in many details, all use cohesion as the major criterion to delimit the species rank. A species is a group of organisms sharing features causing them to remain coherent entities through time, either all remaining in stasis or all responding in similar

ways to common evolutionary forces. These cohesion mechanisms can be either be present in each individual (e.g. because of shared developmental homeostasis or a common ecological niche) or because of interactions between individuals (e.g. gene flow). If cohesion is because of gene flow, these species concepts will demarcate the same species entities as interbreeding species concepts, and implicate the same processes, and the comments under that section apply. The two groups of species concepts only diverge when cohesion does not reflect interbreeding, i.e. there is cohesion without interbreeding, or interbreeding without cohesion. For instance, if divergent or disruptive selection between populations is strong enough, individual populations could each exhibit cohesion despite appreciable gene flow. Such groups would be recognized as multiple species under the cohesion species concepts, but would probably be considered a single species under interbreeding concepts. Conversely, if stabilizing selection is very strong, independent lineages might fail to diverge for an appreciable length of time, leading to the recognition of a single cohesion species but multiple species under interbreeding concepts. Thus, the remaining discussion will focus on whether species recognized on the basis of internal cohesive forces (and that differ from reproductive species) represent a distinct level of biological organization. The coinciding species delimited when cohesion corresponds with interbreeding are discussed in the section on interbreeding species concepts.

Internal cohesion mechanisms suggested to characterize particular species include developmental homeostasis, niche conservatism, and common selective regime. However, these traits, like overall similarity, are continuous variables. They are, however, much more difficult to quantify than traditional phenetic traits, and few or no empirical studies have used direct measurements of such traits (rather than morphological or genetic proxies) to delimit species. As with phenetic similarity, there will be a continuous scale of developmental, ecological and selective similarities: from organisms that are identical in these features, to those that are almost totally different. For instance, monozygotic twins can be expected to share very similar developmental systems, with successively more divergent organisms having less and less in common. Even very distinct organisms can share developmental constraints at some general level (e.g. Raff, 1996). Thus, if similarities in development, ecology or selective regime similarity are postulated to confer cohesion, cohesion – like phenetic similarity – must vary continuously throughout a phylogeny. There is no distinct boundary where these variables change abruptly either qualitatively or quantitatively, and thus no clear biological criterion to decide what shared level of cohesion should be equated with the species rank (e.g. Dupre, 2000; Mishler, 2000). Again, the statement 'organism X belongs in species Y' is unfalsifiable, since the boundaries of species Y can be moved arbitrarily by subjective

changes in the amount of cohesion considered appropriate for the species rank.

Thus, under cohesion species concepts there is no objective criterion for recognizing the species category, and accordingly the 'species' recognized do not have properties qualitatively distinguishing them from other (intraspecific and supraspecific) entities. All the entities above the organismal level recognized under this system, including 'species', are clusters of organisms that share varying degrees of cohesion. Some advocates of this type of species concept have therefore paradoxically questioned the validity of the species rank (e.g. Mallet, 1995).

Monophyly concepts

The monophyletic species concept (Mishler & Brandon, 1987; Mishler & Theriot, 2000) states that all species must be monophyletic entities, and then uses other criteria to determine which clades should be assigned to the species category. Clades '... are ranked as a species rather than at some higher level because they are the smallest monophyletic lineage deemed worthy of formal recognition, because of the amount of support for their monophyly and/or because of their importance in biological processes ...'(Mishler & Theriot, 2000 p. 47).

This concept is problematic firstly because the concept of monophyly, even if generalized to entities such as populations and individuals, is only easily applicable if those entities have nonreticulating relationships (e.g. de Queiroz & Donoghue, 1988). In sexual taxa, individual organisms and populations exhibit reticulating relationships, and thus a single organism from two parents, or population connected by gene flow with other populations, cannot be considered 'monophyletic', i.e. descended exclusively from a single entity of like kind. Because of their mixed ancestries, they cannot be neatly arranged into nested (diverging) hierarchies of clades, some of which can then be ranked as species. Similarly, ancestral populations are paraphyletic with respect to other populations. These nonmonophyletic populations would not be assignable to species at all (e.g. de Queiroz & Donoghue, 1988). The idea of monophyly, and recognition of clades, can only be readily applied to nonreticulating entities with hierarchical relationships. Although reticulation has been argued to be problematic not just for analyses around the species level, but at higher levels too (e.g. Mishler, 2000), it is likely to be a more prevalent at lower levels.

Disregarding this difficulty, let us assume that one can recognize clades of populations upwards, and wishes to divide these into 'monophyletic' species. However, higher taxa are also clades, so determining which clades should be ranked as species, and which as higher taxa, cannot be done objectively. Criteria suggested to determine which clades should be ranked as species rank

are vague and, more problematically, also characterize higher taxa. These include such features as number of synapomorphies, geographical distribution, phenotypic, genetic and ecological distinctness ('cohesion'), overall diversity, geological age, or importance in biological processes. The problems with trying to rank taxa using these criteria have been discussed above, and apply here. As acknowledged by Mishler & Theriot (2000), there are no clear criteria for ranking a clade at one level (e.g. species) rather than another (e.g. genus), and the species-level entities recognized using these criteria will not differ in any qualitative way from entities assigned to other ranks such as genera (de Queiroz & Donoghue, 1988). Indeed, recent works advocating recognition of only monophyletic basal taxa have emphasized that these do not differ from other clades, and thus should not be called species (Pleijel & Rouse, 1999, 2000).

Interbreeding concepts

A group of species concepts use interbreeding to demarcate the species category (rank). The biological, recognition, reproductive competition and generic species concepts identify species as the largest biological entities undergoing (regular or significant) genetic recombination. They differ in emphasizing, respectively, either overall reproductive isolation between different species (Mayr, 1963, 2000a), shared mate recognition systems within a species (Paterson, 1985), common reproductive resources within a species (Ghiselin, 1974), or adaptive genes linked pleiotropically to reproductive incompatibility (Wu, 2001 and accompanying commentaries). These concepts are all designed to delimit species at a given point in time. The cladistic or 'Hennigian' species concept (Meier & Willman, 2000) also uses interbreeding, defining species as the branches between successive cladogenetic events (i.e. successive origins of reproductive isolation). Although the cladistic species concept is largely a diachronic concept for delimiting lineages through time, it can also be applied at a given point in time. If two taxa do not interbreed, they must be separated by at least one cladogenetic event (and are separate species). If they interbreed, they most probably have not been separated by a speciation event and are conspecific (secondary introgression is a less likely possibility, but even here it can be argued that the observed taxon represents a fused individual and thus a single species). Under all five concepts, species at a given point in time are groups of organisms which interbreed with each other and are reproductively isolated from other species. Thus, all five concepts employing gene flow would tend to delimit the same taxa as species, and thus to draw the boundary of the species rank in the same place.

Like other criteria for recognizing the species rank (similarity, cohesion, monophyletic inclusiveness), interbreeding is not all-or-nothing, but a matter of degree.

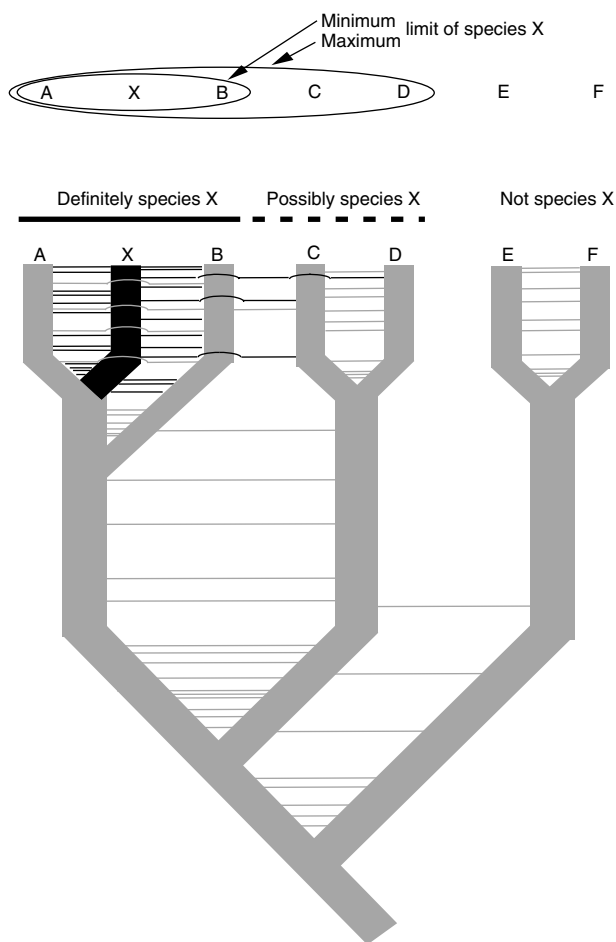


Fig. 1 Determining the limits of the species rank using interbreeding criteria. Thick lines denote populations, thin horizontal lines denote instances of gene flow (interbreeding). The focal population (containing the type series), and its interbreeding connections with other populations, are highlighted in black. With respect to the focal population, most populations can be identified unequivocally as conspecific (A, B) or heterospecific (E, F, and more distantly related populations G–Z not shown). The uncertainty over the position of the species boundary only affects a few populations (C, D).

Two taxa can be totally panmictic, totally isolated, and everything in between (e.g. Mishler, 2000). However, there is one important difference. Unlike the transition between total and zero similarity (or cohesion), the transition between regularly interbreeding entities, and those that never interbreed, is localized to a particular region of a phylogeny. For instance (Fig. 1), imagine we wish to delimit the boundary of the species containing a type organism (or type series of organisms) from a particular (focal) population X. One can observe that some populations (A and B) interbreed regularly with the focal population, a few populations (C and D) interbreed very occasionally with the focal population, and finally all other populations of organisms (which comprise the

vast majority of life on earth) never interbreed with the focal population (E, F, ..., Z). The species boundary – under any interpretation employing interbreeding criteria – must at least include the focal population and freely interbreeding populations A and B, and exclude the reproductively isolated populations E, F, ..., Z. The precise position of the species boundary with respect to a few populations (C and D) is ambiguous, because it is dependent on how much gene flow one decides is enough to warrant inclusion in the same species. Thus, with reference to a particular focal population, most organisms can be unequivocally either deemed conspecific (interbreeds with focal population) or heterospecific (reproductively isolated from focal population). The statement ‘organism X belongs in species Y’ can be empirically evaluated and falsified. In any given phylogeny, the inclusiveness of the species taxa can therefore be objectively defined within finite limits. The species boundaries must be drawn at a level somewhere between entities with regular gene flow, and those with none at all. The hazy intervening region (with partial and irregular gene flow) can be very narrow, e.g. in many higher animals, or rather broad, e.g. in many plants (Hey, 2001). Species boundaries (and the species rank) in any phylogeny, accordingly, lies in the zone where reticulate relationships change to hierarchical relationships.

Such relatively narrow (or at least, not infinitely wide) limits on species boundaries do not occur with other species criteria such as phenetic similarity, cohesion, or monophyletic inclusiveness, as discussed above. For instance, if degree of phenetic similarity is adopted for recognition of the species rank, two taxa would only be invariably recognized as the same species if they are ‘totally’ similar (0% phenetic difference) and invariably as different species if they are totally different (100% phenetic difference). Taxa with an intermediate amount of difference might or might not be assigned to the same species, depending on the amount of similarity one adopts as characteristic of the species category. Unlike the transition from panmixis to reproductive isolation, the transition between 100% phenetic similarity, and 100% difference, which marks the inner and outer allowable limits of the (phenetic) species rank, cannot be shown to occur at a localized region in a phylogeny. Thus, compared with reproductive criteria, phenetic criteria are much hazier with respect to species boundaries. Similar problems beset cohesion and monophyletic species criteria: cohesion and monophyly occur to varying degrees across large stretches, if not most, of life.

Reproductive isolation (or its converse, interbreeding) provides a sharper criterion to objectively define the species category, i.e. what taxa should be accorded the species rank. Because reproductive isolation occurs in degrees, some ambiguity will remain, but much less compared with other proposed criteria. Also, if species are defined as the largest units exhibiting regular genetic recombination, then clear ontological differences would

exist between species, lower taxa, and higher taxa. The species rank would coincide with the level of a phylogeny where gene flow changes from regular to none. Species would be the largest biological entities exhibiting reproductive interaction of parts (interbreeding between component organisms), and would be 'individuals' in the paradigmatic and most restricted sense (e.g. Ereshefsky, 1991, 2001; Sober, 1993; Baum, 1998; Lee & Wolsan, 2002). Lower taxa would be biological populations that interbreed with each other, and thus, the building blocks of (noninterbreeding) species. Higher taxa would be nonintegrated assemblages of lineages (species) united only by shared history, and would not be 'individuals' in the most restricted sense of the term. Even if one extends the term 'individuals' to include such nonintegrated historical assemblages (e.g. Kluge, 1990; Ghiselin, 1987, 1997), the clear ontological divide between integrated species, and nonintegrated clades, remains. In contrast, the species category, if based on phenetic, cohesion or monophyletic criteria, is not qualitatively distinct from higher taxa or lower taxa.

Interbreeding species concepts therefore appear to have more ontological validity, but to be useful must also be workable empirically. This section has focused on the former issue; empirical criticisms of such concepts are addressed below.

A conservative solution to the species problem

The issues over the reality of higher taxon categories (genera, families, etc.) are relevant to the question of the validity of the species category. Despite the voluminous literature on the nature of species, the implications of various species concepts for the delimitation and uniqueness of the species category (rank) have been poorly discussed. It has here been suggested that only species concepts based on reproduction can provide (reasonably) clear criteria for where to draw the species rank, i.e. assigning a given taxon to the species category as opposed to a higher or lower category. Reproductive concepts are also the only criteria that result in a clear ontological divide between species, 'higher taxa', and 'lower taxa'. Species are largest biological entities exhibiting reproductive interaction of parts, whereas lower taxa are these interacting parts, and higher taxa are nonintegrated groups of species united only by shared ancestry. If one wants to advocate the view that species are a distinct ('real') level of biological organization with special properties, one must adopt interbreeding species concepts. This also makes the boundary of each species directly discernable (at least within limits, see below). Conversely, if one uses phenetic, cohesion, or monophyletic criteria for recognizing species, it is hard to determine which taxa should be accorded the species rank. Species defined using such criteria will not be fundamentally distinct from other (higher) taxa, and there will be frequent debates over boundary of each

species, leading to futile splitting and lumping debates. Such problems have been highlighted, accompanied by calls for the rejection of the species category (e.g. Ereshefsky, 2000; Mishler, 2000). These suggestions have often come from workers who allow cohesion or monophyletic concepts of species. Since such concepts do not result in a clear ontological difference between species and other taxa, it is not surprising that workers employing these criteria have argued that the species category is artificial, uninformative and unnecessary.

Though interbreeding species concept have ontological merits, they also have empirical problems which have been repeatedly discussed (e.g. Sokal & Crovello, 1970; Wheeler & Meier, 2000; Hey, 2001). One common argument – that reproductive isolation comes in degrees leading to 'fuzziness' of species boundaries – is not very relevant, since all other proposed species criteria for delimiting the species rank (inclusiveness) fare even worse in this respect. The boundaries of all objects, even apparently discrete ones, e.g. continents and oceans, will become hazy as the scale of perception is reduced, e.g. satellite image vs. walking along the beach (see O'Hara, 1997). Similarly, the argument (Sokal & Crovello, 1970) that interbreeding is rarely directly observed, but is usually inferred through phenotypic or genetic traits, is also not very relevant. Cohesion and monophyletic species are also not diagnosed using those criteria directly (e.g. monophyly is very difficult to directly observe without a time machine), but instead usually diagnosed by character distributions. Higher taxa (clades) are also never directly observed, but again inferred through character distributions (e.g. Hennig, 1966). The definition and diagnosis of a taxon can be logically separated (Rowe, 1987; de Queiroz & Gauthier, 1992). A species can be *defined* as the largest unit exhibiting regular gene flow that includes the type organism(s); the extent of these connections (i.e. species boundaries) are manifested as and *diagnosed* through traits of individual organisms. For some species boundaries, a precise diagnosis will exist, through measured traits that are directly related to reproductive isolation, e.g. F_{ST} , molecular variance, or gene coalescences. For others, only a coarse diagnosis will exist, through measured traits that are only loosely correlated with reproductive isolation, e.g. divergence in phenotype, allozymes or DNA sequences (see Ferguson, 2002; Fitzpatrick, 2002 for recent critiques). Different markers are not always accurate and might give conflicting results. Frequent dependence on the use of additional criteria for diagnosing an interbreeding species does not mean the concept is nonoperational; it just means that other traits can be used as proxies (of varying reliability) for the variable of interest, gene flow. In this connection, adoption of reproductive concepts does not mean rejection of the vast majority of existing species, which have been recognized by phenotypic features. It just means that in those species, the only marker so far used to infer reproductive isolation has been phenotypic

divergence – use of additional markers might lead to refinements, as in the numerous cases of sibling or polytypic species that have been uncovered by genetic analyses.

Allopatric populations which can potentially interbreed (e.g. in artificial crosses) have also been viewed as highly problematic for reproductive species concepts (e.g. Ehrlich & Raven, 1969; Mallet, 1995). However, this difficulty fades if one realizes that even in a panmictic population, every individual is not simultaneously interbreeding with every individual. Rather, the potential for interbreeding between all individuals exists, and is being realized at an appropriate time scale: in this case, a few generations (Sober, 1993; Baum, 1998). The same applies to interbreeding populations in a species. Although each population of a species is not simultaneously interacting with every other population, the potential exists and is being realized over the appropriate time scale: in this case, perhaps dozens or hundreds of generations. Thus, populations isolated from other populations for periods within the appropriate time scale can still be said to be conspecific, in much the same way a temporarily non-reproductive individual can still be said to belong to a particular population. This view also alleviates the need to use the problematic phrase ‘potentially interbreeding’ in definitions of biological species. Populations (like individual organisms) which reproductively interact on the appropriate time scales can be considered interbreeding, whether or not they are doing so at any instant in time.

It has also been widely recognized that interbreeding species do not necessarily correspond to clades. However, despite being argued by some to be problematic for taxonomy (Pleijel, 1999; Ereshefsky, 2000), this mismatch is precisely what makes the species category worthy of special recognition: interbreeding species are *not* merely a type of clade, but a different type of biological entity altogether. The species category reflects a qualitatively different aspect of biological organization – interbreeding rather than ancestry (de Queiroz & Donoghue, 1988). Another common argument against interbreeding concepts is that rigid (or, phrased more positively, ‘consistent’) application of such criteria would recognize overly ‘large’ or ‘small’ species (e.g. Templeton, 1989; Ereshefsky, 2000; Wheeler & Meier, 2000). For instance, many highly distinct plant taxa conventionally assigned to separate species (or even genera) undergo regular genetic interchange (e.g. Ellstr *et al.*, 1996), whereas such phenomena is much rarer in animals (e.g. Dowling & Secor, 1997). Finer scale patterns also occur. Even relative to other animals, the limits to interbreeding are extremely narrow in onychophorans (velvet worms), with multiple almost indistinguishable species occurring in extremely restricted and often sympatric distributions (Trewick, 2000). Consistent application of an interbreeding species criterion would result in individuation of large polytypic plant species,

and narrower animal species epitomised by a plethora of cryptic onychophoran species. Although some have suggested this result is problematic (Dupré, 2000; Hey, 2001), it might instead be viewed as *illuminating*. The species in such classifications would directly reflect biological phenomena: interbreeding is generally wider in plants and more localized in animals, being particularly restricted in onychophorans. In turn, this taxonomy would prompt investigation why barriers to gene flow are more effective in some groups than in others, e.g. because of behavioural complexity, low vagility, or gametic incompatibility. Because a single criterion (interbreeding) has been consistently applied, the resultant species are equivalent (comparable according to that criterion), and differences in their nature (e.g. morphological or ecological diversity) will reflect biological phenomena. All species share something, and the species category means something. In contrast, if strong species pluralism is adopted which encompasses concepts other than those related to interbreeding (e.g. Mishler & Donoghue, 1982; Kitcher, 1988; Dupre, 1993, 2000; Ereshefsky, 2000), there might be a temptation to invoke ‘cohesion’ criteria to subdivide heterogeneous interbreeding plant species into smaller more cohesive ‘species’. Any resultant equivalence between plant and animal species would then be misleading, since they are delimited using different criteria. Conversely, if species in one group are much more diverse than those in another group, this difference will not necessarily reflect biology, but could be artefacts of different species concepts. It has previously been acknowledged that employment of multiple species concepts results in the species category being a heterogeneous and artificial collection of non-equivalent entities (e.g. de Queiroz & Donoghue, 1988; Ereshefsky, 2000; Mishler, 2000). One possible escape from this conundrum is to embrace such species pluralism (Ereshefsky, 2001) and reject the reality of the species category (Ereshefsky, 2000). However, this seems internally inconsistent – many species concepts are acceptable but the species rank itself is not real. The alternative approach is more conservative: to adopt a more monistic view of species that only uses concepts directly implicating interbreeding, and thus salvage the reality of the species category.

In this respect, the ‘general lineage’ concept of species, which attempts to reconcile species pluralism and monism, deserves consideration. This view considers that most modern (i.e. cohesion, monophyletic and interbreeding) species concepts are similar because they all attempt to delimit distinct lineages (de Queiroz, 2000). The definition and illustration of lineages as unbranched, single paths suggests that any two contemporaneous lineages are effectively reproductively isolated from each other. Different species concepts simply employ different criteria as landmarks to determine when one lineage (species) splits into two: phenotypic divergence, genetic divergence, reciprocal monophyly, or gene flow. Speciation

is a gradual process, and even if loss of gene flow is adopted as the sole species criterion, that there will be a grey area during any speciation when gene flow is present but heavily restricted, and it is uncertain whether one or two species exist. If various species concepts all draw the species boundary between in this grey area, they would all individuate entities that consistent with those delimited by the interbreeding criterion. Using the general lineage approach, it might be claimed that all these concepts could be embraced as being (at least indirectly and approximately) capturing the patterns of changes in gene flow. However, this is not the case, as some concepts can draw the species boundary outside the allowable 'grey area'. For instance, the cohesion concept could recognize noninterbreeding but phenotypically similar lineages as a single species, whereas interbreeding concepts would clearly individuate these as separate species. In time those entities will probably become phenotypically distinct and also be separated even under cohesion concepts (de Queiroz, 2000), but this does not address the problem that they are currently inappropriately lumped into the same species using that concept. An analogy with paradigmatic individuals such as humans might be helpful. The time when a pregnant woman becomes a mother and child occurs sometime between formation of the zygote and the severance of the umbilicus. Certain criteria for recognizing when a developing embryo becomes an individual – e.g. gastrulation, neuralation, formation of a brain, childbirth – would correctly identify the transition from one individual to two as occurring within this period. These might therefore all be valid criteria (concepts) to determine when a new individual arises. However, other criteria – e.g. nutritional independence, christening – would inappropriately consider a mother and a (breastfeeding or unnamed) baby as a single person long after they are separate individuals. Given sufficient time, these criteria would correctly split the mother and child into two individuals, but this doesn't change the problem that they are currently inappropriately considered a single person. Although all the concepts for individuating people capture stages in the extended process of human reproduction, some of them more reasonably mark the boundary when an individual becomes two. Based on this reasoning, the general lineage approach could be considered compatible with the rather monistic view of species advocated here, provided that it includes only species concepts compatible with interbreeding, i.e. concepts that consistently individuate species somewhere between reduction and loss of gene flow. It is likely that this requirement would exclude cohesion and monophyletic concepts from the allowable range of concepts, leaving only the tight cluster of similar interbreeding concepts, but this needs to be confirmed empirically.

The above arguments imply that clonal (asexual) species, which do not exhibit interbreeding, cannot

form true species (e.g. Eldredge, 1985; Ghiselin, 1987). They merely form monophyletic clans (clades of organisms) of varying inclusiveness, and no special property can be found to separate 'species-level' lineages from 'higher taxa'. Such organisms might apparently form cohesive assemblages separated by distinct gaps from other assemblages, but closer inspection will probably reveal that such discontinuities exist at all levels in the organismal hierarchy (e.g. Mishler, 1990, 2000). When examined closely, even an apparently homogenous ('basal') lineage of clones will exhibit some internal heterogeneity, with certain individuals being more similar than others (even genetically identical organisms will vary because of phenotypic plasticity, for instance). The situation is, of course, similar in sexual species, leading to problems with recognizing the species rank in sexual species unless interbreeding is invoked. However, in asexual species, the interbreeding criterion is not available to define the species category (rank). The only criteria available to delimit whether a given asexual clan should be assigned to the species rank are phenetic similarity, cohesion and monophyletic inclusiveness – all of which occur throughout phylogeny. Thus, it will be impossible to objectively draw the line between lineages that can be assigned to the species rank, those that merely represent variation within a species, and those that represent groups of species ('higher taxa'). Even if such ranking is done arbitrarily, there will be no clear ontological distinction between the asexual 'species' recognized, and the asexual 'higher taxa' recognized. Although most of life (arguably) consists of clonal organisms, and there is thus an obvious desire to assign them to species using a universally applicable concept (e.g. Templeton, 1989; Ereshefsky, 2001; Hey, 2001), this endeavour could be futile.

Given the entrenchment of the term 'species' across the entire tree of life (and beyond: Kitcher, 1988), and in popular as well as scientific discourse, it is unlikely to be possible to restrict it to interbreeding assemblages of sexual organisms. A pragmatic partial solution would be to at least highlight the different types of entities masquerading as species by always describing the species concept adopted (Hey, 2001). However, this might be cumbersome in most works which use the term species, where the focus is not on systematics. A more solution would be to use prefixes to indicate the species concept employed. Interbreeding species (e.g. many animals) could be termed biospecies (Grant, 1981), cohesion 'species' (e.g. many plants) could be called phylopecies (Ereshefsky, 2000), and asexual 'species' (e.g. bacteria) could be labelled agamospecies (Willman & Meier, 2000). In this way, one can immediately discern whether the entities discussed represent a distinct level of biological organization (biospecies) or taxa arbitrarily ranked as 'species' to facilitate communication or for historical reasons (phylospecies, agamospecies).

Acknowledgments

I thank Marc Ereshefsky, Greg Rouse, John Scanlon, Adam Skinner, Mark Adams and Terry Bertozzi for valuable comments and discussion, and the Australian Research Council and South Australian Museum for financial support.

References

- Baum, D. 1998. Individuality and existence of species through time. *Syst. Biol.* **47**: 641–653.
- Benton, M.J. 2000. Stems, nodes, crown-clades and rank-free lists: Is Linnaeus dead? *Biol. Rev.* **75**: 633–648.
- Bryant, H.N. & Cantino, P.D. 2002. A review of criticisms of phylogenetic nomenclature: is taxonomic freedom the fundamental issue? *Biol. Rev.* **77**: 39–55.
- Cain, A.J. 1954. *Animal Species and Their Evolution*. Princeton University Press, Princeton.
- Cracraft, J. 1983. Species concepts and speciation analysis. *Curr. Ornith.* **1**: 159–187.
- Darwin, C. 1859. *On The Origin of Species By Means of Natural Selection, Or, The Preservation of Favoured Races in the Struggle For Life*. John Murray, London (Penguin Classics reprint).
- Dobzhansky, T. 1937. *Genetics and the Origin of Species*. Columbia University Press, New York.
- Dowling, T.E. & Secor, C.L. 1997. The role of hybridization and introgression in the diversification of animals. *Ann. Rev. Ecol. Syst.* **28**: 593–619.
- Dupre, J. 1993. *The Disorder of Things: Metaphysical Foundations of the Disunity of Science*. Harvard University Press, Cambridge, MA.
- Dupre, J. 2000. On the impossibility of a monistic account of species. In: *Species: New Interdisciplinary Essays* (R. A. Wilson, ed.), pp. 3–22. MIT Press, Cambridge, MA.
- Ehrlich, P. & Raven, P. 1969. Differentiation of populations. *Science* **165**: 1228–1232.
- Eldredge, N. 1985. *Unfinished Synthesis: Biological Hierarchies and Modern Evolutionary Thought*. Oxford University Press, New York.
- Ellstr, N.C., Whitkus, R. & Rieseberg, L.H. 1996. Distribution of spontaneous plant hybrids. *Proc. Natl. Acad. Sci. U.S.A.* **93**: 5090–5093.
- Ereshefsky, M. 1991. Species, higher taxa, and the units of evolution. *Philos. Sci.* **58**: 84–101.
- Ereshefsky, M. 1992. *The Units of Evolution: Essays on the Nature of Species*. MIT Press, Cambridge, MA.
- Ereshefsky, M. 1997. The evolution of the Linnaean hierarchy. *Biol. Philos.* **12**: 493–519.
- Ereshefsky, M. 2000. Species and the Linnaean hierarchy. In: *Species: New Interdisciplinary Essays* (R. A. Wilson, ed.), pp. 285–306. MIT Press, Cambridge, MA.
- Ereshefsky, M. 2001. *The Poverty of The Linnaean Hierarchy: A Philosophical Study of Biological Taxonomy*. Cambridge University Press, Cambridge.
- Ferguson, J.W. 2002. On the use of genetic divergence for identifying species. *Biol. J. Linn. Soc.* **75**: 509–516.
- Fitzpatrick, B.M. 2002. Molecular correlates of reproductive isolation. *Evolution* **56**: 191–198.
- Gauthier, J., Kluge, A.G. & Rowe, T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* **4**: 105–209.
- Ghiselin, M.T. 1974. A radical solution to the species problem. *Syst. Zool.* **23**: 536–544.
- Ghiselin, M.T. 1987. Species concepts, individuality and objectivity. *Biol. Philos.* **2**: 127–143.
- Ghiselin, M.T. 1997. *Metaphysics and The Origin of Species*. State University of New York Press, Albany, NY.
- Grant, V. 1981. *Plant Speciation*. Columbia University Press, New York.
- Greuter, W., McNeill, J., Barrie, F.R., Burdet, H.-M., Demoulin, V., Filgueiras, T.S., Nicolson, D.H., Silva, P.C., Skog, J.E., Trehane, P., Turland, N.J. & Hawksworth, D.L. 2000. *International Code of Botanical Nomenclature (Saint Louis Code)*. Koeltz Scientific Books, Königstein.
- Griffiths, G. 1976. The future of Linnaean nomenclature. *Syst. Zool.* **25**: 168–173.
- Hennig, W. 1966. *Phylogenetic Systematics*. University of Illinois Press, Illinois.
- Hennig, W. 1969. *Die Stammesgeschichte der Insekten*. Waldemar Kramer, Frankfurt.
- Hey, J. 2001. *Genes, Categories and Species: The Evolutionary and Cognitive Causes of The Species Problem*. Oxford University Press, Oxford.
- Kitcher, P. 1988. *Species*. MIT Press, Cambridge, MA.
- Kluge, A.G. 1990. Species as historical individuals. *Biol. Philos.* **5**: 417–431.
- Lee, M.S.Y. 2001. On recent arguments for phylogenetic taxonomy. *Taxon* **50**: 175–180.
- Lee, M.S.Y. & Wolsan, M. Cohesion, individuality, and the nature of species. *Biol. Philos.* In press.
- Mallet, J. 1995. A species definition for the modern synthesis. *Trends Ecol. Evol.* **10**: 294–299.
- Mayr, E. 1963. *Animal Species and Evolution*. Harvard University Press, Cambridge, MA.
- Mayr, E. 2000a. The biological species concept. In: *Species Concepts and Phylogenetic Theory: a Debate* (Q. D. Wheeler & R. Meier, eds), pp. 17–29. Columbia University Press, New York.
- Mayr, E. 2000b. A critique from the biological species concept perspective: what is a species, and what is not? *Species Concepts and Phylogenetic Theory: a Debate* (Q. D. Wheeler & R. Meier, eds), pp. 93–100. Columbia University Press, New York.
- Meier, R. & Willman, R. 2000. The Hennigian species concept. In: *Species Concepts and Phylogenetic Theory: a Debate* (Q. D. Wheeler & R. Meier, eds), pp. 30–43. Columbia University Press, New York.
- Mishler, B. 1990. Reproductive biology and species distinctions in the moss genus *Tortula*, as represented in Mexico. *Syst. Bot.* **15**: 86–97.
- Mishler, B. 2000. Getting rid of species? *Species: New Interdisciplinary Essays* (R. A. Wilson, ed.), pp. 307–315. MIT Press, Cambridge, MA.
- Mishler, B. & Brandon, R.N. 1987. Individuality, pluralism, and the phylogenetic species concept. *Biol. Philos.* **2**: 397–414.
- Mishler, B. & Donoghue, M.J. 1982. Species concepts: a case for pluralism. *Syst. Zool.* **31**: 491–503.
- Mishler, B. & Theriot, E.C. 2000. The phylogenetic species concept (*sensu* Mishler and Theriot): monophyly, apomorphy and phylogenetic species concepts. In: *Species Concepts and Phylogenetic Theory: a Debate* (Q. D. Wheeler & R. Meier, eds), pp. 44–54. Columbia University Press, New York.
- Nixon, K.C. & Carpenter, J.M. 2000. On the other 'phylogenetic systematics'. *Cladistics* **16**: 298–318.
- O'Hara, R.J. 1997. Population thinking and tree thinking in systematics. *Zool. Scr.* **26**: 323–329.

- Paterson, H.E.H. 1985. The recognition concept of species. In: *Species and Speciation* (E. S. Vrba, ed.), pp. 21–29. Pretoria Transvaal Museum, Pretoria.
- Pleijel, F. 1999. Phylogenetic taxonomy, a farewell to species, and a revision of *Heteropodarke* (Hesionidae, Polychaeta, Annelida). *Syst. Biol.* **48**: 755–789.
- Pleijel, F. & Rouse, G.W. 1999. Least-inclusive taxonomic unit: a new taxonomic concept for biology. *Proc. R. Soc. Lond. B* **267**: 627–630.
- Pleijel, F. & Rouse, G.W. 2000. A new taxon, *capricornia* (Hesionidae, Polychaeta), illustrating the LITU ('least-inclusive taxonomic unit') concept. *Zool. Scr.* **29**: 157–168.
- de Queiroz, K. 1988. Systematics and the Darwinian revolution. *Phil. Sci.* **55**: 238–259.
- de Queiroz, K. 1997. The Linnaean hierarchy and the evolutionization of taxonomy, with emphasis on the problem of nomenclature. *Aliso* **15**: 125–144.
- de Queiroz, K. 2000. The general lineage concept of species and the defining properties of the species category. In: *Species: New Interdisciplinary Essays* (R. A. Wilson, ed.), pp. 49–89. MIT Press, Cambridge, MA.
- de Queiroz, K. & Donoghue, M.J. 1988. Phylogenetic systematics and the species problem. *Cladistics* **4**: 317–338.
- de Queiroz, K. & Gauthier, J. 1992. Phylogenetic taxonomy. *Ann. Rev. Ecol. Syst.* **23**: 449–480.
- Raff, R.A. 1996. *The Shape of Life: Genes, Development, and the Evolution of Animal Form*. University of Chicago Press, Chicago.
- Ride, D., Kraus, O., Cogger, H., Tubbs, P., Dupuis, C. & Thompson, C. 1999. *International Code of Zoological Nomenclature*, 4th edn. The Natural History Museum, London.
- Rowe, T. 1987. Definition and diagnosis in the phylogenetic system. *Syst. Zool.* **36**: 208–211.
- Simpson, G.G. 1961. *Principles of Animal Taxonomy*. Columbia University Press, New York.
- Sneath, P.H.A., ed. 1992. *International Code of Nomenclature of Bacteria*. International Union of Microbiological Sciences, Washington, DC.
- Sober, E. 1993. *Philosophy of Biology*. Westview Press, Boulder CO.
- Sokal, R. & Crovello, T. 1970. The biological species concept: a critical evaluation. *Am. Nat.* **104**: 127–153.
- Templeton, A.R. 1989. The meaning of species and speciation. In: *Speciation and its Consequences* (D. Otte & J. A. Endler, eds), pp. 3–27. Sinauer Associates, Sunderland, MA.
- Trewick, S.A. 2000. Mitochondrial DNA sequences support allozyme evidence for cryptic radiation of New Zealand peripatoides (Onychophora). *Molec. Ecol.* **9**: 269–281.
- Van Valen, L. 1976. Ecological species, multispecies, and oaks. *Taxon* **25**: 233–239.
- Wheeler, Q.D. & Meier, R. (eds). 2000. *Species Concepts and Phylogenetic Theory: A Debate*. Columbia University Press, New York.
- Wheeler, Q.D. & Platnick, N.I. 2000. The phylogenetic species concept (*sensu* Wheeler and Platnick). In: *Species Concepts and Phylogenetic Theory: a Debate* (Q. D. Wheeler & R. Meier, eds), pp. 55–69. Columbia University Press, New York.
- Wiley, E.O. & Mayden, R.L. 2000. The evolutionary species concept. In: *Species Concepts and Phylogenetic Theory: a Debate* (Q. D. Wheeler & R. Meier, eds), pp. 70–89. Columbia University Press, New York.
- Willman, R. & Meier, R. 2000. A critique from the Hennigian species concept perspective. In: *Species Concepts and Phylogenetic Theory: a Debate* (Q. D. Wheeler & R. Meier, eds), pp. 101–118. Columbia University Press, New York.
- Wu, C.-I. 2001. The genic view of the process of speciation. *J. Evol. Biol.* **14**: 851–865.

Received 11 November 2002; accepted 22 November 2002