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On the Impossibility of a Monistic Account of Species

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[i]f we can once and for all lay the bogey of the existence of true relationship and realize that there are, not one, but many kinds of relationship—genealogical relationship, morphological relationship, cytological relationship, and so on—we shall release ourselves from the bondage of the absolute in taxonomy and gain enormously in flexibility and adaptability in taxonomic practice.

—J. S. L. Gilmour, "The Development of Taxonomic Theory Since 1851"

By the classification of any series of objects, is meant the actual, or ideal, arrangement of those which are like and the separation of those which are unlike; the purpose of this arrangement being to facilitate the operations of the mind in clearly conceiving and retaining in the memory, the characters of the objects in question. Thus there may be as many classifications of any series of natural, or of other, bodies, as they have properties or relations to one another, or to other things; or, again, as there are modes in which they may be regarded by the mind.

—T. H. Huxley, *Introduction to the Classification of Animals*

Most of the philosophical difficulties that surround the concept of species can be traced to a failure to assimilate fully the Darwinian revolution. It is widely recognized that Darwin's theory of evolution rendered untenable the classical essentialist conception of species. Perfectly sharp discontinuities between unchanging natural kinds could no longer be expected. The conception of sorting organisms into species as a fundamentally classificatory exercise has nevertheless survived. Indeed, the concept of a species traditionally has been the paradigmatic unit of classification. Classification is centrally concerned with imposing conceptual order on diverse phenomena. Darwin's theory, as the title of his most famous work indicates, is about the origins of diversity, though, so it is no surprise that the dominant task in post-Darwinian taxonomy has been to connect classificatory systems to the received, Darwinian, account of the origin of diversity. Attractive though this task undoubtedly is, it has proved unsuccessful. The patterns of diversity that evolution has produced have turned out to be enormously diverse, and in many cases the units of evolutionary analysis have proved quite unsuitable for the basic classificatory aims of taxonomy. Or so I argue.

Why do we classify organisms? A natural and ancient explanation—expressed clearly by, for example, Locke (1689, bk. 3, chap. 5, sec. 9) and

Mill (1862)—is that we do so to facilitate the recording and communication of information. If I tell you some animal is a fox, I immediately convey a body of information about its physiology, habits, and so on. The more you know about animals or mammals or foxes, the more information about that particular animal I convey. If organisms came in sharply distinguished natural kinds, internally homogeneous and reliably distinguishable from the members of any other kind, then the identification of such kinds would be the unequivocal aim of taxonomy. A classificatory system that recognized such natural kinds would be unequivocally the best suited to the organization and dissemination of biological information. But this is just what Darwin has shown us we cannot expect (see e.g., Hull 1965). In a domain of entities characterized, in part, by continuous gradation of properties and varying sharp and frequent discontinuities, matters are much less clear. It is this fact about the biological world that makes attractive the idea of taxonomic pluralism—the thesis that there is no uniquely correct or natural way of classifying organisms and that a variety of classificatory schemes will be best suited to the various theoretical and practical purposes of biology.

Many biologists and philosophers appear to think that pluralistic accounts of species will lead us to Babel (see e.g., Ghiselin 1997, 117–121). Biologists, they suppose, will be unable to communicate with one another if they are working with different species concepts. In this paper, I argue that species pluralism is nevertheless unavoidable. However, I also defend a kind of minimal monism: to serve the traditional epistemic goals of classification, it is desirable to have one general set of classificatory concepts. However, this general taxonomy will need to be pragmatic and pluralistic in its theoretical bases. For specialized biological purposes, such as the mapping of evolutionary history, it may often be necessary to adopt specialized classificatory systems. My monism is merely semantic: I suggest it would be best to reserve the term *species*—which is, as I have noted, the traditional philosophical term for classificatory concepts—for the base-level categories of this general, pragmatic, taxonomy. Such an antitheoretical concept of species will discourage the conspicuously unsuccessful and controversial efforts to find a solution to the “species problem,” and leave it to working biologists to determine the extent to which they require specialized classificatory schemes for their particular theoretical projects.

Monists, needless to say, disagree about which actual species concept biologists should accept. The cheapest way to buy monism might be with a radically nominalistic phenetic concept, as conceived by numerical taxonomists (Sneath and Sokal 1973). If biological classification could be conceived as merely an exercise in recording degrees of objective similarity, then some particular degree of similarity could be defined as appropriate to the species category. But few people now think this can be done. Philosophically, attempts to construe a notion of objective similarity founder on the fact that indefinitely many aspects of difference and of similarity can be discovered between any two objects. Some account of what makes a property bio-

logically interesting is indispensable: there can be no classification wholly innocent of theoretical contamination. Without wishing to deny that phenetic approaches to classification have provided both theoretical insights and practical benefits, I restrict my attention in this essay to more theoretically laden routes to species monism. My conclusions, however, leave entirely open the possibility that a version of pheneticism, modified by some account of what kinds of properties might be most theoretically interesting, may be appropriate for important domains of biology. The classification of bacteria is a likely example (see e.g., Floodgate 1962 and further discussion below).

In the section "Troubles with Monism," I trace some of the difficulties that have emerged in attempting to provide monistic accounts of taxonomy motivated by central theses about the evolutionary origins of diversity. I thereby hope to substantiate my claim that as more has been learned about the diversity of the evolutionary process, the hopes of grounding therein a uniform account of taxonomy in general, or even the species category in particular, have receded. In the final section, I outline my more constructive proposal for responding to this situation.

TROUBLES WITH MONISM

The potential conflict between two main goals of classification has long been recognized. The first and most traditional goal is to facilitate the communication of information or to organize the vast quantities of detailed biological information. From this point of view, a taxonomy should be constructed so that knowing the taxon to which an organism belongs should tell us as much as possible about the properties of that organism. This goal must, of course, be qualified by pragmatic considerations. Indefinite subdivision of classifications can provide, theoretically, ever more detailed information about the individuals classified: assignment to a subspecies or a geographical race will presumably give more information than mere assignment to a species. As the basal taxonomic unit, the species should be defined, therefore, to classify organisms at a level at which the gains from finer classification would be outweighed by the costs of learning or transmitting a more complicated set of categories. If organisms varied continuously with no sharp discontinuities, this balancing of costs and benefits would present a largely indeterminate problem. By happy chance for many kinds of organisms there appear to be sharp discontinuities at a relatively fine classificatory level that are much sharper than any discontinuities at any lower level. To the extent that this is the case, the selection of the appropriate level for assignment of organisms to species appears unproblematic.

In recent years, this goal of organizing biological information has been emphasized much less than a second, that of mapping the currents of the evolutionary process. A recent anthology of biological and philosophical essays on the nature of species carried the title *The Units of Evolution* and the subtitle *Essays on the Nature of Species* (Ereshefsky 1992). Though the idea

that, by definition, species should be the units of evolution is not uncontroversial, it is widely held. What is a unit of evolution? Evolutionary change is not change in the properties of any individual organism, but change over time in the distribution of properties within some set of organisms. (We need not worry here whether these properties are conceived as genetic or phenotypic.) A unit of evolution is the set of organisms in which changes in the distribution of properties constitute a coherent evolutionary process.

Because an evolutionary change is one with the potential to be maintained in future organisms, it is easy to see that the temporal dimension of a unit of evolution must be defined by relations of ancestry. As long as we are concerned with biological evolution in which properties are transmitted genetically (and ignore some complexities of gene exchange in bacteria), then evolution will be constrained within sets of organisms defined temporally by parent-offspring relations. We must then consider what determines the synchronic extent of a unit of evolution. A natural and attractive idea is that a species should include all and only those organisms with actual or potential reproductive links to one another. This condition would determine the set of organisms among whose descendants a genetic change in any member of the set might possibly be transmitted. To the extent that the biological world is characterized by impenetrable barriers to genetic exchange, then there will be distinct channels down which evolutionary changes can flow. The sets of organisms flowing down these channels, then, will be the units of evolution.

Here, of course, is the great appeal of the so-called *biological species concept* (BSC)—until recently the dominant conception of the nature of species. According to this view, a species is conceived as a group of organisms with actual or potential reproductive links to one another and reproductively isolated from all other organisms. Recalling for a moment my brief discussion of classification as mere ordering of information, one might also suppose that the sharp discontinuities that (sometimes) determine the optimal level for making base-level discriminations should correspond to lines of reproductive isolation. The flow of evolutionary change down reproductively isolated channels, after all, should be expected to lead to ever-growing morphological distinctness. Thus, the goals of representing the evolutionary process and of optimally ordering biological phenomena would turn out to coincide after all.

Unfortunately, however, the biological world proves much messier than this picture reveals. Certainly, there are cases in which species can be identified with discoverable lowest-level sharp discontinuities marked by reproductive barriers. But such cases are far from universal, and the appealing picture drawn thus far has a range of important complications to which I now turn.

Asexual Species

A familiar objection to the BSC is that it has nothing to say about asexual species. A fully asexual organism is reproductively isolated from everything

except its direct ancestors and descendants. The leading proponent of the BSC, Ernst Mayr, has concluded that there are, strictly speaking, no species of asexual organisms (Mayr 1987). But asexual species still require classification, and indeed some asexual species are more sharply distinguishable from related species than are some sexual species. Moreover, asexual organisms evolved just as surely as did sexual species. Thus, whichever view we take of the fundamental goal of assigning organisms to species, the exclusion of asexual organisms should lead us to see the BSC as at best one species concept among two or several concepts necessary for encompassing biological reality. A more radical attempt to save the BSC is suggested by David Hull (1989): in asexual organisms, the species are simply organism lineages—that is, an organism and its descendants (p. 107).¹ I take it that although Hull's proposal is attractive theoretically, it will divorce the identification of species in these cases from any practical utility in classification. It should also be noted that even this radical move may not work to give the biological species concept universal applicability. In bacteria, although reproduction is asexual, various mechanisms are known by which bacteria exchange genetic material. The pattern of relationships between bacteria is thus netlike, or reticulated, rather than treelike.² Although I suppose that one might hope to identify a new species as originating at each node in the net, such an identification would imply the existence of countless species, many lasting only a few minutes or even seconds. The impracticality of this idea suggests that we would be better abandoning the idea of applying the BSC, or indeed any evolutionarily based species concept, to bacteria. Many bacterial taxonomists (see Nanney, this volume) indeed seem to have this inclination.³

Gene Flow beyond Sharp Discontinuities

A second familiar difficulty with the biological species concept is that apparently well-distinguished species frequently do, in fact, exchange genetic material. The classic illustration is American oaks (see Van Valen 1976). Various species of oaks appear to have coexisted in the same areas for millions of years while exchanging significant amounts of genetic material through hybridization. Ghiselin (1987) is quite happy to conclude that these oaks form a large and highly diversified species. Two responses should be offered to this conclusion. First, and most obviously, the need to make such a move illustrates the divergence between this kind of theoretically driven taxonomy and the pragmatic goal of providing a maximally informative ordering of nature. This divergence may not much bother the theoretically inclined, but it does illustrate one of the ways in which we cannot both have our cake and eat it in the way indicated in the most optimistic explication of the BSC.⁴ Second, such examples throw serious doubt on the central motivation for the BSC, which is that genetic isolation is a necessary condition for a group of organisms to form a coherent unit of evolution. The example shows that different species of oaks have remained coherent and distinct

vehicles of evolutionary change and continuity for long periods of time. Ghiselin's conclusion looks like nothing more than an epicycle serving solely to protect the BSC from its empirical inadequacy.

The Absence of Sharp Discontinuities

In some groups of plants and of microorganisms, and very probably in other kinds of organisms, there is considerable variation, but no apparent sharp discontinuities. It is even tempting to suggest that within certain plant genera there are no species. A good example would be the genus *Rubus*, blackberries and their relatives. Because *Rubus* lacks sharp differentiation between types, but admits great variation within the genus as a whole, it seems unlikely that there could be any consensus on its subdivision into species.⁵ If we assume that this lack of sharp differentiations is due, in part, to gene flow, the option is again open to call *Rubus* a single and highly polymorphic species. Though less objectionable than in the case where there are sharply distinguished types, as with oaks, this move again separates theory-driven taxonomy from the business of imposing useful order on biological diversity.

Lack of Gene Flow within Sharply Differentiated Species

A somewhat less familiar point is that a considerable amount of research has shown that often there is surprisingly little genetic flow within well-differentiated species (Ehrlich and Raven 1969), most obviously in the case of species that consist of numbers of geographically isolated populations, but that nevertheless show little or no sign of evolutionary divergence. Even within geographically continuous populations, however, it appears that genetic interchange is often extremely local. This kind of situation puts great weight on the idea of *potential* genetic flow in defending the BSC. If populations are separated by a distance well beyond the physical powers of an organism to traverse, should their case nevertheless be considered one of potential reproduction, on the grounds that if, *per impossibile*, the organisms were to find one another, they would be interfertile? The alternative, paralleling Ghiselin's line on oaks, would be to insist that such apparent species consisted of numbers of sibling species, differentiated solely by their spatial separation. Again, one is led to wonder what the point of either maneuver would be. Clearly, to the extent that species retain their integrity despite the absence of genetic exchange, it must be concluded that something other than gene interchange explains the coherence of the species. Contenders for this role in cases like either of the kinds just considered include the influence of a common selective regime and phyletic or developmental inertia. I might finally note that although I do not know whether any systematic attempt has been made to estimate the extent of gene flow in the genus *Rubus*, in the

likely event that the flow is quite spatially limited, the claim that the whole complex group with its virtually worldwide distribution can be seen as reproductively connected is tenuous to say the least.

The conclusion I want to draw at this point is that the BSC will frequently lead us to distinguish species in ways quite far removed from traditional Linnaean classification and far removed from the optimal organization of taxonomic information. Moreover, the theoretical motivation for the BSC seems seriously deficient. The sorts of criticisms I have been enumerating above have led, however, to a decline in the extent to which the BSC is now accepted, and this decline has been accompanied by increasing interest in a rather different approach to evolutionarily centered taxonomy that can be broadly classified under the heading of the *phylogenetic species concept* (PSC). (The definite article preceding the term should not be taken too seriously here, as there are several versions of the general idea.)

The central idea of all versions of the PSC is that species—and, in fact, higher taxa as well—should be monophyletic. That is, all the members of a species or of a higher taxon should be descended from a common set of ancestors. An appropriate set of ancestors is one that constitutes a new branch of the phylogenetic tree. Such a group is known as a *stem species*. The important distinction between versions of PSC is whether a taxon is merely required to contain *only* descendants of a particular stem species or to contain *all* and only such descendants. The latter position is definitive of cladism, whereas the former, generally described as evolutionary taxonomy, requires some further criterion for deciding which are acceptable subsets of descendants.⁶ Two issues arise in explicating a more detailed account of the PSC. First, what constitutes the division of a lineage into two distinct lineages and hence qualifies a group as a stem species? Second, what constitutes a lineage and its descendants as a species (or, indeed, as any other taxonomic rank)?

The traditional answer to the first question is that a lineage has divided when two components of it are reproductively isolated from one another, but the difficulties raised in connection with the BSC suggest that this answer is inadequate. Examples such as oaks suggest that reproductive isolation is not necessary for the division of a lineage, and worries about the lack of gene flow within apparently well-defined species suggest that it is not sufficient either. An illuminating diagnosis of the difficulty here is provided by Templeton (1989), who distinguishes *genetic* exchangeability, the familiar ability to exchange genetic material between organisms, and *demographic* exchangeability, which exists between two organisms to the extent that they share the same fundamental niche (p. 170). The problem with asexual taxa and with a variety of taxa for which gene exchange is limited is that the boundaries defined by demographic exchangeability are broader than those defined by genetic exchangeability. Conversely, for cases in which well-defined species persist despite gene exchange, the boundaries defined

by genetic exchangeability are broader than those defined by demographic exchangeability (p. 178).

In the light of these considerations, Templeton proposes the *cohesion species concept* (CSC). It is not entirely clear how this concept should be interpreted. In the conclusion of his paper, he writes that species should be defined as “the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability” (p. 181). If we assume that the connective “and/or” should be interpreted as inclusive disjunction, this definition would suggest that the “syngameon” of oaks—that is, the set of distinct but hybridizing species—should be treated as a species. But it is clear from earlier discussion that such an application is not what Templeton intends. Earlier, he defines the CSC as “the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms” (p. 168). A central and convincing motivation for this definition is the claim that a range of such mechanisms promotes phenotypic cohesion, of which genetic exchange and genetic isolation are only two. Equally important are genetic drift (cohesion through common descent), natural selection, and various ecological, developmental, and historical constraints. The basic task, according to Templeton, is to “identify those mechanisms that help maintain a group as an evolutionary lineage” (p. 169).

What, then, is an evolutionary lineage? The significance of the conflicting criteria of genetic and demographic exchangeability is that they show it to be impossible to define that lineage in terms of any unitary theoretical criterion. Rather, lineages must first be identified as cohesive groups through which evolutionary changes flow, and only then can we ask what mechanisms promote this cohesion, and to what extent the identified groups exhibit genetic or demographic exchangeability. Presumably, this initial identification of lineages must be implemented by investigation of patterns of phenotypic innovation and descent over time. With the abandonment of any general account of speciation or any unitary account of the coherence of the species, it appears that species will be no more than whatever groups can be clearly distinguished from related or similar groups. This approach may seem theoretically unsatisfying, but to the extent that it reflects the fact that there are a variety of mechanisms of speciation and a variety of mechanisms whereby the coherence of the species is maintained, it would also seem to be the best concept we can hope for.

This conclusion makes pressing the second question distinguished above: How do we assign taxonomic rank, especially species rank, to a particular lineage or set of lineages? A *prima facie* advantage of the BSC is that it provides a clear solution to this problem: a species is the smallest group of individuals reproductively connected (or at least potentially connected) one to another and reproductively isolated from all other individuals. The difficulty is that this definition would leave one with species ranging from huge and diverse syngameons to clonal strains with a handful of individuals. Apart from the theoretical difficulties discussed above, any connection be-

tween the theoretical account of a species and a practically useful classification would surely be severed.

The question that must be faced, then, is whether from the PSC point of view the idea that the species is the basal taxonomic unit—where taxonomy is conceived as providing a practically useful classification—can be maintained. Abandoning the BSC will take care of species that look unsatisfactorily large by allowing a variety of cohesion mechanisms apart from reproductive isolation, but it will tend to imply the presence of disturbingly small species. Frequently there are clearly distinguishable groups of organisms—subspecies, varieties, geographical races—below the species level. There is no reason to suppose that these groups are not monophyletic and no reason to suppose that they are not, at least for the moment, evolving independently. There is no doubt that such groups are often clearly distinguishable, and indeed for many purposes classification at this level is the most important. Stebbins (1987, 198) notes, for instance, that foresters are often more concerned with geographic races than species and indeed can be hampered in their work by the confusing attachment of the same specific name to trees with quite distinct ecological properties and requirements. A judge at a dog show is not much concerned with the criteria that identify something as *Canis familiaris*. Such groups may go extinct, they may merge with other subgroups in the species, or they may be destined to evolve independently into full-blown species or higher taxa. Their evolutionary significance is thus unknown and unknowable. The same, of course, could be said of groups recognized as full species, though the second alternative (merging with other groups) may be rare.

THE CASE FOR PLURALISM

An evolutionarily based taxonomy appears to be faced at this point with only two possible options. The first is to consider species as by definition the smallest units of evolution. Leaving aside the insurmountable difficulty of detecting such units in many cases, my argument so far has been that this option will provide a fundamental classification that is often much too fine to be useful for many of the purposes for which taxonomies have traditionally been used.⁷ Mishler and Donoghue (1982) suggest that this proposal is also conceptually confused. They argue that “there are many evolutionary, genealogical units within a given lineage ... which may be temporally and spatially overlapping” (1982, 498). They suggest, therefore, that it is an error to suppose that there is any such thing as a unique basal evolutionary unit and that the particular evolutionary unit one needs to distinguish will depend on the kind of enquiry with which one is engaged. If there is no unique basal unit, then there is no privileged unit and, from an evolutionary point of view, no theoretical reason to pick out any particular group as the species. Mishler and Donoghue therefore propose the second option, to “[a]pply species names at about the same level as we have in the past, and decouple

the basal taxonomic unit from notions of 'basic' evolutionary units" (p. 497). This process involves seeing species on a par with genera and higher taxa—that is, as ultimately arbitrary levels of organization, chosen on a variety of pragmatic grounds.⁸

Although Mishler and Donoghue see the species as an ultimately arbitrary ranking criterion, they do maintain a version of the PSC and, hence, do not see it as arbitrary from the point of view of grouping. In fact, they endorse the strong, cladistic concept of monophyly as a condition on a group constituting a species (or, for that matter, a taxon at any other level). Their "pluralism," however, entails that "comparative biologists must not make inferences from a species name without consulting the systematic literature to see what patterns of variation the name purports to represent" (p. 500). But given this degree of pluralism, and the rejection of the attempt to equate the basal taxonomic unit with any purportedly fundamental evolutionary unit, one may reasonably wonder why it is desirable to insist nevertheless on the requirement of monophyly. I suspect that part of the motivation for this requirement is the idea that there must be *some* answer to the question what a species *really* is. It was once, no doubt, reasonable to suppose that evolution had produced real, discrete species at approximately the classificatory level of the familiar Linnaean species. Perhaps this supposition was an almost inevitable consequence of the transition from an essentialist, creationist view of nature to an evolutionary view. Acceptance of evolutionary theory would require that it more or less serve to explain biological phenomena as theretofore understood. Nevertheless, a further century of development of the evolutionary perspective has given us a radically different picture of biological diversity. The sharpness of differentiation between kinds and the processes by which such differentiation is produced and maintained have proved to be highly diverse. There is no reason to suppose that evolution has provided any objectively discoverable and uniquely privileged classification of the biological world.

Why, then, should we continue to insist that evolution should provide a necessary condition, namely monophyly, on any adequate biological taxon? I can think of only three possible answers. First, it might be held that a better understanding of evolution is so overwhelmingly the most important biological task that any taxonomy should be directed at improving this understanding. Second, it might be thought that an evolutionarily based taxonomy, despite its problems, would provide the best available taxonomy, or at least a perfectly adequate taxonomy, for any biological project even far removed from evolutionary concerns. Or third—and this, I suspect, is the most influential motivation—it may be held on general methodological grounds that a central concept such as the species must be provided with a unitary definition. This third motivation might be grounded either in a general commitment to unification as a scientific desideratum or on the fear that failure to provide a unified account of the species category will lead to massive confusion as biologists attempt to communicate with one another. I

argue, however, that none of these proposed justifications of the demand for monophyly stand up to much critical scrutiny.

The first answer can be quickly dismissed. Even as distinguished an evolutionist as Ernst Mayr (1961) has emphasized the distinction between *evolutionary* and *functional* biology, the former being concerned with questions about ultimate causation (how did a trait come to exist?), the latter with questions of proximate causation (how does the trait develop or function in particular individuals?). Following Kitcher (1984), I prefer to distinguish these types of questions as historical and structural. It is clear that questions about the ontogeny of the human eye, say, or about the processes by which it provides the individual with information about the environment, have little to do with questions about how humans came to have the kinds of eyes they have. Of course, just noting this fact doesn't show that we need a taxonomy based specifically on structural aspects of organisms, but it does remind us that there is more to biology than evolution. A particularly salient domain, about which I say a bit more below, is ecology.

We should turn, then, to the second, and more promising, line of thought. The fact that a great variety of kinds of investigation takes place within biology certainly does not show that one scheme of classification, based on phylogenetic methods, might not be adequate to all these purposes. To some degree, it should be acknowledged that this question is purely empirical: only the progress of biological enquiry can determine whether different overlapping schemes of classification may be needed. This point needs to be stated carefully. There is no doubt at all that interesting structural or physiological properties crosscut any possible phylogenetically based classification. An investigation into the mechanics of flight, for instance, will have relevance to and may appeal to a group of organisms that includes most (but not all) birds, bats, and a large and miscellaneous set of insects. In general, convergent evolution and the acquisition or loss of traits within any sizeable monophyletic group make it clear that no perfect coincidence between monophyletic groupings and the extension of physiologically interesting traits can be anticipated. Whether this calls for a distinct, nonphylogenetic system of classification is less clear. To pursue the example given, there is no particular reason why the student of flight should attach any particular significance to the miscellaneous group of organisms that fly.

Ecology, on the other hand, raises more difficult issues. Ecology, it may be said, is the microstructure of evolution. Nevertheless, it is not obvious that evolutionarily based taxa will be ideal or even well suited to ecological investigations. Certainly, there are categories—predator, parasite, or even flying predator—that are of central importance to ecological theory and that include phyletically very diverse organisms. There is no reason why phyletically diverse sets of organisms might not be homogeneous (for example as fully substitutable prey) from the perspective of an ecological model. On the other hand, such concepts may reasonably be treated as applying to a higher level of generality than the classification of particular organisms. At a more

applied level of ecology, however, some kind of taxonomic scheme must be applied to the particular organisms in a particular ecosystem. Ecology will often be concerned with the trajectory of a population without addressing competition between different subgroups within that population. It may, that is, abstract from distinctions within a population, perhaps corresponding to distinct lineages, which could be fundamental in understanding the longer-term evolutionary trajectory of the population. Groups of sibling species may prove ecologically equivalent (or demographically exchangeable) and thus provide another example of a kind of distinction that may be phylogenetically significant, but ecologically irrelevant. On the other hand it is possible that behavioral distinctions within a phyletic taxon, perpetuated by lineages of cultural descent, might provide essential distinctions from an ecological perspective. It is at least a theoretical possibility that a group of organisms might require radically diverse classification from phyletic and ecological perspectives. Perhaps a population of rats, consisting of several related species, divide into scavengers, insectivores, herbivores, and so on in ways that do not map neatly onto the division between evolutionary lineages. Ecology may therefore, in principle at least, require either coarser or finer classifications than evolution, and it may need to appeal to classifications that crosscut phyletic taxa.⁹

This distinction leads me to the third objection to pluralism, the meta-theoretical desirability of a monistic taxonomy. Here, it is relevant to distinguish two possible aspects of pluralism. One might be a taxonomic pluralist because one believes that different groups of organisms require different principles of classification, or one might be a pluralist because one thinks that the same group of organisms require classification in different ways for different purposes. Monistic objections to the first kind of pluralism seem to me to have no merit. Taking the extreme case of bacterial taxonomy, there seem to be very good reasons for doubting the possibility of a phylogenetic taxonomy. The various mechanisms of genetic transfer that occur between bacteria suggest that their phylogenetic tree should be highly reticulated, and standard concepts of monophyly have little application to such a situation. The significance of bacteria as pathogens, symbionts, or vital elements of ecosystems make the goals of classification quite clear in many cases regardless of these problems with tracing phylogenies. Of course, it is possible that new insights into bacterial evolution might nevertheless make a phylogenetic taxonomy feasible. But no vast theoretical problem would be created if bacterial taxonomy appealed to different principles from those appropriate, say, to ornithology.¹⁰ In this sense, the assumption that there is *any* unitary answer to "the species problem" is no more than an optimistic hope. The suggestion that the use of different taxonomic principles might lead to serious confusion is absurd. It is of course possible that an ornithologist might mistakenly suppose that a bacterial species name referred to a monophyletic group of organisms, just as it is possible that a nuclear physicist might sup-

pose that the moon was a planet. Not every possible misunderstanding can be forestalled.

The danger of confusion is a more plausible concern regarding the idea that the same organisms might be subject to different principles of classification for different biological purposes. In one sense, I am happy to agree that this type of confusion should be avoided. It would be undesirable for a particular species name, say *Mus musculus*, to be variously defined and to have varying extensions according to the taxonomic theory espoused by various authors. We should aim to agree as far as possible which organisms are house mice. In the concluding section of this paper, I explain how I think such species names should be understood. If, to recall my hypothetical example about rats, it proves useful to treat scavenging rats as a basic kind in some ecological model, it would be misguided to insist that scavenging rats constitute a species. Equally clearly, however, this concession to standardized terminology does not at all require that all species names be conceived as answering to the same criterion of what it is to be a species. The other consequence of insisting on an unambiguous interpretation of particular species names is that we cannot assume a priori that the canonical taxonomy incorporating standard species names will be suitable for all biological purposes. The question here is, again, an empirical one that depends ultimately on how orderly biological nature turns out to be. If it should prove to be disorderly in the relevant sense, then biology would prove to be a more complicated discipline than is sometimes assumed. But once again I cannot see that any unavoidable confusion need be introduced.

CONCLUSION: A CASE FOR TAXONOMIC CONSERVATISM

Many taxonomists and almost everyone who uses the results of taxonomic work have complained about the genuine confusion caused by changes in taxonomic nomenclature. Some of these changes seem entirely gratuitous—for example, changes in the names of taxa grounded in the unearthing of obscure prior namings and in appeals to sometimes esoteric rules of priority. Other changes are more theoretically based adjustments of the extent of particular taxa. Many such theoretically motivated changes have been alluded to in this paper. BSC-committed theorists will urge that discoveries of substantial gene-flow between otherwise apparently good species should lead us to apply one species name to what were formerly considered several species. Phylogenetic taxonomists will want to amend the extensions of any higher taxa that fail their favored tests for monophyly, and strict cladists will promote the breaking up of prior “species” into various smaller units when their favored criteria for lineage splitting demand it.¹¹ Less theoretically committed taxonomists may promote the splitting or lumping of higher taxa on the basis of general principles about the degree of diversity appropriate to a particular rank.

There is no doubt that the taxonomic system we now possess is a highly contingent product of various historical processes. Walters (1961) gives a fascinating account of how the size of angiosperm families and genera can very largely be explained in terms of earlier biological lore available to Linnaeus. Considering the data collected by Willis (1949) in support of the idea that the large families—families, that is, with large number of genera—were those of greater evolutionary age, Walters argues compellingly that the data much more persuasively support the hypothesis that larger families are those that have been recognized for longer. Very crudely, one might explain the point by arguing that the existence of a well-recognized type provides a focus to which subsequently discovered or distinguished types can be assimilated. Thus, plants of ancient symbolic significance, such as the rose and the lily, have provided the focus for some of the largest angiosperm families, Rosaceae and Liliaceae. Walters makes the suggestive observation that even Linnaeus, recognizing the similarities between the Rosaceous fruit trees, apple, pear, quince, and medlar (*Malus*, *Pyrus*, *Cydonia*,¹² and *Mespilus*), attempted to unite them into one genus, *Pyrus*. This attempt was unsuccessful, however, presumably because of the economic significance of these plants, and modern practice has reverted to that of the seventeenth century. Walters comments: "Can we doubt that, if these Rosaceous fruit trees had been unknown in Europe until the time of Linnaeus, we would happily have accommodated them in a single genus?" A general feature of Walters's argument is that our taxonomic system is massively Eurocentric. The shape of taxonomy has been substantially determined by which groups of plants were common or economically important in Europe.

The crucial question, of course, is whether this bias is a matter for concern and a reason for expecting wholesale revision of our taxonomic practices. To answer this question, we must have a view as to what taxonomy is for, and we come back to the major division introduced at the beginning of this essay: should we see taxonomy as answering to some uniform theoretical project or more simply as providing a general reference scheme to enable biologists to organize and communicate the wealth of biological information? The central argument of this paper is that the more we have learned about the complexity of biological diversity, the clearer it has become that any one theoretically motivated criterion for taxonomic distinctness will lead to taxonomic decisions very far removed from the desiderata for a general reference scheme. Of course, the contingencies of taxonomic history will no doubt have led, in many instances, to a scheme that is less than optimal even as a mere device for organizing biological information. On the other hand, in the absence of a theoretical imperative for revision, it is essential to weigh the benefits of a more logical organization of diversity against the costs of changing the extensions of familiar terms. My intuition is that on this criterion taxonomic revisions will seldom be justified.

We might begin by recalling part of Huxley's account of the function of classification (in the epigraph to this essay): to facilitate the operations of the

mind in clearly conceiving and retaining in the memory the characters of the objects in question. Plainly to the extent that taxonomic names are undergoing constant modification, what any one person "conceives and retains in the memory" will be potentially incommunicable to others, and the possibility of reliably adding further information obtained from the work of others will be constantly jeopardized. This is not to say that taxonomic revision is never justified. If a species is included in a genus in which it is highly anomalous, and if that species is much more similar to other species in some other genus, then the goals of organizing information will be better served by reassigning it. It is of course also true that monophyletic taxa will tend to be more homogeneous than polyphyletic taxa, and that in paraphyletic taxa—taxa in which some of the descendants of the common ancestors of a particular taxon are excluded—there will be often be a case, on grounds of similarity, for including the excluded parts of the lineage. My point is just that these consequences rather than monophyly itself should provide the motivation for taxonomic change, and the benefits of such change must be weighed carefully against the potential costs. In this weighing process, the presumption that taxon names retain constant extension should probably be kept as strong as possible to maximize the ability of biologists to maintain reliable and communicable information.

To take perhaps the most familiar example, it seems to me that there is no case at all for revising the class Reptilia (reptiles) to include Aves (birds). This move is required by a strict cladistic concept of monophyly because it is believed that birds are descended from ancestral reptiles. We cannot exclude these avian ancestors from the class that includes modern reptiles because crocodiles, still classed as reptiles, are believed to have diverged from the main reptilian lineage earlier than birds did. The fact remains, however, that most zoologists, I suppose, would consider crocodiles much more like other reptiles than either is like any bird. The attempt to convince the learned or the vulgar world that birds are a kind of reptile strikes me as worse than pointless. It may be said that the only important claim is that Aves should be classified as a lower-level taxon included within Reptilia, and that this classification has nothing to do with our common usage of the terms *reptile* and *bird*. Although it is certainly the case that scientific taxonomic terms frequently differ considerably from apparently related vernacular terms, this differentiation is a source of potential confusion that should not be willfully exacerbated (see Dupré 1993, ch. 1, and forthcoming). It is also unclear what advantage is to be gained from insisting on such a revision. All evolutionists, I suppose, are likely to be familiar with recent thinking on the historical relationships within the main groups of vertebrates, and if they are not, their ignorance is not likely to be relieved by terminological legislation. Similarly, experts on smaller groups of organisms will presumably be familiar with current thinking on phylogenetic relationships within those groups. To celebrate every passing consensus on these matters with a change in taxonomic nomenclature is an inexcusable imposition of a particular professional

perspective on the long-suffering consumers of taxonomy outside these phylogenetic debates.

In conclusion, I am inclined to dissociate myself from the strongest reading of the taxonomic pluralism I advocated earlier (1993; see also Kitcher 1984). In view of the limited success of theoretical articulations of the species category, it would seem to me best to return to a definition of the species as the basal unit in the taxonomic hierarchy, where the taxonomic hierarchy is considered as no more than the currently best (and minimally revised) general purpose reference system for the cataloguing of biological diversity. This system should provide a *lingua franca* within which evolutionists, economists, morphologists, gardeners, wildflower enthusiasts, foresters, and so on can reliably communicate with one another. Where special studies, such as phylogeny, require different sets of categories, it would be best to avoid using the term *species* (the desirability of rejecting this concept is sometimes asserted by evolutionists). Of course, such specialized users will be free to advocate changes in taxonomic usage, but should do so only in extreme circumstances. Although I am inclined to doubt the desirability of a pluralism of overlapping taxonomies, a general taxonomy will evidently draw broadly and pluralistically on a variety of considerations. Perhaps the most important will be history, not an unattractive idea in a science in which evolutionary thought is so prominent: a goal of general taxonomy should be to preserve the biological knowledge accumulated in libraries and human brains as far as possible. In addition, there would be a range of the morphological, phylogenetic, and ecological considerations that have figured in various monistic attempts to define the species. The importance of these considerations may vary greatly from one class of organisms to another. My feeble monism is my recognition of the importance of such a general reference system. My recognition of the likelihood that different enquiries may need to provide their own specialized classifications and my tolerance of diverse inputs into the taxonomic process will leave serious monists in no doubt as to which side I am on.

The position I am advocating provides, incidentally, a quick and possibly amicable resolution to the species as individuals debate. Species, I propose, are units of classification and therefore certainly not individuals. Lineages, on the other hand, are very plausibly best seen as individuals. Often, it may be the case that the members of a species (or higher taxon) are identical to the constituents of a lineage, but of course this coincidence does not make the species a lineage. And it is doubtful whether all species, or certainly all higher taxa, are so commensurable with lineages.

Resistance to or even outrage at the kind of position I am advocating may derive from the feeling that I am flying in the face of Darwin. Darwin, after all, wrote a well-known book about the origin of species, and he was writing about a real biological process, not a naming convention. Of course, the problem is that Linnaeus (or for that matter Aristotle) also talked about

species and had in mind kinds, not things. Arguably, the tension between these two usages is at the root of the great philosophical perplexity that the concept of species has generated in this century. In arguing for reversion to the earlier usage of the term *species*, I am at least honoring conventions of priority. What I am proposing, however, is not much like a Linnaean taxonomy either. As many have observed, Darwin forced us to give up any traditionally essentialist interpretation of taxonomic categories and even any objectively determinate taxonomy. But almost a century and a half of biological work in the Darwinian paradigm have also shown us that evolution does not reliably produce units of biological organization well-suited to serve the classificatory purposes for which the concept of species was originally introduced, so perhaps rather than a reversion to Linnaeus, it would be better to see my proposal as a quasi-Hegelian synthesis. At any rate, if I seem to have been implying that Darwin may have been responsible for introducing some confusion into biology, I am sure no one will take this as more than a peccadillo in relation to his unquestionably positive contributions.

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NOTES

1. It is not entirely clear how to make this idea precise. Obviously, not every organism founds a lineage, unless every organism is to constitute a species. A natural idea is that every organism in any way genetically distinct from its parent should found a new lineage. Given, however, the possibility of the same point mutation occurring more than once, it could turn out that a set of genetically identical organisms might constitute two or more distinct species.

The proposal also leads to the surprising conclusion that the vast majority of species are asexual. As Hull notes, this conclusion may mitigate the well-known difficulty in explaining the origin of sex by showing that sexual reproduction is a much rarer phenomenon than is often supposed (1989, 109). I should also mention that Hull's proposal is made in connection with the thesis that species are individuals, and is thus not necessarily an explicit defense of the BSC.

2. It appears that the same is probably true for some kinds of flowering plants (see Niklas 1997, 74 ff.).

3. This claim is perhaps less true now than it was twenty years ago. An influential evolutionary classification of bacteria was proposed by Woese (1987); see also Pace (1997). On the other hand, Gyllenberg and others (1997) aim explicitly to produce a classification that is optimal from an information-theoretic perspective, a goal that there is no reason to suppose would be met by any imaginable phylogenetic scheme. See also Vandamme and others (1996) for a related proposal. It is clear, at any rate, that any possible phylogenetic classification of bacteria, if it is to be of any practical use, must define taxa with great clonal diversity. Gordon (1997), for instance, reports that the genotypic diversity of *Escherichia coli* populations in feral mice was an increasing function of the age of the mouse, indicating the development of distinct clones during the lifetime of the mouse. I assume one would not want to think of this development as speciation, but

given this clonal diversity, it is difficult to see how any useful taxonomy could avoid being arbitrary from a phylogenetic perspective. The situation is still worse in view of the partially reticulate phylogeny consequent on genetic exchange between bacteria.

4. An extreme statement of this optimistic view can be found in Ruse (1987, 237): "There are different ways of breaking organisms into groups and they coincide! The genetic species is the morphological species is the reproductively isolated species is the group with common ancestors."

5. On *R. fruticosus*, the common blackberry, Bentham and Hooker (1926, 139) wrote: "It varies considerably. The consequence has been an excessive multiplication of supposed species ... although scarcely any two writers will be found to agree on the characters and limits to be assigned to them." The same "species" is described by Schauer (1982, 346) as "aggregate, variable with very numerous microspecies". More optimistically, *The Oxford Book of Wildflowers* (Nicholson, Ary, and Gregory 1960) states that "[t]here are several hundred species and hybrids in the *Rubus* group, and only an expert can identify all of them".

6. See Sober (1992) for a very clear exposition of this distinction. Although the debate here is a fundamental one, it is not of central concern to my essay.

7. See Davis (1978, 334–338) for a discussion of some of the difficulties in subspecific classification of angiosperms.

8. For further elaboration, see Mishler and Brandon (1987). For more general arguments against any fundamental distinction between species and higher taxa, see Ereshefsky (1991 and chapter 11 in this volume) and Mishler (chapter 12 in this volume).

9. Some more realistic examples have been discussed by Kitcher (1984).

10. For references to bacterial taxonomy and brief discussion, see note 3.

11. De Queiroz and Gauthier (1990, 1994) claim that taxonomic changes they advocate will promote constancy of meaning, or definition, for taxa. Mammalia, for example, should be defined as the set of descendants of the most recent common ancestor (i.e., ancestral species) of monotremes and therians. The extension of such a term, however, will be constantly revisable in the light of changes in opinion about the details of evolutionary history. From the point of view of the consumer of taxonomy, at least, I suggest that constancy of extension is surely more valuable than constancy of definition.

12. Subsequent to Walters' paper, the quince appears to have been reconceived as *Chaenomeles* (though not unanimously according to the few sources I consulted on this matter). This reconception effects a conjunction with the ornamental flowering quinces. One might speculate that the increasing obscurity of the quince as a fruit might have exposed it to this annexation, which one doubts could have happened to the apple.

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