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Branches in the lines of descent: Charles Darwin and the evolution of the species concept

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Charles Darwin introduced a novel idea into the concept of species, namely that species are branches in the lines of descent (segments of population lineages). In addition to this novel evolutionary component, Darwin's species concept also retained an older taxonomic component, namely the view that the species category is a taxonomic rank; moreover, he adopted amount of difference as a criterion for ranking lineages as species. Subsequent biologists retained both components of Darwin's species concept, although they replaced Darwin's ranking criterion with ranking criteria that either are more objectively defined or relate more directly to the biological bases of lineage separation and divergence. Numerous alternative ranking criteria were proposed, resulting in a proliferation of species definitions and a controversy concerning the concept of species. That controversy can be resolved by distinguishing more explicitly between the theoretical concept of species and the operational criteria that are used to apply the concept in practice. By viewing the various alternative ranking criteria as operational indicators of lineage separation rather than necessary properties of species, the conflicts among competing species concepts are eliminated, resulting in a unified concept of species. A brief examination of the history of biology reveals that an important shift related to the unified species concept has been emerging ever since Darwin reformulated the concept of species with an evolutionary basis. The species category is effectively being decoupled from the hierarchy of taxonomic ranks and transferred to the hierarchy of biological organization. Published 2011. This article is a US Government work and is in the public domain in the USA. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **103**, 19–35.

ADDITIONAL KEYWORDS: Evolutionary Synthesis – hierarchy of biological organization – incipient species – isolating mechanisms – lineage – phylogenetic systematics – species selection – taxonomic rank.

INTRODUCTION

24 November 2009 was the 150th anniversary of the publication of Charles Darwin's (1859) *On The Origin of Species by Means of Natural Selection*, one of the most influential works in the history of the biological sciences. Its influence transformed almost every field of biology and extended into many other arenas of human culture, including religion, politics, art, and literature. The 150th anniversary of such a significant publication provides an opportunity to re-examine that work in the context of subsequent developments, both to celebrate its historical influence and to highlight important similarities and differences relative to current thought.

The present article examines Charles Darwin's concept of species as described in *The Origin* and its influence on the subsequent evolution of the species concept. Several aspects of Darwin's species concept have been analyzed previously, including its relationship to essentialism (Mayr, 1982), strategic elements that may have helped Darwin to communicate his revolutionary views (Beatty, 1985), and whether Darwin viewed species as artificial or real entities (Kottler, 1978; Coyne & Orr, 2004; Stamos, 2007). Here, Darwin's species concept is examined as a combination of two distinct components: a newer evolutionary component according to which species are conceptualized as segments of population lineages, and an older taxonomic component according to which species are conceptualized as groups of organisms assigned to a particular rank in the hierarchy of

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taxonomic categories. First, these two components are described. Then, a summary is provided of some of the subsequent history of the species concept, describing how many later biologists adopted both components of Darwin's species concept but replaced Darwin's criterion for conferring the rank of species with a diversity of alternatives, creating a controversy about the concept of species. Next, recent developments are discussed that attempt to resolve this controversy, thereby achieving a unified species concept, by retaining the conceptualization of species as segments of population lineages but eliminating the treatment of the species category as a taxonomic rank. Finally, evidence is presented to show that the resulting unified concept of species has been developing ever since the acceptance of Darwin's proposal to equate species with segments of population lineages.

TWO COMPONENTS OF DARWIN'S SPECIES CONCEPT

In this section, the two components of Darwin's species concept are described, and characterizations are supported with quotations from the first edition of *The Origin*.

Species as lineage segments

By considering species in an evolutionary context, Darwin developed a concept of species that differed significantly from those of his predecessors. Although their views undoubtedly varied, most biologists prior to Darwin conceptualized species as self-perpetuating groups of similar organisms that had been endowed with those properties by a creator. As Darwin described those earlier views: 'Generally, the term ["species"] includes the unknown element of a distinct act of creation' (p. 44). By contrast, Darwin departed from then traditional views by considering species as descended from common ancestors, which led him to equate species with 'branches in the lines of descent' (p. 119). Thus, in his famous branching diagram (Fig. 1), the only figure in *The Origin*, the capital letters A through L at the bottom of the diagram represent the species of a genus existing at a particular time. Each is positioned at the top of a dotted line,

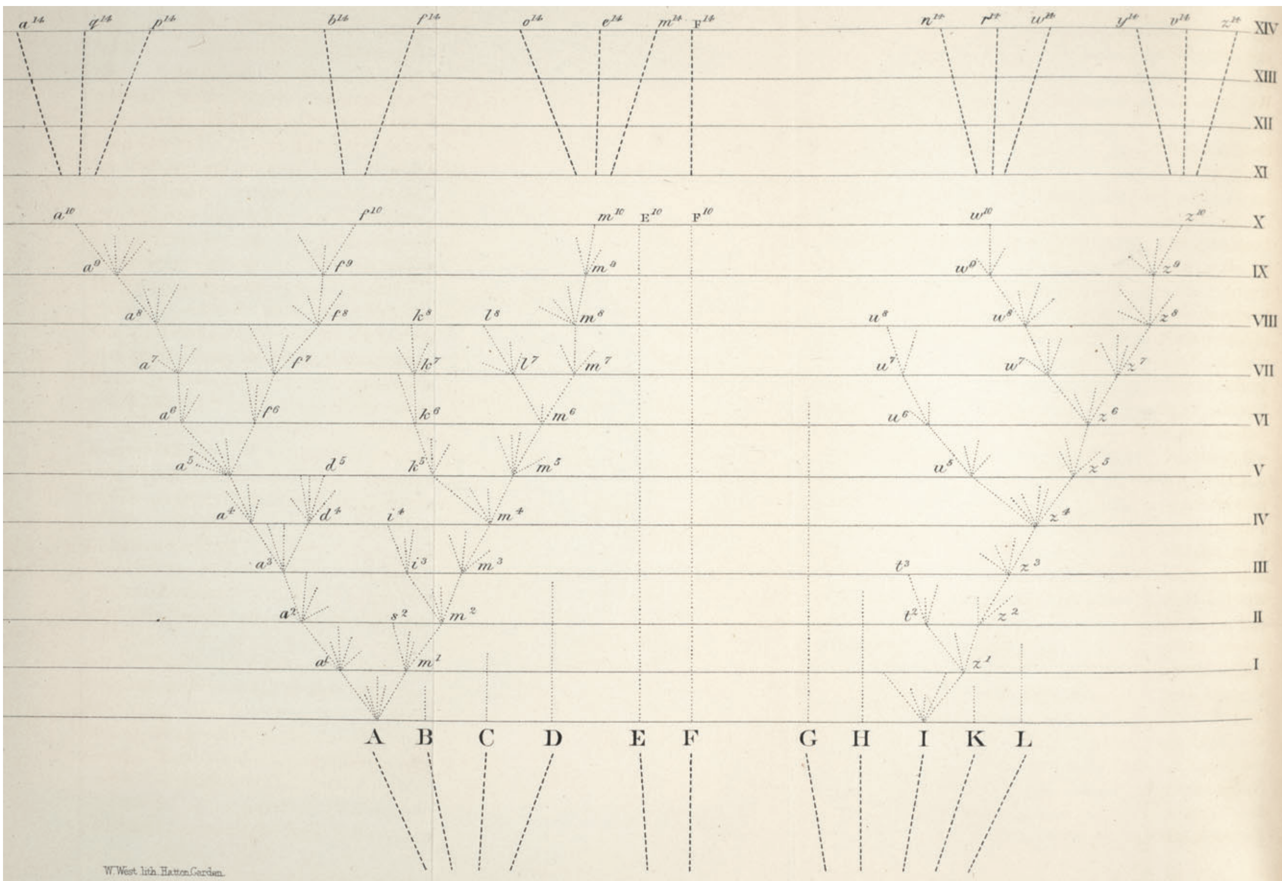

Figure 1. The branching diagram from *The Origin of Species*, which Darwin used to describe the process of descent with modification and how it results in the origin of new species.

representing descent from an earlier common ancestor, and each continues forward in time as either 'a single line of descent' (p. 119), as in the case of species F, or several diverging 'branches in the lines of descent' (p. 119), as in the case of species A. The passage is quoted here with the key phrases highlighted:

As all the modified descendants from a common and widely-diffused species, belonging to a large genus, will tend to partake of the same advantages which made their parent successful in life, they will generally go on multiplying in number as well as diverging in character: this is represented in the diagram by the *several divergent branches* proceeding from (A). The modified offspring from the later and more highly improved *branches in the lines of descent*, will, it is probable, often take the place of, and so destroy, the *earlier and less improved branches*: this is represented in the diagram by some of the lower branches not reaching to the upper horizontal lines. In some cases I do not doubt that the process of modification will be confined to a *single line of descent*, and the number of the descendants will not be increased; although the amount of divergent modification may have been increased in the successive generations. (pp. 119–120, italics added)

In this passage, no mention is made of the branches in the lines of descent being species, although the implication is obvious to 21st Century readers. That equivalency is established in the next paragraph:

After ten thousand generations, species (A) is supposed to have produced three forms, a^{10}, f^{10}, and m^{10}, which, from having diverged in character during the successive generations, will have come to differ largely, but perhaps unequally, from each other and from their common parent. If we suppose the amount of change between each horizontal line in our diagram to be excessively small, these three forms may still be only well-marked varieties; or they may have arrived at the doubtful category of sub-species; but we have only to suppose the steps in the process of modification to be more numerous or greater in amount, to convert these three forms into well-defined species: thus the diagram illustrates the steps by which the small differences distinguishing varieties are increased into the larger differences distinguishing species. (p. 120)

In short, as lines of descent diverge from a common ancestor, their component branches become varieties, subspecies, and ultimately species.

Darwin's equation of species with 'branches in the lines of descent' is also evident in his likening of the proliferation and extinction of species to the growth of a great tree, presented in the summary of the same chapter (Natural Selection) as its powerful climax:

The affinities of all the beings of the same class have sometimes been represented by a great tree. I believe this simile largely speaks the truth. The green and budding twigs may represent existing species; and those produced during each former year may represent the long succession of extinct species. At each period of growth all the growing twigs have tried to branch out on all sides, and to overtop and kill the surrounding twigs and branches, in the same manner as species and groups of species have tried to overmaster other species in the great battle for life. The limbs divided into great branches, and these into lesser and lesser branches, were themselves once, when the tree was small, budding twigs; and this connexion of the former and present buds by ramifying branches may well represent the classification of all extinct and living species in groups subordinate to groups. (p. 129)

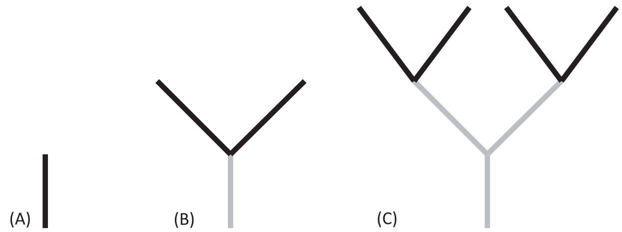

Figure 2. A simplified representation of the branches produced over three years in the life of an actual tree or the species produced over three rounds of speciation in the history of an evolutionary tree: t_1, when only a single branch (species) exists (A); t_2, after the single branch (species) that existed at t_1 has given rise to two descendant branches (species) (B); and t_3, after the two branches (species) that existed at t_2 have given rise to four descendant branches (species) (C). Black lines represent 'green and budding twigs' or extant descendant species; grey lines represent older branches or extinct ancestral species.

This description can be translated more-or-less directly into one in which, on a branching diagram similar to the one used by Darwin himself but simplified further into a contemporary phylogenetic tree, species are represented by the internodes (branches) that make up the various paths (lines of descent) through the tree. A simplified representation covering three years in the life of an actual tree or three generations of species in the history of an evolutionary tree is shown in Figure 2.

In sum, Darwin added a new component to the concept of species that equated species with segments of lineages (branches in the lines of descent). Not surprisingly, this new component was strongly tied to his evolutionary worldview. Moreover, as described in greater detail below, this evolutionary component underlies most subsequent and virtually all contemporary views on species and is fundamental to the modern species concept.

Incorporation of an evolutionary component into the concept of species also led Darwin to explore various consequences of this novel species concept. Here, I support the views of some recent authors, notably Mallet (2008) and Reif (2008), by providing additional evidence that Darwin's views on species and speciation, although often portrayed as lacking or misguided (Mayr, 1942, 1959, 1963, 1982; Futuyma, 1983, 1998; Coyne & Orr, 2004), are in many respects surprisingly modern. For example, contrary to Mayr's (1942, 1959, 1963) assertions that Darwin addressed the modification of species but not the multiplication of species, Darwin discussed the formation of new species in several places in *The Origin* (p. 174, 203, 292). I quote passages from his discussions of the circumstances favourable to natural selection (Chapter IV: Natural Selection) and the absence of transitional forms (Chapter VI: Difficulties on Theory) as examples:

> Lastly, isolation, by checking immigration and consequently competition, will give time for any new variety to be slowly improved; and this may sometimes be of importance in the production of new species. (p. 105)

Similarly:

> In the first place we should be extremely cautious in inferring, because an area is now continuous, that it has been continuous during a long period. Geology would lead us to believe that almost every continent has been broken up into islands even during the later tertiary periods; and in such islands distinct species might have been separately formed without the possibility of intermediate varieties existing in the intermediate zones. By changes in the form of the land and of climate, marine areas now continuous must often have existed within recent times in a far less continuous and uniform condition than at present. But I will pass over this way of escaping from the difficulty; for I believe that many perfectly defined species have been formed on strictly continuous areas; though I do not doubt that the formerly broken condition of areas now continuous has played an important part in the formation of new species, more especially with freely-crossing and wandering animals. (p. 174; see also p. 103 and letter to Moritz Wagner, F. Darwin, 1887: 159)

In these passages, Darwin discussed the role of geographic isolation, a factor considered of paramount importance by Mayr (1942, 1963, 1970), in the formation of new species, including its greater importance in vagile, sexually reproducing organisms (including most birds, the group on which Mayr conducted most of his empirical research). Nor should it be assumed that Darwin's reference to the formation of new species 'on strictly continuous areas' is an endorsement of sympatric speciation (contra Mayr, 1959), for he was contrasting continuous continental landmasses (which exhibit significant internal geographic barriers) with their previous fragmentation into separate islands. On the other hand, Reif (2008) has argued that the roots of most currently recognized speciation models can be found in Darwin's work, including allopatric, peripatric (founder effect), clinal, stasipatric, and sympatric speciation.

A second example of Darwin's forward-thinking views on species is his recognition of most of the phenomena that would later come to be referred to as reproductive isolating mechanisms (Dobzhansky, 1937a, 1970; Mayr, 1942, 1963, 1970). As evidence, I quote some passages from *The Origin*, inserting corresponding terms from the classification of isolating mechanisms outlined by Mayr (1970) in brackets. Thus, in his discussions of circumstances favourable to natural selection (Chapter 4), Darwin stated:

> I can bring a considerable catalogue of facts, showing that within the same area, varieties of the same animal can long remain distinct, from haunting different stations [habitat isolation], from breeding at slightly different seasons [seasonal isolation], or from varieties of the same kind preferring to pair together [ethological isolation] (p. 103).

Later, in his discussion of the causes of the sterility of first crosses and hybrids (Chapter 8), he noted:

> There must sometimes be a physical impossibility in the male element reaching the ovule [mechanical isolation], as would be the case with a plant having a pistil too long for the pollen-tubes to reach the ovarium. It has also been observed that when pollen of one species is placed on the stigma of a distantly allied species, though the pollen-tubes protrude, they do not penetrate the stigmatic surface. Again, the male element may reach the female element, but be incapable of causing an embryo to be developed [gametic mortality: sperm transfer takes place but egg is not fertilized], as seems to have been the case with some of Thuret's experiments on Fuci. . . . Lastly, an embryo may be developed, and then perish at an early period [zygotic mortality] (pp. 263–4).

Darwin then contrasted these situations, in which the male and female elements of different species are functional but incompatible, with cases involving 'the sterility of hybrids [hybrid sterility]' (p. 264), in which the sexual elements are nonfunctional. The only isolating mechanism in Mayr's list that is absent from Darwin's is that of hybrid inviability. Nonetheless, Darwin noted that interspecific hybrids have 'their whole organisation disturbed by being compounded of two distinct species' (p. 277) and implied that this situation would be expected to have unfavourable consequences for vigor (viability) as well as fertility (pp. 277, 461). It is also worth noting that the sets of phenomena covered in the different chapters approximately correspond to the modern distinction between premating and postmating isolating mechanisms.

In sum, Darwin not only introduced the conceptualization of species as segments of population level lineages (branches in the lines of descent), but also he addressed various factors related to that novel view, including the role of geographic isolation in the formation of separately evolving species-as-lineages, and the various intrinsic reproductive barriers ('isolating mechanisms') between organisms of different species-as-lineages that allow them to evolve separately in sympatry.

The species as a taxonomic rank

Despite Darwin's novel evolutionary conceptualization of species as lineage segments, his species concept retained at least one element from an older taxonomic tradition. This second, more traditional component of Darwin's species concept was the treatment of the species category as a rank in the taxonomic hierarchy (Linnæus, 1758; Cuvier, 1817; Swainson, 1835) which, in 1859, consisted of the primary ranks: kingdom, class, order, family, genus, species, variety. Below, two of many passages from *The Origin* that could be quoted to illustrate Darwin's treatment of the species category as a rank are provided:

> Hence, in determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgment and wide experience seems the only guide to follow. (p. 47)

> Many of the cases of strongly-marked varieties or doubtful species well deserve consideration; for several interesting lines of argument, from geographical distribution, analogical variation, hybridism, &c., have been brought to bear on the attempt to determine their rank. (p. 49).

Related to his treatment of the species as a taxonomic rank, Darwin adopted a traditional criterion for assigning the rank of species – amount of difference (along with the absence of intermediates). Thus, according to Darwin:

> . . . in those cases in which intermediate links have not been found between doubtful forms, naturalists are compelled to come to a determination by the amount of difference between them, judging by analogy whether or not the amount suffices to raise one or both to the rank of species. Hence the amount of difference is one very important criterion in settling whether two forms should be ranked as species or varieties. (pp. 56–57)

> Undoubtedly there is one most important point of difference between varieties and species; namely, that the amount of difference between varieties, when compared with each other or with their parent-species, is much less than that between the species of the same genus. (p. 57)

Both the view of the species category as a rank and the adoption of amount of difference as a ranking criterion were tied closely to Darwin's propositions that species do not differ fundamentally from varieties and subspecies, and that they also share certain properties with genera. These propositions formed an important part of Darwin's arguments that varieties are incipient species (i.e. that varieties evolve into species) and that taxa at all ranks in the taxonomic hierarchy can be explained by the process of descent with modification. The quotations below illustrate the absence, in Darwin's view, of a fundamental distinction between species and taxa of lower rank, as well as the similarity, in at least one respect, between species and taxa of higher rank.

> From these remarks it will be seen that I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms. (p. 52)

> Finally, then, the facts briefly given in this chapter [Hybridism, Chapter VIII] do not seem to me opposed to, but even rather to support the view, that there is no fundamental distinction between species and varieties. (p. 278)

> In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. (p. 485)

Various authors have interpreted Darwin's statements about the arbitrary and artificial nature of the species category as suggesting that species are not 'real' (e.g. Hull, 1965: 320; Mayr, 1970: 13; Ereshefsky, 1992: 190; for other examples, see Stamos, 1996, 2007). However, it seems clear from Darwin's proposition that species are segments of lineages (see previous section) that he most certainly considered species to be real in the sense that they exist in nature and not only in the human mind (even if their boundaries are not always sharp to a human observer). That which Darwin considered arbitrary and artificial was not the lineages (species) themselves but the act of ranking those lineages as species rather than varieties or subspecies. Thus, according to Darwin:

> On the view that species are only strongly marked and permanent varieties, and that each species first existed as a variety, we can see why it is that no line of demarcation can be drawn between species, commonly supposed to have been produced by special acts of creation, and varieties which are acknowledged to have been produced by secondary laws. (p. 469)

This passage indicates that Darwin viewed species-as-lineages to be real in the sense of being acted on by 'secondary laws' (natural processes) and that what he considered arbitrary and artificial was the line of demarcation between species and varieties.

Darwin's treatment of the species as a taxonomic rank also explains why he sometimes considered a species to be made up of several diverging (and possibly separately evolving) lines of descent (e.g. the descendants of species A in his diagram; Fig. 1) rather than as single lines (e.g. the descendants of species

F). Because Darwin adopted amount of difference as a ranking criterion, several descendant lineages of a common ancestor could evolve separately for some time before they diverged enough to be considered different varieties, different subspecies, and finally different species. In short, Darwin's treatment of the species as a rank and his adoption of amount of difference as a ranking criterion led him to adopt the implicit position that all species are separately evolving lineages but not all separately evolving lineages are species. Only those separately evolving lineages that had evolved a certain amount of difference from other such lineages were to be ranked as species; those that had not evolved the requisite amount of difference were to be ranked as subspecies, varieties, or nothing at all.

In contrast to the lineage component of Darwin's species concept, which was novel at the time of publication of *The Origin* and closely associated with an evolutionary worldview, the second component of Darwin's species concept, the treatment of the species as a taxonomic rank, was a holdover from the earlier pre-evolutionary era. Nevertheless, it persisted long after the evolutionary worldview became widely accepted, and it was partly responsible for a period of confusion and controversy concerning the concept of species that is only now in the process of being resolved. Fortunately, treatment of the species as a taxonomic rank is not fundamental to the modern species concept; indeed, its elimination appears to be the key to resolving much of the confusion and controversy surrounding contemporary views on species.

POST-DARWINIAN SPECIES CONCEPTS

In this section, the two components of Darwin's species concept described above are discussed in the post-Darwinian era. The aim is not to present a thorough historical analysis, but only to document the status of the two components in the modern era, which, here, is equated with the period starting with the Evolutionary Synthesis (Mayr & Provine, 1980) and continuing to the present time.

Species as lineage segments

Post-Darwinian biologists increasingly accepted the evolutionary component of Darwin's species concept. That they did so is evident in the species definitions of a number of middle and late 20th Century authors, who explicitly equated species with lineages. For example:

> An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies. (Simpson, 1961: 153)

> A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range. (Van Valen, 1976: 233)

> A species is a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate. (Wiley, 1978: 18)

Of course, many other 20th Century authors did not use the term 'lineage' in their explicit species definitions. Instead, they described species as populations or reproductive communities. For example:

> Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups. (Mayr, 1942: 120)

> The biological species is the largest and most inclusive Mendelian population [a reproductive community of sexual and cross-fertilizing individuals which share in a common gene pool]. (Dobzhansky, 1950: 405)

> . . . a species [is] that most inclusive population of individual biparental organisms which share a common fertilization system. (Paterson, 1985: 25)

This difference in terminology (i.e. 'lineage' versus 'population') simply reflects differences in temporal perspective. As Simpson (1951) pointed out, a lineage is a population extended through time and, conversely, a population is a lineage at a particular moment in time (i.e. a temporal cross section of a lineage). This correspondence between populations and lineages is reflected in Simpson's (1951, 1961) own species definition, in which he explicitly equated a lineage with an ancestral–descendant sequence of populations. In this context, definitions that equate species with lineages and those that equate them with populations simply reflect time-extended and time-restricted perspectives on the same general species concept. (Here, I am referring to lineages at the population level, as entities at several other levels of biological organization, such as cells and organisms, also form lineages.)

Some clarifications may be useful here. First, populations form a continuum from small demes to large metapopulations (groups of connected subpopulations). When authors equate species with populations, they generally mean those at the more inclusive end of the continuum. Second, a lineage is not the same thing as a clade, although the two concepts are often confused terminologically. A lineage is a direct line of ancestry and descent (Fig. 3A); by contrast, a clade is a group composed of an ancestor and all of its descendants (Fig. 3B). One important difference is that lineages are unbranched (which is not to say that

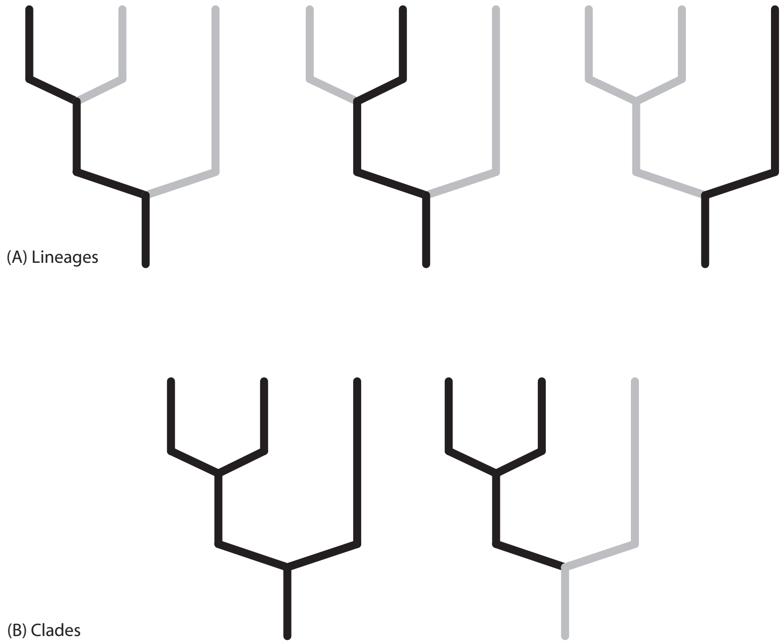

Figure 3. Lineages contrasted with clades. All five trees represent the same phylogeny with three different lineages highlighted in (A) and two different clades highlighted in (B). Note that the lineages are unbranched and partially overlapping, whereas the clades are branched and nested (they may also be non-overlapping).

smaller components cannot separate, as long as they later reconnect); in contrast, clades are generally branched, which is to say that they are generally composed of multiple lineages. On the other hand, the reason that the concepts are commonly confused is probably that a clade originates in a single lineage (the ancestral or stem species). Finally, a species is not an entire lineage but only a segment of a lineage (or, to use Darwin's words, a branch in the line of descent). Thus, under a bifurcating model of speciation (terminology follows Foote, 1996), species are the lineage segments between branching events (i.e. they correspond to the internodes of phylogenetic trees; Fig. 4A), whereas, under a budding model of speciation, species originate, but do not necessarily terminate, in branching events (i.e. they may correspond to several successive internodes; Fig. 4B).

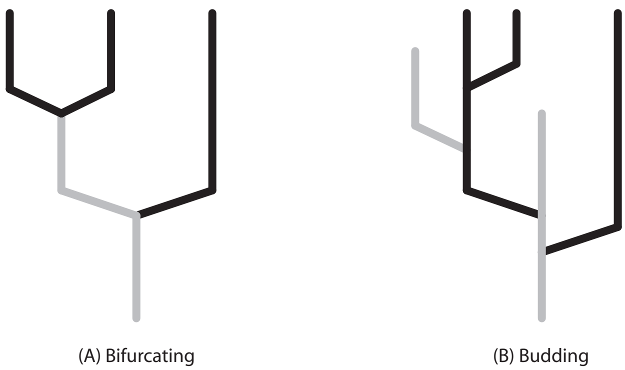

Figure 4. Species as lineage segments. These trees illustrate species under two general models of speciation (Foote, 1996). A, under the bifurcating model, ancestral species become extinct at speciation events. B, under the budding model, ancestral species persist through speciation events. Extant species are represented by black lines; extinct species by grey ones. Note that one of the ancestral species in the diagram illustrating the budding model is extant. Under both models, species are segments of lineages.

The species as a taxonomic rank

In addition to accepting the evolutionary component of Darwin's species concept, many if not most post-Darwinian biologists also accepted (to one degree or another) the older non-evolutionary component of Darwin's species concept: the treatment of the species as a rank in the hierarchy of taxonomic categories. Thus, following Darwin's lead, they treated the species category as a rank to be conferred on a lineage after that lineage had reached a particular stage in the process of divergence. Lineages that had not yet reached that stage (i.e. those that were ranked as varieties by Darwin and his contemporaries) were ranked as subspecies, a rank that became more popular in the post-Darwinian era.

On the other hand, particularly during and after the Evolutionary Synthesis of the mid-20th Century, many biologists adopted different ranking criteria than amount of difference, the criterion espoused by

Table 1. Post-Darwinian species ranking criteria

Criterion	Advocates (examples)
Phenetic cluster	Michener (1970); Sokal & Crovello (1970); Sneath & Sokal (1973)
Intrinsic reproductive barrier	Mayr (1942); Dobzhansky (1970); Coyne & Orr (2004)
Different mate recognition or fertilization system*	Paterson (1985); Masters *et al*. (1987); Lambert & Spencer (1995)
Distinct niche or adaptive zone	Van Valen (1976); Andersson (1990)
Fixed character state difference	Cracraft (1983); Nixon & Wheeler (1990)
Monophyly	Rosen (1979); Donoghue (1985); Mishler (1985)
Exclusive coalescence of alleles†	Avise & Ball (1990); Baum & Shaw (1995)

This table lists species ranking criteria that have been popular among biologists from the period of the Evolutionary Synthesis to the present.
*This criterion is debatably different from the previous criterion, given that intrinsic reproductive barriers include those related to both fertilization and subsequent development. Its treatment as a distinct criterion reflects a perspective that emphasizes the phenomena that unite organisms to form species-as-lineages rather than those that prevent separate species-as-lineages from fusing (de Queiroz, 1998).
†This criterion is debatably distinct from the previous criterion, given that the exclusive coalescence of alleles within a lineage is evidence of monophyly. On the other hand, exclusive coalescence of alleles concerns monophyly at the level of genes, whereas at least some advocates of the monophyly criterion emphasize monophyly at the population level (de Queiroz, 1999).

Darwin and many of his contemporaries. In particular, many post-Darwinian biologists adopted ranking criteria that are either more objectively defined (in that they are based on thresholds rather than a continuum) or that more directly address the biological basis of lineage separation. In effect, such criteria solved the problem with the Darwinian species concept in which the rank of species was considered arbitrary and artificial. For at least some post-Darwinian authors, the species category became objective and natural (Dobzhansky, 1937a; Mayr, 1969a).

Table 1 lists some of the most popular species ranking criteria adopted by middle and late 20th Century biologists. The first, the formation of a distinct phenetic cluster, is similar to Darwin's criterion, although perhaps it emphasizes discontinuities more than amount of difference. Other popular criteria differ to various degrees from that of Darwin. Those criteria include the existence of intrinsic reproductive barriers, the occupation of a distinct niche or adaptive zone, the existence of one or more fixed character state differences, monophyly, and the exclusive coalescence of alleles. If the various ranking criteria are considered in the context of the evolutionary component of the species concept, one can see that each represents a threshold crossed by separately evolving lineages as they diverge from one another. Thus, as lineages diverge, their component organisms form increasingly distinct phenetic clusters; they evolve differences in their fertilization and developmental systems that result in prezygotic and postzygotic reproductive barriers; they evolve distinctive ecologies and fixed character state differences; and their component gene lineages undergo sorting until they become reciprocally monophyletic.

As an aside, I want to point out that, despite differing from the ranking criterion adopted by Darwin, the alternative criteria adopted by modern biologists are not necessarily incompatible with Darwin's views on species. For example, concerning reproductive barriers, although Darwin went to great lengths to argue against the view that different species are always sterile when crossed, he also noted '. . . species within the same country could hardly have been kept distinct had they been capable of crossing freely' (p. 245). Similarly, with regard to the occupation of distinct ecological niches, Darwin noted several times that divergence of character (resulting from natural selection) between descendants of a common ancestral species was closely tied to those descendants 'filling new and widely different places in the polity [economy] of nature' (p. 121; see also pp. 102, 104, 112, 122, 126, 158, 178, 331, 412, 470).

The proliferation of species concepts

Post-Darwinian biologists were unable to agree on which of the various species ranking criteria ought to be adopted. Particularly in the middle and late part of the 20th Century, different groups of biologists advocated different criteria for conferring the rank of species. Moreover, because biologists continued (to one degree or another) to treat the issue of rank as a fundamental component of the concept of species, they viewed different species ranking criteria as the basis of alternative species concepts. The result was a proliferation of species concepts. Indeed, by the end of the 20th Century, biologists had proposed more than 20 different named species concepts (Mayden, 1997; Wilkins, 2006). A more conservative estimate based on distinct ranking criteria (i.e. rather than simply having been called a 'species concept'), such as those listed in Table 1, would still recognize five to seven different concepts (depending on whether a distinct fertilization system is considered a type of intrinsic reproductive barrier and whether monophyly and exclusive coalescence of alleles are considered different). Moreover, the concepts based on distinct ranking criteria are at least partly incompatible in that they sometimes lead to the recognition of different boundaries and numbers of species. For example, the criterion of one or more fixed character state differences (the basis of one of the so-called phylogenetic species concepts) commonly leads to the recognition of more species taxa than the criterion of intrinsic reproductive barriers (the basis of the so-called biological species concept) (Cracraft, 1997). In sum, considerable disagreement exists concerning species ranking criteria, which leads to disagreement concerning the boundaries and numbers of species taxa. This situation has come to be known as the species problem or, more specifically, the species concept problem (de Queiroz, 2005a).

In the context of the two general components retained from Darwin's species concept (lineage and rank), the species problem can be seen as result of different biologists adopting different thresholds in the process of lineage divergence as criteria for ranking lineages as species. Moreover, there is no real hope for agreement because the different thresholds advocated by different groups of biologists go hand-in-hand with the different types of questions that they address. For example, biologists who study hybrid zones tend to emphasize reproductive barriers, systematists tend to emphasize fixed character differences and monophyly, and ecologists tend to emphasize niche differences. Paleontologists and museum taxonomists tend to emphasize morphological differences, whereas population geneticists and molecular systematists tend to emphasize genetic ones. In this context, convincing all biologists to adopt the same species ranking criterion is about as likely as convincing them all to specialize in the same subdiscipline of biology.

A UNIFIED CONCEPT OF SPECIES

The situation described above concerning alternative and partly incompatible species concepts applies to views on species during the second half of the 20th Century that have persisted, to one degree or another, to the present day. Recently, however, a modified concept of species has been emerging. This emerging species concept resolves the conflicts among alternative and incompatible species concepts that differ in terms of their ranking criteria. It accomplishes this first, by retaining the newer evolutionary component of Darwin's species concept, namely the conceptualization of species as segments of population lineages, and second, by eliminating the older (and originally non-evolutionary) component of Darwin's species concept, namely the treatment of the species category as a taxonomic rank (whether based on an arbitrary amount of difference or on a property that bears more directly on the biological basis of lineage separation). The result is a unified species concept: one that reconciles the differences among competing species concepts without denying the importance of the properties that underlie their obvious differences.

Unification

Part of the reason that unification can be achieved is that the two components of Darwin's and many subsequent species concepts are not equal in terms of their theoretical significance. The conceptualization of species as segments of population lineages is more fundamental than the treatment of the species as a taxonomic rank in a couple of different respects. For one thing, in each of the various species definitions incorporating those two components, one must first establish that the entity in question is a population lineage before the ranking criterion can be applied to it. Thus, most of the definitions start by saying that a species is a lineage or a population; then the statement is qualified by stipulating that the lineage or population must possess some additional property, the ranking criterion, to be considered a species. For example, in Mayr's (1970:12) influential species definition, 'Species are groups of interbreeding natural populations', and then the qualifier: 'that are reproductively isolated from other such groups'. Another reason for considering the conceptualization of species as population lineages more fundamental is that this component is common to all species concepts formulated in the context of an evolutionary worldview. By contrast, the ranking criteria differ from one concept to another. Given that none of these criteria is present across all species definitions, none can be considered fundamental to the general concept of species, and this situation calls into question not only whether any given ranking criterion is necessary but also whether it is necessary to treat the species as a rank at all.

In this context, the solution to the species concept problem, as argued previously (de Queiroz, 1998, 1999, 2005a,b,c, 2007), is simply to drop the various species ranking criteria and thus also the treatment of the species as a taxonomic rank. Eliminating the ranking criteria removes the conflicts among alternative species concepts by reducing them to their common denominator: the evolutionary component that traces back to Darwin. Moreover, as argued below, the resulting species concept is more consistent with the significance commonly attributed to the species category by biologists. In any case, under the emerging unified species concept, species are simply separately evolving lineage segments at the inclusive end of the population level continuum. They may or may not evolve various contingent properties (e.g. intrinsic reproductive isolation, distinct ecological niches, or fixed character state differences) during the course of their existence, and they need not possess any of those properties to be considered species.

This emerging species concept can be considered unified not only because it removes the conflicts among rival species concepts, but also because it acknowledges the importance of all of the properties that were responsible for the differences among those rival concepts. Those properties, which can be considered secondary or contingent properties under the emerging unified concept, remain important in at least three different ways. First, all of the properties are useful as lines of evidence concerning the separation of lineages. For example, fixed character state differences and reciprocal monophyly (exclusive coalescence of alleles) are unlikely to be maintained unless the lineages in which they occur are not exchanging genes (i.e. unless the lineages are evolving separately).

Another way in which the properties in question remain important is that some of them are central to explanatory hypotheses concerning the maintenance of lineage separation. For example, at least in organisms with biparental reproduction, the separation of sympatric lineages may be maintained by one or more intrinsic reproductive barriers (i.e. by incompatible fertilization or developmental systems, corresponding to prezygotic or postzygotic barriers, respectively). Alternatively, it may be that the lineages occupy different ecological niches and that separation is maintained, despite considerable interbreeding between their members, by natural selection favouring phenotypes and genotypes that are well adapted to those niches over those of hybrids, as Van Valen (1976) hypothesized for certain species of oaks.

A third way in which the secondary properties remain important is that they can be used as the basis of subcategories of the species category, which bears on the use of species as units of comparison when testing various biological hypotheses. For certain types of questions, it will be most useful to consider, for example, only those species that exhibit intrinsic reproductive barriers; for other types of questions, it will be most useful to consider only those that are monophyletic. Traditionally, these sorts of subcategories have been given overly general and therefore misleading names (e.g. 'biological species' and 'phylogenetic species' for the cases just mentioned). It would be more useful, and more in keeping with the spirit of unification, to give them names that describe their properties more explicitly (e.g. 'reproductively isolated species' and 'monophyletic species' to continue with the same examples).

It is instructive to consider the first of the three roles a bit further because doing so reveals an important cause of the species concept problem. As noted above, all of the former species ranking criteria are useful as lines of evidence for inferring lineage separation and, indeed, they have often been used for that purpose. In this context, many of the alternative species concepts (i.e. those that adopt one or another contingent property of lineages as a necessary property of species) appear to confuse the theoretical concept of species with one or more operational criteria that are used to apply the concept in practice. By contrast, the emerging unified species concept (which rejects the proposition that any of the properties in question are necessary properties of species) distinguishes more clearly between the theoretical concept and its operational criteria. Indeed, the unified concept can be viewed simply as a consequence of embracing that distinction.

A CONCEPTUAL SHIFT

The emerging unified species concept also represents a subtle but important shift in the conceptualization of the species category. Implicit in earlier views (i.e. under all species concepts that both equate species with lineages and treat the species as a taxonomic rank) is the treatment of the species as a stage; specifically, a stage in the process of lineage divergence (for explicit examples, see Darwin, 1859: 51–52; Dobzhansky, 1935, 1937b). To use an analogy from the organism level of organization (Fig. 5), the species category is analogous to the stage category 'adult' (Fig. 5A). Just as an organism is not considered an adult until it acquires some contingent property, such as the cessation of growth, functional gonads, or social maturity, similarly, a lineage at the species level is not considered a species until it acquires some contingent property, such as an intrinsic reproductive barrier, a distinct ecological niche, or a fixed character state difference.

By contrast, under the emerging unified concept, the species is no longer treated as a stage in the process of lineage divergence (Fig. 5B). Because all separately evolving metapopulation lineages are considered species (i.e. regardless of the contingent prop-

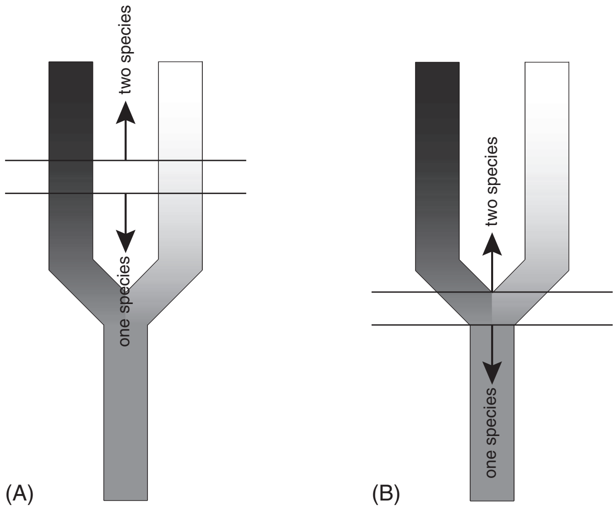

Figure 5. A shift in the conceptualization of the species category. A, older view, in which the species is conceptualized as a stage in the process of lineage divergence, as indicated by the fact that a separately evolving lineage is not considered a species until it has acquired a property indicative of a particular level of divergence (e.g. fixed character state difference, intrinsic reproductive isolation, distinct ecological niche). B, newer view, in which the species is conceptualized not as a stage in the process of lineage divergence but as the entire life span of an entity at a particular level of biological organization and thus the entire separately evolving lineage (segment) is considered a species. Horizontal lines indicate the boundary between a single ancestral species and its two descendant species (two lines are used to indicate that a zone of ambiguity exists regardless of the view). In (A), they represent the acquisition of a property adopted as a species criterion; in (B), they represent the initial separation of descendant lineages.

erties that they have acquired), the species category is no longer analogous to the stage category 'adult'. Instead, it becomes analogous to the (whole) category 'organism' in that it now refers to the entire lineage segment from initial separation to extinction.

This shift, because it involves the elimination of ranking criteria, also represents a change from viewing the species category as a taxonomic rank to viewing it as a level of biological organization. In this respect, the emerging species concept accords well with the theoretical significance commonly attributed to the species category. Biologists commonly assert that species are fundamental biological units, comparable in importance to fundamental units at lower levels of organization, such as organisms and cells (Mayr, 1982). The emerging species concept fits better with this view than do species concepts that treat a particular contingent property of diverging lineages as a necessary property of species. Just as the category 'organism' is more fundamental than the category 'adult', and the category 'cell' is more fundamental than the category 'post S phase cell', similarly, the category 'species' conceptualized as an entire separately evolving lineage segment is more fundamental than the category 'species' conceptualized as a lineage segment only after it has acquired a particular contingent property.

ROOTS OF THE EMERGING SPECIES CONCEPT

Although explicit proposals about how to achieve a unified species concept are relatively new, some components of that proposal have much older roots. Indeed, some can be traced back to Darwin himself. In this section, evidence is presented to show that the unified concept has been developing ever since Darwin introduced an evolutionary component into the species concept.

Darwin

Darwin's most important contribution to the emerging species concept was his novel proposal to equate species with branches in the lines of descent (i.e. with segments of lineages). As described above, this component of Darwin's species concept is the common element in all modern species concepts and the key to achieving a unified concept. Indeed, when the other component of Darwin's species concept (the treatment of the species as a taxonomic rank) is eliminated, the evolutionary component of Darwin's species concept that remains *is* the unified concept. But Darwin's contribution to the emerging unified concept did not end with his novel proposal to equate species with lineage segments. In addition to introducing this evolutionary component to the species concept, he also touched on some logical consequences of that proposal, which, in retrospect, can be viewed as further early developments in the emergence of the unified concept.

Most importantly, despite Darwin's explicit treatment of the species category as a rank, there are elements in his writings that anticipate the rejection of this view. For example, Darwin appears to have recognized a difference between taxa ranked as species and varieties as opposed to those assigned to higher ranks. For one thing, he treated the origin of species and that of genera and higher ranked taxa as two separate questions:

> Again, it may be asked, how is it that varieties, which I have called incipient species, become ultimately converted into good and distinct species, which in most cases obviously differ from each other far more than do the varieties of the same species?

How do those groups of species, which constitute what are called distinct genera, and which differ from each other more than do the species of the same genus, arise? (p. 61)

Moreover, for Darwin, the answers to those questions were different. Varieties transform directly into species through the accumulation of modifications:

Hence I look at individual differences, though of small interest to the systematist, as of high importance for us, as being the first step towards such slight varieties as are barely thought worth recording in works on natural history. And I look at varieties which are in any degree more distinct and permanent, as steps leading to more strongly marked and more permanent varieties; and at these latter, as leading to subspecies, and to species. (pp. 51–52).

By contrast, species do not transform directly into genera and families; instead, genera and families result from the multiplication (and divergence) of species:

Thus, as I believe, species are multiplied and genera are formed. (p.120)

On the principle of the multiplication and gradual divergence in character of the species descended from a common parent, together with their retention by inheritance of some characters in common, we can understand the excessively complex and radiating affinities by which all the members of the same family or higher group are connected together. (p. 431)

In sum, varieties transform directly into subspecies and species through the accumulation of modifications, but species do not transform directly into genera, families, and orders. Instead, species multiply and diverge from common ancestors, and, as they do so, they can be arranged into groups of related species that differ from one another by various degrees, which is reflected in their ranking as genera, families, orders, etc.

Darwin extended his proposition that varieties and subspecies are intermediate stages in the formation of species to an important logical consequence, namely, that varieties (and subspecies) are species in the process of formation, or, as he called them repeatedly, incipient species (and conversely, that species are strongly marked varieties):

I attribute the passage of a variety, from a state in which it differs very slightly from its parent to one in which it differs more, to the action of natural selection in accumulating (as will hereafter be more fully explained) differences of structure in certain definite directions. Hence I believe a well-marked variety may be justly called an incipient species; . . . (p. 52)

These facts are of plain signification on the view that species are only strongly marked and permanent varieties; . . .(pp. 55–6)

Again, it may be asked, how is it that varieties, which I have called incipient species, become ultimately converted into good and distinct species, which in most cases obviously differ from each other far more than do the varieties of the same species? (p. 61)

Nevertheless, according to my view, varieties are species in the process of formation, or are, as I have called them, incipient species. (p. 111)

If varieties are incipient species, then, in an important sense, varieties *are* species. Varieties are simply species at an early stage in their existence. Consequently, the segment of a lineage that is conceptualized (if not ranked) as a species is pushed back much closer to its origin. Darwin's reasoning can be extended further. Just as varieties are incipient species, less modified and therefore unranked earlier segments of lineages can be seen as incipient varieties (i.e. species at a yet earlier stage of their existence). Thus, the segment of a lineage that is conceptualized as a species can be pushed all the way back to its initial separation from other lineages, as it is under the unified concept. In any case, Darwin's recognition that varieties and species are fundamentally the same kind of entity can be viewed as an initial stage in the emerging view of the species category as a level of biological organization rather than a taxonomic rank.

The evolutionary synthesis

During the era of the Evolutionary Synthesis, the concept of species remained firmly rooted in the two general components of Darwin's species concept: lineage and rank. Nevertheless, further developments related to the emergence of the unified species concept occurred. First, as described above (see Post-Darwinian Species Concepts), Darwin's ranking criterion, amount of difference, was replaced with criteria that were less subjective (e.g. fixed character state differences, monophyly) or more directly related to the biological phenomena underlying lineage separation (e.g. distinct ecological niches, intrinsic reproductive barriers).

Second, the idea that the species category differs in some important way from the higher taxonomic categories became more firmly established. That proposition, which is implicit in some of Darwin's writings (see previous section), was stated very explicitly by some of the most influential figures from the period of the Evolutionary Synthesis:

Furthermore, the category of species has certain attributes peculiar to itself that restrict the freedom of its usage, and consequently make it more valuable than the rest. (Dobzhansky, 1937a: 307)

By them [museum workers as well as experimental taxonomists who have come into close contact with the problems], species are seen in the majority of cases to be definable as distinct self-perpetuating units with an objective existence in nature, and therefore on a different theoretical footing from genera or families or other higher categories, which are not definable in this concrete way. (Huxley, 1940: 4)

The unique position of species in the hierarchy of taxonomic categories has been pointed out by many authors. . . . It is the only taxonomic category for which the boundaries between taxa at that level are defined objectively. (Mayr, 1969a: 27)

Such propositions concerning the uniqueness of species were reflected in the distinction between alpha and beta taxonomy (Mayr, Linsley & Usinger, 1953) and the related distinction between microtaxonomy and macrotaxonomy (Mayr & Ashlock, 1991) (i.e. the delimitation and description of species versus the classification of species into higher taxa). As a result of these distinctions, the species category was at least partially decoupled from the other categories of the taxonomic hierarchy.

Another way in which the species category was partially decoupled from the taxonomic hierarchy was an implicit proposal to treat the species category as something other than a taxonomic rank. For example:

Because the species is one of, if not the most significant of, the units of evolution, of systematics, of ecology, and of ethology, the species is as important a unit of biology as is the cell at a lower level of integration. (Mayr, 1982: 296–297).

In effect, the species category came to be viewed as a level in the hierarchy of organization that includes cells and organisms at lower levels (Brown, 1995), although the incompatibilities of this view with the treatment of the species category as a taxonomic rank went largely unnoticed. Both the decoupling of the species category from the taxonomic hierarchy and the recognition of its relationship to the categories ‘cell’ and ‘organism’ can be seen as foreshadowing the complete removal of the species category from the taxonomic hierarchy and its transfer to the hierarchy of biological organization. (Here, I do not mean to suggest that species are no longer treated as taxa or that they are no longer within the purview of taxonomy. The point is that species are no longer treated merely as groups to which organisms, the basic units, are assigned; now species are treated as basic units in their own right.)

Phylogenetic systematics

Species concepts and definitions from the taxonomic reform movement known as ‘phylogenetic systematics’ or ‘cladistics’ continued the trends established during the Evolutionary Synthesis period with regard to the two components of Darwin’s species concept. Thus, some species definitions associated with this movement were similar to definitions associated with the Evolutionary Synthesis in emphasizing the correspondence of species to reproductive communities (Hennig, 1966), whereas others were similar in emphasizing the correspondence of species to population level lineages (Wiley, 1978). Still other species definitions associated with phylogenetic systematics continued the trend from the Synthesis era of replacing Darwin’s species ranking criterion (amount of difference) with criteria that were more objective or had more direct bearing on lineage separation and divergence, such as fixed character state differences (Cracraft, 1983) and monophyly (Rosen, 1979).

Phylogenetic systematics also contributed both directly and indirectly to decoupling the species from the hierarchy of taxonomic categories through propositions related to the concept of monophyly, which reinforced the break between species and taxa of higher rank. In particular, the concept of monophyly was restricted so that only those groups composed of a common ancestor and all (rather than only some) of its descendants were considered monophyletic, or, more importantly, only those groups possessing that property (i.e. clades) were considered to merit recognition as higher taxa (Hennig, 1966; Eldredge & Cracraft, 1980; Wiley, 1981). However, advocates of the restricted concept of monophyly argued either that the concept does not apply to species but only to groups of species (Nixon & Wheeler, 1990), or that the concept applies to species but that species, unlike taxa assigned to higher ranks, are not always monophyletic (Eldredge & Cracraft, 1980). As a consequence of the restricted concept of monophyly, higher taxa were no longer considered ancestors of other higher taxa of the same rank. Given that a monophyletic taxon includes an ancestor and all of its descendants, a family that is ancestral to another family, or a genus that is ancestral to another genus, is not monophyletic because it excludes some of the descendants of the ancestor in which it originated. By contrast, species were still considered ancestors of other species (which is consistent with the proposition that the concept of monophyly does not apply to species or that species are not necessarily monophyletic). As Michael Ghiselin (pers. comm.) has said in various lectures, ‘species speciate, but genera don’t generate’. In short, a fundamental distinction was recognized between species and clades (see also Nelson, 1989; Mishler, 1999), and that distinction reinforced the decoupling of the species category from the hierarchy of taxonomic ranks.

Post-neo-Darwinism

Widely accepted views about the process of evolution that emerged from the period of the Evolutionary Synthesis were often labelled ‘Neo-Darwinian’ (Mayr & Provine, 1980). Two such related views were that natural selection operated primarily at the level of organisms and that large-scale evolution (macroevolution) was nothing more than the sum of changes that took place within populations and species (microevolution). Criticisms of those views, sometimes labelled 'Post-Neo-Darwinian' (Felsenstein, 1986), contributed to the transfer of the species from the hierarchy of taxonomic ranks to the hierarchy of biological organization by developing an hierarchical view of selection that included selection at the level of species (i.e. species selection) and arguing that macroevolution results not only from processes that operate within populations and species, but also from those that operate among them (Stanley, 1975, 1979; Vrba & Eldredge, 1984; Vrba & Gould, 1986; Gould, 2002). The possibility of species selection was complemented by the related view that species are 'individuals' (not in the sense of organisms but in the sense of composite wholes) (Ghiselin, 1974, 1987; Hull, 1976) and therefore can function as units of selection (Hull, 1980). The concepts of species selection and species individuality further reinforced the idea that species are appropriately viewed as biological entities at a higher level of organization than organisms and cells (but exhibiting analogous properties, such as the ability to replicate) and thus further dissociated the species category from the hierarchy of taxonomic ranks.

Species concepts

Additional evidence of the emerging unified species concept can be found in several previous discussions of species concepts that hint at the existence of a single general concept. For example, at least in his early writings, Ernst Mayr clearly distinguished between the general theoretical concept of species, which he termed 'the interbreeding-population concept' (Mayr, 1963) and later 'the biological species concept' (Mayr, 1969b), as opposed to his concise, operational species definition based on the ranking criterion of intrinsic reproductive isolation. However, those distinctions were later obscured and both theoretical concept and operational definition came to be known as 'The Biological Species Concept' (Mayr, 1970; de Queiroz, 2005b). The species definitions of Simpson (1951, 1961) and Wiley (1978) are noteworthy in describing the theoretical concept of species as separately evolving population level lineages without incorporating any operational criteria for species delimitation. Moreover, Mayden (1997) has recognized both that the theoretical concept described by those definitions is common to most modern views on species and that alternative definitions are distinguished primarily by operational criteria. Templeton (1989) explicitly attempted to synthesize a number of alternative propositions about the nature of species in his cohesion species concept. Although his proposed species cohesion mechanisms are related to several commonly adopted operational ranking criteria, they were presented not as ranking criteria but as phenomena hypothesized to unite organisms to form species-as-lineages (de Queiroz, 2005a). All of these proposals at least implicitly acknowledge the existence of a single general species concept.

In sum, there is evidence from the history of biology that what I have called 'the unified species concept' has been developing ever since Darwin's revolutionary proposal to equate species with branches in the lines of descent. Indeed, the emerging unified concept appears to be a natural outgrowth, if not a logical consequence, of accepting an evolutionary underpinning for the concept of species.

CONCLUSION

The concept of species laid out by Charles Darwin in *The Origin of Species* has played a crucial role in the origin and evolution of the modern species concept. Most importantly, Darwin's species concept incorporated a novel evolutionary component, namely the conceptualization of species as branches in the lines of descent (segments of population lineages), that is central to many subsequent and nearly all contemporary views on species. Darwin's species concept also retained a second, older component, namely the treatment of the species category as a taxonomic rank, that was also adopted by most subsequent biologists, although there is evidence of a decreasing emphasis on this second component.

Post-Darwinian biologists have gained numerous insights into the properties of species and the process of speciation through a variety of theoretical, methodological, and technological innovations. None of those developments, however, has led to a radical modification of the evolutionary core of species concept outlined by Darwin (i.e. the conceptualization of species as branches in the lines of descent). Instead, they have led to relatively superficial modifications of Darwin's species concept by replacing Darwin's subjective and not uniquely biological ranking criterion (amount of difference) with criteria that are more objective and often uniquely biological (Table 1). The proposal of several alternative ranking criteria, however, has led to a proliferation of species definitions and concepts, resulting in a controversy concerning the concept of species.

During this same time (from Darwin to the present), a subtle shift has been taking place in the conceptualization of the species category: a shift from treating the species as a taxonomic rank to treating it as a level of biological organization. This conceptual shift is closely associated with the emergence of a unified species concept that retains the evolutionary component of Darwin's species concept (the equation of species with branches in the lines of descent) but eliminates the older taxonomic component (the treatment of the species as a taxonomic rank), which Darwin inherited from earlier naturalists. Interestingly, this conceptual shift, although far from complete, appears to be foreshadowed in Darwin's own writing. Thus, whether because he was the first person to consider the nature of species from an evolutionary perspective, or because of his thoroughness in exploring the consequences of that perspective, Darwin's concept of species remains the foundation of the modern species concept.

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