



Species, Higher Taxa, and the Units of Evolution

Marc Ereshefsky

Philosophy of Science, Vol. 58, No. 1. (Mar., 1991), pp. 84-101.

Stable URL:

<http://links.jstor.org/sici?sici=0031-8248%28199103%2958%3A1%3C84%3ASHTATU%3E2.0.CO%3B2-M>

Philosophy of Science is currently published by The University of Chicago Press.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ucpress.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

SPECIES, HIGHER TAXA, AND THE UNITS OF EVOLUTION*

MARC ERESHEFSKY†

*Department of Philosophy
Washington University*

A number of authors argue that while species are evolutionary units, individuals and real entities, higher taxa are not. I argue that drawing the divide between species and higher taxa along such lines has not been successful. Common conceptions of evolutionary units either include or exclude both types of taxa. Most species, like all higher taxa, are not individuals, but historical entities. Furthermore, higher taxa are neither more nor less real than species. None of this implies that there is no distinction between species and higher taxa; the point is that such a distinction is more subtle than many authors have claimed.

1. Introduction. Biologists draw a number of distinctions between species and higher taxa. For instance, a common distinction found in the literature is that species are units of evolution, or evolutionary units, while higher taxa are not (see Mayr 1982; Wiley 1981; Ghiselin 1987; and Eldredge and Cracraft 1980). Another popular distinction is that species are individuals and real entities, while higher taxa are historical entities and less real (see Eldredge and Cracraft 1980 and Wiley 1981 for the individual/historical entity divide; see Eldredge and Cracraft 1980 and Simpson 1961 for the real/less real divide). In brief, many biologists believe that species are concrete entities which play an active role in the evolutionary process whereas higher taxa are merely an epiphenomenon of that process.

For my part, I am hesitant to adopt this general distinction. I am skeptical of the arguments that species but not higher taxa are evolutionary units. Furthermore, I do not think that higher taxa are any less real than species or that most species fall into a different ontological category than higher taxa. Despite my hesitancy over these distinctions, I still think that there is a divide between species and higher taxa. It is just that the divide is more subtle than many have claimed.

While the bulk of this paper will examine the arguments given for the above distinctions, it will also investigate several controversies on which

*Received July 1988; revised February 1989.

†The author thanks David Hull, John Kirsch, Ernst Mayr, Elliott Sober and an anonymous referee of this journal for their comments on earlier drafts of this paper. Financial support for this paper was provided by Northwestern University in the form of a postdoctorate fellowship.

Philosophy of Science, 58 (1991) pp. 84–101.
Copyright © 1991 by the Philosophy of Science Association.

those distinctions depend. For example, an argument for species but not higher taxa being evolutionary units relies on the assumption that species must be groups of interbreeding organisms. And the claim that species but not higher taxa are individuals turns on the assumption that species are indeed individuals. Both of these assumptions will be reviewed in this paper. Another issue which the distinction between species and higher taxa depends upon is the nature of evolutionary units. Though the phrases "evolutionary unit" and "unit of evolution" are frequently found in the literature, there is little agreement on their meanings. An attempt will be made here to provide some resolution to their meanings.

The next section of this paper will examine the argument that species but not higher taxa are evolutionary units because only the former can be groups of interbreeding organisms. The third section will review other arguments for species but not higher taxa being evolutionary units. Finally, the fourth and fifth sections will respectively address whether the concepts of individuality and realism distinguish species from higher taxa.

Many biologists believe that higher taxa have an inferior role to that of species in the evolutionary process. The main question to be addressed here is whether such a ranking is justified.

2. Evolutionary Units and Reproductive Units. The idea that species are groups of interbreeding organisms separated from all other such groups is well entrenched among biologists. Some even claim that this idea highlights the divide between species and higher taxa and that it explains why the former but not the latter are evolutionary units (see Ghiselin 1987; Eldredge and Cracraft 1980; and Mayr 1970). For example, Eldredge and Cracraft (1980) write:

For organisms among which there is at least occasional sexual reproduction, this unit would conform to the reproductive concept of species. We are led to the ineluctable conclusion that species, when conceived of as reproductive units, are the units of evolution. (pp. 89–90)

That taxa of categorical rank higher than species do not exist in precisely the same sense as do species is crucial. . . . What all taxa, from species up through kingdoms, do share is presumed descent from a single ancestral species. What they do not share are similar reproductive patterns. (p. 249)

[T]here is nothing more to macroevolution than species, inasmuch as taxa of higher rank than species do not exist in the same sense as do species, and thus can in no way be construed as evolutionary units. (p. 327)

According to Eldredge and Cracraft, species but not higher taxa form groups of interbreeding organisms (I will call such groups “reproductive units”). Only reproductive units can be evolutionary units. Hence species but not higher taxa are evolutionary units.

The same argument is found in Ghiselin (1987):

. . . species are those individuals that have to evolve independently of each other. For this to happen, it is a necessary condition that they form separate reproductive units, and a sufficient condition that they have speciated. (p. 137)

It would seem that species do very few things. . . . They speciate, they evolve, they provide their component organisms with genetical resources, and they become extinct. . . . Otherwise, they do very little. Above the level of the species, genera and higher taxa never do anything. Clusters of related clones in this respect are the same as genera. They don't do anything either. (p. 141)

For Ghiselin, the evolutionary unity of a species, that is, its being a distinct species, requires its members to be reproductively connected. Furthermore, what primarily distinguishes higher taxa and clusters of related clones from groups of organisms which Ghiselin takes to be species is that the latter and not the former are reproductive units. Thus species, as reproductive units, can evolve and be evolutionary units. But since higher taxa and clusters of related clones are not reproductive units, they cannot evolve and be evolutionary units.

In this section I want to examine the above argument that species but not higher taxa are evolutionary units because only the former are reproductive units. More specifically, I want to evaluate the premise that evolutionary units must be reproductive units. Accordingly, I will review two interpretations of “evolutionary unit” to see if either of them requires evolutionary units to be reproductive units. In the course of this review I will argue that the first interpretation does not require evolutionary units to be reproductive units. Furthermore I will point out that a number of biologists doubt that the second interpretation requires evolutionary units to be reproductive units.

Before conducting this review, it may be useful to get a better idea of what Eldredge and Cracraft, and Ghiselin mean by “reproductive unit”. In the first quotation given above, we see that Eldredge and Cracraft are interested in groups which have “at least occasional sexual reproduction”. In other words, they take reproductive units to be groups of organisms which are actually interconnected by sexual activity. Such interconnection can range from that found within a well integrated deme, to that which results from occasional migration between the subpopulations of

some species. In a similar vein, Ghiselin describes species as “*the most extensive units in the natural economy such that reproductive competition occurs among their parts*” (1974, 538, emphasis in the text). Reproductive competition requires the members of a species to interact. So reproductive units for Ghiselin are not merely groups of sexual organisms, or organisms which have the potentiality to sexually interact; they are groups of organisms which actually sexually interact.

The first notion of evolutionary units I would like to consider is found in Rosenberg (1985):

[T]o describe the units of evolution, we coin the biological neologism ‘clan’. . . . A *clan* is a set of biological entities and all the descendants of the members of the set.¹ (1985, 139)

According to Rosenberg, an evolutionary unit, or a clan, is a monophyletic taxon. In this paper, I will use the term “lineage” to denote such entities. Some authors (for example, Hull 1980) use the term “lineage” to denote just single descendent-ancestor sequences, that is, single branches of a phylogenetic tree. In this paper, however, I will use the term to denote both single descendent-ancestor sequences and groups of such sequences which share a common and unique origin.

In Rosenberg’s description of evolutionary units, we find the requirement that evolutionary units must consist of organisms which are connected by heredity relations. As we shall see throughout this paper, this requirement is found in all descriptions of evolutionary units. I assume the reason for this is that evolutionary explanations, as a type of explanation, require such heredity connections. When Darwin wanted to explain the distribution of the different types of organisms in the world he posited the hypothesis of evolution (Sober 1984, 21). According to that hypothesis, the distribution of biological types is explained by the passing down and subsequent alteration of traits. This paradigmatic type of explanation is subsequently employed by evolutionary theorists to explain the distribution of traits among the organisms of a lineage, whether the lineage is a phylum, a species, or a local population. In other words, evolutionary units must be groups of organisms which are connected by heredity relations simply because that is how post-Darwinian evolutionary theory explains the distribution of biological phenomena.

Turning to the main question of this section, must evolutionary units, as lineages, consist of subpopulations which exchange genetic material through gene flow? On the face of it, this conception of what it is to be

¹The term “clan” is from Mary Williams’s (1970) axiomatization of evolutionary theory. As we shall see, Williams thinks Darwinian subclans (another type of entity in her axiomatization) not clans are the units of evolution.

an evolutionary unit does not require the existence of gene flow between a unit's members. All such units need do is display a pattern of descent with modification. So the only process requirement this conception of evolutionary units places on such units is the existence of heredity processes within them. Nevertheless, it would be well to point out that a change in the gene frequencies of a lineage does not occur unless some process is causing such a change. In answering whether evolutionary units must be reproductive units we need to see if the processes causing such change require evolutionary units to be reproductive units.

There are a number of processes which can cause a lineage to evolve: selection, mutation, random drift, and recombination. If a lineage is to evolve by organismic selection, the following three factors must be present: the organisms within a lineage must vary in their traits; that variation must cause differential survival and reproduction among the organisms; and their traits must be heritable.² Selection may cause lineages to evolve by working at other levels of biological organization than that of the organism, but I will not take up that issue here.

Must a lineage which evolves as the result of organismic selection be a reproductive unit? I do not think so. Imagine a local population of asexual plants in which half the plants have a tolerance to high temperatures and the other half does not. In addition, suppose that having a tolerance to heat is heritable, and that the temperature of the zone where that population is found is rather high. As long as there are no forces countering the effects of selection for heat tolerance, the next generation of that population will have a higher frequency of genes for that trait. Moreover, we can imagine this selection process going on for a number of generations. In brief, a population or a lineage can evolve by selection without being a reproductive unit. (The same case can be made for lineages consisting of reproductively isolated groups of sexual organisms.)

Lineages consisting of asexual organisms and lineages consisting of reproductively isolated groups of sexual organisms can evolve by processes other than selection. A change in the gene frequency of such lineages can occur because a mutation arises within their organisms or as the result of random drift. Furthermore, recombination can occur within sexual organisms which belong to lineages consisting of reproductively isolated populations. (Though the occurrence of recombination in the organisms of a lineage does not change the gene frequency of that lineage, it allows the formation of new genotypes in it and thus is a source of variation.)

In sum, those processes which can cause a lineage to evolve do not

²A *ceteris paribus* clause needs be added to these conditions: selection causes a lineage to evolve only if there are no forces counteracting its forces.

require such lineages to be reproductive units. Recall the main question of this section; namely, must evolutionary units be reproductive units? If we follow Rosenberg's suggestion that evolutionary units are just lineages which evolve, then evolutionary units need not be reproductive units.

Some authors, however, have suggested that there is more to being a unit of evolution than merely being a lineage. For example, Williams (1985, 584–585) aligns evolutionary units with the Darwinian subclans of her axiomatization of evolutionary theory. A Darwinian subclan is not merely a lineage, but a lineage of organisms “which is held together by cohesive forces so that it acts as a unit with respect to selection” (Williams 1970, 357; also see 1985, 582, 584–585). The same conception of evolutionary units is found in Wiley (1981, 25) and Simpson (1961, 153). Hull also suggests that such units may be more than just lineages:

[A]sexual species and monophyletic higher taxa are much in the same position. Both possess at least one of the characteristics necessary to function as units of evolution—continuity in time—but doubt exists if they possess sufficient unity and, if they do, how this unity is maintained. (1976, 184)

Thus a number of authors think that a unit of evolution is a lineage which has “evolutionary unity”, “cohesiveness” or “coherence”. Unfortunately the nature of such unity or coherence is far from clear. Nevertheless a few observations can be made concerning its nature. First, when Hull (1976), Williams (1985), and Wiley (1981) claim that evolutionary units have a certain cohesiveness, they allow that one of several processes (for example, gene flow, genetic homeostasis or exposure to common selection regimes) may cause such cohesiveness. Second, when Hull (1984), Williams (1985), and Wiley (1981) maintain that evolutionary units have coherence they are not asserting that the members of an evolutionary unit share an essential trait. Third, such unity does not require the members of an evolutionary unit to have some uniformity over time, since, according to Hull (1976, 182), evolutionary units have the capacity to evolve indefinitely. What is left, and what I take to be the sort of cohesiveness the above authors are alluding to, is some sort of uniformity among the members of an evolutionary unit at a time. And over time, this uniformity may be in the form of stasis or it may be uniformity in change.

Returning to the main question of this section, we need to see if the above conception of evolutionary unit requires such units to be reproductive units. More specifically, we need to ask if a lineage's having some sort of evolutionary uniformity requires those lineages to be reproductive units.

Numerous biologists hold that many species, and thus evolutionary units, consist of subpopulations which do not exchange genetic material through

gene flow (see, for example, Ehrlich and Raven 1969, 1230; Wiley 1981, 36–37; Eldredge and Gould 1972, 114). In fact, a number of authors believe that *most* species are distinct evolutionary units despite their lacking the cohering effect of gene flow (see, for example, Ehrlich and Raven 1969, 1231; Lande 1980, 467; and Grant 1980, 167). Thus numerous authors believe that many if not most species need not be reproductive units.

There are three reasons why these biologists are led to this belief. First, empirical studies indicate that many sexual species consist of subpopulations which do not exchange genetic material through gene flow. Second, empirical studies in the lab and in the field show that even the presence of gene flow within some groups of organisms may not cause those groups to be distinct evolutionary units. And third, most biologists recognize some groups of asexual organisms as distinct species or evolutionary units, yet the members of such groups obviously do not exchange genetic material through gene flow.

These considerations have led many biologists to investigate other processes besides gene flow that may cause species to be distinct evolutionary units. For example, some biologists have suggested that the members of a species may contain similar homeostatic genotypes (see Mayr 1970; Ehrlich and Raven 1969; and Wiley 1981). Such genotypes could cause the organisms in a species to produce the same basic phenotype despite the occurrence of mutations or variation in the environment. It has also been proposed that a species may maintain its unity by having its organisms exposed to similar selection regimes (see Lande 1980; Mishler and Donoghue 1982; and Ehrlich and Raven 1969). So not only do a number of biologists recognize that there are evolutionary units which are not reproductive units, but they have posited alternative processes which can be used to explain why such evolutionary units need not be reproductive units.

Returning to the main question of this section, how does the claim that evolutionary units must be reproductive units fare on the assumption that evolutionary units are lineages with some sort of uniformity? According to the above biologists, such uniformity is not restricted to reproductive units. Moreover, there may be processes other than gene flow which cause such uniformity. Thus according to a number of biologists, the assertion that evolutionary units must be reproductive units cannot be substantiated by the second conception of what it is to be an evolutionary unit.

In summary, we have looked at two proposals concerning what it is to be an evolutionary unit. According to these proposals, evolutionary units are mere lineages or they are lineages with some sort of uniformity. In the first case, I have argued that being a mere lineage does not require the existence of gene flow between the members of such units. In the

second case, we saw that numerous biologists present several reasons for doubting that lineages with some sort of uniformity must be reproductive units. Recall that Eldredge and Cracraft (1980) and Ghiselin (1987) present the following argument: Only reproductive units can be evolutionary units; species but not higher taxa are reproductive units; hence species but not higher taxa are units of evolution. The above examination of two conceptions of evolutionary units should give us reason to doubt the premises of this argument. Consequently, the alleged evolutionary unit divide between species and higher taxa is not established (at least according to the numerous biologists cited above) by which entities are and are not reproductive units.

3. Other Constraints on Evolutionary Units. In the previous section, I examined the argument that species but not higher taxa are evolutionary units because only the former are reproductive units. I would now like to look at two other arguments which purport to show that species but not higher taxa are evolutionary units.

One of those arguments involves the claim that species but not higher taxa have ongoing processes. Wiley, for example, writes:

Cohesion in a species is maintained by reproductive ties (in the case of sexual species), evolutionary stasis (asexual and sexual species), and similar responses of the component organisms of the species to extrinsic factors of evolution. In contrast, there is no active cohesion within a natural supraspecific taxon because it is comprised of individual evolutionary units which have the potential to evolve independently of each other. . . . [N]atural supraspecific taxa have only a historical continuity of descent from a common ancestral species. In other words, species show both historical and ongoing continuity whereas supraspecific taxa have only historical continuity. These important distinctions result in a simple characterization of species and higher taxa; species are the units of evolution, and higher taxa containing more than one species are not units of evolution. (1981, 75)

Thus according to Wiley, species but not higher taxa have the “ongoing” or “active” processes of gene flow, genetic homeostasis and exposure to common selection pressures. The existence of such processes in species causes them to have “ongoing continuity”. On the other hand, higher taxa lack such processes; thus they do not have any “ongoing continuity”. As a result, species but not higher taxa are the units of evolution.

I have the following objection to this argument: I am skeptical of the claim that species and higher taxa are distinguished by the former but not the latter being exposed to ongoing unifying processes. Of course, it is commonly held that gene flow is a process that works among the sub-

populations of a species but not among the different species of a higher taxon. However, in the previous section we saw that a number of biologists believe that many species consist of subpopulations which are not connected by gene flow. Thus according to those biologists, gene flow is not a process which distinguishes many species from higher taxa. But what about the other two unifying processes which Wiley claims are found in species but not higher taxa? Should Wiley assume that the processes of genetic homeostasis and exposure to common selection regimes are unique to species?

I think Wiley makes this assumption too quickly. Genetic homeostasis, for example, may play a role in unifying some higher taxa. At least one author has made this suggestion. In explaining why one taxon of sibling species has less morphological diversity than another, Mayr maintains that the genetic homeostasis in one taxon may be stronger than it is in the other (1970, 35–36). In making this observation, Mayr is asserting that there are ongoing homeostatic processes among the organisms of these taxa. In addition, he is asserting that such a process can cause one of those taxa to have less morphological diversity, that is, more evolutionary unity, than the other.

There are plausible reasons for speculating that taxa higher than species may be subject to such unifying homeostatic processes. All the species in a taxon share a common ancestry, and this may cause their organisms to have some common genetic constraint on their characteristics. Whether there are such constraints in higher taxa, and how strong those constraints are, is ultimately an empirical matter. The point here, however, is that Wiley is too quick to rule out the existence of such processes in higher taxa.

I would also like to argue that Wiley is too quick to rule out the possibility that the members of a higher taxon may be exposed to similar selection regimes. Consider the ground finches and the large insectivorous tree finches of the Galapagos Islands. Each of these groups of birds is a taxon. And according to Lack ([1953] 1980), the major difference between the species within each of these groups is the size of their birds' beaks. This difference has been interpreted as an adaptation to their species-specific foods, and has caused Lack to point out that their niches vary in the food items their birds consume. But besides that variation, the niches associated with the species within each group are pretty much the same. If this is the case, then it is implausible to assert that the species in each taxon do not share some sort of common selection regime. I am fairly confident that the same case can be made for other higher taxa as well.

In brief, Wiley should not foreclose the possibility that higher taxa, like species, can have the ongoing processes of genetic homeostasis and exposure to similar selection regimes. As we have already seen, a number

of biologists believe that many if not most species lack the cohering effect of gene flow. Thus we have reason to believe that none of the ongoing processes Wiley cites distinguish all species from higher taxa. In turn, we have reason to doubt Wiley's claim that species but not higher taxa are units of evolution because only the former are exposed to such processes.

I would now like to consider the second argument that species but not higher taxa are evolutionary units. According to Mayr (1970, 1982) and Eldredge and Cracraft (1980), species but not higher taxa are evolutionary units because only the former are the source of evolutionary change. To better appreciate what this might mean, let's turn to Mayr's, and Eldredge and Cracraft's descriptions.

According to Mayr:

The origin of new higher taxa and of all evolutionary novelties ultimately goes back to a founder species. The species, therefore, is the basic unit of evolutionary biology. (1982, 296; also see 1970, 373–374)

Similarly, Eldredge and Cracraft write:

In terms of the Linnaean hierarchy, there is nothing more to macroevolution than species, inasmuch as taxa of higher rank than species do not exist in the same sense as do species, and thus can in no way be construed as evolutionary units; rather they are . . . expressions of the branching pattern produced by many speciation events through time. (1980, 327; also see p. 250)

Thus these authors provide the following argument that species but not higher taxa are the units of evolution: Most evolutionary differences arise during speciation events. Speciation events occur in species and not higher taxa. So species but not higher taxa are the true nexus of evolutionary change. Hence species but not higher taxa are the units of evolution.

This is a nice argument, but it is vulnerable to the following charge: If higher taxa are not evolutionary units because speciation events do not occur in entire higher taxa, then a similar case can be made against species being units of evolution. Consider Mayr's (1970) model of allopatric speciation. According to that model, speciation occurs when a population becomes isolated from the main body of its species. Because such a population is both genetically isolated and relatively small, selection pressures may cause it to diverge radically from the rest of its parental species. Thus such a population may undergo what Mayr calls a "genetic revolution" and become the founding population of a new species. The relevant point here is that such speciation events do not occur in entire species but only in their founding populations. (Gromko and Bradie 1987

make a similar observation.) As we just saw, Mayr, and Eldredge and Cracraft argue that higher taxa are not evolutionary units because speciation events do not occur in entire higher taxa. However, the same argument counts against species being units of evolution as well: Just as speciation events do not occur in entire higher taxa, speciation events do not occur in entire species either. Given the criterion that evolutionary units are the nexus of speciation events, species are no more evolutionary units than are higher taxa.

In summary, we have seen three arguments for species but not higher taxa being evolutionary units: Wiley's process argument; Mayr, and Eldredge and Cracraft's speciation argument; and the reproductive unit argument presented in the previous section. I have maintained that none of these arguments show that species but not higher taxa are evolutionary units. As a result, doubt should be cast on the claim that a major distinction between species and higher taxa is that the former but not the latter are evolutionary units (Mishler and Donoghue 1982 express a similar doubt).

More importantly, this analysis reveals that the distinction between species and higher taxa may be of a different sort than is usually maintained in the literature. In the above arguments, we see that the distinction between species and higher taxa is based on the idea that certain processes occur only in species. More specifically, the above arguments hold that gene flow occurs in species but not in higher taxa, that other ongoing unifying processes occur in species but not in higher taxa, and that speciation occurs in species but not in higher taxa. Despite these claims, the discussion in this and the previous section suggests that the difference between species and higher taxa is not their being exposed to different processes, but their being exposed to mostly the same processes to a different degree. Let me explain.

As we have seen, a number of authors believe that many if not most species lack the unifying effect of gene flow. Such species, they suggest, may be caused to have their own evolutionary uniformity as the result of genetic homeostasis or exposure to similar selection regimes. These two processes, as I have suggested, may give higher taxa some sort of evolutionary unity as well. If many species lack gene flow, then perhaps higher taxa and many species are exposed to the same types of unifying processes. If that is the case, then the difference between species and higher taxa is not so much their being exposed to different types of processes, but the different degree of exposure they have to those processes. Of course, deciding whether this is in fact true is in part an empirical matter. Nevertheless, I think that the arguments presented here suggest that we depart from the commonly held process distinction and consider the distinction I have introduced.

This suggestion may draw the following criticism: If there is no process distinction between species and higher taxa and the distinction between those categories is only a matter of degree, then species and higher taxa do not exist as distinct categories. In other words, it might be thought that if the boundary between species and higher taxa is vague, then the distinction between those categories is an illusion.

I do not think the above suggestion implies that the divide between species and higher taxa is in some sense unreal. Think of the analogous situation with the distinction between being bald and not being bald. The borderline between being bald and not bald is undoubtedly vague, nevertheless we believe that there is a distinction between the two. The same goes for oxygen and nitrogen (see Sober 1980). Though there are discrete jumps on the periodic table between the atomic numbers 14 and 15, there is a period of time when atoms transmuting between those elements have an indeterminate atomic weight. In other words, the boundary between having the atomic number 14 and the atomic number 15 is vague. Nevertheless, we still think that nitrogen and oxygen are distinct categories.

In brief, I suspect that the divide between many empirical categories, categories which we accept as real categories, is vague, and that such vagueness is a fact of nature.³ If that is the case, then my suggestion that the divide between species and higher taxa is vague should not cause us to doubt the existence of those categories.

4. Ontological Distinctions. Another distinction drawn between species and higher taxa is that species but not higher taxa are individuals. For instance, Wiley (1980, 78; 1981, 74ff.) writes that species are individuals, while higher taxa are historical entities. This distinction is found in Eldredge and Cracraft (1980; 90, 275) as well. Mayr (1987, 166) adopts it, but with a twist; while Mayr agrees that higher taxa are historical entities, he thinks that species are populations and not individuals.

In what follows I will argue that the individual/historical entity distinction does not signal a true divide between species and higher taxa. Instead, I will contend that higher taxa and many species fall into the same ontological category, namely that of being a historical entity. This point can be brought out through a brief analysis of the recent debate over the ontological status of species.

This debate started with reasons for why species are not natural kinds. The traditional conception of kinds holds that the members of a kind must share a kind-specific essence. In other words, it requires the existence of

³This is not to say that the categories, or the kinds, of nature do not have essences. It may be the case, as Sober (1980) has suggested, that there are kinds with correspondingly vague essences.

a property which is possessed by all and only the members of a kind and which is useful in explaining the other necessary properties had by the members of that kind (see Sober 1980 and Dupré 1986 for an elaboration of this latter point). The traditional account also maintains that the names of kinds are the predicates found in laws of nature. Since such laws are supposed to apply universally, the account holds there can be no spatio-temporal restrictions on the members of a kind.

Many authors have argued that species do not fit this description of kinds. For example, Ghiselin (1974) and Hull (1965, 1976, 1984), among others, have insisted that there are no interesting biological properties which all and only the members of a species must have.⁴ Furthermore, Sober (1980) has maintained that species essentialism is both theoretically unnecessary and at odds with post-Darwinian evolutionary theory. Another argument against species being kinds is the one used by Hull to show that species, unlike kinds, consist of members which are spatiotemporally restricted. Hull (1976, 1984) argues as follows: Species are entities which are capable of evolving by selection. Such evolution requires the organisms of a species to be connected by parent-offspring relations. These relations, in turn, require the organisms of a species to be spatiotemporally connected. As a result, species, unlike kinds, consist of members which are spatiotemporally connected and thus spatiotemporally restricted.

This last argument not only casts doubt on species being kinds, but it has led some authors to think that species are individuals. For example, Rosenberg (1985) and Ghiselin (1987) contend that the mere spatiotemporal continuity of species suffices to show that species are individuals. Agreement on this, however, is not universal. Both Hull (1976, 1984) and Williams (1985) believe there is more to being an individual than being a spatiotemporally continuous entity. Hull writes:

[I]ntegration by descent is only a necessary condition for individuality; it is not sufficient. If it were, all genes, all organisms and all species would form but a single individual. A certain cohesiveness is also required. . . . (1976, 183)

Similarly, Williams (1985, 581) suggests that a lineage's being spatiotemporally continuous does not suffice to make it an individual; she adds that it must be cohesive with respect to natural selection as well.

Nevertheless, Williams (1985, 583ff.) and Hull (1976, 183–184; 1984,

⁴Kitcher (1984) argues that the members of a species have essences because there are properties which all the members of a species must have. Even if Kitcher were correct in showing that species have necessary properties, this would not be enough to show that they have essential properties; essential properties are necessary *and* sufficient properties. See Ereshefsky (1988) for details.

627ff.) maintain that species are individuals because they believe that species are spatiotemporally continuous and cohesive entities. It should be noted that the cohesiveness which Hull and Williams attribute to species is just the one we saw earlier in the discussion of evolutionary units. Again, the claim attributes no essential properties to the members of a species, merely some sort of uniformity to them. Hull (1976, 1984) provides no further information about the nature of this uniformity. Williams, however, describes a group of organisms as being cohesive when its members react in a relatively similar fashion to similar selection pressures (1970, 356–357).

According to Hull (1976, 1984) and Williams (1985), there are several processes which can cause cohesiveness in species. Both Hull (1976, 183; 1984, 631) and Williams (1985, 584) suggest that gene flow may be a process which can cause species to be cohesive units. But as we saw earlier, numerous biologists believe that many if not most species lack the cohesifying force of gene flow. For instance, Ehrlich and Raven write:

Our suspicion is that, eventually, we will find that, in some species, gene flow is an important factor in keeping populations of the species relatively undifferentiated, but that in most it is not. (1969, 1231; also see Grant 1980, Lande 1980)

In accordance with such considerations, Hull (1984, 630–631) and Williams (1970, 356–357; 1985, 584) suggest that species lacking adequate gene flow may be cohesive wholes because of genetic homeostasis or exposure to similar selection regimes.

I will grant that those species which are caused to be cohesive by gene flow may be individuals. But I doubt that species lacking the cohesifying effect of gene flow are individuals. It is true that the members of the latter species are spatiotemporally connected to a common ancestor. And perhaps the cohesiveness found among the members of such species is due to similar kinds of processes working on those members, namely similar selection regimes or homeostatic genotypes. Nevertheless, individuality seems to require more than spatiotemporal continuity and cohesiveness due to similar but independent processes. It seems to require that the parts of an individual be causally connected in some appropriate fashion as well.

I would like to put forth the following suggestion: An entity is an individual only if its being that entity requires some appropriate causal connection between its parts. Furthermore, it is the theory governing that entity (if such a theory exists) that determines whether its parts must be causally connected and, if so, in what manner they must be causally connected.⁵ This suggestion gains support when one examines those entities,

both in and outside of science, which generally are thought to be individuals. Take for instance an ordinary cup. According to physics and chemistry, cup parts do not form a single cup unless they are causally connected by certain electrostatic forces. The same consideration, I suspect, applies to whether the entity is an organism, a country, or a solar system. In contrast to individuals, when one examines those entities which generally are thought to be *non*individuals, the theories governing those entities do not require their constituents to be causally connected. Take for example the natural kind gold or all the bullets shot in World War II. Nothing in the theories governing these entities require their constituents to be causally connected.

This causal requirement on individuality has the following consequence for the ontological status of species. Those species which owe their evolutionary unity—that is, their being distinct species—to gene flow may be individuals. Those species which lack adequate gene flow but maintain their unity through genetic homeostasis or exposure to common selection regimes are not individuals. If, as numerous authors argue, many species lack the cohering effect of gene flow, then the causal requirement I am proposing implies that many species are not individuals.

Ruse (1987) and Guyot (1987) have used similar arguments to show that species are not individuals. They also think that such arguments lead to the conclusion that species are natural kinds. I disagree. As we saw earlier, species are spatiotemporally continuous entities and they lack species-specific essences. Because of this, I agree with Hull and Ghiselin that species are not kinds. If species are not kinds and those species lacking gene flow are not individuals, what are we then to make of their ontological status?

I propose that such species are merely historical entities, akin to Wiley's (1981) description of higher taxa (Mishler and Donoghue 1982 make a similar suggestion). According to Wiley (1981, 74ff.) a higher taxon consists of species which are historically connected to a common ancestral species, yet the species within such a taxon lack any active cohesion between them. In other words, a higher taxon for Wiley is a spatiotemporally continuous entity whose members are not causally connected in any biological manner. This is analogous to the situation faced by many species: Their subpopulations have a common ancestor, yet their subpopulations are not causally connected in any biological manner either. In sum, some species may be individuals, but many species are merely historical entities. I believe that this result provides a more accurate de-

³This type of suggestion is not a new one among philosophers. Shoemaker (1979), Armstrong (1980) and Slote (1979) have all proposed similar causal requirements on individuality. See Ereshefsky (1988) for a review of such requirements.

scription of the ontological status of species than has generally been offered in the literature.

Besides clarifying the ontological status of species, this result casts doubt on the distinction introduced at the beginning of this section. Recall that Wiley (1980, 1981), Eldredge and Cracraft (1980), and Mayr (1987) contend that species are individuals (populations in Mayr's case), while higher taxa are historical entities. If many species are not individuals, then this division does not separate many species from higher taxa. In fact, the above result suggests that many species and higher taxa fall into the same ontological category: that of being merely historical entities.

5. Species, Higher Taxa and Realism. There is one other alleged distinction between species and higher taxa I would like to consider briefly, namely that species are real and higher taxa are not. This distinction amounts to no less than the claim that species exist in nature whereas the existence of higher taxa is in some way mind dependent. Hennig (1966, 78) cites a number of authors who held this view in the first half of this century. And such claims are found in Simpson (1961, 57), Mayr (1969, 91–92), and Eldredge and Cracraft (1980, 249–250, 327).

Why would one think that higher taxa are less real than species? According to the last four authors, it is because species evolve, yet higher taxa do not. In other words, as Mayr (1982, 296), and Eldredge and Cracraft (1980, 249–250, 327) put it, it is because species but not higher taxa are evolutionary units. The distinction that species but not higher taxa are evolutionary units is also the basis on which Wiley (1981, 75) and Eldredge and Cracraft (1980, 275) make the claim that species but not higher taxa are individuals. Likewise, Hull (1976, 183–184) maintains that species are individuals because they are evolutionary units, and higher taxa would be individuals if they were evolutionary units (Hull leaves this latter point unresolved).

In sections 2 and 3 of this paper we saw several arguments for species but not higher taxa being evolutionary units. These arguments are all based on the contention that certain processes occur in species but not in higher taxa. For example, it is argued that only species have the cohering effect of gene flow, that only species have ongoing unifying processes, and that species are the locus of speciation events. In each case, I have responded that such process distinctions do not divide species from higher taxa: both species and higher taxa can lack gene flow, both can be exposed to ongoing unifying processes, and neither are the locus of speciation events. In sum, the process distinctions argued for in the literature do not show that species but not higher taxa are evolutionary units. As a result, claims concerning the reality of species and unreality of higher taxa based on the evolutionary unit divide should be viewed with suspicion. The same

applies to the argument that species but not higher taxa are individuals because only the latter are evolutionary units.

Perhaps doubt over the existence of higher taxa comes from a different source. According to Hull (1988), most systematists do not use any explicit method for the recognition and ranking of higher taxa, and those who do must choose from principles which lead to the construction of quite different classifications. Doubt about the existence of higher taxa may be due to doubt about the inference procedures systematists use to construct representations of those taxa. If that is the case, then skepticism concerning the existence of higher taxa is the result of mistaking an epistemological problem for an ontological problem.

The same problem infects our classifications of species; there are a number of species concepts which lead to the construction of quite different classifications of species. Yet despite this problem, the degree of skepticism concerning the existence of species is much less. Why this is, is no small question. It might have something to do with our ability to easily recognize nondimensional species (see Hull 1988). Putting considerations concerning the human perspective aside, there is very little in the evolutionary process which demands that we treat species and higher taxa as differently as some have claimed.

REFERENCES

- Armstrong, D. (1980), "Identity Through Time", in P. van Inwagen (ed.), *Time and Cause: Essays Presented to Richard Taylor*. Dordrecht: Reidel, pp. 67–78.
- Briggs, D. and Walters, S. M. (1984), *Plant Variation and Evolution*. 2d Ed. Cambridge, England: Cambridge University Press.
- Dupré, J. (1986), "Sex, Gender, and Essence", in P. French, T. Uehling Jr. and H. Wettstein (eds.), *Midwest Studies in Philosophy*, vol. 10. Minneapolis: University of Minnesota Press, pp. 441–457.
- Ehrlich, P. and Raven, P. (1969), "Differentiation of Populations", *Science* 165: 1228–1232.
- Eldredge, N. and Cracraft, J. (1980), *Phylogenetic Patterns and the Evolutionary Process, Method and Theory in Comparative Biology*. New York: Columbia University Press.
- Eldredge, N. and Gould, S. (1972), "Punctuated Equilibria: An Alternative to Phyletic Gradualism", in T. Schopf (ed.), *Models in Paleobiology*. San Francisco: Freeman, Cooper & Company, pp. 82–115.
- Ereshefsky, M. (1988), "The Ontological Status of Species: A Study of Individuality and its Role in Evolutionary Theory", Ph.D. Dissertation, University of Wisconsin.
- Ghiselin, M. (1974), "A Radical Solution to the Species Problem", *Systematic Zoology* 23: 536–544.
- . (1987), "Species Concepts, Individuality, and Objectivity", *Biology and Philosophy* 2: 127–143.
- Grant, V. (1980), "Gene Flow and the Homogeneity of Species", *Biologisches Zentralblatt* 99: 157–169.
- Gromko, M. and Bradie, M. (1987), "Species Problems and Population Solutions", Paper presented at the 1987 Summer Conference in the History, Social Studies, and Philosophy of Biology.
- Guyot, K. (1987), "Specious Individuals", *Philosophica* 37: 101–126.

- Hennig, W. (1966), *Phylogenetic Systematics*. Translated by D. David and R. Zangerl. Urbana: University of Illinois Press.
- Hull, D. (1965), "The Effect of Essentialism on Taxonomy", *The British Journal for the Philosophy of Science* 15: 314–326.
- . (1976), "Are Species Really Individuals?" *Systematic Zoology* 25: 174–191.
- . (1980), "Individuality and Selection", *Annual Review of Ecology and Systematics* 11: 311–332.
- . (1984), "A Matter of Individuality". Reprinted in E. Sober (ed.), *Conceptual Issues in Evolutionary Biology: An Anthology*. Cambridge, MA: MIT Press, pp. 624–645. Originally published in (1978), *Philosophy of Science* 45: 335–360.
- . (1988), "Common Sense and Scientific Classifications", unpublished manuscript.
- Kitcher, P. (1984), "Species", *Philosophy of Science* 51: 308–333.
- Lack, D. ([1953] 1980), "Darwin's Finches". Reprinted in B. W. Wilson (ed.), *Birds*. San Francisco: Freeman, pp. 99–102.
- Lande, R. (1980), "Genetic Variation and Phenotypic Evolution During Allopatric Speciation", *The American Naturalist* 116: 463–479.
- Mayr, E. (1969), *Principles of Systematic Zoology*. New York: McGraw-Hill.
- . (1970), *Populations, Species, and Evolution*. Cambridge, MA: Belknap Press of Harvard University Press.
- . (1982), *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Cambridge, MA: Belknap Press of Harvard University Press.
- . (1987), "The Ontological Status of Species: Scientific Progress and Philosophical Terminology", *Biology and Philosophy* 2: 145–166.
- Mishler, B. and Donoghue, M. (1982), "Species Concepts: A Case for Pluralism", *Systematic Zoology* 31: 491–503.
- Rosenberg, A. (1985), *The Structure of Biological Science*. Cambridge, England: Cambridge University Press.
- Ruse, M. (1987), "Biological Species: Natural Kinds, Individuals, or What?" *The British Journal for the Philosophy of Science* 38: 225–242.
- Shoemaker, S. (1979), "Identity, Properties, and Causality", in P. French, T. Uehling Jr. and H. Wettstein (eds.), *Midwest Studies in Philosophy*, vol. 6. Minneapolis: University of Minnesota Press, pp. 321–342.
- Simpson, G. (1961), *The Principles of Animal Taxonomy*. New York: Columbia University Press.
- Slote, M. (1979), "Causality and the Concept of 'Thing'", in P. French, T. Uehling Jr. and H. Wettstein (eds.), *Midwest Studies in Philosophy*, vol. 6. Minneapolis: University of Minnesota Press, pp. 387–400.
- Sober, E. (1980), "Evolution, Population Thinking, and Essentialism", *Philosophy of Science* 47: 350–383.
- . (1984), *The Nature of Selection: Evolutionary Theory in Philosophical Focus*. Cambridge, MA: MIT Press.
- Wiley, E. (1980), "Is the Evolutionary Species Fiction?" *Systematic Zoology* 29: 76–80.
- . (1981), *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. New York: Wiley & Sons.
- Williams, M. (1970), "Deducing the Consequences of Evolution", *Journal of Theoretical Biology* 29: 343–385.
- . (1985), "Species are Individuals: Theoretical Foundations for the Claim", *Philosophy of Science* 52: 578–590.

LINKED CITATIONS

- Page 1 of 3 -



You have printed the following article:

Species, Higher Taxa, and the Units of Evolution

Marc Ereshefsky

Philosophy of Science, Vol. 58, No. 1. (Mar., 1991), pp. 84-101.

Stable URL:

<http://links.jstor.org/sici?sici=0031-8248%28199103%2958%3A1%3C84%3ASHTATU%3E2.0.CO%3B2-M>

This article references the following linked citations. If you are trying to access articles from an off-campus location, you may be required to first logon via your library web site to access JSTOR. Please visit your library's website or contact a librarian to learn about options for remote access to JSTOR.

[Footnotes]

³ **Evolution, Population Thinking, and Essentialism**

Elliott Sober

Philosophy of Science, Vol. 47, No. 3. (Sep., 1980), pp. 350-383.

Stable URL:

<http://links.jstor.org/sici?sici=0031-8248%28198009%2947%3A3%3C350%3AEPTAE%3E2.0.CO%3B2-7>

⁴ **Species**

Philip Kitcher

Philosophy of Science, Vol. 51, No. 2. (Jun., 1984), pp. 308-333.

Stable URL:

<http://links.jstor.org/sici?sici=0031-8248%28198406%2951%3A2%3C308%3AS%3E2.0.CO%3B2-I>

References

Differentiation of Populations

Paul R. Ehrlich; Peter H. Raven

Science, New Series, Vol. 165, No. 3899. (Sep. 19, 1969), pp. 1228-1232.

Stable URL:

<http://links.jstor.org/sici?sici=0036-8075%2819690919%293%3A165%3A3899%3C1228%3ADOP%3E2.0.CO%3B2-Q>

NOTE: *The reference numbering from the original has been maintained in this citation list.*

LINKED CITATIONS

- Page 2 of 3 -



A Radical Solution to the Species Problem

Michael T. Ghiselin

Systematic Zoology, Vol. 23, No. 4. (Dec., 1974), pp. 536-544.

Stable URL:

<http://links.jstor.org/sici?sici=0039-7989%28197412%2923%3A4%3C536%3AARSTTS%3E2.0.CO%3B2-B>

The Effect of Essentialism on Taxonomy--Two Thousand Years of Stasis (I)

David L. Hull

The British Journal for the Philosophy of Science, Vol. 15, No. 60. (Feb., 1965), pp. 314-326.

Stable URL:

<http://links.jstor.org/sici?sici=0007-0882%28196502%2915%3A60%3C314%3ATEOEOT%3E2.0.CO%3B2-P>

Are Species Really Individuals?

David L. Hull

Systematic Zoology, Vol. 25, No. 2. (Jun., 1976), pp. 174-191.

Stable URL:

<http://links.jstor.org/sici?sici=0039-7989%28197606%2925%3A2%3C174%3AASRI%3E2.0.CO%3B2-L>

Individuality and Selection

David L. Hull

Annual Review of Ecology and Systematics, Vol. 11. (1980), pp. 311-332.

Stable URL:

<http://links.jstor.org/sici?sici=0066-4162%281980%2911%3C311%3AIAS%3E2.0.CO%3B2-2>

A Matter of Individuality

David L. Hull

Philosophy of Science, Vol. 45, No. 3. (Sep., 1978), pp. 335-360.

Stable URL:

<http://links.jstor.org/sici?sici=0031-8248%28197809%2945%3A3%3C335%3AAMOI%3E2.0.CO%3B2-X>

Species

Philip Kitcher

Philosophy of Science, Vol. 51, No. 2. (Jun., 1984), pp. 308-333.

Stable URL:

<http://links.jstor.org/sici?sici=0031-8248%28198406%2951%3A2%3C308%3AS%3E2.0.CO%3B2-I>

LINKED CITATIONS

- Page 3 of 3 -



Genetic Variation and Phenotypic Evolution During Allopatric Speciation

Russell Lande

The American Naturalist, Vol. 116, No. 4. (Oct., 1980), pp. 463-479.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0147%28198010%29116%3A4%3C463%3AGVAPED%3E2.0.CO%3B2-8>

Species Concepts: A Case for Pluralism

Brent D. Mishler; Michael J. Donoghue

Systematic Zoology, Vol. 31, No. 4. (Dec., 1982), pp. 491-503.

Stable URL:

<http://links.jstor.org/sici?sici=0039-7989%28198212%2931%3A4%3C491%3ASCACFP%3E2.0.CO%3B2-B>

Biological Species: Natural Kinds, Individuals, or What?

Michael Ruse

The British Journal for the Philosophy of Science, Vol. 38, No. 2. (Jun., 1987), pp. 225-242.

Stable URL:

<http://links.jstor.org/sici?sici=0007-0882%28198706%2938%3A2%3C225%3ABS NKIO%3E2.0.CO%3B2-6>

Evolution, Population Thinking, and Essentialism

Elliott Sober

Philosophy of Science, Vol. 47, No. 3. (Sep., 1980), pp. 350-383.

Stable URL:

<http://links.jstor.org/sici?sici=0031-8248%28198009%2947%3A3%3C350%3AEPTAE%3E2.0.CO%3B2-7>

Is the Evolutionary Species Fiction?-A Consideration of Classes, Individuals and Historical Entities

E. O. Wiley

Systematic Zoology, Vol. 29, No. 1. (Mar., 1980), pp. 76-80.

Stable URL:

<http://links.jstor.org/sici?sici=0039-7989%28198003%2929%3A1%3C76%3AITESFC%3E2.0.CO%3B2-W>

Species Are Individuals: Theoretical Foundations for the Claim

Mary B. Williams

Philosophy of Science, Vol. 52, No. 4. (Dec., 1985), pp. 578-590.

Stable URL:

<http://links.jstor.org/sici?sici=0031-8248%28198512%2952%3A4%3C578%3ASAITFF%3E2.0.CO%3B2-B>

NOTE: *The reference numbering from the original has been maintained in this citation list.*