



Species as individuals

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Abstract. There is no question that the constituents of cells and organisms are joined together by the part-whole relation. Genes are part of cells, and cells are part of organisms. Species taxa, however, have traditionally been conceived of, not as wholes with parts, but as classes with members. But why does the relation change abruptly from part-whole to class-membership above the level of organisms? Ghiselin, Hull and others have argued that it doesn't. Cells and organisms are cohesive mereological sums, and since species taxa are like cells and organisms in the relevant respects, they, too, are cohesive mereological sums. I provide further reasons in support of the thesis that species are mereological sums. I argue, moreover, that the advocate of this thesis is committed to a form of pluralism with respect to the species concept.

Introduction

Traditionally, species taxa have been considered natural kinds. Natural kinds are special sorts of classes that exist independently of our systems of classification and the way the world turns out to be. Since natural kinds are demarcated by real essences, objects are members of natural kinds in virtue of their intrinsic properties. Although there are still thinkers who support the thesis that species taxa are natural kinds,¹ a different approach to species has in recent years achieved wide recognition. According to this approach, which was first suggested by Ghiselin and later developed by Hull and others, the organisms of species taxa are joined together by the part-whole relation rather than by that of class membership.² Species taxa are not classes but mereological sums that are cohesive the way organisms are. Consequently organisms and species taxa belong to the same ontological category, namely that of spatio-temporal individual rather than that of class.

This paper elaborates on the species-as-individuals thesis. It is quite clear that the crude idea that species taxa are spatio-temporal individuals does not provide any criteria to determine which aggregates of organisms are species taxa. I shall argue, however, that not only does the species-as-individuals thesis not give us a criterion

¹ E.g. Putnam (1975), Ruse (1998), Mahner and Bunge (1997). See also Thom (1972), Kauffman (1992), Goodwin et al. (1993). Kauffman and others have defended an approach to species taxa sometimes called 'process structuralism'. According to this view, a developing organism is a chaotic system for which certain generic forms (a set of genetic factors) are attractors. As Griffiths has recently pointed out, 'the mistake made by the process structuralists is to assume that a causal homeostatic mechanism must take the form of a set of essential intrinsic properties' (1996, p. S5). These essences are almost like Putnam's genetic essences akin to the atomic structure of chemical elements.

² See e.g. Ghiselin (1966, 1997), Hull (1984, 1989), chapter 5, Hull (2001), chapter 10).

of this sort, but also the advocate of this thesis is committed to the view that a plethora of criteria can be used correctly to determine which mereological sums we should label 'species taxa'.

The class conception

One reason that species taxa have been considered classes is that they were thought to be natural kinds on a par with gold, oxygen, water and nitric acid. Many definitions have been given of 'natural kind', but nearly all of them have it that natural kinds are spatio-temporally unrestricted and have members that share a unique set of traits in common.

The problems with this conception are manifold. Organisms are members of natural kinds, not in virtue of heredity relations, but in virtue of intrinsic properties. But the evolution of a species taxon requires that heredity relations join together the organisms of the taxon. So if species taxa are natural kinds, they cannot evolve. One might accept this consequence of the natural kind thesis. But if species taxa cannot evolve, then how do new species taxa develop? One answer is that they don't. Natural kinds, one might argue, do not have a place in space and time. Since they are spatio-temporally unrestricted, they do not come into existence in the course of the universe, and they do not transmute. Lead would not change or go out of existence if you were to transmute all the lead in the world into gold; only the samples undergoing the process would. If species taxa were natural kinds they, too, would not come into existence, change or go out of existence. All species taxa (past, present, and future) would already be in existence whether they had actual members or not. Organisms born without the essential features of their ancestors would fit, not into the ancestral taxon, but possibly into some other taxon.

Perhaps this response to the objection from evolution is coherent. But there are other difficulties. The natural kind thesis presupposes that a species taxon has a real essence that determines whether or not an organism belongs to it. An organism is a member of a species taxon when and only when some proper subset of its intrinsic properties is identical to the real essence of the species taxon. However, we tend to think that even if genealogical relations do not determine species taxa, then at least they should be co-extensive with whatever determines them; the taxonomic tree should converge on the genealogical tree. If these intuitions concerning species taxa are correct, then organisms do not fit into a species taxon in virtue of intrinsic properties. Of course, the obvious structural similarity to be found within a cluster of organisms such as human beings or domestic dogs, as well as the differentia that make such clusters easily distinguishable from other clusters suggest that structural features may contribute in some way to the stability of species taxa. But there is no guarantee that clusters of structurally similar organisms coincide with clusters of organisms that share a recent common ancestor. As Mayr (1987), p. 146) points out, no one, evidently, has any problem telling apart a chickadee from a starling in one's garden, but what seems to be a paradigm species of chickadee might vary so much geographically that two distinct races may appear as two distinct species taxa.

Of course, what counts as intrinsic features must be extended to encompass features, not only at the level of the phenotype, but also at that of the genotype. Essences of species taxa are sometimes thought to be genetic essences akin to the atomic structure of chemical elements.³ But not even structural similarity at the level of the genotype is always coextensive with heredity relations: structural similarity at the level of the genotype may arise among parts of different species taxa. Hull gives the following example of the dodo, which is now extinct:

As unlikely as it might be, perhaps a species of wild turkey might produce a species that is genetically identical to the dodo. The same array of genomes that characterized the dodo at one point in its evolution (if we knew what this array actually was) also characterizes the newly evolved species. Do these organisms belong to one species or two? (1989, p. 155)

Most of us will almost certainly insist that the dodo and the species resulting from a species of wild turkey belong to different species taxa. But if two aggregates of structurally similar organisms belong to two different species taxa, inclusion within a species taxon cannot ultimately be based on the possession of genotypic or phenotypic traits.

Mereological sums

What is the alternative to the natural kind thesis? Hull has argued that evolutionary theory supports the view that organisms stand to species taxa the way genes stand to cells and cells to organisms. But if organisms are similar to species taxa in this respect, then it is unlikely that it should be the class-membership relation that joins together the organisms of species taxa when it is the part-whole relation that joins together the cells of organisms. As Hull puts it:

There is no question that genes, cells, organisms and kin groups are related by the part-whole relation. Genes are part of cells, cells are part of organisms, and organisms are part of kin groups. The point of the dispute is whether the relation changes abruptly from part-whole to class-membership above the level of organisms and possibly in kin groups. (1989, p. 84)

The genes found in cells are not members of the cell, and the cells that constitute an organism are not members of the organism. Cells and organisms are wholes with parts. Since wholes with parts are mereological sums of some sort, cells and

³ See e.g. Putnam (1975).

organisms are mereological sums. If species taxa are like cells and organisms in the relevant respect, they, too, must be sums.⁴

The idea that species are mereological sums is preferable to the natural kind thesis in many ways. The framework of classical extensional mereology is non-Platonistic, which means that mereological sums are closer to the changing world of flesh-and-blood reality than are natural kinds. This is because a whole is nothing but its parts. Since the parts are concrete individuals, the whole too is a concrete individual. Species taxa conceived as mereological sums are correspondingly less mysterious. If species taxa are concrete individuals, then there is logical space for arguing that heredity relations join together their parts. So it is not ruled out in advance that species taxa evolve. Not so for natural kinds, since relations of structural similarity join together their members. Moreover, if the parts of a mereological sum do not exist, then neither does the whole. But if species taxa are conceived as natural kinds, then there can be species taxa without members.

Though the thesis that species are mereological sums has its advantages compared to the natural kind thesis, I can think of at least three reasons that one might want to reject it. One is that the parthood relation is transitive. So if species taxa are mereological sums, then organisms are not the only parts species have; any part of, or combination of parts of, the organisms would also be parts of the species taxon. I do not believe this is a problem. It might seem odd to treat your elbow as belonging to the species of human beings. But I believe the oddness of this view stems from our habit of treating species as classes with members. Since your elbow is part of you, and you are part of the species of human beings, why not say that your elbow too is part of the human species?

The second concern one might have is that where species taxa evolve and so persist through radical change, extensional mereological sums cannot persist through any sort change. This worry, I believe, originates from a failure to distinguish between three-dimensional and four-dimensional approaches to species. On the three-dimensional approach, species taxa endure through change. For that reason they cannot be treated as extensional mereological sums. If the parts of a sum change, then the whole ceases to exist. Yet species could be treated as non-extensional mereological sums provided that the idea of non-extensional mereological sum is coherent.⁵ What's more, species taxa may be treated as four-dimensional entities.⁶ If species taxa are regarded as four-dimensional entities, then the suggestion that species taxa contain structurally diverse organisms that exist at different

⁴ We should here specify what we mean by 'sum'. If we take a mereological sum to be a sum of its parts no matter their arrangement, then it would be possible for it to be the same sum even if its parts were organized in an entirely different way. If, on the other hand, we take a mereological sum to be a sum of its spatial parts, temporal parts, and spatiotemporal parts, then the sum could not have had the same parts arranged differently (the notion of a temporal part at T of a spacetime worm, for example, is: the (atemporal) fusion of all the parts of the worm that are located only at spacetime points in T). Either way, species taxa, like organisms, need not have their parts essentially. That is, a species taxon might have consisted of parts different from those it consists of in actuality.

⁵ Peter Simons has devoted a whole book to this and related issues. See his (1987). So far no one has fully worked out a mereology of species. For a mereology of niches, see Smith and Varzi (1999).

⁶ For a defense of the general thesis of four-dimensionalism, see Heller (1990).

times poses no problem. This is because classical extensional mereology has been conceived in such a way as to allow unrestricted summation even in relation to diverse objects which exist at different times. On the four-dimensional approach, a species taxon can be said to change or evolve to the extent that it has different temporal parts with different properties, which stand to each other in genealogical/historical relations. Of course, if we want to hold onto the view that species taxa could have been different from what they in fact are, we cannot say that species taxa construed four-dimensionally are identical to the mereological sums that constitute them. It is better to say that species taxa are the mereological sums that constitute them only coincidentally. What this means is that a species taxon, though it probably could not have had a different ancestor, could have been an entirely different sum with entirely different parts. Even so it is still true to say that if an entity is a species taxon, then it is a mereological sum.

This leads us to the third, and related, worry, which is the concern that some mereological sums have parts which seem to be utterly unrelated to each other. For example, Napoleon and your left foot are not related to each other in any interesting way, but the sum of Napoleon and your left foot is a mereological sum nonetheless. It is not entirely clear, however, that this should be a worry at all. If the worry is that mereological sums do not and cannot have any structure, then it is unmotivated. A mereological sum preserves the order and location that the parts already have, since a sum just *is* its parts (as they exist outside the sum). It is true that classical extensional mereology has resisted coherent extension of a sort which would allow it to represent the structure of the objects in its domain, for example, classical extensional mereology cannot represent *when* such objects (for example the fusion of Napoleon and your left foot) should properly be said to exist. But it is not true that a mereological sum *has* no structure. Suppose the name '*a*' represents the sum of *b* and *c*. If *b* exists at a time T1 and *c* exists at a later time T2, then the sum, *a*, has parts that exist at different times. Of course, the representation, ' $a = b + c$ ', does not represent these temporal features. But the fact that no real structure is represented does not entail that the individual denoted by '*a*' does not have any structure. The operator of mereological fusion preserves all inter-object relations, and it thus preserves the order and location of objects which fall within its grasp: if two objects are linked together in nature, then they are linked together also within their mereological fusion. In this sense mereology leaves everything as it is.

Perhaps the only worry left is that the thesis that species taxa are extensional mereological sums is not sufficient for a complete account of species. The parts of species taxa are kept together in ways the mereological sum of Napoleon and your left foot is not, since the sum of Napoleon and your left foot is kept together by nothing but the mere existence of its parts at different times and at different places. If organisms are parts of species taxa in much the same way in which cells are parts of organisms, then the parts of species taxa, too, stick together in ways in which the parts of the sum of Napoleon and your left foot do not. Of course, a mereological sum comes with the specific order and arrangement of its parts that already obtain among its parts. But mereology does not yield a uniform segmentation of organisms into species taxa.

Not even this worry is motivated. For notice that the allusion to mereology made

above and elsewhere is not meant to be a suggestion that all we need to say about species is that they are mereological sums. There are lots of mereological sums that do not, and should not, qualify as species taxa. But this does not constitute an objection to the thesis that species taxa are mereological sums. Rather, it merely shows us that there is an additional problem of finding criteria that can enable us to determine which of the many mereological sums that exist are the ones we should label 'species taxa'.

Kitcher's objection

Kitcher (1989) has objected to the idea that species are spatio-temporal individuals. The idea was that organisms are parts of species in much the same way in which cells are parts of organisms. Kitcher's objection has two parts. The first is substantive: that individual organisms are cohesive in ways that species are not. It is possible, Kitcher argues, to destroy the organization of cells in a multicellular organism while each cell persists. If the organization is destroyed, the organism, too, will be destroyed, even if the cells are intact. But the same is not the case for species taxa; a species taxon, says Kitcher, continues to exist if we disrupt the relations among the organisms that are members of it. As he puts it:

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. (1989, p. 186)

The very idea that species taxa evolve and hence that their population structure, geographic range, and ecological role can change over time, unpredictably, and sometimes abruptly suggests that Kitcher is right when he says that 'we' can disrupt the relations among the organisms of a species taxon without destroying the species taxon. But notice that this claim of Kitcher's is not an objection to the claim that species taxa are mereological sums. Since by saying that species taxa are mereological sums, we do not claim that species taxa do in fact have stability. And we do certainly not say that the same sorts of relations have to hold among all of the organisms that belong to the species. The idea that only those mereological sums that are cohesive in much the same way as individual organisms are species taxa is an additional claim.

But if Kitcher's claim is not an objection to the claim that species taxa are mereological sums, then what is his concern? His concern, I believe, is that the species-as-individuals thesis places species taxa in the same ontological category as organisms. But, he argues, the fact that species taxa continue to exist even if the relations between the organisms are disrupted is enough reason for placing species taxa and organisms in two different ontological categories. I don't believe this is right. Most species taxa can withstand some disruption of their population structure but some cannot. Conversely, most organisms cannot continue to exist if their internal structure were moderately changed; but other organisms can withstand

some tearing apart. But notice that these may be differences of degree, not kind. If so, then these differences need not suggest that species taxa could not belong to the same ontological category as organisms.⁷

The second point of Kitcher's is formal. Claims about species as individuals can be translated into claims about species as sets, using as your criterion of set inclusion historical/genealogical connection. In other words, if species are as dependent on the relations among organisms as organisms are on the relations among cells, Kitcher argues, then it could be claimed that species is 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 the species" (1989, p. 186). Where a set, for example in the sense defined by Cantor, is a logical or conceptual unit of concrete entities which do not necessarily have anything in common, a set in Kitcher's sense is a unit whose members belong to the set in virtue of their historical/genealogical connections.

On the face of it, it seems that historical sets have the same problems as mereological sums, no more, no less. If species taxa are conceived as three-dimensional entities, then the historical sets of Kitcher's would have to be non-extensional entities, that is, entities that could remain the same in spite of having different members at different times, and I see no reason why we could not develop a time-indexed form of set theory without the commitment to extensionality just as we could develop a mereology of this sort.⁸ The problem with historical sets, as with all sets, is that sets are abstractions. Sets do not preserve the order and location their members have outside the set. In Kitcher's case historical/genealogical relations are used as a criterion to determine which organisms are members of the same set. But the set does not represent or capture these historical/genealogical relations. A set of members is like a list of names of people attending a sports club. All the names on the list denote people who are related to each other in interesting ways, and to get your name on the list you must be related to the other people whose names are on the list in the same way as they are to each other. But the names on the list are not related to each other in that way. We can change the order and arrangement of the names on the list without losing any important information. The fact that a name appears on the list shows that the person it names is in the same club as the rest of the people named. Yet the list *is not* identical to, and does not coincide with, the club with its people and their activities. Similarly, the organisms that are taken to be members of a historical set are members of the set because they stand to each other in historical/genealogical relations. So the set *represents* in certain ways the concrete aggregate of organisms under consideration but it is not identical to it, and does not coincide with it.

What the historical set and the historical mereological sum have in common is that they are both the result of some collecting together into a whole. But

⁷ Of course, one will need to divide the metaphysical category of individual into further subcategories. The species category, then, does not belong to the same subcategory as the organism category.

⁸ See Simons (1987).

customarily the difference between them is this:⁹ that where the resulting whole for the case of sets is an abstraction, the resulting whole for the case of sums is concrete, and where mereological sum preserves order and location, the members of sets exist within the set without order or location—they can be permuted at will and the set remains identical.

In response to this rejoinder it might be said that historical sets are supposed to be concrete entities. But then the dispute is in name only, since a concrete historical unit of organisms is the kind of thing the species-as-individuals thesis claims a species taxon is. If Kitcher's sets are concrete (and they preserve order and location), then it does not matter that the claims about species as individuals can be translated into claims about species as sets, using as your criterion of set inclusion historical/genealogical connection, since these sets have everything (important) in common with the mereological sums postulated by the advocates of the species-as-individuals thesis.

What unifies species taxa?

Unless the species-as-individuals thesis is but a crude claim about the ontological status of species taxa, more is needed. The reason is that mereology yields no uniform segmentation of organisms into species. We are left with the additional task of finding criteria for determining which mereological sums we should label 'species taxa'. Of course, the only candidates for the species taxon are the sums that have organic wholes as parts. But we are still left with an indefinite range of overlapping mereological sums most of which should not be regarded as species taxa. When we say "should not be regarded as species taxa" it seems to be the case that we have some impartial, pre-theoretical ideas of what a species taxon can or cannot be. I believe we do have such ideas, that is, ideas prior to any attempt to define the species concept, not necessarily ideas prior to any theories of evolution or theories of science in general. These ideas most likely issue from conceptual considerations, evolutionary theory, and our acquaintance with paradigm species.

One pre-theoretical thesis concerning species taxa is that they must be mutually

⁹ I say 'customarily' since attempts have been made to combine mereology and set theory. Lewis (1991), for example, has developed a set theory based on the singleton set and the part-whole relation. Lewis shows how, with the help of this one single notion, all the standard axioms of set theory can be derived within a mereological framework. He first of all defines the notion of what he calls a class, which is a set in whose content the empty set plays no role. He then shows how the theory of classes can be formally identified with the theory of mereological sums (or 'fusions') of singletons. The advantage of this theory compared to mereology is that in mereology, if an object falls within the range over which you quantify, then so also do all the object's parts. Lewis's theory can block this automatic recognition of an object's parts (in effect by wrapping the object in a set-theoretic coating). The disadvantage is that the set is built up mereologically not out of its elements but out of its singletons, and the singleton operator has the effect of stripping away the various sorts of linkages which obtain between the objects to which it is applied as these exist in nature. It sets them apart from their surroundings and seals them off from each other and from all the effects of time and change.

exclusive and together constitute a (rather) comprehensive taxonomy; consequently adequate grouping criteria do not lead to overlapping species taxa, and all organisms that form species taxa must be parts of a species taxon or an intermediary aggregate perhaps changing into a new species taxon.

Another thesis is that species should play some important role in evolution. As Hull and others have advocated, species taxa should be the units that evolve as a result of the evolutionary process, and so they should be relatively stable units that originate as the result of a speciation event, and which eventually themselves speciate or go extinct.

Yet another (perhaps entailed by the second) is that the parts of species taxa should stand to each other in genealogical relations. But since all organisms on earth presumably stand to each other in genealogical relations, we should probably say that there should not be gaps in the pattern of ancestry relations.¹⁰ A mereological sum consisting of hominids that lived around 100,000 years B.C. and hominids that are alive now should not constitute a species taxon.

Finally, it should be allowed that species taxa can have a certain size and distribution that surpass the size and distribution of populations. A population consists of closely related organisms that share a recent common ancestor, and since they occupy a more or less well-defined geographic region they are more likely to interact with each other than with members of other populations. Thus, populations appear to possess features which we might expect that species taxa possess as well, but it should not be ruled out in advance that species taxa can consist of several populations.

The four pre-theoretical constraints are satisfied by the so-called phylogenetic species concept.¹¹ The phylogenetic species concept sorts organisms based on their common descent and so derive from biological systematics. One version of this concept is the internodal species concept, which was first discussed by Hennig (1966) and was later coined as a term by Nixon and Wheeler (1990), p. 213.¹² The idea here is that populations belong to the same species iff they are components of the genealogical network between two permanent splits or between a permanent split and an extinction event (Kornet (1993), p. 408).¹³ The main problem with the internodal concept considered as a definition of the species category, is that it presupposes that we can determine which events are permanent splits, which are extinction events, and which are the appearances of new evolutionary trends within

¹⁰ Notice, however, that the third pre-theoretical constraint does not exclude that some species taxa consist of several populations that do not actually interbreed, provided that the populations are continuations of the same recent ancestral population.

¹¹ For an in-depth analysis of this concept, see Wheeler (1996).

¹² For other versions of the phylogenetic species concept, see Mishler and Donoghue (1982).

¹³ There is a general problem of deciding whether the general requirement of a species concept concerns its constituent populations, the separate organisms or the genomes of the separate organisms. The most plausible unit is that of a population. For suppose the criterion is that reproductive isolation leads to speciation. Then if a single organism cannot reproduce, then it would no longer belong to the species taxon from which it originated. But this seems wrong. So I shall take the isolating units to be populations throughout.

one and the same species taxon. How can we determine that Neanderthals and human beings are not both part of the same genealogical network between two events of the relevant sort?

As Mishler and Brandon (1987) point out, two components of a proper species concept should here be distinguished: one to give us criteria for grouping organisms together into a taxon (grouping), and one to determine the threshold at which the taxon is designated a species taxon (ranking). Given this distinction it seems that the main problem with the phylogenetic species concept is that fails to provide a ranking criterion (or perhaps both a ranking criterion and additional grouping criteria). It is unclear how to determine the cut-off point at which an aggregate of genealogically related organisms is designated a species taxon. As a result the advocates of the phylogenetic species concept must embrace additional criteria in order for it to give rise to an unambiguous taxonomy of all organisms into monophyletic taxa.

Since the phylogenetic grouping criterion is required in order for our third pre-theoretical constraint to be satisfied, all species concepts must satisfy this criterion. Species concepts get into trouble if they try to avoid the genealogical requirement. And as a matter of fact they rarely do. Indeed other species definitions tend to presuppose that the organisms are related by descent in the relevant way, and so they implicitly or explicitly take the genealogical requirement of the phylogenetic species concept to be a necessary constraint on the species category. Since the members of the same genealogical network between to speciation events will be related by reproductive links, all plausible species concepts refer implicitly or explicitly to these links, for example by requiring that species taxa be lineages.¹⁴

Additional grouping criteria

A horde of distinct species concepts provides additional criteria that might serve to cut off the genealogically related organisms that should be designated species taxa. Let me mention a few. One is Mayr's biological species concept. The grouping criterion is that of interbreeding ability. Two populations are conspecific just in case they belong to the same lineage and they are able to interbreed.¹⁵ The ranking component is taken to be the largest aggregate that satisfies the grouping criterion.

Notice here that without the genealogical requirement the biological concept would be faced with Hull's dodo problem. Imagine that a population of wild turkey genetically identical to the dodo has the ability to interbreed with the dodo. Potentiality alone does not make them one and the same species taxon. The population of wild turkey and the dodo constitute two different sections of the genealogical tree; so they should not be counted as one species taxon. Not even

¹⁴ I take a lineage to be an entity that changes indefinitely through time as a result of replication and interaction of its constituent parts.

¹⁵ It should be clear that genealogical relations (and even immediate ancestral relations) are different from reproductive links. Two genealogically related populations may not be able to interbreed, and two populations that are able to interbreed may not be genealogically related.

co-existing populations that are able to interbreed should always count as one species taxon. Two drops of mercury might be potentially one; for example, if they come into contact with each other. But until they do, then these drops remain two drops, not one. The potentiality requirement is more plausible when it is combined with the genealogical requirement. If two separate populations are conspecific, then they result from a common ancestor population, and they and all the intertwining populations too must be able to interbreed.

The problem with the biological species concept so formulated is that it leads to overlapping species taxa. The reason is that the ability to interbreed is not transitive. The fact that a population *a* is able to interbreed with a population *b*, and *b* is able to interbreed with a population *c* does not imply that *a* and *c* are able to interbreed. So if this scenario were to obtain, population *b* would be a part of two distinct species taxa. A good example of this is a ring species such as the black-backed gulls that circles the Arctic. It is composed of chains of populations in which each link can reproduce with its neighbors, but populations removed from each other by a number of links cannot, even if they make contact.¹⁶ Were the biological species concept correct, such 'ring species' would be not one but several overlapping species taxa. The same objection applies if the constraint on conspecific populations were actual reproduction. What this shows is that although the reproductive link might be sufficient for conspecificity, it is not necessary. So it might be true that any two populations of a lineage which can, or do, interbreed are conspecific, but we must abandon the idea that if two populations of a lineage are conspecific, then they can, or do, reproduce.

A relation comparable to the reproductive link is gene flow. Even though a case can be made for the non-transitivity of gene flow, we can stipulate a related transitive notion. Since gene flow is transitive by stipulation, it will do to avoid the above counterexample. But gene flow is non-symmetric. Gene types from one population might be manifested in a second population through reproductive links if an organism from the one population is absorbed into the other. So we still get overlap: the fact that *a* stands to *b* and *c* in the relation of gene flow does not imply that *b* and *c* stand in that relation. And if they do not, then *a* is a part of two distinct species taxa. What we need is a relation akin to those of reproduction and gene flow but transitive and symmetric, perhaps that of contributing to the same (protected) gene pool. We can define 'contribution to the same gene pool' in terms of 'actual reproduction' (*R*). Two populations *a* and *b* contribute to the same gene pool if and only if there is some ascending chain $A, x_0 R x_1 R \dots (x_i \leq A; i \in \mathbb{N})$, of which both *a* and *b* are parts. Thus, contribution to the same gene pool is transitive and symmetric. So if *a* contributes to the same gene pool as *b* and *c*, then *b* and *c* contribute to the same gene pool. Now, since contribution to the same gene pool requires actual reproductive links between 'neighboring' populations, the lineage requirement is redundant. The revised biological species concept may be formulated

¹⁶ See Sterelny and Griffith (1999), p. 189.

as follows: two populations *a* and *b* are parts of the same species taxon if and only if *a* and *b* contribute to the same gene pool.¹⁷

It is commonly objected that the biological concept has the odd consequence, sometimes embraced by its exponents, that asexual populations cannot form species taxa.¹⁸ This problem can be done away with in one of two ways. Either the restriction can be tolerated, or the biological concept can be supplemented with additional criteria, as suggested by Templeton. Templeton (1989), p. 25) argues that relations other than sexual reproduction confer cohesion on the species taxa. The resultant cohesion concept takes a species to be the largest group of organisms having the ability to interbreed and/or occupy the same sort of niche. Of course, if it is required that the asexual organisms that form a species taxon also form a lineage, then the resulting species taxon is an organism lineage (the progeny of a single organism), since strictly asexual organisms form no higher-level lineages; they alone are the products of replication and interaction.

A second possible relation for partitioning the domain of organisms into species taxa is that of structural similarity. If it is required that species taxa are lineages, the structural requirement does not face the same difficulties here as within the theory of natural kinds. But the notion of structural similarity is vague. How structurally similar must two populations be in order for them to satisfy the structural requirement? Even if we could answer that question, there are other difficulties. The structural concept is faced with challenges similar to those meeting the biological concept. The relation of structural similarity is not transitive. If a population *a* is structurally similar to a population *b* and *b* is structurally similar to a population *c*, it does not follow that *a* is structurally similar to *c*. What we need is a relation akin to that of structural similarity, which is both symmetric and transitive. Something like 'contribution to the same pool of phenotypic traits' might fulfill that need. We can define 'contribution to the same pool of phenotypic traits' in terms of 'structural similarity' the way we defined 'contribution to the same gene pool' in terms of 'actual reproduction'. 'Contribution to the same pool of traits', unlike 'contribution to the same gene pool', does not require actual reproductive links between 'neighboring' populations. So 'contribution to the same pool of traits', unlike 'contribution to the same gene pool', does not meet the lineage requirement. We can define the structural concept of conspecificity as follows: two populations *a* and *b* are parts of the same species taxon if and only if *a* and *b* are parts of the same lineage and contribute to the same pool of phenotypic traits. There is, of course, an analogue notion at the level of genotypes. In need of a better term we might call it 'contribution to the same pool of genotypic traits'. But it should be kept distinct from that of contributing to the same protected gene pool. Where 'contribution to the same protected gene pool' requires reproductive links between 'neighboring' populations, 'contribution to the same pool of genotypic traits' is best defined in

¹⁷ To avoid interbreeding gaps in the species taxon (i.e. two populations that do not interbreed) one might take a species taxon to be a continuous series of interbreeding wholes (i.e. wholes composed of populations that contribute to the same gene-pool).

¹⁸ See e.g. Ghiselin (1989), pp. 74–75).

terms of 'genetic similarity'. The notion of genetic isolation may turn out to be co-extensive with reproductive isolation (*a* is genetically isolated from *b* if and only if *a* is reproductively isolated from *b*), even though the notion of genetic similarity is not co-extensive with potential or actual interbreeding.

A third grouping criterion is provided by the ecological species concept. Advocates of the ecological species concept argue that the stability of species is primarily due to ecological forces.¹⁹ They argue that a species is a lineage which occupies its own distinctive adaptive zone or niche, and the distinct set of selection forces in each niche is accountable for the continuance of species taxa as separate taxonomic units. Notice that to occupy the same adaptive niche is not, of course, to occupy the very same region of geographic space. In fact, 'niche occupancy' can be defined in terms of 'demographic exchangeability', the ability of organisms of distinct populations to exchange adaptive zones. The advantage of the ecological species concept compared to the original biological concept is that the relation of niche occupancy is transitive. If a population *a* occupies the same niche as a population *b* and *a* occupies the same niche as a population *c* then *a* occupies the same niche as *c*. It is furthermore symmetric. If *a* occupies the same niche as *b*, then *b* occupies the same niche as *a*. As a result, if *a* occupies the same niche as *b* and *c*, then *b* and *c* occupy the same niche. So the ecological species concept does not lead to overlapping species taxa. The greatest problem with the ecological species concept is a practical one, namely that of finding an adequate niche concept, which does not define the niche category in terms of the species concept. Though a practical difficulty might constitute a reason for leaning toward other concepts in praxis, practical issues should not cast doubt on the internal coherence of a concept.

A fourth possibility is to define the species category in terms of populations that exchange organisms. Populations are neither purely ecological nor purely genealogical. Usually they are taken to occupy a more or less well-defined geographic region and exhibit reproductive continuity from generation to generation. Since they are easily identifiable integral wholes of the right sort, they are themselves good candidates for being species taxa. But they do not seem to satisfy the fourth pre-theoretical requirement; they are often enough too small. A more plausible species concept rests on the idea of a sum of populations linked by an exchange of organisms. As Hull points out, 'although some species of sexual organism are made up of a single population, most include several populations that are at least periodically distinct. As long as the constituent populations exchange an occasional organism, such species can be considered a single, integrated whole' (1980, p. 324). A maximal group of populations that occasionally exchange organisms might be labeled a 'species taxon', provided that we find a notion of exchange that is transitive as well as symmetric. Notice that a case could be made for understanding this concept as an ecological concept defined in terms of actual demographic exchange rather than demographic exchangeability. Since the organisms in a cluster that frequently exchange organisms are in some sense competing

¹⁹ See e.g. Anderson (1990).

for a limited number of living spaces, they may be regarded as occupying the same adaptive zone.²⁰

Pluralism

All of the above concepts lead to plausible taxonomies, and all of them support the thesis that species are individuals. Of course, ecological and structural species may be less like individual organisms than, say, biological species, since they need not be causally integrated in the same way you and I are causally integrated. Where the three-dimensional time-slices of ecological species may consist of causally disconnected parts, the only parts of us that are causally disconnected lie in two dimensions. But, as mentioned, this difference may very well be one of degree, not kind. Thus, we have a number of alternative, plausible taxonomies. But they are incompatible. The Australian Pacific gray duck, for example, hybridizes freely with the mallard duck. Structurally they are two species; biologically they are one. But in that case which concept gets things right?

I believe that an important consequence of the species-as-individuals thesis is that they all might. If we treat species taxa as natural kinds there is a good reason for saying that one and only one species concept gets things right. If species taxa are natural kinds, although it will be accidental which species taxa have actual members, it will not be accidental which species taxa there are. Since natural kinds are universals, they exist independently of the way the actual world turns out to be. So for the case of natural kinds, there is a principled taxonomy of organisms into kinds. When we treat species as spatio-temporal individuals rather than as natural kinds there is no overwhelming reason for saying that one and only one species concept gets things right. No real essences to go by. If species taxa are individuals, the only way to determine (impartially) which mereological sums are species taxa is to decide which mereological sums satisfy our pre-theoretical constraints. This excludes some mereological sums from being species taxa but leaves us with an indefinite number of correct ways of dividing up all the organisms on earth.

One might notice that any plausible species concept must require that species taxa be lineages that are isolated from other lineages in such a way that the evolutionary innovations within them can be preserved. But isn't reproductive isolation the only isolating mechanism that will preserve such innovations? I don't think it is. An ecospecies might survive the split into two large populations that do not interbreed but are ecologically linked. The genes of the two populations derive from a single gene pool but the two populations do not contribute to the same gene pool; instead they exhibit the capacity for demographic exchange, and so they are ecologically isolated. Similarly, a structural species might survive the split into two large populations that do not interbreed but are structurally similar because they derive from a common ancestor. Again the genes of the two populations derive from a single gene pool, but the two populations do not contribute to the same gene pool;

²⁰ For other species concepts discussed in the literature, see e.g. Mayr (1996), Ereshefsky (1992a), Wilson (1999).

they share a common set of genes and/or traits, which is necessary though not necessarily sufficient for mating with each other. The genes and/or traits isolate them from other species taxa, which means that they are probably reproductively isolated even if they do not or cannot interbreed.

The upshot is that all of the aggregates (biospecies, ecospecies, structural species, etc.) contribute in one way or other to the continuation of the genealogical network. All three aggregates are stable units that evolve as a result of the evolutionary process (the events of replication and interaction). None of them seems best fitted for all situations. As Sterelny and Griffith (1999) point out, “the Queen’s corgis are not a new species of dog, however scrupulously their pedigrees are preserved” (1999, p. 188). Why not? Well, perhaps in part because of the structural similarity between the corgis and other dogs. So why should only one of them have the right to the name ‘species taxon’? The answer is, they shouldn’t. We will have to accept a multiplicity of concepts that combine genealogical factors with morphological, genetic, ecological or behavioral parameters, just as long as they satisfy our pre-theoretical constraints.²¹

Since the range of mereological sums that satisfy our pre-theoretical constraints is indefinite, the consequence of taking species taxa to be mereological sums is pluralism. As Mishler and Brandon (1987) argue, two kinds of pluralism should be distinguished. One sort of pluralism is the view that there are many incompatible but legitimate taxonomies depending on the needs and interests of particular taxonomists.²² The other says that there are a number of legitimate species approaches but different approaches apply to different groups of organisms, and no more than one approach is applicable to a group of organisms.²³

The second form of pluralism has been criticized for being an *ad hoc* strategy, and for giving rise to incomparable, and perhaps overlapping, species taxa.²⁴ The resulting taxonomy of ecospecies, biospecies, and what have you, is oddly miscellaneous, almost like the category of my left tennis shoe, W. V. Quine, and the Taj Mahal. The first kind of pluralism has been criticized for equivocating on the concept of species, and for leading to inconsistency and intellectual laziness.²⁵ In defense of this form of pluralism, Ereshefsky (1992b) has suggested that pluralism

²¹ Kitcher (1984a, 1984b) defends a somewhat similar view, but his view allows non-historical species concepts, including the class conception of species. He thus ignores the second pre-theoretical conception, which says that species taxa must play an important role in some evolutionary process. But a species concept that fails to satisfy this conception is faced with all the aforementioned absurd consequences. Species taxa can evolve only if heredity relations join together their parts. So non-historical species taxa cannot evolve, and so they play no evolutionary role worth mentioning.

²² See e.g. Dupre (1981), Kitcher (1984a, 1984b).

²³ See Mishler and Donoghue (1982).

²⁴ See De Queiroz and Donoghue (1988).

²⁵ For criticisms, see e.g. Sober (1984a), Hull (1987), Ghiselin (1987). These criticisms pertain especially to a pluralism of the sort defended by Dupre (1981). Dupre defends what he calls ‘promiscuous realism’. This sort of realism is based on the fact that ‘there are many sameness relations that serve to distinguish classes of organisms in ways that are relevant to various concerns; the promiscuity derives from the fact that none of these relations is privileged’ (1981, p. 82). But as Ereshefsky points out, Dupre’s pluralism is too promiscuous: ‘Taxonomies based on cooking lore are taken on a par with those based on contemporary evolutionary biology’ (1992b, p. 687).

be treated as a form of reductionism-as a realization of the fact that 'species' is ambiguous or perhaps vague. Forces of evolution have brought about divergent kinds of fundamental lineages (interbreeding, ecological, etc.) that classify the world's organisms, and we have inaccurately applied one and the same term to all of them. In order to disambiguate the concept we should talk, not about 'species taxa' but perhaps about 'biospecies', 'ecospecies', etc. He calls the result 'eliminative pluralism'.

Eliminative pluralism is perhaps the approach most in the spirit of the species-as-individuals thesis, as the underlying idea is that "there is one genealogical tree of life, but that the tree is segmented by different evolutionary forces into different lineages" (Ereshefsky (1992b), p. 681). The genealogical tree of life can be described in terms of facts of mereology and facts of ancestry. That is, there is a totality of organisms (past, present, future) that are related to each other one way or another. Some organisms are direct ancestors of others, some are siblings, some have a common ancestor that existed millions of years ago, etc. This tree of life has an indefinite number of overlapping aggregates of organisms as parts. It is one such set of aggregates of organisms we can designate or put in the foreground of our attention depending on which organizing principle we choose to focus on. Though the resulting taxonomy will reflect our interests, each taxonomy will consist of disjoint mereological sums, which exist independently of our interests, and which would have existed even if no one had thought of labeling them 'species taxa'. In Wilkerson's language, it is just a fact about the world, not a fact about us, that some mereological sums consist of genealogically related organisms that are able to interbreed, that some mereological sums consist of related organisms that occupy the same niche, that some mereological sums consist of related organisms that are structurally similar, etc.²⁶ The only relevant fact about us is that if we are interested in interbreeding units, we will concentrate on one set of mereological sums; if we are interested in ecologically stable units, or structurally similar groups, then we will concentrate on a rather different set; and so on.

In response to eliminative pluralism it might be said that there could be methods for determining impartially which mereological sums are species taxa other than that of asking which mereological sums satisfy our pre-theoretical constraints.²⁷ But which ones would they be?

Perhaps some well-documented evolutionary process requires the existence of species taxa resulting from one grouping criterion but not from any other. One possibility is that a species taxon is a cluster of organisms that function in the evolutionary process. It might be thought that organisms are integrated objects whose parts interact in ways that benefit the whole, because they function as wholes in selection processes. We might wonder whether species taxa are integrated objects

²⁶ Wilkerson (1993), p. 11).

²⁷ Ereshefsky (1992b) adds further constraints on the species concept. Some of these, I believe, are pre-theoretical and impartial, and therefore acceptable within the framework presented here. One further acceptable constraint is that our justification for our sorting principles should be consistent with well-established hypotheses in other scientific disciplines.

for the same reason. If they are, then perhaps only the species taxa falling under one of the plausible species concepts play this role.

As Hull points out, selection can act only on spatio-temporally localized entities, and “If it is to act on entities more inclusive than organisms in the same sense in which it acts on organisms, these entities must be cohesive wholes and not classes or groups” (1980, p. 314). Thus, if species are cohesive individuals, it is not ruled out in advance that they are interactors or vehicles. Some thinkers such as Sober (1984b) and Wilson (1983) argue for species selection in a weak sense in which the differential success of species can be explained in terms of features of the component organisms (brain size), or statistical properties that are in some sense additive (e.g. average brain size). The differential success of species with larger brains, for example, need not be the result of any process at the level of species, but may simply be the result of the differential success of individual organisms with larger brains. We have species selection in a genuine sense when the differential success of a species is caused by selection for features of the species themselves (e.g. demographic structure). In order for species taxa to be units of selection in the genuine sense, they must possess emergent, heritable species properties that causally can influence their survival.

It is not unlikely that they do. Sterelny and Griffith (1999), for example, argue that geographic and ecological distribution, and phylogenetic plasticity—the capacity of a lineage to change over evolutionary time—are emergent properties of this sort, which may be both heritable and causally relevant to extinction and speciation. Distribution, for example, is causally relevant to survival, since a widespread species taxon is more likely to survive (e.g. a meteor or a local climate change) than is a geographically and ecologically limited species. It is also heritable since a species taxon might become even more widespread than before as the result of a selection process. Suppose a lineage survives an extinction event because it is more widespread than its rivals, then the lineage will be able to expand further into vacated ranges and niches. So the lineage becomes even more widespread. It survives the next extinction event, and the process recurs. Thus, distribution is amplified as the result of a selection process.

I believe this story is plausible, but I do not believe that the idea of species selection will help us determine which species concept is the correct one. How would it help us? Perhaps the lesson learned above is that the aggregates called ‘species taxa’ must be geographically and ecologically widespread, since being widespread will causally influence survival. This would rule out the ecological species concept, since an ecospecies cannot survive extending into newly vacated niches. This will not do, however. Being widespread might causally influence survival, because if a species taxon is widespread it is more likely to have organisms that will be outside the range of ecological challenges. But so might narrowness. If a species taxon is narrow, then it is less likely to get hit by a meteor or a local climate change than if it is widespread. So it’s more likely that it will survive. My bet is that correct stories about species selection can be told no matter which of the plausible species concepts we embrace. So if species selection occurs at all, then all of the clusters labeled ‘species taxa’ in line with some plausible species concept probably

occasionally function in the evolutionary process. As a result, the idea that the correct species concept is that which leads to species taxa that function as units of selection is amiss.

Concluding remarks

The species-as-individuals thesis makes a claim about the ontological status of species taxa. The claim is the part-whole relation rather than that of class membership joins together the organisms of species taxa. Thus, species taxa are mereological sums rather than classes of organisms. The mereological account, however, does not yield a uniform segmentation of organisms into species. So it does not give rise to a comprehensive taxonomy but only to overlapping sums most of which are a long, long way from being paradigm species. Since a species concept must give rise to a rather exhaustive taxonomy of mutually exclusive species taxa, the crude form of the species-as-individuals thesis is not a species concept. If the species-as-individuals thesis is intended to be a species concept, it must embrace additional grouping criteria that can determine which of the many mereological sums are species taxa. The question is, which criteria should be embraced? If species were natural kinds, there would be an unambiguous taxonomy of organisms into species taxa, since which natural kinds there are does not depend on the way the world happens to be, or on our classifications. But if species taxa are individuals, there is nothing to species taxa over and above their constituent parts. There are no mysterious real essences that secretly bracket together all organisms in such a way as to result in a large unambiguous taxonomy. We have certain impartial, pre-theoretical constraints (e.g. concerning the origin of species) that to some extent confine the permissible compositions of species taxa, but a plethora of grouping criteria is consistent with these constraints. So the result of accepting the more involved form of the species-as-individuals thesis is a brand of pluralism in keeping with which several taxonomic criteria yield correct, though incompatible, taxonomies.²⁸

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