

# A (Not-so-radical) Solution to the Species Problem

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**ABSTRACT:** What are species? One popular answer is that species are individuals. Here I develop another approach to thinking about species, an approach based on the notion of a lineage. A lineage is a sequence of reproducing entities, individuated in terms of its components. I argue that one can conceive of species as groups of lineages, either organism lineages or population lineages. Conceiving of species as groups of lineages resolves the problems that the individual conception of species is supposed to resolve. It has added the virtue of focusing attention on the characteristic of species that is most relevant to understanding their role in evolutionary processes, namely, the lineage structure of species.

**KEY WORDS:** Species, lineage, individual, class, evolution, organism, population.

## 1. INTRODUCTION

What are species? The question seems simple enough, but its intractability is all too familiar to anyone who has given it serious thought. One answer that has gained currency is that species are individuals (see, for example, Ghiselin 1974, 1987; Hull 1976, 1978, 1987; Eldredge 1985). The application of the concept of an individual to species has been helpful in resolving some of the problems posed by a conception of species as classes of organisms. Unfortunately, however, because the concept of an individual has gotten so much attention, a more useful concept has been neglected, namely, the concept of a lineage. References to lineages appear frequently in discussions of species, but one searches in vain for a precise characterization of what a lineage is. In what follows, I will articulate one conception of a lineage and consider its value in addressing the question 'What are species?' I am not to be understood as denying that species are individuals; I am simply claiming that it is the concept of a lineage, and not the concept of an individual, that is most relevant to understanding the role that species are thought to play in evolutionary processes.

## 2. SPECIES AS CLASSES

Before focusing on the concept of a lineage, it is helpful first to examine the roots of the view that species are individuals. That view was developed in response to the apparent inadequacies of another conception of species, a conception of species as classes of organisms. On the class conception of species, species are definable in terms of biological properties of organisms that are necessary and sufficient for species membership. The class conception, however, is inadequate for at least two reasons. First, it does not take into account the importance of genealogical relations between organisms in understanding what species are. The conception of a class that is normally invoked in this context does not allow for the use of genealogical relations in defining the relevant classes; only “spatiotemporally unrestricted” classes are permitted, classes defined in terms of properties that do not make reference to particular entities (see, for example, Hull 1976, 1978, 1987). (Kitcher (1984, 1987) has pointed out that the conception of a class invoked by Hull is different from the conception of a set as understood by contemporary logicians and that one can conceive of species as sets of organisms; see Wilson (1991) for a further development of this approach.)

The second problem with the class conception of species, according to those who reject it, is that it is not compatible with a central idea in contemporary Darwinian theory, namely, that species are important units of evolution. Hull compares the incompatibility between a class conception of species and evolutionary theory with the incompatibility between Newtonian and Einsteinian conceptions of space and time: “According to Newtonian conceptions of space and time, the speed of light should not remain constant when measured from different reference frames – but it does! Similarly, if species are classes, it is difficult to see how they can evolve – but they do!” (1976, p. 175). The problem is this: Suppose that one defines a particular species as a class having as members all and only those organisms that have some particular biological properties. If one does so, then that species cannot evolve with respect to the properties referred to in the definition without thereby becoming a new species. But, the argument goes, the evolution of a species is not subject to such constraints: there are no properties such that a species cannot evolve with respect to them. Admittedly, more needs to be said to fully support this criticism of the class conception of species. Here it is important only to recognize the need for a conception of species that is compatible with the claim that species evolve.

It was from this background that the view that species are individuals emerged. Very roughly, to say that species are individuals is to say that they are spatiotemporally bounded entities having some sort of internal organization or cohesion (see Hull 1976, 1978, 1987; Eldredge 1985; Mishler and Brandon 1987). A conception of species as individuals, it is claimed, does not suffer from the inadequacies of a class conception of species. First, genealogical relations between the organisms of a species can be explicitly taken into account; they are

(at least part of) what gives a species the organization or cohesion that is characteristic of individuals. Secondly, if species are individuals, then understanding how they can change through time without losing their identity, how they can evolve, is no more problematic than understanding how other individuals, such as organisms, can do so.

A conception of species as individuals, then, appears to be helpful in overcoming some of the inadequacies of a class conception of species. There is, however, another approach, one that I believe is even more helpful in resolving these issues. That approach is based on a notion that has figured prominently in many discussions of species, the notion of a lineage. These two approaches are not necessarily incompatible; Hull (1981), for example, claims that lineages are special sorts of individuals. My claim, to be argued for below, is that it is the notion of a lineage, not the notion of an individual, that best helps us to understand how species can evolve.

### 3. WHAT IS A LINEAGE?

The notion of a lineage has been employed in a number of different areas of biology. For example, Dawkins (1982) has suggested that one can understand the notion of an adaptation in terms of benefits conferred on gene lineages. Buss (1987) argues that the evolution of multicellularity from unicellularity is to be understood in terms of cell lineages and selection pressures on them. More important here are references to lineages that appear in definitions of the term 'species'. Wiley, for example, defines a species as "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" (1978, p. 18). Van Valen (1976, p. 233) defines a species as "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." Mishler and Brandon (1978) make reference to lineages in their "phylogenetic species concept" (see also Mishler and Donoghue 1982). However, little attention has been given specifically to the notion of a lineage. What, exactly, is a lineage and how does understanding what lineages are help one to answer the question "What are species?"

One person who has discussed the notion of a lineage is David Hull (1978, 1980, 1981). In one place, he characterizes lineages as "spatiotemporal sequences of entities that causally produce one another" (Hull 1981, p. 146). The conception of a lineage to be developed here incorporates the main idea in this characterization, that lineages are composed of entities that "causally produce" one another. To this, however, I make a further addition: the entities of which a lineage is composed are entities that are capable of producing more entities of the same sort, they are *reproducing* entities. A lineage, then, is a sequence of reproducing entities, causally related to one another via reproduction.<sup>1</sup>

What sorts of entities are capable of producing more entities of the same sort?

Some obvious examples of such entities are cells and organisms. I will refer to lineages in terms of the sorts of entities of which they are composed: lineages composed of cells will be called 'cell lineages', those composed of organisms, 'organism lineages', and so forth.

In giving a more precise definition of the term 'lineage', one can adopt either of two approaches: a forward-looking approach or a backward-looking approach.<sup>2</sup> Using a backward-looking approach, one would begin with a particular reproducing entity, e.g., a sexually-reproducing organism, and identify lineages by reference to the ancestors of that organism. This approach emphasizes the ancestral relations between organisms. So understood, an organism lineage would be composed of more and more organisms as one went backward in time.

Alternatively, one could adopt a forward-looking approach: one could begin with a particular reproducing entity (for the sake of simplicity, consider an asexually-reproducing organism) and identify lineages by reference to the descendants of that organism. This approach emphasizes the descendant relations between organisms. So understood, an organism lineage would be likely to be composed of more and more organisms as one went forward in time. I will adopt a forward-looking approach in defining the term 'lineage'. The main reason for this is that a backward-looking approach suggests a static conception of a lineage: focusing on an organism (or other reproducing entity) and identifying lineages by reference to its ancestors de-emphasizes the ongoing production of new entities by those that are presently components of the lineage. A forward-looking approach, on the other hand, focuses on the descendant relations between organisms; consequently, the emphasis is on the production of new entities from old, on the projection of a lineage through time.

The term 'lineage' can be defined inductively:

- (i) Any single entity that is capable of producing entities of the same sort is a lineage of a single component (namely, the entity);
- (ii) If  $L$  is a lineage, then  $L$  and any entity produced by a component of  $L$  constitute a lineage, where the entity produced by a component of  $L$  is of the same sort as that component.

By condition (i), single cells and organisms are lineages; a particular organism, for example, would be an organism lineage, albeit a somewhat trivial one. By condition (ii), an organism together with any or all of its offspring would also constitute a lineage. (A lineage, as defined here, is similar to a subclan in Williams' axiomatization of a part of Darwinian theory; see Williams 1970, p. 350ff.).

The notion of a lineage can be made more precise by specifying identity conditions for lineages. Lineages, on the account developed here, are individuated in terms of their components: two lineages are identical if and only if they are composed of the same entities. For example, the organism lineage composed of my father and myself is a different lineage from the organism lineage composed of my mother and my sister. And both of these are different lineages from the organism lineage composed of my father's father, my father

and myself, although the first and third lineages here are related in an important way. (I am ignoring questions about whether a single sexually-reproducing organism can produce more entities of the same kind and am simply assuming that in sexually-reproducing organisms both parents stand in the relevant reproductive relation to their joint offspring.)

The identity conditions for individuals cannot be so simply stated. While having exactly the same parts is presumably a sufficient condition for two individuals to be identical, it does not seem to be a necessary condition: I am not composed of the same parts now as I was a year ago, but presumably I am the same individual. The identity of individuals seems to require some sameness of organization, not composition. Here I want only to make it clear that the conception of a lineage articulated here is not identical to the conception of an individual commonly employed in discussions of species.

There are two other important terms that will be used in the following discussion. First, it will sometimes be useful to talk about the lineage composed of a single entity,  $e_0$ , and all of the entities produced by  $e_0$ , and so forth, up until a given time,  $t$ ; I will call this the 'maximal lineage of  $e_0$  at  $t$ ' (see Figure 1a). (One can think of the maximal lineage of  $e_0$  as the lineage having as components  $e_0$  and all of  $e_0$ 's descendants up until  $t$ .) Secondly, in many instances a particular lineage,  $L$ , will be identical to the initial segment of a distinct lineage,  $L^*$ , a lineage that has as components all of the components of  $L$  and one or more entities produced by the most recent components of  $L$  (see Figure 1b). I will call  $L^*$  a 'temporal projection' of  $L$ . There may, of course, be many different temporal projections of  $L$ , some actual and some merely possible. A given lineage may have an actual temporal projection if the most recent component of the lineage is suitably distant in the past. For example, a temporal projection of the organism lineage having as component my father's father and my father would be the actual lineage having as components my father's father, my father and myself. However, if one considers a lineage the most recent components of which exist at present, then a reference to a temporal projection of that lineage into the future should be understood as a reference to any one of an indeterminate number of possible lineages. The distinction between "actual" and "possible" temporal projections of a lineage will be relevant when considering how thinking about species in terms of lineages is helpful in understanding the basis of a species' capacity to evolve.

#### 4. SPECIES AND ORGANISM LINEAGES

Species, on virtually all accounts, are made up of organisms: organisms belong to species. Given that, we can begin by considering how the notion of an organism lineage might be helpful in thinking about species. Are species simply organism lineages? To answer that, let us first consider the simplest case, namely, species of asexually-reproducing organisms, e.g., bacteria. (Some, for example, Mayr 1987 and Hull 1987, apparently would deny that asexually-

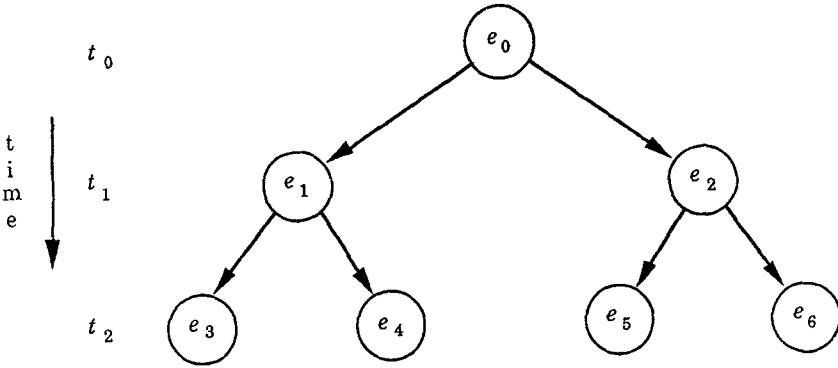


Fig. 1. (a) the maximal lineage of  $e_0$  at  $t_2$ . (b) A temporal extension of a lineage. Let  $L$  be the lineage composed of  $e_0, e_1, e_2$ , and let  $L^*$  be the lineage composed of  $e_0, \dots, e_6$ .  $L^*$  is a temporal extension of  $L$ .

reproducing organisms form species. Thus, the problems encountered here would not trouble them. Nevertheless, equally troublesome problems arise when one considers species of sexually-reproducing organisms.)

*Species of asexually-reproducing organisms.* Bacteria are single-celled organisms that typically reproduce by fission: a single bacterium splits into two (virtually) genetically identical organisms). Consider a particular bacterium,  $b_1$ . Suppose that  $b_1$  splits, giving rise to  $b_2$  and  $b_3$ , and that  $b_2$  and  $b_3$  split, giving rise to  $b_4, b_5, b_6$  and  $b_7$ . Now suppose that  $b_4$  mutates and splits, giving rise to  $b_1^*$  and  $b_2^*$  and further suppose that  $b_1^*$  and  $b_2^*$  are genetically and morphologically different from  $b_1, b_2, b_3, b_5, b_6$  and  $b_7$  (see Figure 2, ignoring for the moment  $b_3^*$  and  $b_4^*$ ).

One can identify a number of different organism lineages within this group of organisms. For example,  $[b_1, b_2, b_4]$  is an organism lineage, as well as  $[b_1, b_2, b_4, b_5, b_1^*, b_2^*]$  and  $[b_1, b_3, b_6, b_7]$  (where the symbols enclosed in square brackets represent organisms that are appropriately reproductively related and where the ordering is temporal). The maximal lineage of  $b_1$  is  $[b_1, b_2, b_3, b_4, b_5, b_6, b_7, b_1^*, b_2^*]$ .

If it made sense to think of each species of asexually-reproducing organisms as an organism lineage, then presumably each recognized species would be identifiable with some particular lineage. How might the bacteria in this example be grouped into species? One way of grouping bacteria into species is on the basis of shared genetic and morphological characteristics (see Gordon 1978). If one adopts this approach, these bacteria could be grouped into species as follows:  $b_1, b_2, b_3, b_4, b_5, b_6$ , and  $b_7$  belong to one species (species A) and  $b_1^*$  and  $b_2^*$  belong to a separate species (species B). If so, then species A could be identified with an organism lineage but species B could not, since  $b_1^*$  and  $b_2^*$  do not constitute an organism lineage.

There are, however, other plausible groupings of these bacteria into species.

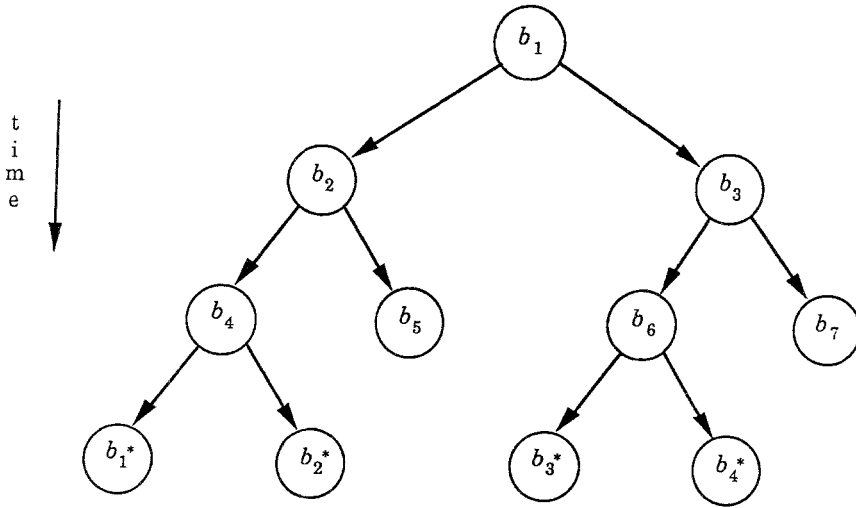


Fig. 2. A lineage of bacteria. (Arrows represent reproductive relations between organisms.)

One might group  $b_4$  in species  $B$ , rather than species  $A$ , since it is the founder organism of the new species. Or one might group  $b_4$  in species  $A$  prior to the occurrence of the mutation, and in species  $B$  after the mutation, on the grounds that a genetic mutation in a bacterium can generate a new species, to which the mutated bacterium belongs. If one adopted either approach, both species  $A$  and species  $B$  could then be identified with single organism lineages.

Even so, not all species of asexually-reproducing organisms can be identified with single organism lineages. Consider a more complex situation: suppose that the same mutation that occurred in  $b_4$  occurs in  $b_6$  and that  $b_6$  produces two offspring,  $b_3^*$  and  $b_4^*$ , such that  $b_3^*$  and  $b_4^*$  are genetically and morphologically similar to  $b_1^*$  and  $b_2^*$  (see Figure 2). Using the criteria of genetic and morphological similarity, one could plausibly include  $b_1^*$ ,  $b_2^*$ ,  $b_3^*$  and  $b_4^*$  in species  $B$ . But  $b_1^*$ ,  $b_2^*$ ,  $b_3^*$  and  $b_4^*$  do not comprise a single organism lineage, and including  $b_4$  and  $b_6$  in the species is no help.

It would appear that species of asexually-reproducing organisms, identified on genetic and morphological grounds, cannot always be identified with single organism lineages. This might lead one to conclude that the notion of an organism lineage is of limited utility in thinking about species of asexually-reproducing organisms. However, that conclusion would be premature; all that has been shown is that the application of this notion to such species is not a simple matter. The organisms belonging to the bacterium species  $B$ , in the second example, do not comprise a single organism lineage. However, consider the organism lineages  $[b_4, b_1^*, b_2^*]$  and  $[b_6, b_3^*, b_4^*]$ . The organisms that comprise these two lineages include all of the organisms that belong to species  $B$  (at least all that have so far been identified). Thus, one might identify species  $B$ ,

not with a single organism lineage, but with a group of lineages, two lineages having genetically and morphologically similar founders, viz., the lineages  $[b_4, b_1^*, b_2^*]$  and  $[b_6, b_3^*, b_4^*]$ .

*Species of sexually-reproducing organisms.* Those who deny that asexually-reproducing organisms form species are not likely to be moved by the preceding discussion. More pertinent are species of sexually-reproducing organisms. How might the notion of an organism lineage be employed in connection with species of sexually-reproducing organisms? Here the situation is more complicated. Lineages of sexually-reproducing organisms differ from lineages of asexually-reproducing organisms in that the former do not form simple branching sequences.<sup>3</sup> Consider a relatively simple scenario, beginning with four organisms,  $s_1, s_2, s_3,$  and  $s_4$ . Now suppose that  $s_1$  mates with  $s_2$ , producing two offspring,  $s_5$  and  $s_6$ , and that  $s_3$  mates with  $s_4$ , producing two offspring,  $s_7$  and  $s_8$ . Furthermore, suppose that  $s_6$  and  $s_7$  then mate, producing two offspring,  $s_9$  and  $s_{10}$ , and that  $s_5$  and  $s_8$  mate, producing  $s_{11}$  and  $s_{12}$  (see Figure 3). Among the organisms  $s_1$ - $s_{12}$ , one can identify a number of different organism lineages, e.g.  $[s_1, s_5, s_6, s_9, s_{12}]$ ,  $[s_2, s_6, s_{11}]$  and  $[s_4, s_8, s_9, s_{10}]$ . There is, however, no single organism lineage that is comprised solely of organisms  $s_1$ - $s_{12}$  (although if one includes other organisms as well, namely organisms that existed at earlier times, it is certainly possible that there be some single organism lineage having  $s_1$ - $s_{12}$ , as well as other organisms, as components). This will be true of most groups of sexually-reproducing organisms found in nature: it is highly unlikely that the organisms that belong to a particular group will comprise a single organism lineage. Rather, the organisms of a group will be components of a number of different organism lineages.

To see clearly the virtual impossibility of identifying a species of sexually-reproducing organisms with a single organism lineage, we need to consider a situation in which the beginning of the species is reasonably clear. Consider a species,  $A$ , of sexually-reproducing organisms that has a well-defined population structure:  $A$  is composed of populations,  $A_1, \dots, A_n$ , within which there is frequent interbreeding, between which there is occasional interbreeding and outside of which there is little or no interbreeding (see Figure 4). In other words, the organisms that belong to  $A$  will form interbreeding clusters throughout the range of the species. Suppose that a population,  $A_k$ , of species  $A$  becomes geographically isolated from the other populations of  $A$ , so that there is no interbreeding between  $A_k$  and the other populations of  $A$ . Now suppose that  $A_k$  is subject to selection pressures different from those affecting the other populations of  $A$  and that  $A_k$  evolves, eventually becoming completely reproductively isolated from other populations of  $A$ . This would be a paradigmatic case of speciation via geographic isolation:  $A_k$  would be deemed to be the founder population of a new species,  $B$ , a species composed of the organisms belonging to  $A_k$  and all of their descendants. But it is highly unlikely (although not logically impossible) that the organisms of  $A_k$  would themselves constitute a single organism lineage, since they would not all be descendants of some single



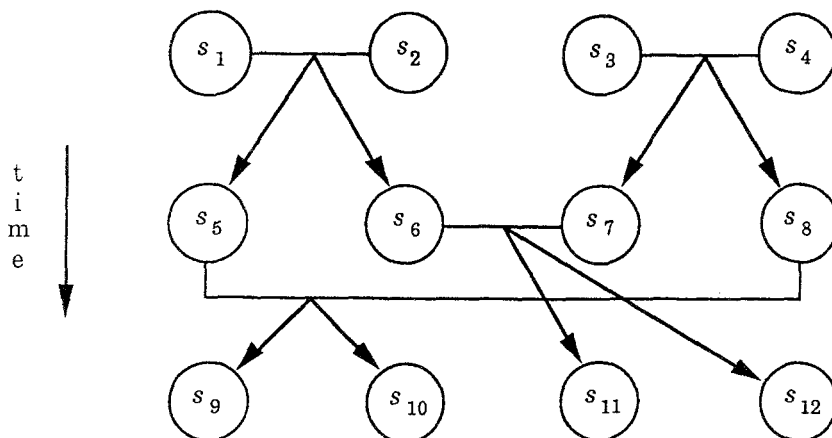


Fig. 3. Sexually-reproducing organisms. (Single lines represent interbreeding relations between organisms; arrows represent reproductive relations.)

organism in the population. And if  $A_k$  were not a single organism lineage, then  $A_k$  together with the offspring of the organisms belonging to  $A_k$  would not comprise a single organism lineage. Thus, the new species,  $B$ , could not be identified with a single organism lineage.

In the example represented by Figure 2, I suggested that a species of asexually-reproducing organisms could be identified with a group of organism lineages. The same strategy can be employed here: one can identify the new species,  $B$ , with a group of organism lineages, rather than a single organism lineage. For example, one can identify the species  $B$  with the group of maximal lineages of each of the organisms that belong to the founder population,  $A_k$ . The maximal lineages of each of the organisms in  $A_k$  will, collectively, include all and only organisms belonging to  $B$  (assuming that there is no immigration or emigration after the geographic isolation occurs).

The preceding considerations suggest a general way of employing the notion of an organism lineage in connection with species: a species can be thought of as a group of organism lineages. This alone does not indicate *which* groups of organism lineages are species; it expresses only a minimal necessary condition for being a species. Before discussing how the relevant organism lineages might be identified, it is helpful to consider another way one might make use of the notion of a lineage in connection with species.

## 5. SPECIES AND POPULATION LINEAGES

The definitions of 'species' offered by Wiley and Van Valen are couched in terms of population lineages. Given that, one might take the relevant reproducing entity to be the population and the relevant lineages to be population

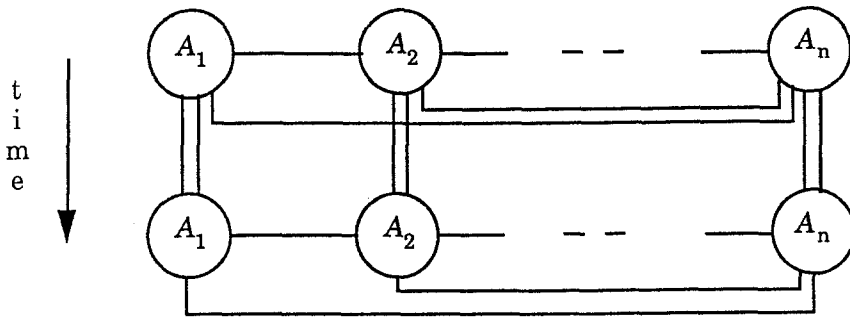


Fig. 4. Interbreeding populations. (Single lines represent interbreeding relations between populations; double lines represent relations of identity through time.)

lineages. This approach holds the most promise in connection with species of sexually-reproducing organisms, since it is here that the term 'population' has its clearest application.

Suppose that we have an adequate account of what populations are, i.e., that we can identify populations and determine when one population produces another. Now consider the example of speciation by geographic isolation discussed above. Suppose that the founder population,  $A_k$ , after becoming geographically isolated from the rest of species  $A$  produces a distinct population,  $B_1$ , and that  $B_1$  produces a distinct population,  $B_2$  (see Figure 5). Suppose also that interbreeding occurs between all three populations (although not as frequently as it occurs within a population) owing to immigration and emigration. The founder population,  $A_k$ , would be the initial population of a population lineage, and the new species,  $B$ , could be identified with the population lineage composed of the founder population,  $A_k$ , and the populations descended from it, i.e.  $B_1$  and  $B_2$ .

Thus, if the relevant reproducing entity is the population, we can, in this case, identify species  $B$  with a single population lineage. However, that is not always so: not all speciation occurs as just described, as a result of the geographic isolation and subsequent reproductive isolation of a single founder population. For example, a new species could arise from the hybridization of two existing species. Two (or more) hybrid populations could originate independently, but both might be included in the new species, if, for example, they were eventually to merge into a single population. Another scenario in which a new species could originate from more than one founder population is one in which two (or more) populations become geographically isolated from the original species as well as from one another. If, owing to similar selection pressures, both populations evolve along similar paths until both are reproductively isolated from the original species but not from one another, one could plausibly deem them to belong to a single new species (particularly if they eventually come into contact and interbreed). In cases such as these, one could not identify a species with a

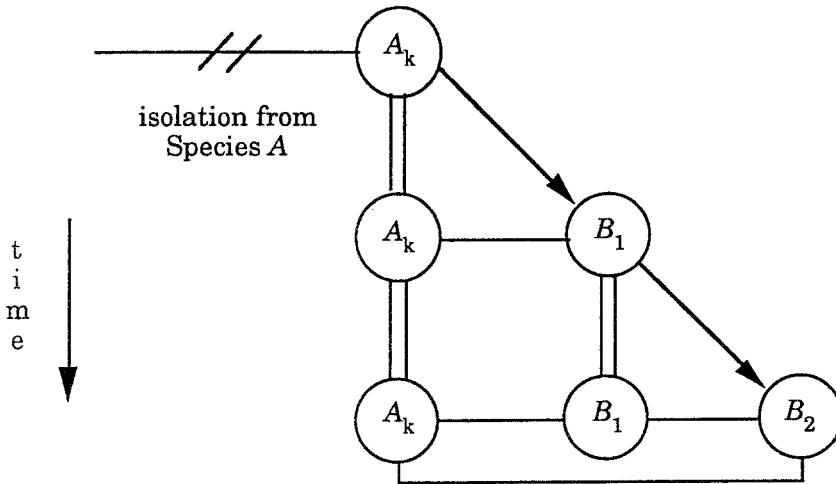


Fig. 5. Speciation by geographic isolation. (Single lines represent interbreeding relations between populations; double lines represent relations of identity through time; arrows represent reproductive relations between populations.)

single population lineage, since the populations included in the species are not all descended from a single population. One could, however, identify the species with a *group* of population lineages, as was done earlier when considering organism lineages. The relevant groups of lineages here would be the maximal lineages of those populations that mark the beginning of the new species.

I have suggested that species can be thought of as groups of lineages, either organism lineages or population lineages. Kitcher (1984) makes a somewhat similar suggestion in his discussion of the unisexual lizard species *Cnemidophorus tessellatus*. *C. tessellatus* is believed to have arisen from a cross of *C. tigris* and *C. septemvittatus*, mostly likely from some single hybridization event. However, Kitcher asks us to perform the following thought experiment: "Imagine that the entire initial population of *C. tessellatus* was wiped out and that the species was rederived after a second incident of hybridization between the two parental species" (Kitcher 1984, p. 315). If, as Kitcher claims, "rederivation" of *C. tessellatus* is the appropriate way to describe this sequence of events, then the organisms that belong to the species would be those organisms belonging to either of the two (temporally discontinuous) lineages of unisexual lizards (see also Holsinger 1987). I will have more to say about the relation between Kitcher's and my position below. Here I want to point out only that Kitcher seems to view lineages as tools that are sometimes useful in picking out the organisms that belong to a particular species; he is not explicitly claiming that all species are composed of lineages (although in a trivial sense, every group of organisms is composed of lineages of single organisms).

One might, then, make use of the notion of a lineage, either organism lineages

or population lineages, in thinking about species. The question now is: Is there any reason to do so?

## 6. EVALUATION OF THE LINEAGE CONCEPTION OF SPECIES

Recall the two deficiencies of the class conception of species that the “species as individuals” view was supposed to remedy: the class conception fails to take into account the importance of the genealogical relations between the organisms of a species and it is also incompatible with the apparent role of species in evolutionary processes. The first of these deficiencies will be addressed here; the second will be addressed more fully in the following section. Although I have not yet specified how the relevant groups of lineages are to be identified, that identification would *not* be on the basis of some set of necessary and sufficient properties possessed by all of the lineages of which a species is composed. Furthermore, since lineages are composed of genealogically-related entities, a conception of species as groups of lineages explicitly takes into account the genealogical structure of a species. On this point, then, the lineage conception of species is preferable to the class conception. But Kitcher (1984) suggests that a conception of species as *sets* of organisms defined by reference to a founder population avoids this problem as well (see also Wilson 1991). How does the lineage conception sketched here differ from Kitcher’s view?

The main difference was alluded to earlier: for Kitcher, it is not an essential characteristic of species that there be genealogical relations between the entities of which the species is composed. Genealogical relations simply provide one possible way of defining the set of organisms that belongs to a particular species. On the other hand, if species are groups of lineages, then the genealogical structure of a species is of fundamental importance. This difference is connected with Kitcher’s “pluralism” regarding species. Kitcher is willing to countenance any number of different ways of grouping organisms into species; his view

rests on the idea that our objective interests may be diverse, that we may be objectively correct in pursuing biological inquiries which demand different forms of explanation, so that the patterning of nature generated in different areas of biology may cross-classify the constituents of nature. (1984, p. 330)

In contrast, the lineage conception of species is based on the notion that species are, first and foremost, important genealogical entities; like the “species as individuals” view, the lineage conception is aimed at shedding light on how it is that species can evolve. Consequently, the criteria used for identifying the groups of lineages that constitute species will be based on current views about evolutionary processes. One requirement for a group of organisms to function as an evolutionary unit is that there be genealogical continuity within that group. Thus, in the lizard example mentioned earlier, the temporally discontinuous (imaginary) group of lineages of asexual lizards that Kitcher would treat as a

single species, *C. tessellatus*, would not constitute a species on the lineage conception, since that group of lineages could not function as a single evolutionary unit. In light of this, we can formulate a minimal condition for a group of lineages to constitute a single species: there must be some genealogical connection between some components of the lineages at some time; the lineages can not be completely spatiotemporally isolated from one another. (Of course, this would exclude grouping bacteria into species using the criteria of genetic and morphological similarity, as was suggested for Figure 2 above).

## 7. LINEAGES AND THE EVOLUTION OF SPECIES

The second deficiency of the class conception of species is that it is not compatible with the evolution of species. How does conceiving of species as groups of lineages help one to understand the evolutionary character of species?

In asking about the value of a lineage conception of species in understanding the evolutionary character of species, one could have in mind at least two different questions. First, one might be asking whether or not one can make sense of claims about the evolution of *particular* species in terms of lineages. Secondly, one might be asking whether or not conceiving of species as groups of lineages is helpful in understanding more generally the basis of the evolutionary capacities of species. The view that species are individuals seems to be directed primarily toward answering the second question: insofar as we have an understanding of the basis of the capacities of individuals to change, that understanding should carry over to species (see, for example, Hull 1978).

Consider the first question: How might one understand, in terms of lineages, the claim that a particular species, *A*, has evolved (or is evolving) with respect to some trait, *t*? Before we can answer that question, something needs to be said about how the claim that species *A* has evolved with respect to trait *t* is to be understood. There are at least three different ways of construing that claim; which one will be correct will depend on the particular circumstances of *A*. First, the claim that species *A* has evolved with respect to trait *t* may mean that, at one time, the organisms that belonged to *A* did not have trait *t* and that, at a later time, the organisms that belonged to *A* did have trait *t*. Secondly, that claim may mean that the proportion of the organisms that have trait *t*, relative to those that do not, has changed in time. Thirdly, that claim may mean that, at one time, the organisms that belonged to *A* had trait *t* and that, at a later time, the organisms that belonged to *A* had a modified form of trait *t*. In the following discussion, I will focus on the first of these possibilities; with appropriate substitutions, the conclusions reached here will be applicable to the second and third construals as well.

If one conceives of species as groups of lineages, how is a claim about the evolution of a particular species to be understood? I will assume that one has identified the species in question with the relevant group of lineages, either organism lineages or population lineages. If so, then that claim can be under-

stood as a claim about differences within and between the lineages of the group with which the species has been identified. For example, suppose that species *A* has been identified with a group of organism lineages,  $L_1, L_2, \dots, L_n$ . Now consider the claim that *A* has evolved with respect to trait *t*: that claim can be understood in terms of differences between the organisms that are components of the lineages at early points in time and organisms that are components of the lineages at later points in time. Thus, to say that *A* has evolved with respect to *t* is to say that the components of  $L_1, L_2, \dots, L_n$ , that existed prior to some time in the past,  $t_n$ , did not have trait *t*, and that the components of  $L_1, L_2, \dots, L_n$ , that existed after some later time,  $t_{n+k}$ , did have trait *t*, and that one could trace the emergence of the trait between  $t_n$  and  $t_{n+k}$  by considering the components of the lineages that existed during that time period. (For a similar analysis of claims about the evolution of a species in set-theoretic terms, see Kitcher 1984; Wilson 1991.)

Here it may be helpful, for purposes of comparison, to consider how one might understand a claim about the evolution of a particular species if one thinks of species as individuals. On that view, organisms are understood to be "parts" of species (see Hull 1976, 1978; Eldredge 1985). Presumably, then, a claim about the evolution of a particular species would be understood in terms of relations between the parts (i.e., the organisms) of the species. For example, the claim that species *A* has evolved with respect to trait *t* would be understood as the claim that, at some time in the past,  $t_n$ , the parts of *A* did not have trait *t* and that, at a later time,  $t_{n+k}$ , the parts of *A* did have trait *t*. The similarities to the treatment in terms of lineages should be obvious: on the lineage conception, claims about the evolution of a species are understood by reference to the components of lineages; on the individual conception, claims about the evolution of a species would, presumably, be understood by reference to the parts of individuals. Given that, a conception of species as groups of lineages would seem to be roughly equal to a conception of species as individuals in terms of its usefulness in formulating claims about the evolution of particular species.

The important remaining question is whether or not conceiving of species as groups of lineages helps one to understand how it is that species can evolve. The answer to that question is yes; briefly stated, it is owing to the possibility of there being temporal projections of the lineages that comprise a species at any given time that species have the capacity to evolve. To see why, consider again a particular species, *A*, that has been identified with a group of lineages,  $L_1, L_2, \dots, L_n$ . Unless *A* is an extinct species (or a species on the verge of extinction), the group of lineages that will be identified with *A* in the future will be temporal projections of lineages  $L_1, L_2, \dots, L_n$ . This is so because as the components of these lineages produce more of the same (organisms or populations), the group of lineages with which the species will be identified will change. Furthermore, the temporal projections of lineages  $L_1, L_2, \dots, L_n$  could have components that differ in biologically interesting ways from the components of  $L_1, L_2, \dots, L_n$ , owing, for example, to mutation and recombination, selection, or drift. On the view of species suggested here, a species' capacity to evolve is simply a

consequence of imperfect reproduction: as new entities are produced from old, the lineages identified with a (nonextinct) species are likely to display changes in the characteristics of their component organisms. Simply put, species have the capacity to evolve because organisms (or populations) have the capacity to reproduce (see also Hull 1978, p. 341). Admittedly, this observation is not exactly earth-shattering; Darwin made essentially the same observation (descent with modification). But if it is true that species are important evolutionary units, then our conception of species should be one that makes clear the basis of their evolutionary capacities.

## 8. LINEAGES AND INDIVIDUALS

At this point, one might ask why a conception of species in terms of groups of lineages is preferable to a conception of species as individuals. The answer lies in the differences between the two with respect to their relevance to the concerns of biologists. Recall the brief discussion (in section 2) of one of the problems facing the class conception of species: the class conception is incompatible with the status of species as units of evolution. Conceiving of species as individuals is supposed to provide a solution to this problem: individuals can change through time, so if species are individuals then presumably they can evolve. My worry is that this approach does not go very far toward helping us to understand how it is that species can evolve. Locating the problem of understanding the evolution of species in the framework of individuals requires us first to address several general philosophical issues regarding the concept of individuality. But even if those issues can be resolved, the concept of individuality makes only a limited contribution to our understanding of the basis of a species' capacity to evolve.

The philosophical issues that need to be resolved include the following. First, we need a clear account of the general notion of individuality, an account that is precise enough to enable us to identify the individuals (in the broad sense, not just organisms) in the world. Secondly, we need a clear account of how individuals undergo change through time. Thirdly, we need to combine these two accounts in a way that enables us to determine when one individual has changed enough to constitute a distinct individual. Only then can we hope to profit from approaching the problem of understanding the evolution of species in terms of the change of individuals.

Advocates of the view that species are individuals have attempted to address these issues. For example, Hull gives the following abstract characterization of an individual:

Individuals are spatiotemporally localized entities that have reasonably sharp beginnings and endings in time. Some individuals do not change much during the course of their existence, others undergo considerable though limited change, and still others can change indefinitely until they eventually cease to exist. But regardless of the change that may occur, the entity must exist continuously through time and maintain its internal organization. (1980, p. 313)

This is a first step toward a resolution of the issues mentioned above, but more needs to be said (see also Hull 1976, 1978; Mishler and Brandon 1987). Ereshefsky suggests a more specific approach to the identification of individuals: "An entity is an individual only if its being that entity requires some appropriate causal connection between its parts" (1991, p. 97). Which causal connections are appropriate is determined by "the theory governing that entity" (p. 97). Ereshefsky's suggestion could possibly be developed further to provide an account of how individuals change; it might also enable us to determine when one individual has changed into another.<sup>4</sup>

But even if we do manage to resolve these difficult philosophical issues, it is not clear that we will have a much better understanding of the basis of a species' capacity to evolve. Of primary interest from the point of view of the evolutionary biologist are the characteristics of *species* that are relevant to understanding evolutionary change, not the characteristics shared by individuals such as atoms, organisms and planets in virtue of which all have the capacity to change. A conception of species as groups of lineages emphasizes the characteristics of species that are relevant to their evolution, namely, the relations of descent among the components of the lineages which comprise a species. Furthermore, the conception of a lineage developed here is precise enough to allow one to identify lineages and to understand what it means for a lineage (or, by extension, a group of lineages) to change through time. All that remains to make full use of this notion is to consider how to identify the relevant groups of lineages, those that constitute species. As I suggested earlier, the criteria to be used will depend on our most current theories about what is responsible for the maintenance of important evolutionary units among the lineages in question. In many lineages of sexually-reproducing organisms, gene flow between organisms is responsible for maintaining distinct evolutionary units. In other cases, there is reason to think that gene flow is less important than stable selection pressures (Ehrlich and Raven 1969) or "homeostatic epigenetic programs" (Mishler 1985). But in any case, conceiving of species as groups of lineages focuses our attention as directly as possible on that characteristic of species that is most relevant to understanding their role in evolutionary processes, namely, the lineage structure of species. And that is not so radical a view after all.

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## NOTES

<sup>1</sup> The entities of which a lineage is composed are similar to Dawkins's replicators. Dawkins (1982, p. 83) defines a replicator as "anything in the universe of which copies are made" (a better term for this, suggested by Robert Brandon, might be 'replicatee'). What I have in mind might be called "self-replicators", entities which make copies of themselves, if the notion of a copy is relaxed to allow anything that produces something of the same sort to be something of which a copy is made. See also Hull (1980, 1981) for a discussion of replicators.

<sup>2</sup> Robert Brandon pointed out the possibility of alternative approaches here.

<sup>3</sup> In fact, not all asexual reproduction is as simple as represented here; there are some asexually-reproducing organisms which do exchange genetic material.

<sup>4</sup> It is worth noting that Ereshefsky then goes on to argue that, on his account of individuality, not all species are individuals.

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