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is not an effort to solve arcane technical problems. It is not an effort to apply what gets taught in one academic department to what gets researched in another. Rather it is a serious attempt to unify knowledge as a whole. As such it is uncompromisingly monistic.

# Answers to These Comments

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I had attempted to restrict my presentation to ontological issues. Unfortunately almost all of the discussants have added a discussion of epistemological problems, that is questions pertaining to the definition of the species category. Since I have discussed these epistemological issues in great detail elsewhere (Mayr 1986 b) I shall not discuss here why I reject the morphological species concept and endorse instead the biological one. However I must point out that there is no real conflict between statements of mine relating to the species taxon and others relating to the species category, as claimed by some of the readers. For instance, Ghiselin states "on the one hand they [= Mayr] want(s) species to be individuals - so they can evolve. On the other hand they want them to be classes of ecologically similar organisms." Yet Ghiselin fails to produce any argument that ecological autonomy could not be just as much a characteristic of species individuals as reproductive isolation (see below). A similar confounding of the nature of the species taxon ("a thing") with the criteria of the species category ("a class") can be found in many of the comments on my paper.

When Hull says that the argument is about "the issue of the ontological status of the species category", I doubt that he really means this. I thought everyone now agreed that the species category is a class (Mayr 1976b), and that the argument concerns entirely the status of the species taxon. As a matter of fact, this is what Hull actually discusses in his paper.

## CROWE

Crowe emphasizes that a species has characters-in-common among which the Specific-Mate Recognition System is most important. This set of

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isolating mechanisms is perhaps the most cohesive factor holding the parts of a species together.

### GHISELIN

As far as the ontology of species is concerned, there is no disagreement between Ghiselin and myself, except for the question whether or not singular and multiple individuals should both be designated by the term individual, which to any non-philosopher signifies singularity and indivisibility. Like most naturalists I have treated species taxa as individuals from my earliest publications on.

Like Hull, Ghiselin is much concerned about the issue of laws. What is the connection between the ontological status of species and the recognition of laws in nature? I will not discuss this in detail, since in my opinion this is largely a semantic question (see my answer to Hull). That innumerable generalizations are possible in biology is something that every scientist would accept. But would they qualify as "laws of nature" as defined in the classical philosophy of science? Smart said that they would not, and I agree. Popper's falsification principle was to a large part based on the universality of laws. What Ghiselin and others have done is to greatly modify the concept of laws, by now applying this term to any statistically based generalization. If such a shift is accepted by the philosophers of science, then, of course, I will no longer deny that there are laws in biology. But what is gained by this transformation? Also, where is the demarcation between laws and facts? The more so-called laws I have looked at, the more they have looked to me as if they were simply statements of fact. Is the statement that birds have feathers a fact or a law? A paleontologist may claim that it is a law because in fossil birds feathers are usually not preserved, and it is only the law "birds have feathers" which permits him to say that the fossil birds also had feathers. Or is this an altogether wrong argument? Does the term law refer only to processes? It would seem to me that my challenge should induce somebody to produce a more up to date treatment of the concept of law than we seem to have in the literature at the present time.

Ghiselin says that Simpson (1961) confused matters by saying that we classify "groups not individuals". Actually the shoe is on the other foot. Simpson used the word individual in the traditional vernacular sense, and what he called groups were not at all classes but populations, that is, multiple individuals in the technical sense of the philosophers. The confusion to which Ghiselin refers was introduced not by Simpson but by the philosophers when they took a term from everyday life, a term signifying singularity and indivisibility, and transferred it to a multiple object.

Let me take up once more the ecological criteria of the species category. When I lately added the qualifying clause "that occupies a specific niche in nature", I had no intention at all of doing so in order to be able to classify asexual organisms. It occurred to me only much later that this criterion might help in the classification of asexual clones. The real reason why I added this clause was that it seemed to me that no population has completed the process of speciation until it is able to coexist with its nearest relatives. Reproductive isolation is one of these factors, but avoidance of competitive exclusion is another one. This is not at all a "watering down" of the biological species concept, as Hull says, but rather a "toughening it up". It adds one more constraint to the concept of the biological species. Time will show whether this additional qualification is useful or confusing.

In a recently published history of species concepts (Mayr 1986 b), I have given a detailed critique of the evolutionary species concept. I reject it as categorically as does Ghiselin, but for different reasons. However, referring to ecological criteria in a species definition does not make it an evolutionary concept, as far as I am concerned. In my argument I always go back to the nondimensional situation. Two populations may not be able to coexist because they are not reproductively isolated, that is they would immediately interbreed and fuse into a single species. However, two populations may also not be able to coexist at one locality because they have not yet acquired such niche exploiting capacities as would preclude competitive exclusion. This is of course superimposed on the primary criterion of reproductive isolation. It would seem to me that the process of speciation is not completed until such mutual ecological tolerance has been achieved. One of the characteristics of the species, as individual, is ecological autonomy. It should be very evident from my discussions that. nothing is further from my mind than to treat species as classes of ecological similars, as Ghiselin implies.

The greatest difficulty, rather neglected by both Ghiselin and myself, is the fact that in certain groups of organisms, particularly plants, fungi, and prokaryotes, there are entities of nature usually treated by the taxonomists as species, that have little resemblance to the classical biological species of sexually reproducing higher organisms. I reaffirm my support for Ghiselin's position to postpone a discussion of these nontraditional entities until full clarity has been achieved concerning both ontology and epistemology of the traditional biological species.

# HULL

I still insist that the question of laws has nothing to do with choosing class or individual (population) as the status of the species taxa. If I were to deny the existence of regularities in nature, I would not be a scientist. What I question is whether the term law, as defined and used in physics, is the appropriate term for the regularities found in the living world. To me it seems that the statistically calculated regularities found in living nature are not the same thing as the laws of physics and therefore should not be designated by the same term: laws. In contrast to Hull and Ghiselin, I find this terminology misleading with respect to the regularities described by the biologist. As I said, the issue class versus individual can be discussed and perhaps decided without any reference to the problem of the terminology of regularities.

The question whether species are always correctly identified in folk taxonomy is a question of epistemology rather than of ontology. Natives are always best in that which they are most interested in. Natives living at the seashore may be able to identify every mollusk and other edible or toxic invertebrate in the intertidal zone and yet be remarkably ignorant of the plant species of the adjacent forest. Yet such ignorance has no bearing on the ontological status of species taxa.

The whole concept of "characters-in-common" seems to be alien to philosophy. Therefore philosophers make no distinction between essence and characters-in-common. In reality there is a fundamental difference between the two concepts. No one will question that the members of such species as wolf or nightingale have characters-in-common. But this aggregate of characters-in-common has a number of characteristics that are incompatible with the definition of essence. First, they are variable, actually and potentially, and secondly, they can evolve, that is they can change in time. By contrast, an essence has no variability and has no potential for change. This is a vitally important distinction. What is also important to recognize is that the characters-in-common are a consequence of the fact that the respective taxon is a species. We are dealing here with the same chain of causation, as described by Simpson (1961), for identical twins. Two siblings are identical twins not because they are so similar, but they are so similar because they are monozygotic.

As far as the question of the history of species as individual is concerned, Hull misses the point of my historical analysis. What is involved is not the question of priority. After all, Ghiselin himself pointed out quite correctly that the concept of species being an individual goes back "at least to Buffon". What is important is the fact that most biologists for 200 years agreed that species taxa are not classes but "things" (= individuals), but this was totally ignored by the philosophers until Ghiselin brought it to the attention of D. Hull. As far as priority is concerned, Ghiselin certainly deserves credit for finally making the philosophers acknowledge what biological taxonomists had been saying for more than 100 years. Contrary to Hull's claims, the scientists had the right idea for a long time, but they were unfamiliar with the terminology, classes versus individuals, and therefore never made an issue of this question. Actually, the shift from the essentialistic to the biological species definition represented automatically a shift from the class to the individual concept of the species taxon.

## KITCHER

Kitcher implies in his "ghostly whispers" allegations that Ghiselin and I, in the individual vs. class controversy, argue against obsolete philosophics and terminologies. This is a demonstrably wrong claim. There are literally scores of articles on the individual versus class problem in the recent philosophical journals. Kitcher carefully refrains from listing "the recent philosophical literature about species" with which we "fail so conspicuously to come to terms with", except for four of his own papers among the six listed under his references. Where are all those papers on the philosophy of species in "the pertinent technical literature" that we "have failed to immerse" ourselves in? Also, does Kitcher think that his settheoretical framework, because it is newer is therefore better, as claimed in the slogan of the advertising industry?

Kitcher's comments, for a number of reasons, have greatly disappointed me. Other philosophers have realized in recent years how important it is to avoid equivocation, and how important to break up heterogeneous assemblages by providing a specific term for each component. The discrimination of *teleonomic*, *teleomatic*, and *adapted* among the confusing uses of the word teleological is an example. Many of the recent introductions of new terms have eliminated previously existing ambiguities.

Now Kitcher tries to reverse the trend. Instead of accepting the distinction between two assemblages, class and individual, or three, by accepting population, he lumps all aggregates of more than a single entity under the heading of set. For him a species taxon is a set, as is, to cite his own example, the combination of "Queen Victoria, the manuscript of *Finnegan's Wake*, and the number 7." The members of the species nightingale are a set as is the contents of my waste paper basket. All previously recognized discriminations are abandoned and the drastically different kinds of multiples one finds in this world are all lumped under one heading. I fail to find in his comments any response to my criticism of this procedure. His further discussion of set theory does not accomplish this in the slightest.

If one were to adopt Kitcher's set terminology, one would have to recognize various subcategories of sets, in order to bring at least some homogeneity to the different kinds of grouping one discovers in nature. Some of them would correspond to "class" and "individual" of traditional philosophy, and then we would be right back where we were at the beginning. So, what is the good of the set terminology? Gregg (1950, 1954) tried it before and produced only confusion.

From his discussion one gains the impression that Kitcher has an essentially numerical conceptualization of the world. He is apparently completely insensitive to the fact that there is a fundamental difference between a chance aggregation of items, like the contents of my waste paper basket, or an aggregate held together by a defining property, like hairy objects, or, finally, a cohesive species population that has all the properties by which philosophers recognize individuals. To ignore all these differences might be good enough for a mathematician, but not at all for those who work with these phenomena, for instance the students of species. Frankly, Kitcher's set-theoretic analysis has left me totally bewildered. I have been unable to establish any connection between it and the real world of biological species.

Kitcher seems to have no appreciation of the non-dimensional situation, the only one where species taxa can be delimited against each other unequivocally. Fission in protozoans and in other vegetatively reproducing organisms shows that the origin of new individuals can be a gradual process, corresponding to a similarly gradual origin of new species.

Perhaps the greatest weakness in Kitcher's species concept is that it is strictly "additive." This means that what members of a species have in common is that they belong to the same set [just like hairy objects belong to the set of hairy objects]. What is left out entirely, and that is what makes species "individuals," is the interaction of the members of the species. They exchange genes with each other in every generation, they form a common gene pool, and stabilizing selection controls the limits of their variation. There is nothing equivalent to this among sets of inanimate objects. Let a mathematician ignore such a fundamental difference, but for a biologist it would be suicidal to do so. If he treated biological species as being no different from sets of inanimate objects, he would no longer be a biologist.

One more minor point. Kitcher talks of parents producing an individual that is a different species. In sexually reproducing species this occurs only very rarely, for instance in the case of polyploidy, and contra-Sober, such an individual is not a member of the parental population. It would lead to a most perverted concept of population to accept the proposition that members of two different species could be members of a single population.

## ROSENBERG

Since Rosenberg and I agree in the conclusion that species are not classes but that which philosophers call individuals, there is no major disagreement between us. Whether it is worthwhile or merely confusing to make a distinction between singular individuals, that which everybody calls an individual, and multiple individuals, that which the biologist calls populations, is something the future will tell. In my comments on Rosenberg's paper I shall argue about relatively minor points.

In his early discussion Rosenberg deals with the species as if it were simply the lowest in the Linnaean hierarchy of categories, a merely classificatory phenomenon. However, as almost every biologist who has written about species in recent years has pointed out, the species taxon plays an important biological role in nature, particularly in ecology, while the higher categories are merely classificatory devices without particular biological significance. Evidently, the species has a different biological significance from the higher categories.

Both evolutionary biologists and philosophers tend to conflate Darwin's various evolutionary theories. It is by no means correct to say "the theory of natural selection is an account of the origin of species". Take any modern account of natural selection, let us say Sober's (1985) and quite rightly you find little if anything in it about the origin of species. Correspondingly, in modern arguments about allopatric speciation, parapatric speciation, or sympatric speciation, you will probably find no reference whatsoever to natural selection. Nevertheless Ghiselin is entirely correct when saying that "if species were not individuals, they could not evolve, indeed they could not do anything whatever. Classes are immutable, only their constituent individuals can change". Classes can change only by the saltational change of their essences. Hence there is no evolution of the chemical elements, but only a saltational origin of new elements. Hence a discussion of speciation is not going to add anything to the conclusion that species are "individuals". If species originated by new origins, as claimed by some of Darwin's opponents, then it could be accommodated within an essentialist framework. This no doubt was one of the reasons for Darwin's insistence on gradualism in evolution.

Rosenberg's endeavor to find theories about the causes of morphological differences is irrelevant. We have a great deal of morphological differentiation within species, and we have numerous sibling species without morphological differences. This again, of course, demonstrates the invalidity of the essentialistic species concept. Much of this has more to do with the epistemology rather than the ontology of species. In the end, I was pleased to see that Rosenberg firmly endorses the non-class status of species and provides excellent arguments in favor of this point of view.

### STEBBINS

I greet in Ledyard Stebbins a co-professional. Like him I have recognized

species in the field and described valid new species already more than 50 years ago. So I listen to what he says with great sympathy. I would wish, however, that he had read my paper more carefully. When he claims: "Mayr says that he can recognize species only on the basis of inference", I wonder where he got that idea. As I stressed in my article, and for 30 years, one can recognize species without any difficulties in the nondimensional situation. It is only when one deals with isolated populations in space and time that one has to fall back on inference. And such inferences are always based on numerous factual pieces of evidence. They are not simply wild guesses.

And what is so bad about inference? There are few insights in science that are based exclusively on direct observation. Nearly always inferences are also involved. If I were to go through Stebbins's writings I would surely discover literally hundreds of instances where he relied on inferences.

Stebbins brackets me with Ghiselin as upholding species as indivisible entities. Actually, in my paper I have opposed this viewpoint and saw in the divisibility of species a major reason for replacing individual by the term biopopulation. Stebbins rejects both class and individual as designation for species, but says nothing about my proposal of calling species biopopulations. Instead, he says we should call them systems. To be sure, species are systems, but so many other kinds of things in this world are also systems, especially in the inanimate realm, that one can hardly consider system a particulary characteristic designation for species taxa. Almost all the arguments I have heard against biopopulation as a designation of species would be equally valid against the term system.

## WILLIAMS

I entirely agree with Williams that species are individuals within the technical philosophical meaning. This is true as long as one accepts that individual is the only alternative to class. However, I argued, the term individual implying singularity and indivisibility, is remarkably inappropriate for an entity that is neither singular nor indivisible. A biological species may consist of millions of individuals and is rather subdivided in most polytypic species. I appreciate the effort of Williams to provide a definition of individuality that would preserve singularity and at the same time be applicable to species. However her "absolute criterion," under which she says that neither populations nor organisms will be individuals, likewise prevents many species from being individuals. I would judge that it would fail with respect to many polytypic species taxa as well as with those that are geographically variable with respect to ecological attributes. Hence I would consider it not a particularly valid species criterion. I am not certain that the relative criterion would work either. There are many

species that bud off founder populations, incipient species, and eventually, full species. Which of these populations are individuals with respect to evolutionary theory?

Williams's proposal leads to a much deeper question, which has come up in connection with many of the comments. As I have emphasized over many years, the major biological significance of the species is in the nondimensional situation. This is what interests the students of biota, the ecologist, and the student of behavior. This is where the isolating mechanisms, the species recognition systems, come into play. What the relationship is of far removed populations of a widespread polytypic species is biologically relatively unimportant. I have always been somewhat troubled by attempts to place the species concept too strictly on evolutionary theory. I have even gone so far as to suggest that under certain circumstances it might be legitimate to give species status to a nonevolving species. And I am sure that it is possible to demonstrate the reality of species as aspects of nature, without invoking the theory of evolution.

It seems to me that Williams argues a little too strongly for the maintenance of the term individual when virtually all of her arguments would be equally valid if she would use the word biopopulation instead of the misleading term individual. There is no argument about the underlying facts, it is only that the bridge between philosophers and scientists is so much more easily established if philosophers would give up or modify the usage of certain terms that for the average person have a very different meaning.

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