The Ontological Status of Species: Scientific Progress and Philosophical Terminology

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ABSTRACT: (1) Biological species are not classes, as traditionally defined, because they have no essence and because they have various properties (see 2 and 3) that are incompatible with the class concept.

(2) Among non-class properties of species are their spatiotemporal localization, their boundedness, their internal cohesiveness, and their capacity to change (evolve).

(3) Other non-class properties of species are their propensity for splitting (speciating), for fusing (by hybridization), and for becoming extinct, none applicable to classes.

(4) To call a species a set, and defining as set any aggregate of more than a single entity, would completely destroy the usefulness and unique characterization of the species in biological science.

(5) Properties in common of taxa of all ranks are not essences, since they are variable and have the potential for evolution.

(6) Even though ignored by philosophers, the non-class nature of species was recognized by naturalists from John Ray (1686) and Buffon (1753) to the 1960s. By that time it was virtually unanimously recognized by biologists.

(7) In order to make the non-class nature of biological species more visible, Ghiselin (1974) and Hull (1976) have proposed to consider them individuals.

(8) Most biologists and some philosophers have however been unhappy about calling a species an individual, when it actually may consist of millions or billions of individual organisms and show much less cohesion than a single individual.

(9) It is proposed that the term population, applied by naturalists to species for more than 100 years, be added to the vocabulary of the philosophers of science to designate a phenomenon of nature, biological species, for which neither the term class (set) nor the term individual is appropriate.

(10) Only sexually reproducing organisms qualify as species. Some other terminology, for instance paraspecies, will have to be found for uniparentally reproducing forms. Higher taxa are neither classes nor individuals but may be designated, following Wiley, as 'historical groups.' Grades are classes.

KEY WORDS: Species, classes, individual, population.

Certain problems of ontology seem to be exceedingly refractory to solution. Opposing viewpoints continue to be firm, neither side being able to produce the kind of arguments that would be able to convert their opponents. Such a situation seems to pertain at the present time to the

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ontological status of species. Are they classes, are they individuals, or what are they if they are neither classes nor individuals?

My major objective in the following discussion is not so much to produce a final solution to this problem, but rather to show what the reasons for this stalemate are. I shall try to show that a purely philosophical solution is impossible unless and until the factual basis has been clearly established. In other words, clarity must first be achieved on the biological nature of species before this can be expressed appropriately in philosophical terminology. A second reason is that a controversy may be prolonged because the ontological vocabulary of neither camp is adequate. Both of these factors are clearly involved as far as the solution of the ontological species problem is concerned. More than 50 papers on this question have been published in the last several decades and we still seem to be far from any consensus.

Two matters require clarification before the basic issue can be taken up. First, there is the question of whether observed species have reality in nature. This question can be answered only for the *nondimensional species*[1] at a given place and a given time. No naturalist would question the reality of the species he may find in his garden, whether it is a catbird, chickadee, robin, or starling. And the same is true for trees or flowering plants. Species at a given locality are almost invariably separated from each other by a distinct gap. Nothing convinced me so fully of the reality of species as the observation I made 60 years ago that the Stone Age natives in the mountains of New Guinea recognize as species exactly the same entities of nature as a western scientist. Actually, the question of realism has nothing to do with the current controversy since both individuals and classes can be real.

Secondly, a major advance in conceptualization and terminology of the taxonomist is curiously unknown to many philosophers. I am referring to the difference between the species as a category ("species definition") and the species as a taxon ("species delimitation"). A species taxon is an object in nature recognized and delimited by the taxonomist. The species category is the rank given to a species taxon. That the species category is a class is not disputed by anybody. What is involved is the ontological status of the species taxon. It is a serious shortcoming in the writings of most philosophers that they confound taxon and category so often in their analyses, although in principle most of them are fully aware of the distinction. In order to determine the species status of a population or taxon, one must attempt to apply to it the species definition and see whether the situation is consistent with it. What is involved has been excellently illustrated by Simpson (1961) in the case of monozygotic twins. Two persons are monozygotic twins not because they are so similar, but they are so similar because they are monozygotic twins. Two populations belong to two different species, not because they can tolerate coexistence without interbreeding, but rather they can tolerate such sympatry because they are species. Probabilistic inference is the major method in systematics for determining species status of a population. It can be observed directly only in the nondimensional situation and not always even there. In all dimensional situations (with longitude, latitude, or time added) species status can be determined only by inference. No working naturalist can escape this simple fact of nature.

It is the objective of the present analysis to remove, as much as possible, all semantic ambiguities and factual misunderstandings. In my treatment I shall concentrate on the crucial issues and largely ignore a discussion of certain side issues that have been introduced into some of the arguments, such as the role of exemplars (Mayr 1984) and the applicability of laws to individuals and classes.

THE SPECIES CONCEPT OF CLASSICAL TAXONOMY

In classical taxonomy, species were simply defined as groups of similar individuals that are different from individuals belonging to other species. Thus a species is a group of animals or plants having in common one or several characteristics. Each species represents a different type of organism. The diversity of nature is seen as the reflection of a limited number of unchanging universals. This concept ultimately goes back to Plato's concept of the *eidos* or, as it was referred to by some later authors, to the essence or "nature" of some object or organism. The similarity of the members of a species was due to the joint possession of this eidos or essence. Variation was interpreted as due to an imperfect manifestation of the eidos resulting in "accidental" attributes.

SPECIES AS CLASSES

The philosophers adopted exactly the same criteria as the basis of their concept of species as the early taxonomists with their typological species concept. The time honored concept of the species held by the philosophers was that of a class. Membership in a class is determined strictly on the basis of similarity, that is on the basis of the possession of certain characteristics shared by all and only members of that class. In order to be included in a given class items must share certain features which are the criteria of membership or, as they are usually called, the "defining properties." Even in such essentialistically defined classes members of a class can have more in common than the defining properties but they need not. These other properties may be variable. This is important in connection with the problem whether or not classes may have a history. For the traditional philosopher the word species meant "kind of" and simply designated a degree of similarity (Quine 1969). This was the traditional species concept of Linnaeus and his contemporaries. Although abandoned by the majority of modern taxonomists (see below), it is still upheld by a few schools such as the pheneticists, certain pattern cladists (Nelson, Patterson) and a few botanists (Cronquist 1978). Under this concept members of a species can be identified by their diagnostic characters (defining properties). Each class or species is characterized by its "essence," that is its fixed, unchanging defining properties. The concept is widely applicable to inanimate objects. For instance one can recognize a class of chairs as consisting of pieces of furniture built in such a way that a human can sit on them. By far the most important defining property of a class is its constancy, a necessary correlate of its being based on an essence. At the same time class membership is not spatiotemporally restricted. For instance, if there were two-legged hominoids on Mars and they had constructed pieces of furniture with the defining properties of chairs, these would belong to the class of chairs. Nor is there any special relation among members of a class such as one finds among parts of an individual. Clearly there is no relation among the members of the class *chair*. In other classes there is sometimes an indication of relationship but such relationship is not part of the definition.

The class concept of species was fully understood by most taxonomists and rejected because it did not correspond to the situation found among biological species. It was referred to as the typological species concept, which "treats species as random aggregates of individuals that have in common the essential properties of the type of the species" (Mayr 1963: 20—21). Adoption of the typological or class concept of species was one of the major impediments not only in accepting evolution but also in accepting particular theories of evolutionary change. For instance it required speciation to be saltational, that is to consist of the production of a new species essence by a single mutation. For the classical philosopher the species simply was a lower ranking class than the genus. As stated by Jevons (1877: 701) "a genus means any class whatever which is regarded as composed of minor classes or species."

The nonphilosopher has considerable difficulties in reading the analyses of philosophers because class is not the only term used for aggregates of items. I have encountered also the terms natural kinds, clusters, and in recent years most frequently, sets. Not fully understanding the differences among these terminologies and rather bewildered by opposing statements by philosophers themselves, I shall not attempt to discuss this heterogeneity of terminology in full detail.

Let me say a few words, however. Natural kinds have been discussed by philosophers from Mill to Quine (1969). Most recently this designation has been supported by Schwartz (1981: 301) and by Kitts and Kitts

(1979), but its usefulness has been questioned by Ghiselin (1981: 271) and by Sober (1984: 335). Since the defenders of the natural kinds terminology apparently make no difference between inanimate objects and living populations I agree with those who find it a sterile terminology. The same would seem to be true for so-called cluster concepts, favored at least by some modern philosophers (Caplan 1981: 285).

What puzzles me particularly is why certain philosophers want to apply the term *set* to species (Kitcher 1984*a*, *b*). In contrast to a class a set, if I understand Kitcher correctly, does not require any defining properties. According to his definition, any aggregate consisting of more than a single item is a set, no matter how heterogenous. To illustrate his concept of a set without a defining property Kitcher lists "Queen Victoria, the manuscript of *Finnegan's Wake*, and the number 7." By abandoning the traditional defining properties of a class Kitcher arrives at a definition of set which by necessity must include species, for every species taxon is composed of more than one item (organism). This concept of set is so different from the traditional definition of class that none of the arguments against class in the classical controversy on the ontological status of species is any longer applicable.

Frankly, a biologist is utterly bewildered. For more than 100 years biologists have worked very hard to discover and describe how biological species differ from other phenomena of nature and whether there is only one kind of species or several different ones. All this is obliterated if all variable phenomena of nature are dumped into a single highly heterogeneous receptacle, the set. Nor does Kitcher seem to make any distinction between species category and species taxon. Items of a set and members of a species are consistently equated. This omits any consideration of variation and population thinking. I have not found a criterion in Kitcher's discussion indicating how one could distinguish definitionally a biological species from a set characterized by some arbitrary property. For instance hairy objects including mammals, hairy caterpillars, hairy seeds of certain plants and other hairy objects, would make a legitimate set for Kitcher. Likewise not only species taxa but also higher taxa, the whole animal kingdom, the whole living world as well as the contents of the top drawer of my desk or of my wastepaper basket would be sets. At the same time I sense in his discussions seeming inconsistencies such as his disclaimer that his analysis would imply "a general way of replacing talk of objects with talk of sets" (1984*b*: 617), and yet this is what he seems to suggest in the rest of his discussion. Occasionally he seems to notice where his axioms lead him and thus he rejects the idea "that organisms are just sets of cells." And yet this is precisely what they are on the basis of his definitions. I found no criterion in his writings that would make such a definition of organisms inadmissible. There is no criterion by which one can decide which multiples of objects are sets and which others are not.

Nor of how a set that is a species differs from a set of hairy objects. Indeed Kitcher seems to consider it a virtue to have such a sweepingly defined and heterogeneous category like set. This permits him to consider any set of individuals a species which any biologist or taxonomist had ever called a species (on the basis of no matter what criterion). To me it would seem that a species concept based on such a broad and vague set of theoretical criteria loses all scientific usefulness. As both Hull and Ghiselin have pointed out, the great virtue of the newer ways of defining species is that they permit all sorts of evolutionary predictions.

FROM THE TYPOLOGICAL SPECIES TO THE REPRODUCTIVE COMMUNITY

Almost up to modern times it was similarity which revealed whether two items belonged to the same species. In the world of inanimate objects this criterion worked very satisfactorily. However in the world of life, as the knowledge of kinds of animals and plants increased, similarity failed occasionally. In spite of their great difference, caterpillar and butterfly clearly belong to the same species. In other cases, male and female of a species were more different from each other than one of these sexes in a series of related species. How could one cope with such variability? (Mayr 1982: 256). Toward the end of the 17th century John Ray proposed an entirely novel solution. Regardless of degrees of variation all those variants should be considered members of a species that had sprung "from the seed of one and the same plant" or, in the case of animals, been produced by the same parents. Reproduction was here for the first time introduced into the species definition. In the case of Ray it was problems of practical taxonomy that led to this shift. In the case of Buffon a similar shift occurred, but on an entirely different basis (Sloan 1986). Buffon had a great interest in individual development and it greatly puzzled him why the offspring on the whole was always so similar to the parent. This led to his famous proposal of the internal mold, derived from Plato's developmental eidos, which controlled the constancy throughout time of the species-specific characteristics. "This power of producing its likeness, this chain of successive existences of individuals . . . constitutes the real existence of the species" (Buffon 1954: 233, 238). Buffon explicitly rejected considering the species a class because then each organism would be "a creature by itself, isolated and detached, which has nothing in common with other beings, except in that which it resembles or differs from them" (Ibid., p. 355). As Sloan points out quite rightly, this is not an intrinsically biological argument. Even though there is reproductive continuity from parent to offspring and its offspring, one finds in Buffon no trace of population thinking or of the concept of a reproductive community. Buffon does not think and talk like a naturalist (much less like an evolutionist), but rather like a student of embryology. What Buffon had actually done, and this clearly distinguishes him from Linnaeus and other taxonomists of the period, was to replace Plato's eidos (which is a typological essence) by Aristotle's eidos (which is a genetic program). In spite of this forward step, Buffon's *moule interieure* is as constant and eternal as Plato's essence. Yet it was a step in the right direction, and it was much easier to go from Buffon's species (as constant as it was) to the reproductive community of the biological species than it would have been to take this step from the Platonian species of Linnaeus. What helped the subsequent developments even more was Buffon's idea that if two parents had the same *moule interieure* they would be able to produce fertile offspring. And this, indeed, would permit a reproductive community.

Buffon's species concept, sometimes combined with that of Ray, rapidly displaced the strictly typological species definition of Linnaeus. Happily it was also consistent with creationist dogma. The members of a species were the descendants of the first pair created by God at the beginning. This is what the antievolutionist von Baer (1828) had in mind when he defined the species as "the sum of the individuals that are united by common descent." Cuvier and many naturalists in the first half of the 19th century supported similar definitions. Increasingly often not only generation ("descent") but also common reproduction was made part of the definition. As stated by Gloger (1856) "a species is what belongs together either by descent or for the sake of reproduction." Voigt (1817), Oken (1830), and others of their contemporaries adopted similar definitions (Mayr 1957: 9). In one species definition after the other during the ensuing 125 years the emphasis was on the reproductive community. This is well stated in the species definitions of Poulton (1903) and Jordan (1905). Plate (1914) stated it in these words: "The members of a species are tied together by the fact that they recognize each other as belonging together and reproduce only with each other." It was the species concept of the naturalists who participated in the evolutionary synthesis. There are numerous unequivocal statements on the non-class nature of species in the writing of Dobzhansky and Ernst Mayr. Dobzhansky stated it particularly clearly: "A Mendelian population is a reproductive community of sexual and cross-fertilizing individuals which share in a common gene pool. . . . The biological species is the largest and most inclusive Mendelian population" (1951: 577). And in another place he called the species "a supraindividual biological system . . . more than a group concept. A species is composed of individuals as an individual is composed of cells. . . . A biological species is an inclusive Mendelian population; it is integrated by the bonds of sexual reproduction and parentage" (1970: 353—354). None of these characteristics are those of a class.

My own species concept (1942—1982) has clearly always been that of a concrete entity. Eldredge, in a recent historical analysis, stated: "If it is true that Mayr did not invent the notion that species are real entities, it is nonetheless indubitable that the underlying basis for all the various recent approaches to looking at species as entities or individuals rather than as classes of individuals stems from Mayr's species concept" (Eldredge 1986: 49).

In 1963 I enumerated three properties of species which "raised the species above the typological interpretation of a class of objects. The nonarbitrariness of the biological species is the result of this internal cohesion of the gene pool" (1963: 21). In 1969 I characterized the species as follows: "the members of a species form a reproductive community. The individuals of a species of animals recognize each other as potential mates and seek each other for the purpose of reproduction. . . . The species, finally, is a genetic unit consisting of a large, intercommunicating gene pool. . . . These . . . properties raise the species above the typological interpretation of a 'class of objects'." (Mayr 1969: 26).

These developments were not altogether ignored by philosophers, for J. Gregg reports that two different taxonomists had advanced the notion "that species are composed of organisms just as organisms are composed of cells: according to this argument, a species is just as much a concrete, spatio-temporal thing, as is an individual organism, though it is of a less integrated, more spatio-temporally scattered sort" (Gregg 1950: 424–425). I know that I was one of these taxonomists, and either A. J. Cain or Dobzhansky was the other. Gregg rejected this notion, and all other philosophers up to the 1970s ignored it. They ignored it so much that as recently as 1984 Kitcher refers to the "traditional thesis that species are sets." Hull (1976), Caplan, Rosenberg, and Sober have made similar statements. Owing to their ignorance of the taxonomic literature they all credit a shift in thinking on the subject to Hull's discovery (1976, 1978) of Ghiselin's papers (1966, 1974*a*, *b*) in which the species-as-class concept is rejected. It is remarkable that among philosophers Hull made only few converts for the non-class concept of species (Rosenberg, Sober, and M. Williams). Most other philosophers who joined the controversy in recent years have continued to defend the species-as-class concept, failing to see a difference between "species" of inanimate objects and biological species.

Anyone reviewing this literature is puzzled why the virtually universal rejection of the concept of the species as a class by evolutionary biologists was so completely ignored by the philosophers. Undoubtedly there were several reasons. One of them is that philosophers of former periods almost completely ignored the scientific literature, so that it was necessary for a biologist (Ghiselin) to bring the shift in thinking to their attention. Another reason, as I shall discuss below, is the insufficiency of the terminological and conceptual repertory of the philosophy of science. A few examples of the writings of philosophers will show how little they understood the biological nature of species. For instance: "The concept of species was introduced to answer certain theoretical desiderata" (Kitcher 1984*b*: 636). Or, species are primarily "an answer to a practical need" (Rosenberg 1985: 203).

THE SPECIES AS INDIVIDUAL

The historical analysis clearly reveals a curious discrepancy. The biologists, on the whole, considered species to be something entirely different from what the philosophers accepted. Even though there were still quite a few taxonomists who adhered to the typological species concept, far more of them, as I showed, treated them as non-class phenomena. Indeed I do not know the writings of a single evolutionary taxonomist in the period from the 1930s to 1970 who did not reject the class concept of the species. But this went entirely unnoticed by the philosophers. Evidently they did not read the writings of the biologists and vice versa. It was not until a biologist (Ghiselin) translated the views of the biologists into philosophical language that the conflict was discovered; and even then not at once. In 1966 Ghiselin clearly stated "biological species are, in the logical sense, individuals . . . a species name is a proper noun" (1966: 208—209). But this went unnoticed, and Hull in 1967 still treated the species as a class. Not until Ghiselin had amplified his thesis (1974*a*, *b*) and had pointed out that it was by no means a new proposition, but went back at least to Buffon, did Hull (1976) take notice and become converted. Considering how unequivocally the non-class status of species had previously been maintained by one biologist after the other, it is quite possible that Ghiselin's claim would have remained equally ignored if Hull had not taken up the issue and given it a broad foundation couched in philosophical terms.

I am deliberately using the terminology of the non-class status of species because, as the ensuing controversy reveals, two different issues were involved. The first is indicated by the question, Is it correct to consider the biological species a class?; and the second by the question, If it is decided that the biological species is not a class, is the term individual the appropriate term for it, or should a different terminology be chosen?

THE NON-CLASS PROPERTIES OF BIOLOGICAL SPECIES

Ghiselin (1974*a*, 1981), Hull (1976, 1978, 1981, 1984), Beatty (1983), Holsinger (1984), and Sober (1984) have specified a lengthy list of properties of species that are not properties of classes as traditionally defined. Some of these putative non-class properties of species raise problems which I shall now attempt to discuss.

Species are spatio-temporally localized. They occur at specific places and at specific times. A given species taxon cannot occur on earth and also on the Andromeda nebula. Within their spatio-temporal localization species are on the whole continuous and it is this continuity which often permits in cases of doubt the inference as to what belongs to a single individual. For instance, that caterpillar and butterfly are the same individual is inferred not from any similarity in their appearance, but from this continuity. The continuity of different organisms within a species is provided by their historical (common descent) connection. Ghiselin (1974*b*: 536) correctly stresses that the spatio-temporal continuity does not need to be physically continuous. The fact that Alaska and Hawaii are not physically contiguous with the other 48 states does not exclude them from being parts of the "individual" called the United States.

Physical discontinuity of parts of an "individual" is one of the major causes of difficulty for the student of polytypic species. How can one determine whether or not an isolated "individual" is part of a larger individual? That Alaska is part of the United States can be documented because she adheres to the Constitution of the United States. In the case of animal populations, the relation of isolated populations to other populations must be inferred on the basis of the biological species concept. The Ipswich Sparrow, although completely isolated on Sable Island off Nova Scotia, is part of the Savannah Sparrow because it is inferred that it shares with the Savannah Sparrow the same isolating mechanisms. Species status or not is determined on the basis of inference on the reproductive relation to other presumably related "species." Ghiselin missed this ned for testing species status when he said "if a species is an individual it hardly matters whether it is interbreeding at any given time" (1974*b*: 538). This has things upside down, because, in the case of every isolated population, it is precisely the inference we make on its reproductive isolation which tells us whether it is a separate individual or a part of a larger individual. Until the inference on reproductive status is made, we do not know whether or not the population is a separate individual.

Discreteness. Individuals are reasonably discrete in space and time, they are bounded rather than being potentially unlimited, as are classes. However, since species speciate and sometimes merge, their borders are sometimes "fuzzy" and the point at which one species leaves off and another begins is often arbitrary, as is also true for mountains and many other objects of nature that are individuals (Rosenberg 1985: 208). Owing to their discreteness, species are particular things with proper names.

Internal Organization. By far the most important definens of an individual is its internal cohesiveness. Organisms that together form a species have intimate connections with each other not found among the members of a class of objects, as classically defined. This is due to the fact that they are derived from the joint gene pool of the species, and that they jointly contribute their genotypes to form the gene pool of the next generation. There is thus a continuity and interconnection among the organisms of which a species is composed that is altogether absent from the members of a class. Organisms that belong to a species are part of the species, not its members. This statement to its full extent is true only for the sexually reproducing biological species in which genetic recombination among the various genotypes occurs normally in every generation. The compatibility of the genotypes of conspecific mates, as documented by the production of viable new genotypes in their offspring, indicates that the species population has the kind of internal harmony one would expect to find in parts of a single system. The numerous, often fatal, incompatibilities one usually encounters in hybrids produced in species crosses reveal that the parental species are not part of the same system, that they are not parts of a single individuals. The parts of an "individual" (in the broad sense of the terminology of logic) are "integrated in one way or another — joined as by physical or social forces or common descent" (Ghiselin 1981: 271). Also there must be some mechanisms by which the unity of the biological species is maintained, through the joint possession of isolating mechanisms (e.g. reciprocal fertility and a behavioral recognition capacity).

DOES A SPECIES HAVE AN ESSENCE?

No one questions the fact that organisms which belong to a species are united by the joint possession of a set of isolating mechanisms, perhaps also of a niche occupation potential, structural characteristics and other joint properties of the genotype. Proponents of the species-as-class concept have suggested that this joint genotype should be considered the essence of the species and that this proves that species are classes. Indeed, I have heard a philosopher ask: Is not any reference to the joint properties of the members of a species "a flirtation with essentialism?" This suggestion reveals a regrettable confusion between essence and properties in common. Of course the parts of an individual have certain properties in common. No one will question "that tigers have an underlying trait that makes them tigers and not giraffes or turtles, just as there is an underlying trait that makes gold gold, or water water" (Schwartz 1981: 302). Furthermore, all monophyletic groupings of organisms, from the population to the highest taxon, have of course something in common. How else would we otherwise determine whether a certain organism is a butterfly or a vertebrate? But a property in common and an essence are two entirely different things. To be sure every essence is characterized by properties in common, but a group sharing properties in common does not need to have an essence. The outstanding characteristic of an essence is its unchanging permanence. By contrast, properties in common of a biological group may be variable and have the propensity for evolutionary change. What is typical for a taxon may change through evolution at any time and then no longer be typical.

It was precisely the variability of species populations that led to population thinking, a dramatic departure from essentialism. The shift from the concept of species-as-a-class to species-as-individuals was an inevitable byproduct of the shift from essentialistic to population thinking.

Unfortunately the word essential with reference to species has often been employed ambiguously. If someone refers to the essential characters of a species, he might mean (and usually does mean) certain indispensable properties, such as the isolating mechanisms which maintain the integrity of the species. Some philosophers, however, have interpreted this as a reference to Platonic species essences. If Kitts (1984) argues that species have an essence, it would seem to me that he has fallen victim to this equivocation. There is nothing in a biological species that corresponds to the Platonic concept of a fixed and transcendental essence. If species had such an essence, gradual evolution would be impossible. The fact of their evolution shows that they have no essence. And since they do not have an essence, they do not form classes. Some philosophers recognize classes without an essence, but such a shift in terminology is too vague to be of any practical use.

Parts of a species display a three-fold variability. First there is the variability of organisms within a population. As a result, no two individuals in a sexually reproducing species have the same genotype. Such individuals may agree with each other in 85 per cent or 90 per cent or 95 per cent or even 98 per cent of their genotype, but even this identical component of the genotype of conspecific individuals has the potential not only to vary but also to evolve. The Platonic essence has neither capacity. This is the crucial distinction between a genotype and a Platonic essence. Furthermore, there is variation in space, that is the geographic variation of populations of a species. Finally, there is evolution, that is variation in time. Individual variability, variation in space, and variation in time are compatible with the species concept if organisms and populations within a species are considered parts of an individual but are incompatible with the species concept if the species is considered a class with the defining properties of an essence.

INDIVIDUAL AND EVOLUTION

The properties of a particular object, an individual, may change over time. Applied to the species-as-individual it means that the evolutionary capacity of species confirms their status as individuals. Indeed, all biological species seen today, except a few that originated by an instantaneous process (e.g. polyploidy), are the result of evolution. The process of geographic speciation illustrates the difference between class and species particularly well. Dividing a class never results in a change of the properties of the new subdivisions. But if a species is split by a geographic barrier, the two separate populations inevitably begin to differ and have even the capacity to evolve into two separate species.

To include the capacity to evolve among the evidence in support of the claim that the species is an individual, has been frequently criticized. Is evolutionary change a diagnostic difference between class and individual? Is it not also possible for a class to evolve? Has there not been an historical change concerning the class of chairs in the last several hundred years? Indeed, if we compare three sets of chairs, those in use in 1780, those in use in 1880, and those in use in 1980, we may discover considerable change. If it had been part of the defining criterion of the 1780 chair that the supporting structure is of wood, this definition would no longer be appropriate in an age of steel and plastic. But 'being made of wood' was never a truly defining criterion of chair. What had changed over the centuries was not the essence of chairness, but rather some accidental properties of chairs that are not part of the defining essence. A class, having a constant essence, cannot evolve.

Species have the capacity to evolve. Yet, the provision "develops continuously through time" is presumably not a necessary aspect of the species-as-individual. The validity of this assumption is indicated by the fact that many punctuationists believe that most species do not evolve at all after the original speciation event but may go into complete stasis until they become extinct. It may be well to remember at this time the preevolutionary species concept of Buffon (Sloan 1986), Cuvier, and von Baer. The aspect of the species they emphasized most was the internal continuity and coherence of the species, resulting from the fact that all members of the species were derived from the original pair created by God. In that respect their species clearly had more the characteristics of an individual than those of a class, even though the criterion of constancy made them a class. Owing to mutation, genetic recombination and selection, every species is changing over time. But such change does not need to qualify as evolution. For instance, as a thought experiment, one could conceive of a very widespread, very populous species existing in our time that lives in such a stable environment that it has reached a steady state stability without evidence of any seeming evolution.

Species have some other non-class properties, they can speciate (split into two), they can hybridize (fuse), and they can become extinct. No class can ever become extinct. Generalizations made concerning particular species are not laws, but simply facts about particular spatio-temporally localized objects.

There is no conflict between individual and class, they are simply different aspects of nature. Even though organisms are parts of a species, one may also recognize classes of organisms such as sexes, age stages, sessile, hermaphroditic, migratory, and other assemblages based on defining properties. Even though cells are part of an individual and genes are part of the genotype, one can recognize classes of cells such as red blood cells, connective tissue cells, epidermal cells, or classes of genes such as lethal genes, enzyme-producing genes, etc. But none of this is in conflict with the fact that species, organisms, cells, and genes are individuals. Both individuals and classes can be hierarchically organized. Hierarchical organization thus is not a feature which distinguishes individuals from classes.

OBJECTIONS TO THE SPECIES-AS-INDIVIDUAL TERMINOLOGY

When attempting to call the attention of the philosophers to the fact that the biologists consider the species a non-class, Ghiselin (1966, 1974*a*) chose for these composite wholes the term individual, so frequently used by philosophers as the opposite of class. Ghiselin realized the seeming inappropriateness of this term and commented, "Some readers will find it easier to call composite wholes 'collections,' 'aggregations,' or the like, but 'individuals' is the traditional term in logic" (1981: 270). Actually Ghiselin was not the first to apply this terminology, since exactly 100 years earlier Haeckel had called the species *ein Individuum* (Haeckel 1866 II: 30). It would require a rather tedious search through the literature to determine whether this terminology had also been used by others. Be that as it may, the choice of this terminology raises two kinds of objections. Even several of those authors who fully agreed that species are not classes were unhappy over the selection of this particular term. After all, the word individual stresses singularity more than anything else, and is used in the daily language of nonphilosophers almost exclusively to express such singularity. It is quite counterintuitive to apply it to an assemblage of individuals. Indeed, as Kitts and Kitts (1979: 617) have remarked correctly, it is "flying in the face of convention." The human species consists of more than 4 billion individuals, so how can one call it *an* individual? Even Hull, a vigorous defender of the non-class status of species, was seemingly uncomfortable with the term individual because he ended his major discussion of the problem with the statement "I think I have adduced ample reasons in this paper for concluding that, at the very least, species are not classes" (1976: 190).

Some of the objections, however, have gone much further. The word individual, derived from the Latin, basically means that which is indivisible. This is indeed essentially true for most real individuals, whose integrity is ordinarily seriously compromised by removing any parts of it.

A human without his head, his heart, his parathyroid, his liver, and various other organs, is unable to live. Even the removal of less vital organs, like the eyes, an arm, a leg, the stomach, or many other parts, seriously alter the individual, converting it into something it was not before. By contrast, a species of a million organisms is not seriously affected if 10,000 or even 100,000 of them should be removed by sudden death. Indeed, this sort of thing happens in nature periodically in catastrophic seasons caused by drought, disease or other disasters. The damage is quickly repaired in the ensuing seasons. It is only in the lower invertebrates and in many kinds of plants that a seriously mutilated individual can be restored as quickly as a decimated species.

The nature of organization (cohesiveness) is also very different. In a genuine individual all parts interact with each other and do so directly. By contrast the interaction of parts of a species is for most of its members quite loose and indirect, consisting only of the propensity for gene exchange. But such gene exchange is virtually nonexistent in those many species which consist of highly isolated colonies or subspecies. The "organization" of such species is less cohesive by several orders of magnitude than that of a true individual.

Furthermore the species-as-individual terminology invites misunderstandings in discussions of natural selection. There is now rather broad agreement that the individual is normally the target of natural selection. Calling the species an individual, does this imply that the species as a whole is one of the targets of natural selection?, as has indeed been suggested by some authors. Since most biological groups answer the logician's definition of individual, does this terminology legitimize the concept of group selection? These are not frivolous questions, because these questions have actually been raised in the literature.

Those who transfer the term individual to composite wholes are forced to find another term for what everybody up to now has called an individual. In biology they use the word organism as replacement term; but organism is actually a term that is used at various hierarchical levels. There is no implication as to level in such usages, as in "turtles are long-lived organisms." When using the word organism one may have individuals in mind, or species, or higher taxa. It avoids a great deal of misunderstanding to return the word individual to its traditional usage.

THE PROBLEM OF TERMINOLOGY

It is evident from my analysis that neither the term class nor the term individual expresses the ontology of biological species satisfactorily. Rather, it would seem necessary to introduce a new term, so far not in use in the terminological repertory of philosophy. Here is not the only place in recent years where a deficiency in vocabulary seems to have been the major cause for controversy in philosophy. What happens particularly often is that philosophers use a single technical term for several objects or processes that are factually quite different from each other. Perhaps the most instructive instance of this is provided by the concept of teleology. I have recently shown (Mayr 1974) that when certain philosophers (e.g. Nagel, Woodfield) used the term *teleological* they were applying this term indiscriminately to four entirely different kinds of natural phenomena. Obviously, one cannot solve the problem of teleology as long as one treats such a melange as if it were a uniform entity. It happens not infrequently that scientific analysis leads to a partitioning of a phenomenon which up to that time had been referred to by a single scientific or philosophical term. A philosophical analysis of such problems will be incomplete or even misleading if it does not keep up with these scientific developments. Let me cite some additional examples. What in most of the philosophical literature is referred to as the *Darwinian theory* (in the singular) actually consists of five major and at least four minor evolutionary theories (Mayr 1982, 1985), all with separate histories and philosophical problems. Any discussion of evolution that does not keep these theories apart is liable to be confusing. A number of authors has recently discussed whether or not group selection occurs. Most of them paid no attention to the fact that as far as selection is concerned, at least four different kinds of *groups* must be distinguished (Mayr 1986). Other equivocal terms are *category* (including taxon), *selection* (including elimination), *evolution* (both transformational and variational) (Lewontin 1983), and *development* (ontogeny and phylogeny), to mention merely a few (see also Ghiselin 1984). It is quite impossible to carry out a constructive ontological analysis unless it has been preceded by a careful factual analysis. All heterogeneity must first be eliminated. It strikes me as an unfortunate backward step when Kitcher lumps the biological species together with all sorts of other unrelated phenomena into his category "set." Sober has stated quite correctly, "that species are populations (i.e. physical objects — individuals — of a certain kind) was the idea that filled the vacuum left by the demise of the view that species are natural kinds" (1984: 336). Bunge (1981: 284) and Salthe (1981: 301) also endorse population as the proper designation of species: "The preferable term for this entity is population because that appears to be the simplest or smallest unit of which most of these things can be predicated."

For a biologist the individual-like properties of biopopulations are obvious. Unfortunately, a few philosophers coming from mathematics or the physical sciences have equated populations with classes. This became particularly clear to me when I read Caplan's discussion in which he claimed that Stebbins had ascribed all sorts of biological and evolutionary phenomena to "sets of organisms" (1981: 132). Such a usage by a biologist seemed to me so improbable that I consulted the publication to which Caplan referred (Stebbins 1977), where I discovered that Stebbins had not used the word *set* (or for that matter, *class*) even a single time. What he referred to on page after page was "population." Evidently Caplan was not trying to misrepresent Stebbins, but for him populations were sets of organisms. He thereby revealed the deep difference between an essentialist, for whom populations are classes or sets, and a populational biologist, for whom populations are of the nature of individuals, as correctly recognized by Sober (1984: 336). How much difficulty some philosophers have in understanding what a biological population is, is indicated by Kitcher's assertion "there seems to be no implication that if *x* and *y* belong to the same population, then they are conspecific" (1984: 622). The concept of *population* has up to now been totally missing from the conceptual framework of nearly all philosophers of science. As a result they were forced to translate the term population into something with which they were familiar, usually the term class or set. It is Ghiselin's outstanding achievement to have called attention to this error.

There is no real conflict between the terms individual and population, for a biopopulation has the spatio-temporal properties, internal cohesion, and potential for change of an individual. If a single organism is considered a "singular individual," a population can perhaps be considered a "multiple individual." The crucial properties of the biopopulation that make it an individual are maintained by the two-way street — generation after generation — between conspecific organisms and the gene pool of the species.

The term population for a species is preferable to the term individual for three reasons:

(1) because it has been traditionally used by biologists for species ever since the typological concept of natural kinds had been given up,

(2) because the term conveys the impression of the multiplicity and composite nature of species, whereas the term individual implies a nonexisting singularity, and

(3) because it provides a far more suitable basis for the discussion of evolutionary phenomena, particularly speciation.

Most of the objections to the species-as-individual terminology listed above are met with by the species-as-population terminology.

THE BOUNDING OF THE SPECIES TAXON

The problem of the bounding of a species individual remains to be discussed. If we accept the Darwinian concept of gradual evolution, then every species originates gradually (regardless of how fast) from a parental species, and gives rise by gradual evolution to daughter species. The only sharp bounding is provided by the extinction of a species. An individual organism is born, lives, and dies. Thus it is bounded at the beginning and at the end. By contrast, the birth of a new species is given by sharp boundary only in cases of saltational speciation. In all other cases speciation is gradual and not clearly delimitable. This is equally true whether the new species arises through phyletic gradualism (as believed by many paleontologists) or by allopatric speciation.

The absence of a sharp boundary is, of course, not a decisive argument against the "species is an individual" concept. A stage of intermediacy is quite characteristic for many cases of the origin of new individual organisms. For instance, when a protozoan divides, at what moment does it become two individuals? When the chromosomes divide and move to the opposite poles? Or when the division of the nucleus is completed by the formation of a new nuclear membrane? Or when the cytoplasm has completed its fission and the two daughter cells have separated completely? Thus the origin of new individuals is often a gradual process, and the fact that most speciation, even rapid peripatric speciation, is gradual is no argument against the individuality of species. The process of evolution, in particular the gradualness of most speciation, precludes the drawing of sharp boundaries. In the case of peripatric speciation[2] it has been found convenient by some philosophers to choose the moment of the spatial isolation of the new founder population as the boundary between the parental and the daughter species. This is not correct biologically, since the development of the isolating mechanisms, the true sign of species status, requires many generations. Sharp boundaries can be established only if one adopts the nondimensional species concept as I have urged for so many years.

The most frequent problem in species delimitation is the uncertain status of virtually all isolated populations. Every student of geographic speciation knows scores, if not hundreds, of cases where an isolated population is on the threshold of becoming a separate species. The crucial test whether or not it has passed this threshold cannot be applied, since there is no physical contact with a sister or parent species. The isolated population clearly qualifies as an individual. But what we cannot determine except by somewhat uncertain inferences is whether it is part of a larger individual (a more widespread polytypic species) or is indeed a separate species. This is not quite as serious a practical problem as a philosopher might imagine, because for most biological researches it is rather immaterial whether such borderline cases are listed as species or subspecies.

For the logician a considerable problem is caused by the possibility of three populations (individuals) *a, b*, and *c* "such that *a* and *b* but not *c* are conspecific even though *a* and *c* are genealogically closer than *a* and *b*" (Kitcher 1984: 625). Such cases indeed are not rare in island regions.

As an example I might name the kingfisher *Tanysiptera galatea* in which the mainland populations *a* and *b* on New Guinea are conspecific, but some island populations (*c, d*) are good species although one (*c*) was derived from mainland population *a* and the other (*d*) from mainland population *b*. To me at least it is simpler and more easily explained if the relevant entities are referred to as populations rather than as individuals. The open-endedness of most species as well as their potential for continuing evolution, can be more easily accommodated by the species-as-population terminology than by the species-as-individual terminology. No doubt this is one of the reasons why all along the word population has been the key word in definitions of the biological species.

DIFFICULTIES WITH THE TERM POPULATION

Like almost all terms in science and philosophy the term *population* does not have a single well-defined connotation. Its original use in the English language was that for the subjects of a ruler, the population of a politically defined area. Eventually it was used for any component of the human species, and later of animal and plant species. Unfortunately the meaning of the term was eventually still further expanded, and mathematicians sometimes spoke of populations when referring to sets. Several population geneticists used the term more in this mathematical sense than in that of actual populations of organisms. Finally, the ecologists expanded it even further, beyond the limits of a single species, when speaking of the plankton population of a lake or of the population of savannah animals. Populations in such broadened sense lack the most characteristic features of biological populations, their internal cohesion and variability. This was clearly seen by Bunge (1981: 284) who refers to the interbreeding, conspecific population of the biologist, as the *biopopulation*. It would be most helpful if the use of the word *population* or at least biopopulation would be restricted to this focal meaning of the word population, and in particular, if the misleading use of the word population in the sense of set were abandoned. The heterogeneity of usages of the word population has been evident for some time and I have referred to it on a previous occasion (Mayr 1963: 136—138).

One can recognize a hierarchy of biopopulations ranging from the local population (deme) up to the species ("the largest Mendelian population" of Dobzhansky). This is, of course, no more an argument against the adoption of the population terminology, than it would be in the case of class and individual, which can also be organized hierarchically.

ARE THERE DIFFERENT KINDS OF SPECIES?

Systematists, presumably all the way back to Darwin, have been aware of the heterogeneity of species-like phenomena in nature. To this problem I devoted an entire chapter (*Kinds of Species*) of my 1963 book (pp. 400–423). In the most elaborate attempt to discriminate among kinds of species, Camp and Gilly (1943) recognized 12 categories of plant species. One other well known enumeration of kinds of species is that of Cain (1954) who recognizes four kinds.

The clarification of the ontological status of species makes it mandatory to examine these so-called kinds of species and determine whether they all have the qualifying criteria of biological species, particularly the internal cohesion and spatio-temporal definiteness of individuals-populations. Even a quick survey of the literature makes it quite clear that there are entities in nature (like asexual clones or strains of prokaryotes) which do not qualify under the biological species concept. The frequency of these exceptions is very different in different groups of organisms. In birds there are none so far as I know. In prokaryotes they might amount to about 100 per cent. In the vascular plants of a local flora they may comprise about 15 per cent. Actually, an improved understanding of the biological species concept has led to a reduction in the percentage of recognized exceptions. In 1957 Grant wrote "there are a few botanists who adopt the so-called biological species concept" (p. 43). Twenty-five years later Stebbins implied that a majority of plants can be classified as biological species (1982).

To the species that unequivocally qualify as populations belong all regularly sexually reproducing species, all those allopolyploids in which sexuality has been fully restored, and all evolutionary species (sensu Simpson-Wiley).

Uniparentally reproducing organisms

There are many lineages of organisms which perpetuate themselves without sexual reproduction. This includes for instance stabilized species hybrids that have reverted to uniparental (asexual) reproductions. It includes all other forms of permanent uniparental reproduction, particularly obligatory parthenogenesis and obligatory hermaphroditism, as well as various forms of vegetative reproduction. All these lineages are clones that are independent of each other, that is they do not share in a common gene pool. Owing to their mode of origin, such uniparental entities could theoretically originate several times independently, and yet be indistinguishable for all practical purposes. Such a case was actually discovered by M. J. D. White in Australia. The parthenogenetic species *Warramaba virgo* consists of two allopatric populations that were derived from different strains of the two parental species (White 1980).

All these asexual entities fail to qualify as biological species, and the question has been much discussed in the literature as to what ontological status they should be given. Many different solutions have been proposed, which are best presented as three different options:

(a) To accept a concept of species that would apply across all the kingdoms of living organisms. Kitcher's proposal to consider species as sets would be such a solution. It would mean watering down the species concept to the extent that it would apply to any kinds of organisms, even the most aberrant ones. There would seem to be little that recommends this solution. It has two very serious flaws. By confounding various fundamentally different natural entities under one name, it would do again what has already caused so much trouble in the history of philosophy (e.g. definition of teleological, selection, group, adaptation, etc.). To apply a single term to a heterogeneous assemblage is bound to cause trouble sooner or later. Inevitably in such a broadened concept of species, all those criteria will have to be excluded that are particularly characteristic for the majority of species, that is the characteristics of biological species.

The second flaw is that this solution can be adopted only by going back to a strictly nominalistic or typological species concept such as that suggested by the botanist Cronquist, for whom "species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means" (1978: 3). A group of taxonomists, the so-called pattern cladists (e.g. Rosen 1979), have also returned to the typological species of essentialism. In one of their papers they defined the species as "the smallest detected samples of self-perpetuating organisms that have unique sets of characters" (Nelson and Platnick 1981: 12). Since asexual organisms are the only self-perpetuating organisms in nature, this species definition curiously (presumably contrary to the intentions of the authors) applies only to asexual organisms. Also each clone that differs by even a single detectable mutation would be a separate species. In conclusion, it would seem rather obvious that it is an unrealistic objective to try to find a useful species concept that applies equally to all forms of life on earth.

(b) To recognize several different kinds of species. Such a pluralism has been the traditional way of dealing with this problem. It consisted of recognizing biological species, agamospecies, chronospecies, etc. (Cain 1954). Although this solution seemingly gets rid of the problem, it actually does nothing of the sort. For instance, it does not come to grips at all with the problem as to whether these several kinds of species are individuals, populations, or classes. It is by no means a scientifically or philosophically adequate solution.

(c) To restrict the term species to the biological species, the largest cohesive population. This solution has recently been proposed by Ghiselin (1986) and is clearly the most honest solution. This is the species which the modern biologist, whether evolutionist, geneticist, or ethologist, means when he uses the word species. Only that which has the propensity for speciation, says Ghiselin, deserves to be called a species, and this does not include asexual entities.

Unfortunately even this is not a perfect solution. The fact remains that there are entities in nature that do not qualify as biological species, but which fill the same place in the ecosystem as do biological species. They cannot be ignored in any study of niche occupation, utilization of resources, and competition. An ecologist will say that some of them occupy the same place in nature as do genuine species, and that some way of dealing with them must be found. Although by descent they have continuity in time within the clone, they lack the internal cohesion characterizing a gene pool. Therefore they are classes and not individuals-populations. One possible compromise solution would be to recognize them under a special name, let us say as paraspecies.

HIGHER TAXA

That higher taxa are not ordinary classes is agreed upon by all recent authors who have given serious thought to their ontological status (Ghiselin 1981; Hull 1976; Fink 1981; Wiley 1981*a*). They share many characteristics with individuals, particularly their spatio-temporal restriction and their capacity to change (evolve). On the other hand, they differ from individuals (populations), because they lack the most characteristic property of the individual, the internal cohesion. This lack of cohesion is well demonstrated by every striking evolutionary departure, such as that of the birds from the archosaurians or the mammals from the therapsids. Wiley (1980, 1981) has proposed the felicitous term *historical groups* for higher taxa. This is not the place to discuss to what kind of groups the term historical groups should be delimited, but personally I can see no merit in restricting it to holophyletic groups.

Grades are characterized by certain joint properties but not by any internal cohesion. Clearly they are therefore not individuals. When monophyletic they might qualify for the status of historical groups; when polyphyletic they are clearly classes.

NOTES

[1] The term 'nondimensional' species designates the coexistence of several species at a given locality without the dimensions of space and time. The term nondimensional is to be taken colloquially, not in a strict mathematical sense. It simply refers to the relationship of a local population (deme) of a species to the demes of other coexisting species, this relationship consisting of "noninterbreeding." Each deme is a reproductive community.

[2] Peripatric speciation is that form of allopatric speciation in which a founder population beyond the present species range becomes a new species while thus isolated.