Laudan, L. (1981). *Science and Hypothesis. Historical Essays on Scientific Methodology.* Dordrecht: Reidel Publishing.

Laudan R. (1982). The role of methodology in Lyell's geology. *Studies in History and Philosophy of Science* 13: 215–250.

Laudan, R. (1987). *From Mineralogy to Geology. The Foundations of a Science, 1650–1830.* Chicago: The University of Chicago Press.

Lloyd, E. (1983). The nature of Darwin's support for the theory of natural selection. *Philosophy of Science* 50: 112–129.

Lloyd, E. (1984). A semantic approach to population genetics. *Philosophy of Science* 51: 242–264.

Lyell, C. (1830–1833). *The Principles of Geology.* (3 vols.) London: John Murray.

Powell, B. (1855). *Essays on the Spirit of the Inductive Philosophy, the Unity of Worlds and the Philosophy of Creation.* London: Longman.

Recker, D. (1987). Causal efficacy: the structure of Darwin's argument strategy in the *Origin of Species. Philosophy of Science* 54: 147–175.

Ruse, M. (1971). Natural selection in the *Origin of Species. Studies in History and Philosophy of Science* 1: 311–351.

Ruse, M. (1975). Charles Darwin's theory of evolution: an analysis. *Journal of the History of Biology* 8: 219–241.

Ruse, M. (1976). Charles Lyell and the philosophers of science. *British Journal for the History of Science* 9: 121–131.

Ruse, M. (1979). *The Darwinian Revolution: science red in tooth and claw.* Chicago: University of Chicago Press.

Suppe, F. (ed.) (1974). *The Structure of Scientific Theories.* Urbana: University of Illinois Press.

Thagard, P. (1978). The best explanation: criteria for theory choice. *Journal of Philosophy* 75: 76–92.

van Fraassen, B.C. (1980). *The Scientific Image.* Oxford: Clarendon Press.

Waters, C.K. (1986). Taking analogical inference seriously: Darwin's argument from artificial selection. In A. Fine and P. Kitcher (eds) *PSA 1986* 1: 502–513. East Lansing, Mich.: The Philosophy of Science Association.

Whewell, W. (1837). *History of the Inductive Sciences.* (3 vols) London: Parker.

Whewell, W. (1840). *Philosophy of the Inductive Sciences* (2 vols) London: Parker.

Some Puzzles About Species

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In the Fall of 1974, my second year of teaching philosophy, I was giving a course in philosophy of science to a dozen or so bright undergraduates. After about three weeks, one of the students came to see me in my office. 'We find this material interesting,' he explained, 'but most of us are pre-meds, and the science we know best is biology. It would really help if you could give us some examples from biology, and not talk about physics quite so much.' The point was a good one. Like many philosophers of science of my generation, the standard examples came from physics – when I needed an illustration, I pointed to Newtonian dynamics, optics, electromagnetic theory, thermodynamics, and only occasionally ventured as far afield as chemistry. However, it was clear that the course would be improved if I honored my student's reasonable request, so I set off for the library in search of a key to reform.

I was lucky. There on the shelves was David Hull's *Philosophy of Biological Science*, relatively newly published in the Prentice-Hall series I knew and loved. I took it out and began to read. Almost immediately it was clear that this would not simply be a Useful Source of Improving Examples (although it did fulfil that function for my grateful students). Reading David's lucid discussions of reductionism and of the character of evolutionary theory, I realized that there were deep and important issues of which I had previously been ignorant, and a body of science that I would find difficult to integrate with the philosophical ideas I had absorbed in graduate school. It was clear that I needed re-education, and David's book pointed the way.

Other philosophers of biology of my generation probably have similar stories to tell. All of us owe Daivd Hull an enormous debt. For, at a time when biology was almost invisible in the graduate education of philosophers of science, he showed how exciting and significant the philosophy of biology could be. Moreover, the high scientific standards set in David's work made it clear that there could be no room for mere dabbling: biology, like physics, is serious, difficult, and demanding, and those who philosophize about it had better do their homework. David's example led many of us to the ever-hospitable Museum of Comparative Zoology at Harvard and to regular interchanges with the local population of biologists.

As I have eradicated some of my initial innocence about biology, I have learned more and more from David's own work. On many topics, his discussions have influenced my own ways of thinking, probably beyond the extent to which I am aware. But there is one issue on which we are in deep disagreement. Following a provocative article by Michael Ghiselin, David has argued at considerable length for a view of species that seems to me to bypass the main questions that arise in this area of the philosophy of biology.[1] The aim of the present essay is to continue the debate between us. But it seemed to me wrong to launch into the arguments without some prefatory acknowledgement of my intellectual debts. And perhaps those who champion David's view of species may draw the obvious moral from my story: the re-education stopped too soon.

1. Individuality again

According to (Ghiselin 1974, Hull 1976, Hull 1978) biological species are not 'spatio-temporally unrestricted classes' but 'historical individuals.' What does this claim mean? And why does it matter?

I have argued (Kitcher 1984a, 1984b, 1987) that there are conceptual difficulties in the position that Ghiselin and Hull wish to oppose: they are stalking a broken-backed chimera. What is a spatio-temporally unrestricted class? The obvious response is to say that a class is spatio-temporally unrestricted just in case, for any finite region of space-time that one chooses, there are members of the class that lie outside the region. But this will not do, since no class of physical objects is spatio-temporally unrestricted in this sense. Hull recognizes the point and proposes that a class is spatio-temporally unrestricted if its definition allows for the presence of instances that lie outside a spatio-temporal boundary. But this, I suggest, is a confused hybrid notion. Classes (or sets) as I understand them are entities that have their properties independently of the particular ways in which we choose to talk about them. Set-theoretic identity is extensional: $a = b$ just in case a and b have the same members.

So what? Well, let $\{a_1,...a_n\}$ be any finite set of physical objects. Let B be some finite region of space-time that includes all the a_i. We can pick out the set in two different ways: as the extension of the predicate '$x = a_1 \vee x = a_2 \vee ... \vee x = a_n$' or as the extension of the predicate '$(x = a_1 \vee x = a_2 \vee ... \vee x = a_n)$ & x lies within B'. Here I assume that the names a_i do not pick out their referents in ways that restrict those referents to particular regions of space-time. (If they do, choose different names). Now we ask if the set $\{a_1, ..., a_n\}$ is spatio-temporally unrestricted. Answer: yes, because the first way of specifying it sets no spatio-temporal boundary within which its members must lie. Answer: no, because the second way of picking it out does set a spatio-temporal boundary, *viz. B*, within which its members must lie. Both definitions identify sets with exactly the same members, and

therefore, by the extensionality of set-theoretic identity, they pick out the same set. So, the set we have identified is both spatio-temporally unrestricted and spatio-temporally restricted. But that set was an arbitrary finite set of physical objects. Thus we can conclude that any finite set of physical objects is both spatio-temporally unrestricted and spatio-temporally restricted.

The contradiction arises because the notion of spatio-temporally unrestricted class with which we have been working mixes properties of entities with properties of their definitions. The *first* issue about the ontology of species is whether species are sets (with organisms as members) or whether they are mereological wholes (with organisms as parts). In his (1976) and (1978), Hull offers a number of arguments for thinking that species are individuals. He appeals to the character of evolutionary theory, the nature of natural selection, and the absence of laws about individual species. If these arguments are taken as directed at the conclusion that species are wholes rather than sets, then I think they fail to reach their target. As I have argued at length (Kitcher 1984a, 1984b), all of our discourse about evolution can be reconstructed equally well within set theory or within mereology. The moral that I draw from this – and that I shall develop in some detail below – is that the point Hull (and Ghiselin) really want to make has nothing to do with ontology. There is a *second* issue about the delineation of the species category on which Hull and Ghiselin offer a significant (though controversial) proposal, and this issue is orthogonal to the question whether species are individuals or sets.

Before presenting that issue, I want to consider a line of argument that Hull has recently offered.[2] The kind of reasoning that leads us to think of a species as a set of organisms, he suggests, should also induce us to think of an organism as a set of cells. Because of our size and perceptual abilities, we are able to see the gaps that separate the parts of species from one another, and thence arises the temptation to view the species as a set of organisms. But the accidents of epistemological access should not lead us to attribute an ontological difference where there is none.

I find this argument interesting, challenging, and ultimately unsuccessful. First, let us ask why we do not think that organisms are sets of cells. One important, and fairly obvious, point is that an organism consists of cells and extra-cellular matrix and the latter may play a crucial role in its development and physiology. Another is that the organism (conceived as existing over time) would be better viewed set-theoretically as a function mapping any time at which it exists onto the set of space points occupied at that time. Since Carnap and Reichenbach, this has been a standard way of thinking about physical objects in general, and organisms can be treated as special cases.

But there is a deeper point that can be appreciated by recognizing that there are some organisms that we can easily conceive as collections of cells (or, more accurately, there are some *stages* of organisms that we can view in this way). In such organisms as *Hydra* and *Dictyostelium* cells can function with a high degree of independence, and we can think of the organism as continuing to survive (albeit

in a different form) even when the cells are dissociated. But this is not the rule with organisms. The distinction between an organism and a set of cells is vividly brought home to us when we recognize that it is in principle possible for the organization of the cells that make up a complex organism to be destroyed while each cell persists. The set of cells remains but it is no longer an organism.[3]

Let us ask the analogous question about species. Does a species continue to exist when we disrupt the relations among the organisms that are (on the set-theoretic view) members of it? I believe that a case can be made for an affirmative answer. If an endangered species becomes scattered so that human intervention is required if its remaining members are to reproduce, then there remains a chance of preserving the species: that, of course, is what motivates efforts that people sometimes make. Provided that there is a set of organisms belonging to the species, the species persists. Here we have a clear disanalogy with the relationship between organisms and cells, and Hull's argument is blocked.

However, if it is suggested that species are as dependent on the interactions among organisms as organisms are on the relations among cells, it is possible to make a different reply to Hull. Waiving qualms about obligatorily asexual species, let us suppose that it is crucial to the persistence of a species that some of its member organisms be combining their genes in the production of progeny.[4] Now we can say that a species is a set-theoretic entity, to wit a set of organisms subject to a particular relation (or, more precisely, the ordered pair of a set and a relation) where the relation obtains just in case there is that kind of reproductive behavior that is supposed to be crucial to the persistence of species. Could we conceive of organisms after the same fashion, treating them as sets of cells and pieces of extra-cellular matrix subject to relational conditions? Perhaps. However, at the present state of our knowledge, we can only guess at the complexity of the relations that would have to be adduced. We have not the slightest idea how to define organisms as sets of cells and pieces of matrix (whereas the specification of the relational properties that are required in the case of species seems relatively straightforward). Two points follow. First, the organization of organisms appears much more intricate than that of species – another disanalogy between organisms and species. Second, there is no firm basis for saying that organisms could not be identified with sets subject to a complex of relations (a complex which encapsulated *all* the intricacy of organization), since we have no idea what the explicit specification of the organization of organisms would look like.

I conclude that Hull's argument does not tell against the claim that species are sets. For, depending on your views about what is essential for the persistence of species, it is possible either to find a relevant disanalogy or to find a defensible version of the conclusion that organisms (better: organism-stages) are sets.

On to issues of greater biological significance. The traditional species problem was to delimit the species category by saying which superorganismal entities count as species taxa. If we decide the first question by saying that species are sets, then we can formulate this second problem as that of explaining which sets whose members are organisms are species taxa. Alternatively, if the first question is answered by claiming that organisms are individuals then the second task is to specify which individuals with organisms as parts are species taxa. Notice that it is not a consequence of the set-theoretic view of the ontology of species that *any* set with organisms as members counts as a species. Nor is it a consequence of the mereological approach to species that *any* individual with organisms as parts counts as a species.[5] There are numerous sets with organisms as members and numerous individuals with organisms as parts, and the vast majority of these sets and individuals are of no biological interest whatsoever. To solve the traditional species problem, further specification is needed.

As I interpret them, both Hull and Ghiselin disguise an interesting answer to the second question as a thesis about the ontology of species. The significant point is that species are 'historical individuals', chunks of the genealogical nexus. What makes an individual historical? In general I think that this is a hard question to answer, but, in the case of interest, it seems fairly clear that historical connectedness is critical. So, talking in the mereological idiom, we conceive of an individual with organisms as parts to be historically connected just in case for any organismal parts x and y such that x precedes y and for any organism z, if z belongs to a population that descended from a population containing x and that is ancestral to a population containing y then z is also part of the same individual as x and y. Note that the criterion for historical connectedness can easily be reformulated as a condition on sets. A set of organisms is historically connected just in case it satisfies the following condition: for any organisms x, y and z, if x and y are in the set and if z belongs to a population that is descendant from a population which has x as a member and that is ancestral to a population that has y as a member then z is in the set. Hull and Ghiselin *might* have expressed their proposal by saying that species are historically connected entities and shown a studied neutrality on the question whether they are individuals or sets.[6] In my view, of course, this reformulation would have avoided considerable confusion and would have forestalled attempts to give a priori arguments for significant biological theses.[7]

In its neutral version the Hull-Ghiselin proposal is still at odds with Ernst Mayr's biological species concept. For Mayr's account allows for the possibility of species that are not historically connected. Imagine that a species A splits into two parts at t_0, one part consisting of almost all organisms in A and the other of a small isolated population. A (or the bulk of A) persists unmodified, but the peripheral isolate evolves so that, at t_1, it has descendants that are reproductively isolated from A and constitute a new species B. However, the evolutionary change consists in a small genetic modification that is reversed in an isolated population that descends from B, so that, at time t_2, there are descendants of B that make up a population C that is reproductively compatible with A. (See Figure 1). On Mayr's account, the organisms in C are conspecific with the organisms in A. But now it is clear that A is
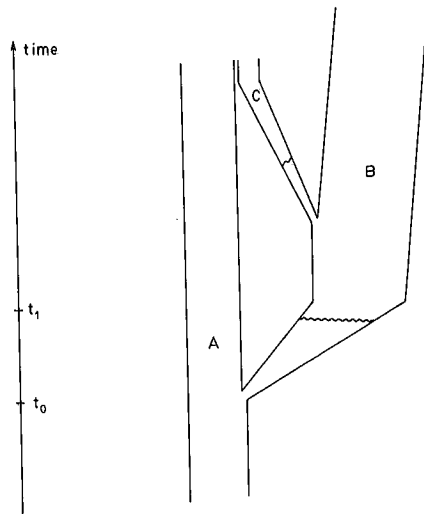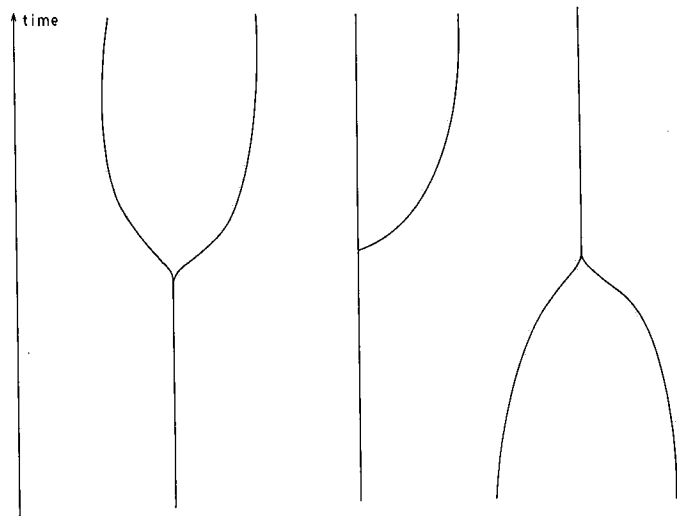
Fig. 1. Hull and Ghiselin *versus* Mayr.

Fig. 2. Three modes of Phylogenetic Change (after (Hull 1978)).

not historically connected. For there are organisms – those in B – that belong to a population ancestral to a population of A and descendant from a population of A but that are not themselves included in A. Hence the biological species concept does not require species to be historically connected.

However, even though the Hull-Ghiselin proposal diverges from the most celebrated answer to the traditional version of the species problem, that proposal does not constitute a complete rival answer to the traditional question. Saying that species are historical entities narrows the range of candidate species taxa but still allows us different ways of splitting up the genealogical nexus. The whole of life – past, present, and future – is one very big historical entity, and, at the opposite extreme, timeslices of particular populations also count as historical entities. Somewhere between these extremes are the species, and, in his (1978) Hull canvasses some possibilities for delineating them. The diagrams that he presents (see Figure 2) are persuasive devices for leading us to think that the problem of breaking up the nexus has been solved – or can be solved relatively easily. But I want to urge that the diagrams conceal deep and important problems, that there are serious questions about what the lines and branch points actually mean.[8] The rest of this essay will be devoted to explaining what needs to be done to complete the Hull-Ghiselin account and why the task strikes me as formidable. I hope that the neutrality of the formulation of the ontological issue (sets versus individuals) will be apparent throughout.[9]

2. The trouble with populations

On the account of historical connectedness that I offered above, the historical connectedness of a species depends on the holding of certain relations among populations. This reference to populations in accounts of species is as necessary on the Ghiselin-Hull approach as it is to Mayr's well-known biological species concept. But what is a population?

One way to define the standard biologist's notion of *local population* is to take a local population to comprise all the organisms of a chosen species that are present in a particular place at a particular time (see, for example, Futuyma 1979, p. 506). There is no objection to using this definition for purposes of exposition, supposing that the notion of species can be taken as already well-understood, but it is useless in a context in which we are trying to use the notion of population to analyse the concept of species. However, Mayr has attempted to do better. He offers the following characterization:

All members in a local population share in a single gene pool, and such a population may be defined also as 'a group of individuals so situated that any two of them have equal probability of mating with each other and producing

offspring', provided, of course, that they are sexually mature, of opposite sex and equivalent with respect to sexual selection. The local population is by definition and ideally a panmictic (randomly interbreeding) unit. An actual local population will, of course, always deviate more or less from the stated ideal. (Mayr 1963, p. 136; 1970, p. 182).

This passage offers a compelling picture that seems to encapsulate the ways in which many naturalists and theoretical biologists think about populations. Start with a particular sexual organism a. Consider all the organisms in the same region as a (where 'region' is defined as a specified function of the distance that a can be expected to travel to mate). Call the totality of these organisms T. Within T we are going to pick out those organisms b such that for any organism c in T, the probability that a mates with b is greater than or equal to the probability that a mates with c. (Here mating requires both copulation and the production of viable offspring). Let S_1 consist of all the b's that meet the condition just stated; intuitively, S_1 comprises the opposite sex of a within the local population. We now assume that, for any b belonging to S_1 there is a unique totality S_2 within T consisting of b's most probable mates (i.e. of those organisms c such that for any d in T the probability that b mates with c is greater than or equal to the probability that b mates with d), that S_2 is the same for each b in S_1, and that a belongs to S_2. Subject to these assumptions, the total local population to which a belongs consists of the organisms in S_1 and S_2.

There are a number of obvious worries that we might have about this picture. In some cases there will be organisms that are not among the most probable mates of their most probable mates. If a male bird of paradise has dull plumage, his potential mates will include females who do not include him among their potential mates. Examples like this – and it is easy to see that they are legion – prompt Mayr's suggestion that we treat the notion of population as an ideal, abstracting from the actual differences in sexual selection. Of course, once we demand that mating must involve not only copulation but production of viable offspring, then we encounter troubles with those organisms carrying alleles that are not concordant with the alleles found in members of the opposite sex. If we do not make the demand, then we shall have trouble with populations in which males have the propensity to copulate with females of closely related species as well as with their conspecifics.

For present purposes, however, let us restrict our attention to the difficulty posed by sexual selection, and ask what is meant by claiming that various mating probabilities are equal or unequal. Imagine that a male organism a_1 actually mates with a female a_2 and does not actually mate with another female a_3. Assume that all these organisms are, from the naturalist's standpoint, members of the same population. If Mayr's account of population is to be accepted, then we need to defend the claim that the probability that a_1 mates with a_2 is the same as the probability that a_1 mates with a_3. In making this claim we are obviously expanding our horizons from contemplation of the actual situation alone. We envisage a range

of possible situations and suggest that the proportion of situations in which a_1 mates with a_2 is the same as the proportion of situations in which a_1 mates with a_3. The actual world was, as it were, 'selected' from this range of situations, and the 'selection' produced a situation in which a_1 mates with a_2 and not with a_3. Now what determines the appropriate range of situations, the situations that we tacitly envisage in making our judgment of equiprobability? Or, to put the point another way, what features of the organisms do we allow to vary across this range of possibilities, and which do we hold constant?

Plainly if *all* the features of the actual situation are held fixed, then our consideration is limited to a unique situation, so that the proportion of cases in which a_1 mates with a_2 is 1, and the proportion of cases in which a_1 mates with a_3 is 0. If *no* features of the actual situation are held constant, then we shall be confronted with a range of possibilities so vast that it seems that the proportion of cases in which a_1 mates with any particular organism will be effectively 0. Our probability judgment rests on our striking just the right balance between these two extremes, in abstracting from some features of the actual situation and holding others fixed, so that the probability judgments made in applying Mayr's picture will identify 'local populations of conspecific organisms'.

A full account of what a population is must tell us how to strike this balance. It must explain how the conception of probability is to be applied here, specifying the class of possible situations that are to fall under our consideration. What properties of the organisms should be held fixed? Which features can be idealized? To see how difficult these questions are, let us consider some cases, which I describe from the perspective of a naturalist who uses the concept of species without analysis.

1. A local population of a social species with a dominance hierarchy in which smaller, weaker males rank lower, contains some males – the smallest and weakest – who do not mate at all. In judging that they have a nonzero probability of mating with high-ranking and low-ranking females, we abstract from the size of these males (i.e. from the characteristic on which their position in the dominance hierarchy depends).

2. Populations of two species, one of which is the dwarf form of the other, inhabit the same region. In judging that dwarf-dwarf matings are more probable than dwarf-normal matings, we do not abstract from considerations of size.

3. Two small populations of related species occur in a marginal habitat at the peripheries of the ranges of both species. In this region, hybridization occurs as frequently as mating between conspecifics. We avoid lumping the two populations by judging that each organism has a greater probability of mating with an organism from its own species. This judgment rests on abstracting from the composition of the fauna of the region. We distinguish the populations by considering what would happen if the region were not so sparsely

populated, which would raise the relative frequency of mating among conspecifics.

4. In a highly polytypic species, showing a continuously distributed range of morphological types, individuals of each type may have a greater propensity to mate with one another than with individuals of different types. Consider a region in which a small number of organisms of the species, exhibiting different types, meet and mate freely. We judge this group of organisms to be a single population, taking the probabilities of cross-type mating to be equal to those of intra-type mating, because, in this case, we do not abstract from the composition of the local fauna.

5. Two species may be reproductively isolated from one another by differences in the times at which they are active. (The differences can consist in differences between the daily cycles of activity and rest or in differences between breeding seasons.) If two such species occur in a given region, we judge the probabilities of various types of mating by holding fixed the times of activity of the organisms concerned. Were we to abstract from the differences in these times, the probability of interspecific matings would be as great as that of intraspecific matings.

6. In some cases, a species may include organisms with a broad range of times of activity. Extreme individuals may be debarred from mating because their times of activity do not overlap. Yet we may count these organisms as belonging to the same local population, by abstracting from the differences in times of activity, so that the probabilities of mating become equal across the species.

I claim that if 'species' is used as naturalists and theoretical biologists alike use it, then there are numerous examples answering to the descriptions 1–6. What these examples show is that properties of the organisms in question which are held constant in arriving at probability judgments in some cases are allowed to vary in other cases. In other words, the collection of possible situations, with respect to which the probabilities of mating are judged, cannot *obviously* be characterized in any uniform way.[10] If Hull and Ghiselin hope to deploy the concept of population to articulate the idea that species are historical individuals, then they need to articulate the principles we use in setting up the space of 'real possibilities' that underlies our probability judgments.

Since Hull has differed with Mayr's use of modal notions (*viz.* the *possibility* of gene exchange) and has insisted that our delineation of species should be based on the pattern of *actual* matings, it is worth exploring briefly whether there is any plausibility to the idea that we can avoid talk of possibilities and probabilities, either explicating the notion of a population in a nonmodal way or bypassing it and building up the concept of historical connectedness from the actual matings among organisms. One obvious trouble results from the fact that, in many species, vast

numbers of organisms belonging to the same population do not mate at all. This difficulty could be overcome by supposing that organisms whose parents belong to the same population and that inhabit the same region belong to the same population. Unfortunately, that supposition would debar *by fiat* the possibility of instant speciation, and would yield counterintuitive results in the known cases in which polyploidy results from a single generation event.

Another worry stems from the fact that hybridization does occur in nature, and it is quite probable that there are some organisms that only mate with members of different species. Not only will such instances draw the boundaries of populations in the wrong ways, but, if they are accompanied by instances of relatives that engage in some matings with conspecifics, there is the obvious possibility that the transitivity of the relation *belonging to the same population* will lead to identifications of 'populations' that are assemblages of members of different species – perhaps even species that are quite distantly related but connected by a chain of close relatives.

Although both problems are serious, the most fundamental trouble for those who hope to avoid the modal intricacies of Mayr's concept of population seems to me to be a consequence of the fact that populations may have significant internal structure and may fall into groups that have been reproductively disconnected for a number of generations. In some instances in which this occurs there may be incipient speciation; in others not. I deny that we can distinguish the two types of case by appealing to the pattern of actual matings.

Let's consider two examples in which the conspecifics in a region are fragmented into reproductively disconnected groups. The first is an idealization of what actually occurs among the Serengeti lions. Imagine that the females of a species divide into small groups, that these females mate with one or two males who become associated with a group for short periods, and that each male only has one chance to become associated with a group. Under these conditions there is no chain of animals in the population such that *a* mates with *b* who also mates with *c* who also mates with *d* ..., so that ultimately every member of the species in the region is connected to every other member. Moreover, if there is a large number of groups, and if there is a strong tendency for males to take over groups including offspring of the females in their mothers' groups, then there are likely to be males and females 'in the same population' who have no common ancestor in recent generations.

The second example is focused on our own species. It is all too familiar that there have been groups with very strong taboos or laws against various kinds of miscegenation. There are probably some instances in which these taboos have been and are still effective, so that, within a given region, people with different phenotypes have been reproductively disconnected for many generations. I doubt that we want to classify these cases as examples of incipient speciation or to declare that the people concerned belong to different populations. Instead, we want

to talk of an extreme of assortative mating *within* a single population.

The moral of this section should by now be apparent. If the Hull-Ghiselin account is to be developed as a reply to the traditional problem of delineating the species taxa, then there is a serious task of analysing the notion of population or of devising some surrogate. If we are even to *understand* the thesis that species are 'historical entities', the difficulties that I have indicated must be faced and overcome.

3. The idiosyncrasies of isolating mechanisms

The breaks in the genealogical nexus that are depicted in branching diagrams and that Hull uses to indicate the views about species he regards as serious contenders are typically connected with the attainment of reproductive isolation between populations. Two populations are said to be reproductively isolated from one another if there are mechanisms that prevent interbreeding between their members where they occur together in nature or that would prevent interbreeding between their members if they did occur together in nature. Of course, organisms from populations that are reproductively isolated from one another may produce hybrid progeny in captivity, in the laboratory, or even in places where disturbances of the habitat have produced a large disruption of the normal way of life.[11] Moreover, it is possible for there to be some gene flow between reproductively isolated populations, for example, across stable hybrid zones. Introgression is not precluded, but it must not proceed on so wide a scale that the evolutionary autonomy of either species is threatened.

There is an apparent tension within those accounts that make reproductive incompatibility central to speciation, whether they do so in the classic way of Mayr (the biological species concept) or whether they pursue the idea that species are 'historical entities' whose boundaries are marked by episodes of speciation that involve the attainment of reproductive incompatibility. The tension arises from ideas about evolutionary autonomy, specifically:

(a) A small amount of introgression is compatible with reproductive isolation between populations.

(b) A low rate of migration between spatially separated populations (of the same species) is sufficient to ensure that these populations are not (effectively) isolated from one another.

Simultaneous acceptance of (a) and (b) seems problematic. If limited migration between spatially separated populations serves as the 'glue' that binds those populations together, making them parts of a single (scattered) species, why does limited gene exchange between populations that are classified as belonging to different species not serve equally effectively to bind those populations into the same kind of genetic/evolutionary unit?[12]

Notice that it won't do to try to solve the problem by insisting that *whenever* there's limited gene exchange the populations in question belong to different species – for, as we saw in the last section, we want to allow for assortative mating within a single species and for island populations of a continental species. There may well be limited gene flow among some subgroups of *Homo sapiens*, among some subgroups of Serengeti lions, among some groups of anoline lizards in the Caribbean, and among oaks in California and Quebec.[13] What we need is a principle for drawing the species boundary, and, in defining the task, it is helpful to pose the issue of what exactly we are attempting to map by speaking of species in the first place.

Remarks by Dobzhansky, and subsequently by Mayr, make plain the motivation for insisting on reproductive isolation. In a famous passage (1937, pp. 311–312), Dobzhansky introduces the notion of reproductive isolation as the key to the understanding of local diversity. Without the attainment of reproductive isolation, he suggests, gene flow would be uninterrupted, so that, in any locale, the effects on one group of organisms would be felt by the rest of the living residents. Dobzhansky's case for the importance of reproductive isolation presupposes a thesis about the homogenizing effects of gene flow. Even small amounts of gene exchange are taken to threaten the obliteration of genetic differences. Hence the principled division that we sought one paragraph back should explain just how much gene flow can be tolerated without making one group's 'evolutionary tendencies and fate' felt by the other.

But it is possible to question the presupposition on which the connection between speciation and the attainment of reproductive isolation depends. As several empirical studies have shown, gene flow in some groups of organisms is far weaker than orthodox evolutionary theorists had supposed: for example, detailed research on dispersal of pollen by insects and by wind has supported the conclusion that '[p]ollen and seed dispersal are either exclusively local or highly leptokurtic' (Levin and Kerster 1974, p. 202). Given this result, it is not easy to see how reproductive community serves as an explanation for the genetic (morphological, ecological) uniformity found in some widely distributed species. As two of the most influential critics conclude: 'Our suspicion is that, eventually, we will find that, in some species, gene flow is an important factor in keeping populations of the same species relatively undifferentiated, but that in most it is not. As this becomes widely recognized we will see the disappearance of the idea that species, as groups of actually or potentially interbreeding populations are evolutionary units 'required' by theory' (Ehrlich and Raven 1969, p. 1231).

Theoretical considerations also reveal that reproductive isolation is not a *sine qua non* for the development and maintenance of diversity. It is at least theoretically possible for considerable differences to evolve within an interbreeding

population: even in the absence of barriers to gene flow, sharp differences in the frequencies of alternative alleles can be maintained (see Endler 1977, Roughgarden 1979, pp. 240–254).[14] Combining the theoretical study of clines with empirical results about gene flow, it becomes hard to sustain the thesis that attainment of reproductive isolation is necessary and sufficient for two groups of organisms to be subject to distinct evolutionary 'fates'.

Hull's account of the historical individuals that count as species is, I have suggested, incomplete, but his remarks about species fission (and possible fusion) seem wedded to the notion that the genealogical nexus is broken into species at those points at which reproductive isolation is attained (see his 1978, pp. 344–349). Not only is this approach vulnerable to the familiar objections about the status of species in nonsexual organisms, but, given the considerations that I have been raising here, we need a serious defense of the view that reproductive isolation is necessary and sufficient for the integrity of historical individuals (or for those historical entities that constitute species). It is not just that Hull and Ghiselin have failed to say which among several proposals for splitting the genealogical nexus they are inclined to favor, but we are owed an account of why *any* proposal involving the interruption of gene flow among populations should be seen as theoretically crucial to species diversity.

Let me extend the point by taking note of a response that proponents of the biological species concept have offered to suggestions that gene flow may be insufficient to promote the cohesion of 'conspecific' populations. Mayr writes:

> Physiologists and embryologists, likewise, have published evidence for a remarkable uniformity of physiological constants through the range of most species. The essential genetic unity of species cannot be doubted. Yet the mechanisms by which this unity is maintained are still largely unexplored. Gene flow is not nearly strong enough to make these species anywhere nearly panmictic. It is far more likely that all the populations share a limited number of highly successful epigenetic systems and homeostatic devices which place a severe restraint on genetic and phenotypic change. (Mayr 1963, p. 523; see also Mayr 1970, pp. 300–301).

This response threatens the priority of the concept of reproductive isolation by hinting at a quite different approach to the delimitation of species taxa. Each species taxon is to be associated with an epigenetic system (or a small family of such systems). The persistence of uniform phenotypes across the broad range of a species is to be explained by the difficulty of introducing new alleles that perturb the phenotype, and, by the same token, the distinctness of species is grounded in their having distinct epigenetic systems. No mention need be made of reproductive isolation. It might turn out that the distinctness of epigenetic systems coincided with the possession of isolating mechanisms, or that it did so in most cases, but the division of organisms into species (on this approach) would not rest on the fact of

reproductive isolation. What would make organisms belong to different species would be their possession of different epigenetic systems.

If Mayr's account of the persistence of uniformities in phenotype through the prevalence of imperturbable epigenetic systems were correct, then not only would the biological species concept fail to identify the crucial features on which species identity and species difference rest but, more to our present point, species would not need to be characterized as historical entities. Species taxa would be individuated by (families of) epigenetic systems. Of course, we could impose the *additional* requirement that organisms sharing epigenetic systems (of the same family) belong to the same species only if they belong to populations that are historically connected. However, if one believed that it is the presence of the epigenetic systems themselves that explains uniformities and differences, then it would be hard to see this additional requirement as anything other than an *ad hoc* salvaging of the Hull-Ghiselin thesis. Why should we care about reproductive connections if evolutionary fates are fixed by the (family of) epigenetic systems?

I shall conclude my worries about reliance on the notion of reproductive isolation, by considering a disturbing possibility. One of the intuitive, pre-theoretical, ideas that we might have about species is that organisms are either conspecific or not, and that, in either case, there is no relativization to any third factor. Given the organisms, their intrinsic properties and the relations between them, the answer to the question 'Are they conspecifics?' is fixed. I do not wish to claim that this pre-theoretical idea is entirely precise, or that it is sacrosanct. However, if we appeal to reproductive isolation as a criterion for species distinctness (or as a criterion for the occurrence of a speciation event that has split the genealogical nexus) then it seems quite possible that there will be a necessary relativization to the environment. This could occur in numerous cases where there are actual or potential disruptions of the habitat with consequences for the cycles of activity of organisms that do not normally overlap. However, I want to consider a pure example in which a mechanical barrier to gene flow might be breached by the environment.

Fertilization in sea urchins involves three fusions between sperm and egg. The first of these involves the acrosome (at the head of the sperm) and a jelly that surrounds the egg: a receptor molecule on the surface of the sperm responds to glycoproteins in the jelly and the result is a change in the pH of the acrosome, a change that allows for release of acting and (ultimately) for the penetration of the egg by the sperm. Two species of sea urchins are distinguished by different glycoproteins at the egg surfaces and by different molecules that bind the glycoproteins to the sperm. The result is that sperm of *Strongylocentrotus purpuratus* cannot fertilize eggs of *S. franciscanus* because the reaction is blocked at the first stage. However, in the presence of trypsin, the glycoproteins *will* bind to the sperm, and, in consequence, hybrid progeny are produced.

To the best of my knowledge, *S. franciscanus* and *S. purpuratus* are isolated only

by the mechanism just described. But it is plain that the isolation is environment-relative. In a trypsin-rich environment, there would be no barrier to gene flow between the two species. Now it is doubtful that there are any such environments inhabited by sea urchins – at least outside the laboratory. However, the example[15] points to a general possibility: populations may be reproductively isolated simply because a particular reaction in the formation of a zygote is blocked; however, the presence of certain molecules in the environment – perhaps as a result of abiological features, perhaps because of the presence of further organisms – might allow the reaction to go forward; thus it is quite possible that there are organisms that are reproductively isolated in one environment and not isolated in another (slightly different) environment. If the *very same* organisms had been situated slightly differently, the question whether they are conspecifics would have received a different answer. But perhaps the appropriate moral to draw here is that our initial view about the non-relativity of species relationships is faulty, and that, in our normal speech, we tacitly relativize to the kinds of environments that actually occur.

4. Segmentation and serendipity

Imagine that the problems of previous sections have been overcome and that we have successfully made sense of the concept of a population and of a principled notion of reproductive isolation. I'll suppose that we have understood a *lineage* to consist of organisms in some original population (the *founding* population) plus all their descendants, and that our residual task is to segment lineages by using the notion of reproductive isolation to characterize *separation events*. When a separation event occurs, some stages of the lineage just after the event belong to a different species than stages of the lineage from which they descended. The problem is to articulate the idea, specifying exactly how reproductive isolation relates to segmentation.

One proposal is to allow for speciation by anagenesis. Two lineage stages belong to different species if, had they coexisted, they would have been reproductively isolated. This proposal, essentially Simpson's, faces certain obvious difficulties of application – especially within the context of a gradualistic approach to evolutionary change. Notoriously, it has inspired some systematists to express their gratitude for the incompleteness of the fossil record, on the grounds that the gaps allow the delimitation of species taxa![16]

For many contemporary systematists, there is no hope of finding a principled division of lineages while allowing for anagenesis. Instead, we should recognize that the genealogical nexus is broken at those points where speciation produces two contemporary populations that are reproductively isolated from one another. Cladogenetic speciation is completed when the post-speciation descendants of the

stages of the lineage preceding the speciation event divide into two groups that are reproductively isolated from one another. For Hennig, a species comprises the organisms on a branch of a lineage bounded by consecutive speciation events: 'The limits of the species in a longitudinal section through time would consequently be determined by two processes of speciation: the one through which it arose as an independent reproductive community, and the other through which the descendants of this initial population ceased to exist as a homogeneous reproductive community' (1956, p. 58). Hennig is committed to two claims that distinguish his account from Simpson's: (1) speciation by anagenesis cannot occur; (2) ancestral species cannot survive the events in which they give rise to daughter species.

Wiley (1981) has amended Hennig's approach to avoid one source of controversy, and his formulation of an evolutionary conception of species is explicitly designed to wed Simpsonian and Hennigian insights. On Wiley's account each species comprises the organisms on a branch of a lineage bounded by speciation events (not necessarily consecutive). Thus Wiley takes over (1), but does not commit himself to (2). He writes: 'Ancestral species may become extinct during speciation events if they are subdivided in such a way that neither daughter species has the same fate and tendencies as the ancestral species' (1981, p. 25). It is fairly clear what Wiley has in mind. If speciation occurs by geographical isolation of a very small population of the ancestral species, so that the full range of antecedent genetic (behavioral, ecological, morphological) variation is retained in that portion of the ancestral species that is *not* isolated, then, in a very obvious sense, the evolutionary history of the branch of the lineage containing the unisolated moiety is unaffected by what occurs on the branch that contains the isolate. Had a cataclysm simply eliminated the organisms that were actually geographically isolated, the subsequent evolution of the unisolated organisms would (at least initially) have been no different. But in this case, there would have been no speciation event, and hence no principled splitting of the lineage into two 'sibling' species that succeed one another temporally. Wiley proposes that ancestral species can survive speciation events if their range of variation is not substantially depleted, and this eminently reasonable idea enables him to cope with cases that Hennig finds troublesome.

The differences among Simpson, Hennig, and Wiley are easily displayed diagrammatically (see Figure 3). Hull (1978) reproduces similar diagrams, and points out, quite correctly, that it is a significant and difficult issue to choose among the corresponding positions. In the remainder of this section, I want to underscore the difficulties. The Hull-Ghiselin thesis that species are historical entities is committed to the view that there is some principled way of segmenting the genealogical nexus. I hope to show how each of the available principles of segmentation is problematic.

Here is the strategy. In motivating Wiley's departure from Hennig, I developed an argument that contrasts the actual course of evolution with a slightly different

possible situation. In the transition from the actual history of the world to this possible situation, the intrinsic properties of and direct relations among stages of one branch of the lineage were left unmodified. Yet Hennig's criterion for species delineation was found to yield different conclusions for the organisms on this branch in the two cases. What discredits the criterion is our acceptance of the following principle:

> (*) A proposal to count lineage-stages as stages of the same species should depend only on the intrinsic properties of and direct relations among those stages. It should give the same results in cases which differ only in the existence or properties of organisms occupying a different branch of the lineage.

I shall now try to show how appeals to (*) cast doubt on some of the most basic features of the idea that species are segments of the genealogical nexus.[17]

Let us begin with the thesis that Wiley shares with Hennig, (2), the ban on anagenesis. There is an old worry about this thesis. It is apparently possible that a lineage should evolve quite dramatically without splitting: imagine a world in which the lineage is founded by a population of protists and then evolves into *Homo sapiens* by the sequence of genetic changes that actually link us to our protist ancestors. On the Hennig-Wiley criterion, all the organisms in this lineage would belong to a single species.[18] This strikes many people as counterintuitive (even insane). I shall defend the example and develop it so as to make clear the source of the trouble.

Notice first that the Hennig-Wiley criterion cannot be protected by dismissing the imagined possibility as unreal. It will not do to protest that, in any world in which there was an undivided lineage linking the protists to humans, the laws of nature would have to be very different so that the Hennig-Wiley criterion would be inapplicable. We can describe a world, like our own in certain critical respects, in which the lineage is realized. At each point corresponding to a speciation event in the actual world the same kind of thing happens. Part of the ancestral population takes the first step toward speciation, and, as it does so, the relict of the ancestral population is wiped out. Objection: the story cannot be quite parallel, because the organisms that were eliminated would have exerted selection pressures on the evolving lineage, and, in their absence, the course of evolution cannot be the same. Reply: the selection pressures have to be made up in other ways; one possibility is to suppose that another (distinct) group of protists gives rise to a branching lineage in which organisms evolve to exert the right kinds of pressures on the unbroken lineage.

The heart of the problem can be understood by beginning with the hypothetical situation of the last paragraph and tracing a continuous path back toward actuality. Choose any of the actual branching points along the protist-human lineage – say the event in which the first mammalian species originated from part of the ancestral population. In the hypothetical world, we assume that the first mammalian species
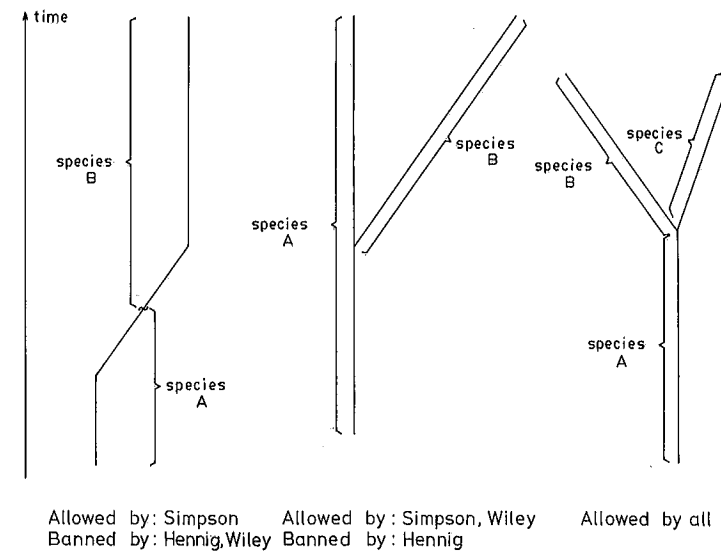
Allowed by: Simpson   Allowed by: Simpson, Wiley   Allowed by all
Banned by: Hennig, Wiley   Banned by: Hennig

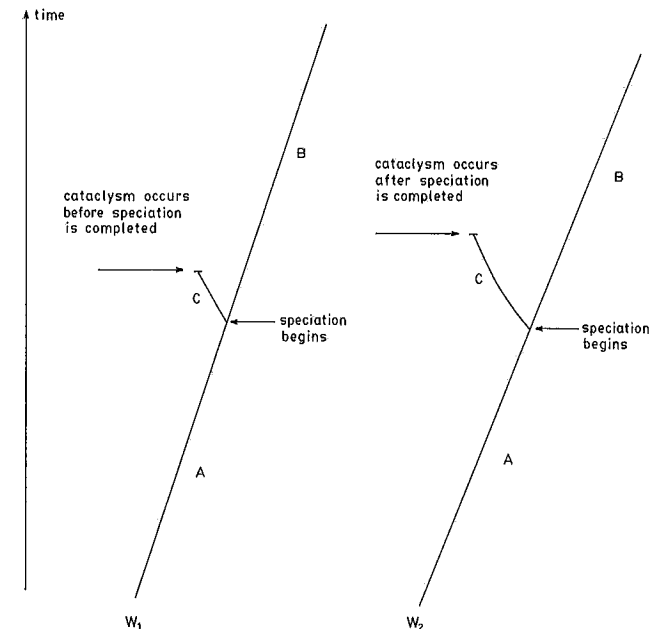*Fig. 3.* Three Proposals for Splitting Lineages.

Fig. 4. A Puzzle for the Hennig-Wiley Criterion.

survived a cataclysm in which the rest of the ancestral population was wiped out. Now let us suppose that the time of the cataclysm is slightly postponed – the avalanche comes or the river floods a day later than before. As we delay the time of the catastrophe, we finally obtain a situation in which the relict branch achieves reproductive isolation from the main lineage. At this point, the Wiley-Hennig criterion demands that the original lineage is to be split into two distinct species.

The thought-experiment is easier to grasp by reference to Figure 4. Here W_1 is a world in which A and B (and C, for that matter) are lineage segments belonging to the same species. In W_2, by contrast, A and B (at least) count, by the Hennig-Wiley criterion, as distinct species. To defend the 'Simpsonian intuition' that lineage splitting is forced even in unbranching lineages, one should focus on cases like those contrasted here, and invoke (*). In W_1 and W_2, the intrinsic properties of the organisms in the $A+B$ lineage are the same: the same ranges of genetic, morphological, behavioral, and ecological variation occur at each stage. The same reproductive connections hold along the lineage. All that differs is the timing of a catastrophe that affects only organisms on a *different* branch. Appealing to (*), I claim that the difference is extraneous to the organisms in $A+B$, and that a proper division of the organisms of $A+B$ into species ought to yield the same result in each case.

Allowing for anagenesis would, of course, leave us with the puzzle of *how* to allow for anagenesis. That topic deserves a paper of its own, and I shall not pursue it here. Instead, I want to pose a problem, of the same general form, that strikes at all versions of the thesis that species are historical entities – including those that articulate the thesis along the lines indicated by Simpson. Unlike the argument just offered, we do not have to countenance any exotic possibilities to appreciate the force of the puzzle. It arises form the simple possibility of 'dumbbell allopatry' as a mode of speciation.

Imagine an evolving lineage which, at time t, is divided into two roughly equal halves by the interposition of a geographical barrier. Assume that, at t', the descendant populations on each branch of the lineage have diverged to a sufficient extent that each behaves as a good species with respect to the other. The criterion of species distinctness can be reproductive isolation – or something different, provided only that termination of speciation should conform to a familiar biological fact, to wit that speciation need not be instantaneous and that it is possible to talk of lineages as undergoing events of speciation (not necessarily at a uniform rate). Suppose, further, that from t' a condition of stasis prevails, so that the two lineage branches persist unmodified for a million years, until they become extinct. Finally, let us add the condition that the divergence of both branches is minimal for complete speciation. If the ancestral lineage had persisted unchanged beyond the point of geographical bifurcation, its subsequent stages would not be sufficiently distinct from the stages on either branch to count as a separate species. In other words, each incipient branch retained the full range of variation present in the ancestral lineage, there are evolutionary changes along both branches, and these
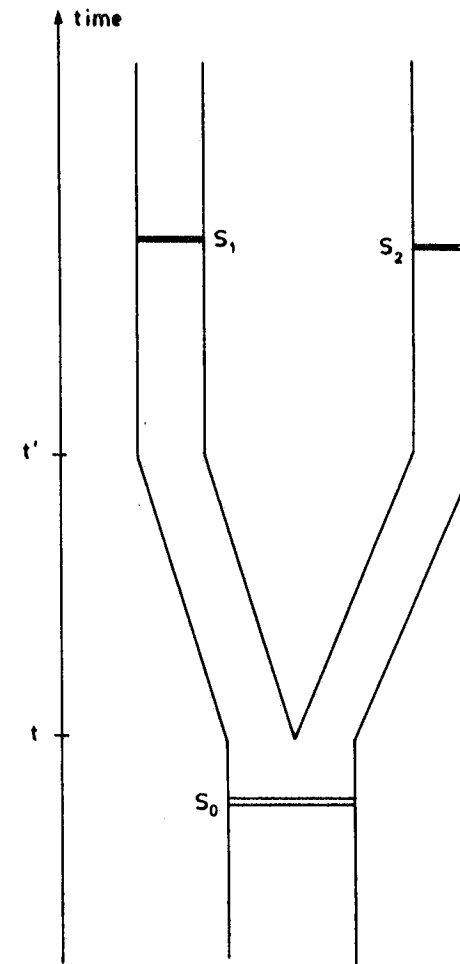
Fig. 5. Species Survival and Identity.

are, together but not separately, sufficient for speciation.

The envisaged situation is represented in Figure 5, where the horizontal axis represents whatever kind of change is taken to be relevant to speciation. By the criterion for speciation S_1 and S_2 are stages of different species. However, by the same criterion, S_1 and S_0 count as conspecific, and so do S_0 and S_2. Hence we face an apparent paradox: there is a species that embraces S_1 and S_0 and a species that embraces S_0 and S_2, but no species that embraces S_1 and S_2.

Formally, this is not a paradox. No contradiction arises unless one holds that for any organism there is at most one species to which it belongs. But if one retains that principle then one must decide which of the judgments about conspecificity to abandon. One approach (Hennig's) is to declare that the ancestral species becomes

extinct at t, at which point two daughter species are born. This response falls foul of the argument given in motivating Wiley's departure from Hennig. Had either branch become extinct shortly after t, we would be happy to count the residual branch as a continuation of the ancestral species. Moreover, the situation is symmetrical. Worlds in which either branch survives and the other terminates are happily seen as worlds in which an evolving lineage gets about half way through what looks like anagenesis – and then stops.

Whatever condition is proposed for guaranteeing the persistence of the ancestral species – retention of full range of genetic variation, for example – can be built in to the scenario. Once again our judgments of conspecificity are grounded in (*). Because the time of extinction of one branch does not make a difference to the intrinsic properties of stages on the other branch, or to the direct relations among them, whether or not those stages belong to the same species cannot depend on whether or not the first branch persists.

If cases like this were to occur (and perhaps they do) a purely formal solution to the problem could be obtained by allowing the same lineage-stage to belong to two different species.[19] Just as two different roads can overlap on the same piece of tarmac, so, we might say, the same lineage-stage can be included in two different species. Biologists, I suspect, will not find this formal solution attractive. A more plausible way of treating such instances is to let one's judgments about division into species conform to the current needs of biological research. For someone investigating the acquisition of reproductive isolation, it might be appropriate to count both branches as distinct daughter species. On the other hand, a biologist concerned with the developmental constraints imposed upon organisms by the facts of their ancestry might prefer to view the branches and the ancestral lineage as constituting an (unusual) single species. Judgments about such cases seem to rest on whether one is more interested in the distinctness of the descendant branches or in their kinship with their common ancestor. I believe that there is no single, objectively right, way to segment the entire lineage into species. Various ways of proceeding offer partial solutions, emphasizing some biological features of the situation and downplaying others. I propose (once again) that we take a pluralistic view of species, allowing that there are equally legitimate alternative ways of segmenting lineages – and indeed legitimate ways of dividing organisms into species that do not treat species as historical entities at all.

5. Conclusions

To say more about pluralism and its virtues would change the focus of this paper. What I have been attempting to show is the extent of the work that needs to be done if Hull's conception of species as historical entities is to cope with the diversity of organisms. Pluralism enters the discussion only because it offers a way out of an

apparent difficulty in segmenting lineages. Hull (1987) has complained that pluralism is the counsel of despair, and that monistic proposals for understanding species deserve a run for their money. There is surely a sound point here. Numerous instances from the history of science reinforce the judgment that theories need time to overcome apparently devastating objections. However, what concerns me about the proposal that species are historical entities is that the *difficult* problems about delimiting species taxa seem to have become invisible. As I read the recent literature – for example (Eldredge 1985, Mayr 1987, Ghiselin 1987, Hull 1987) – an unarticulated version of the proposal seems to be serving as the basis for suspiciously a-priori-looking arguments about evolutionary processes, while issues about the articulation of the proposal are ignored. My aim here has been to bring *some* of the problems back to center stage.

Of course, not all apparent puzzles deserve serious and sustained attention. Most philosophers are familiar with the dismaying degeneration that characterizes fields in which energy is lavished on counterexamples of no theoretical importance. One of the great merits of David Hull's approach to philosophy of biology has been his plea for the use of realistic examples and his dismissal of worries based on unconstrained philosophical fictions. I hope that the examples I have constructed are simply pure types of actual biological situations, so that they will strike him as the kinds of puzzles that his account of species will have to overcome. In this spirit I offer him, not a knockdown argument for pluralism, but just some puzzles about species.

Acknowledgement

Notes

1. The debate about 'the ontology of species' begins with (Ghiselin 1974), (Hull 1976, 1978). Criticisms are launched in (Kitts and Kitts 1979) and (Caplan 1981). Hull replies to these in his (1981). My own objections to the Hull-Ghiselin view are presented in my (1984a, 1984b, 1987), and some of my concerns are addressed in (Hull 1987). Sober (1984) is a reply to my (1984a) and my (1984b) attempts to rebut Sober's objections.
2. The following argument is briefly presented in (Hull 1987), but Hull has offered a more extensive version of it in conversation.
3. Talk of the persistence of sets all of whose members are physical objects is tricky. In one obvious sense, any set is an abstract object and therefore exists atemporally. But there is another notion of persistence that underwrites the intuition about the organization of organisms that I am attempting to articulate here. According to this notion, a set of physical object persists just so long as all of its members exist. When I speak of the

persistence of sets of physical objects, I shall be employing this latter notion.

4. This is the type of organization that Hull appears to emphasize in his (1978) – see for example p. 342. He has made the point even more explicitly in conversation.

5. This elementary logical point seems to have been very difficult to grasp – see for example Mayr's confession of bewilderment in his (1987) and Hull's (1987) acknowledgement that he shares Mayr's bewilderment. My (1987) tries to forestall the confusion, but perhaps I can make the point even more obvious by noting that the claim 'All *A*'s are *B*'s' ('All species are sets', 'All species are individuals') doesn't entail 'All *B*'s are *A*'s' ('All sets are species', 'All individuals are species').

6. It is worth noting that the concept of historical connection that I have just introduced isn't strong enough to generate Hull's 'conceptual point' (Hull 1978, p. 349) that species cannot re-evolve. To require that species can't become extinct and then reappear, one needs a condition of *complete historical connection*: an entity with organisms as parts (or members) is completely historically connected just in case for any two organisms belonging to the entity there is a sequence of populations, all of the organisms in which belong to the entity, such that each population in the sequence is either an immediate ancestor or an immediate descendant of its predecessor and such that the organisms in question belong to the first and last members of the sequence, respectively. I don't hold Hull and Ghiselin to this requirement, because it seems to me to be incorrect. In my (1984a), I offered a hypothetical case based on what we know about species of the genus *Cnemidophorus* to suggest that the same species might have a discontinuous career. Examples of a similar kind are probably legion among microorganisms, and the fact that we are eukaryotes shouldn't prevent us from seeing the need for a species concept that can be applied to bacteria and viruses as well.

7. A paradigm example seems to me to be (Eldredge 1985), where I think that some very important ideas are obscured by developing and defending them in quite the wrong way.

8. A cautionary note: it is easy to draw branching diagrams and to canvass possibilities by appealing to them. But it is always worth asking how we link the organisms that the naturalist observes to the branching diagram. By this I do not simply mean to pose the cladists' central question of 'retrieving phylogeny' (in Elliott Sober's apposite phrase) but also to point out that we need to be told *precisely* what the phylogenetic branching diagram is supposed to represent. As Hull himself noted in a classic paper (1968), there is all the difference in the world between asking how we obtain evidence for a classificatory judgment and what the classificatory judgment means. So we should wonder not only how we are to find branch points and how we are to assign organisms to lineages, but what 'branch point' and 'lineage' *mean*.

9. Exercise for the reader; show that any statement made in subsequent pages that uses set-theoretic notions (e.g. *is a member of*) can be replaced without modification of empirical content by a mereological expression (e.g. *is a part of*) provided that the translation is done systematically, and that the converse is also true. Ambiguous expressions (*belongs to*) can be read either way.

10. The point that I have been making is an attempt to articulate what I regard as a deep insight in the critique of the biological species concept advanced by Sokal and Crovello (1970). The worry is not just that we cannot obtain *evidence* for reproductive community without introducing considerations of phenotypic similarity, but that the *concept* of reproductive community presupposes a projection from the events of actual mating, a projection itself defined by continuities and discontinuities in biological properties. Sokal and Crovello present their case in terms of the decision procedure of a field naturalist, but many of the observations they make can be freed from the emphasis on 'operational critria for application' and reformulated as points about the concept of reproductive community.

11. A classical example is that of the towhees (*Pipilo erythrophtalmus* and *Pipilo ocai*) which occur together in some places without interbreeding, but which hybridize freely where agricultural disturbance has disrupted their habitat. For concise discussion, see

Mayr 1970, pp. 73–74, 1963, p. 121.

12. Roughgarden (1979, Chapter 12) provides a review of some basic results about conditions under which migration of alleles among spatially separated populations is likely to be an evolutionarily significant force. He considers the relative strength of effects of migration and drift, and the interplay between migration and a spatially variable selection pressure. However, I have not seen any detailed discussion of the question when introgression in peripheral populations of a species becomes sufficient to break down the autonomy of the species. The conditions for introgression to be important can be expected to depend on (a) the spatial distribution of the populations of both species, (b) the migration rate among conspecific populations, (c) the selection pressures operating on different loci in different populations, and (d) the effective sizes of the populations in question. It seems possible that the phenomenon of introgression in hybrid zones should be asymmetrical: in other words, that genetic changes in one population should spread into the other population, but that there should be no significant flow in the opposite direction. Were this to occur, there would be a fundamental difficulty in talking about reproductive isolation as a symmetrical relation between populations.

13. The last example is due to Leigh van Valen. See his extremely interesting – and underread – (1976).

14. My formulation here is deliberately conservative. Many writers would insist that morphological differences and isolating mechanisms can evolve without the interposition of a geographical barrier. See, for example, (Bush 1975), (White 1978), and, for a response, (Futuyma and Mayer 1980). If they are correct, then the case for making reproductive isolation crucial to the understanding of species diversity is even weaker than I have portrayed it as being.

15. For information and discussions relevant to this example, I am extremely grateful to William Loomis. For details on sea urchin fertilization, see (Vacquier 1979) and (Podell and Vacquier 1984).

16. See, for example, a first-rate textbook in paleontology, (Raup and Stanley 1978, p. 111). I should note that Raup and Stanley also lament the 'valuable information' that has been lost, so they do perceive the gappiness of the record as a *mixed* blessing.

17. Note that (*) is connected with the intuition that I canvassed in the last section in discussing the possible environment-relativity of species divisions. I don't rule out the possibility that we might ultimately want to reject (*), but I think that any such rejection would have to be based on a thorough scrutiny of the central ideas, aims and presuppositions of systematics, the type of investigation for which I have argued in my (1984b, pp. 628–630). In a line, philosophical discussion of species concepts ought to return to the issue of what we are after in devising a scheme for mapping organismic diversity, the issue that was originally posed by Mayr and Dobzhansky in the 1930s and 1940s, but that has become lost in subsequent discussions. The puzzles of this paper are intended as motivational preludes for the return.

18. One can't duck the issue by claiming that all the organisms belong to a single *taxon, Eucaryota*. For, if we believe that every organism belongs to a species, then trivially for each organism in the lineage there is a species to which it belongs. By the Wiley-Hennig criterion, any two organisms in the lineage are conspecific. Hence there is a unique *species* to which every organism in the lineage belongs. It makes little difference whether one calls this species *Eucaryota integra* or *Homo sapiens*.

19. Aficionados of the literature on personal identity will recognize the problem I have posed and the line of solution I indicate here. A similar puzzle and similar canvassing of possible solutions is given by Laurance Splitter in a forthcoming paper.

References

Bush, G.L. (1975) Modes of animal speciation. *Annual Review of Ecology and Systematics* 6: 339–364.

Caplan. A. (1981). Back to class: a note on the ontology of species. *Philosophy of Science* 48: 130–140.

Dobzhansky, T. (1937). *Genetics and the Origin of Species.* New York: Columbia University Press.

Ehrlich, P.R. and Raven, P.H. (1960). Differentiation of populations. *Science* 165: 1228–1232.

Eldredge, N. (1985). *Unfinished Synthesis.* New York: Oxford University Press.

Endler, J. (1977). *Geographic Variation, Speciation, and Clines.* Princeton: Princeton University Press.

Futuyma, D. (1979). *Evolutionary Biology.* Sunderland MA: Sinauer.

Futuyma, D. and Mayer, G. (1980). Non-allopatric speciation in animals. *Systematic Zoology* 29: 254–271.

Ghiselin, M. (1974). A radical solution to the species problem. *Systematic Zoology* 23: 536–544.

Ghiselin, M. (1987). Species concepts, individuality, and objectivity. *Biology and Philosophy* 2: 127–143.

Hennig, W. (1966). *Phylogenetic Systematics.* Urbana: University of Illinois Press.

Hull, D. (1968). The operational imperative – sense and nonsense in operationism. *Systematic Zoology* 17: 438–457.

Hull, D. (1976). Are species really individuals? *Systematic Zoology* 25: 174–191.

Hull, D. (1978). A matter of individuality'. *Philosophy of Science* 45: 335–360.

Hull, D. (1981). Kitts and Kitts and Caplan on species'. *Philosophy of Science* 48: 141–152.

Hull, D. (1987). Genealogical actors in historical roles. *Biology and Philosophy* 2: 168–184.

Kitcher, Ph. (1984a). Species. *Philosophy of Science* 51: 308–333.

Kitcher, Ph. (1984b). Against the monism of the moment: a reply to Elliott Sober. *Philosophy of Science* 51: 616–630.

Kitcher, Ph. (1987). Ghostly whispers: Mayr, Ghiselin and 'the Philosophers' on the ontology of species. *Biology and Philosophy* 2: 184–192.

Kitts, D.B. and Kitts, D.J. (1979). Biological species as natural kind. *Philosophy of Science* 46: 613–622.

Levin, D. and Kerster, H. (1974). Gene flow in seed plants. *Evolutionary Biology* 7: 139–220.

Mayr, E. (1963). *Animal Species and Evolution.* Cambridge MA: Harvard University Press.

Mayr, E. (1987). The ontological status of species: scientific progress and philosophical terminology. *Biology and Philosophy* 2: 145–166.

Podell, S. and Vacquier, V. (1984). Wheat germ agglutin blocks the acrosome reaction in *Strongylocentrus purpuratus* sperm by binding a 210,000 mol. wt. membrane protein. *Journal of Cell Biology* 99: 1598–1604.

Raup, D. and Stanley, S. (1978). *Principles of Paleontology.* San Francisco: Freeman.

Roughgarden, J. (1979). *Theory of population genetics and evolutionary ecology.* New York: Macmillan.

Sober, E. (1984). Sets, species and evolution: comments on Philip Kitcher's 'species'. *Philosophy of Science* 51: 334–341.

Sokal, R. and Crovello, T.J. (1970). The biological species concept: a critical evaluation. *American Naturalist* 104: 127–153.

Vacquier, V. (1979). The interactions of sea urchin gametes during fertilization. *American Zoologist* 19: 839–849.

Van Valen, L. (1976). Ecological species, multispecies, and oaks. *Taxon* 25: 233–239.

White, M.J.D. (1978). *Modes of Speciation.* San Francisco: Freeman.

Wiley, E.O. (1981). *Phylogenetics.* New York: Wiley.

The Rational Weight of the Scientific Past: Forging Fundamental Change in a Conservative Discipline

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Introduction

(One of the recurrent foci in David Hull's research has been the character of history, especially history of science. He has, indeed, been an eloquent defender of enlightened whiggism in history of science during decades when, for all the wrong reasons, whiggism has gone out of fashion. At the heart of the debates between anti-whigs and people like David Hull has been a disagreement about whether the past has a legitimate *justificatory* role in contemporary debates about science. I have written this essay for this volume as an effort to sketch out a picture of one important kind of justification which the history of science has often been expected to provide.)

For well over a century, scientists and philosophers of science have been struck by various apparent continuities in science. Thus, it has been commonly maintained (1) that earlier theories are limiting cases of later theories, (2) that successor theories explain all the successes of their predecessors, and (3) that later theories entail their predecessors. The conviction that there are pervasive temporal continuities in science was, of course, a cornerstone of both positivist and pre-positivist accounts of scientific knowledge. Within recent times, virtually all these claims have been seriously and (in my view) successfully challenged.[1]

However, as the case for wholesale retention of empirical content through theory transitions has been rapidly crumbling, many philosophers of science have begun to seek for continuities elsewhere – specifically in the aims and standards of the scientific enterprise. On this view, even if the *content* of our beliefs about the world shifts dramatically from epoch to epoch, there are nonetheless certain broad epistemic goals and methodological standards which have characterized science since its inception. Scientists, we are told, are and always have been seeking to find out the truth about the world and have utilized familiar methods of observation and experiment to ferret out those truths. This supposed constancy at the level of methods and aims avowedly gives science its coherence and individuates it from other, more ephemeral intellectual practices, lacking a fixed mooring in sound methods. Unfortunately, this view of the fixity of the aims and methods of science