Species as family resemblance concepts: the (dis-)solution of the species problem?

Massimo Pigliucci

Summary

The so-called ''species problem'' has plagued evolutionary biology since before Darwin's publication of the aptly titled *Origin of Species*. Many biologists think the problem is just a matter of semantics; others complain that it will not be solved until we have more empirical data. Yet, we don't seem to be able to escape discussing it and teaching seminars about it. In this paper, I briefly examine the main themes of the biological and philosophical literatures on the species problem, focusing on identifying common threads as well as relevant differences. I then argue two fundamental points. First, the species problem is not primarily an empirical one, but it is rather fraught with philosophical questions that require—but cannot be settled by—empirical evidence. Second, the (dis-)solution lies in explicitly adopting Wittgenstein's idea of ''family resemblance'' or cluster concepts, and to consider species as an example of such concepts. This solution has several attractive features, including bringing together apparently diverging themes of discussion among biologists and philosophers. The current proposal is conceptually independent (though not incompatible) with the pluralist approach to the species problem advocated by Mishler, Donoghue, Kitcher and Dupré, which implies that distinct aspects of the species question need to be emphasized depending on the goals of the researcher. From the biological literature, the concept of species that most closely matches the philosophical discussion presented here is Templeton's cohesion idea. *BioEssays* 25:596–602, 2003. © 2003 Wiley Periodicals, Inc.

The problem that never goes away

The so-called ''species problem'' is one of those topics of discussion among evolutionary biologists that has been present since before Darwin's publication of the aptly titled *Origin of Species* (Darwin himself referred to it as an already old problem), and will probably never go away. Furthermore, biologists have a schizophrenic attitude toward the whole issue: on the one hand, they tend to turn away in disgust when species concepts are brought up by colleagues, are the subject of papers, or are discussed at conferences. On the other hand, they simply cannot resist the temptation to offer graduate seminars on the topic and avidly reading anything that is published on the subject. Just in the last two years, two of the major journals of evolutionary biology have devoted several papers in special issues to the ever-burning question of exactly what species are (*Journal of Evolutionary Biology*, volume 14, 2001, pp. 889 ff.; and *Trends in Ecology and Evolution* volume 16, 2002, pp. 326 ff.).

In this paper, I will argue two points: First, the reason why the species problem has not gone away is because it is not as much an empirical problem (contrary to what has been argued, for example, by Hey, Ref. 1), but rather one that has strong philosophical overtones. Indeed, the philosophical literature on the definition of species is as extensive as the biological one, with some biologists contributing to both.[2–6] This does not mean that empirical information is not relevant here, but rather that the problem represents a paradigmatic example of a philosophical question that requires empirical information (provided by science) to be settled, not of a scientific problem with unwelcome philosophical characteristics.

Second, the problem does in fact have a satisfying philosophical solution based on Wittgenstein's idea of ''family resemblance'' or cluster concepts,[7] as was proposed early on by Hull[8] in a different context (he was interested in the taxonomists' apparent historical inability of letting go of essentialist concepts of species). I wish to cast this solution in modern terms to my biology colleagues (as well as represent it to many philosophers), while naively and optimistically suggesting that there is no reason why this should not be the end of the controversy.

The controversy: the biological side

It is not my intention here to provide the reader with a history or comprehensive review of either the biological or philosophical literature on the species question. That would be a fascinating endeavor, but it would require a book-length treatise, something I hope a philosopher and a biologist will eventually get together to write. However, in order to substantiate my two points, it is helpful to have an idea of what has occurred so far in the debate.

Departments of Botany, Ecology & Evolutionary Biology, and Philosophy, University of Tennessee, Knoxville, TN 37996-1100.
E-mail: pigliucci@utk.edu; URL www.genotype-environment.org
Funding agency: NSF (Grant DEB-0089493).
DOI 10.1002/bies.10284
Published online in Wiley InterScience (www.interscience.wiley.com).

From the perspective of the biological literature, besides the two recent special issues of major journals mentioned above, there have been several books[9–12] and of course countless articles. A brief history of the species concept can be found in Grant,[13] a recent empirical example of how easily different concepts of species don't mesh even for the same group of organisms is provided by Gleason et al.,[14] and Mayden[15] provides a (incomplete) list of a whopping 21 species concepts!

Before investing any more time on this matter, one could reasonably wonder why bother. Part of the answer is obvious to any biologist: species are considered a fundamental level of organization of the biological world (though this also is hotly disputed), and as such they are pivotal to several fields of investigation as well as to practical applications of evolutionary biology. To mention a few, researchers interested in the study of the process of speciation (obviously), evolutionary geneticists, evolutionary ecologists, systematists, and conservation biologists all deal directly with questions for which—it would seem—understanding what constitutes a species is of paramount importance in order to make progress.

Or is it? One can actually argue that progress in all of the above areas (including, paradoxically, our understanding of the process of speciation) has actually been achieved *despite* all the discussion on what species are (or, more charitably, independently of it). To paraphrase a famous American judge, many biologists seem to agree that—like the case of pornography—it is impossible to define species, but it is certainly feasible to recognize them when you see them (notwithstanding some taxonomic wrangling). Indeed, some[16] even go so far as to suggest that it is because of entanglement with such "semantic" (a pejorative term in biology) issues that evolutionary biology has not achieved the recognition as a science that, say, physics has (I actually think that particular problem is caused by much more fundamental factors, and in some respects is not a problem at al, Ref. 17).

Be that as it may, it is instructive to go over the list of species concepts that have emerged so far, in search of common themes. Here, I will assume that the reader is familiar with at least the major species concepts proposed by biologists and some of their pitfalls. Commonalities among species concepts are actually not difficult to find: Table 1 lists what one might consider the "top 9" species concepts (in alphabetical order, I am not taking sides here), together with brief definitions conveying the focus that they put on specific biological aspects

Table 1. Some of the major species concepts proposed so far (the list is incomplete and arranged in simple alphabetical order), short definitions, and some relevant references

Species concept	Brief definition	References
Biological (including recognition concept)	Groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups.	Mayr 1940
Cohesion	The most inclusive population of individuals having the potential for genetic and/or demographic exchangeability.	Templeton 1989
Ecological	A lineage which occupies an adaptive zone minimally different from that of any other lineage in its range, and which evolves separately from all lineages outside its range.	Van Valen 1976
Evolutionary	A lineage evolving separately from others and with its own unitary evolutionary role and tendencies.	Simpson 1961
Genetic	Group of organisms so constituted that a hereditary character of any of these organisms may be transmitted to a descendant of any other.	Simpson 1943
Morphological	The smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means.	Cronquist 1978 (though proposed as early as the 1920s)
Phenetic	The level at which distinct phenetic clusters can be observed.	Sneath 1976
Phylogenetic (several variants)	The common feature of these concepts is the attempt to identify the smallest biological entities that are diagnosable and/or monophyletic.	E.g., Nixon and Wheeler 1990; McKitrick and Zink 1988
Population-level lineages	Lineages identified at the level of evolving populations, before they become clades.	de Queiroz 1998, 1999

Cronquist A. Once again, what is a species? In: Ramberger JA, editor. Biosystematics in Agriculture. Monclair, NJ: Allanheld and Osmun. 1978. 3–20.
de Queiroz K. The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. In: Howard DJ, Berlocher SH, editors. Endless Forms: Species and Speciation. Oxford, England: Oxford University Press. 1998. 57–75.
de Queiroz K. The general lineage concept of species and the defining properties of the species category. In: Wilson RA, editor. Species: New Interdisciplinary Essays. Cambridge, MA: MIT Press. 1999. 49–89.
Mayr E. Speciation phenomena in birds. American Naturalist 1940;74:249–278.
McKitrick MC, Zink RM. Species concepts in ornithology. Condor 1988;90:1–14.
Nixon KC, Wheeler QD. An amplification of the phylogenetic species concept. Cladistics 1990;6:211–223.
Simpson GG. Criteria for genera, species, and subspecies in zoology and paleontology. Annals of the New York Academy of Sciences 1943;44:145–178.
Simpson GG. Principles of Animal Taxonomy. New York, NY: Columbia University Press. 1961.
Sneath PHA. Phenetic taxonomy at the species level and above. Taxon 1976;25:437–450.
Templeton AR. The meaning of species and speciation: a genetic perspective. In: Otte D, Endler JA, editors. Speciation and its consequences. 1989. 3–27.
Van Valen L. Ecological species, multispecies, and oaks. Taxon 1976;25:233–239.

that are considered essential to each concept. We can see that there are broadly speaking only three factors entering into the equation: phylogenetic relationships, genetic continuity (sometimes specifically concerned with reproductive traits, sometimes more broadly defined) or similarity, and ecological similarities, broadly construed. Furthermore, one could argue that even these three themes are obviously not independent, since genetics, phylogeny and ecology are tightly intertwined when it comes to determining the fate of any population of organisms. There are, it seems, more commonalities among the various species concepts than one might at first suspect.

Indeed, one author, de Queiroz,[6,18] claims to have solved the species problem by pointing out that no matter what specific characteristics one uses to study species in particular instances, all definitions share the fact that species are population-level lineages. I cannot here provide a detailed assessment of this proposal, but a few points deserve attention. First, while it is often confused with variants of the phylogenetic concept, it is distinct enough from it because the author makes a distinction between lineages and clades, where the first may become an instance of the latter, but not necessarily. Second, this proposal still looks for an *essence* defining species, an approach that I consider at the core of the species problem (see below), and that needs to be abandoned. Third, the ''essence'' proposed as common to species (i.e., being population-level lineages) is too broad to be useful for at least two reasons: on the one hand, it is not clear what sets aside species from population-level lineages that do not diverge enough to become species (if the criterion invoked is cladogenesis, then we fall back into the phylogenetic concept); on the other hand, many other characteristics are also necessary (but not sufficient) to talk about something being a species: for example, being comprised of living organisms, being subjected to a variety of evolutionary forces, and so on. The problem when one wishes to identify the *essence* of a concept is not to pick some necessary condition (there are often many available), but to identify a set of conditions that are necessary and sufficient. Being a population-level lineage is not sufficient for being a species.

The controversy: the philosophical side

As in the case of the biological literature, the philosophical outpour on the species problem is vast and complex, and I cannot possibly attempt here to do it justice. However, it is interesting to note the main threads, particularly as they partly overlap with the concerns of biologists (some of whom, as noticed above, have in fact participated actively to this side of the debate as well) while maintaining a characteristically philosophical flavor (biologists often do wonder what exactly philosophers write about biology anyway).

Like its biological counterpart, the philosophical discussion can best be understood as focusing on a small number of basic themes, which are summarized in Table 2 (which, again, is certainly not to be taken as an exhaustive list). First, in an overlap with the biological literature, there are discussions of species concepts proposed by biologists, mostly focusing on the biological species concept and, to a lesser extent, on the many flavors of the phylogenetic species concept. These are the discussions that, understandably, have seen the major contributions by biologists to the philosophical literature[2–5] Ruse[19] suggested early on that biologists prefer one well-defined species concept (and are therefore very unlikely to go for any of the pluralistic proposals briefly outlined below) because they are looking for *the* answer to the problem and because they want this answer to be embedded within general laws and be derived logically from first principles of biology. Giray[20] produced one of the early criticisms of morphological species concepts and proposed a synthesis of different variants of the biological species concept that had been put forth by biologists up to that point. Mishler and Brandon[21] compared the biological and phylogenetic concepts in terms of the idea that species are individuals (which is fundamental to theories such as species selection, Refs. 22,23). Horvath[24] examined the consequences of the phylogenetic species concept, while Sterelny[25] is unusual (for a philosopher) in defending the evolutionary species concept as opposed to the two dominant ones (biological and phylogenetic).

On the matter of what sort of ''things'' species are, Kitcher,[26] contrary to Mishler and Brandon, proposed that species are

Table 2. Some of the major themes dominating philosophical discussions of the species problem. The list is certainly not comprehensive, and the references mentioned are but a small portion of those available in the literature. However, the table should provide biologists with a feeling for the threads underlying the debate among philosophers, as well as an entry in the relevant literature

Theme	Representative references
Discussions of species concepts proposed by biologists, mostly the biological and phylogenetic one.	Ruse 1969; Giray 1976; Mishler & Brandon 1987; Splitter 1988; Sterelny 1994; Horvath 1997.
What kinds of ''things'' are species? Are they individuals or sets? Are they natural kinds?	Giray 1976; Kitcher 1984; Splitter 1988; de Queiroz 1999.
Pluralism: do we need more than one concept because of inherent heterogeneity of purposes within the biological sciences?	Mishler and Donoghue 1982; Kitcher 1984; Dupré 1993.

not individuals, but rather sets, from which idea one can derive the limitations of the biological species concept. Splitter[27] suggests that species are not natural kinds, an idea that—with an interesting twist that includes arguments concerning human brain's physiology—has been revisited by biologist Hey in a recent book.[10]

We then come to pluralism, the suggestion—put forth in different fashions by Mishler and Donoghue,[28] Kitcher,[26] and Dupré[29]—that the reason there are many species concepts is because biologists are legitimately interested in a heterogeneous group of questions, each of which requires logically independent, and equally valid, concepts of species. The idea is that there are at least two such components to biological endeavors, which Kitcher terms the historical/evolutionary and the structural/functional inquiries. These two (epistemologically equivalent) views of biological evolution translate for Dupré into a genealogical and an ecological conception of species, neither one of which has logical priority. In other words, if one wishes to emphasize historical relationships, one must adopt a phylogenetic concept of species and speciation; but one could also equally validly be interested in the ecology and function of organisms, in which case something along the lines of the biological or ecological species concepts would serve the purpose better.

Why the problem has not gone away

I come now to the first of the two points that I wish to articulate in this article: the species problem has not gone away for the all-important reason that it is not the sort of empirical problem that can be solved by biologists alone. This, however, is not to say that it cannot be solved or, worse, that there is no real problem (i.e., it's "just" a matter of semantics, Ref. 16). On the contrary, it is a prime example of a philosophical question that requires input from empirical science and that can provide a useful return to the practice of that science. I will defend this claim in two steps: first by briefly discussing the relationship between philosophy of science and science and why some scientists have a misguided conception of it, and, second, by detailing my case in the specific instance of the species problem.

The relationship between philosophy and science is a complex one, and entire books have been written on its turbulent nature on both sides of the cultural divide.[30,31] Perhaps one of the best examples of the misgivings that scientists often have concerning philosophy can be found in an essay written by Nobel prize physicist Steven Weinberg, aptly entitled "Against philosophy".[32] In it, Weinberg accuses philosophers of not having contributed to the advancement of science in a single instance and, in fact, of having positively retarded it in at least one case (the negative influence that logical positivism and its abhorrence of unobservable quantities allegedly had on the acceptance of quantum mechanical theory). This is not the place to mount a comprehensive criticism of Weinberg's position, but it is instructive to ask a simple question: given that the principal aim of philosophy of science is to understand how science works, not necessarily to solve scientific puzzles, why *would* we expect philosophy to have contributed significantly to answering specific scientific questions? Another way to put it would be to ask, equally legitimately one would think, the question the other way around: how many cases can we think of in which science has actually solved a problem being debated in philosophy of science? It is interesting to ponder why the latter question sounds immediately specious, while its reverse seems quite plausible.

Let us now come to the specific problem posed by the debate on species concepts. Hey[1] has suggested that the main reason that the problem is still unsettled is because "we [biologists] are not acting like scientists. We are acting like some philosophers." Besides betraying the same sort of questionable attitude toward non-scientific disciplines that characterizes Weinberg, Hey is saying that the knot of the problem lies in the fact that we simply don't have enough information to make up our mind on what species really are. Yet, he himself is incredulous at this suggestion, since in the same article he asks: "How could our knowledge, upon which the species debates have been built, be missing something?" How indeed: after all, we have been studying species and speciation for many decades now. Hey's answer (further elaborated upon in his book, Ref. 10) is in fact interesting, and it's probably part of the more comprehensive picture that we should draw as far as the species concept wars are concerned. According to Hey, the problem is that we evolved as pattern-recognition animals, but that this ability is far too crude to match the sophistication of nature when it comes down to the make-up of species. The result is that the species that we perceive as natural categories (a philosophical term) have in fact little correspondence with the real thing (he is making another philosophically contested assumption, as we have seen: that species are indeed natural entities of some sort). I think Hey has a good point here, but he perhaps pushes it a bit too much as the principal explanation of why we have a species problem. At any rate, the presence or lack thereof of correspondence between natural categories as they are and as they are perceived by the human brain is an empirical question that awaits further study.

What I maintain, however, is that more empirical data will not be sufficient to solve the species question simply because this is by its nature a problem with strong philosophical overtones, not just a scientific one. Scientists have been able to function in practice very well without apparently agreeing on what a species is, even when it comes to empirical studies of species and speciation. I think this independence of scientific progress in an area from the solution of a "semantic" problem related to that same area is a hallmark of questions that are more philosophical than scientific in nature. Analogously, research on the neurobiology of consciousness is proceeding at a fast pace[33] despite strong disagreements about what

consciousness really is.[34] This line of reasoning, of course, opens up again the question of why should biologists care about philosophical questions (which I think they should, in a limited manner—see below), but right now my concern is with showing that as biologists we have simply being barking up the wrong tree in considering the species problem.

The (dis-)solution of the problem: species as family resemblance concepts

My second point is, as I mentioned at the beginning, that species are actually best seen as what Ludwig Wittgenstein[7,35] saw as "family resemblance" concepts, as was already realized among others by Hull (who, incidentally, is *both* a biologist and a philosopher) in a different context back in the mid 1960s.[8] The idea was endorsed by numerical taxonomists,[36] but has been rarely cited since the demise of that particular intellectual movement.

Let us briefly look at Wittgenstein's concept (Fig. 1) and how it applies to the species problem (Fig. 2). Wittgenstein was interested in the nature of human language and proposed the idea that humans engage in what he referred to as "language games," an iterative social negotiation of the meaning of terms made possible by the continuous interaction among individual human beings. At one point in his *Philosophical Investigations* he finally gets around to addressing the obvious question of what he means by "language games." (He had used the idea up to that point to great effect, just as biologists use "species" in practice, without need for a formal definition.) As a way to answer this, Wittgenstein considers an example: what do we mean by a complex concept such as "game"? He immediately notices that, hard as one might try to, it is simply not possible to come up with a single, all-encompassing definition of what a game is. This is because things as disparate as board games, card games, ball games and sports, to name a few instances of activities to which we attach the label of "game,"do not share one essential quality. Rather, Wittgenstein suggests, there are many threads that crisscross the multidimensional linguistic landscape occupied by the concept of game. Some of these threads connect several types or instances of games, others connect additional instantiations of the word, and yet other threads run through some (but not all) examples of different classes of games. Game, in other words, is defined by a *cluster* of characteristics, or what Wittgenstein refers to as "family resemblance" (in analogy to the very biological fact that members of a human family share some characteristics or others, but that no single trait identifies, say, the Wittgenstein family as distinct from all others).

Interestingly, Wittgenstein directly addresses the practical problem posed by cluster concepts, a problem similar to the question of how we can possibly use the concept of species if we don't agree on what species are: "How should we explain to someone what a game is? I imagine that we should describe games to him, and we might add: 'This and similar things are called games.' And do we know any more about it ourselves? Is it only other people whom we cannot tell exactly what a game is?" (69). Indeed, as biologists we *teach* our students what species are by example, exposing them to courses in systematic and natural history where they can see firsthand what the professionals consider the same or distinct species.

Furthermore, Wittgenstein goes on to explain why the above situation does not constitute a problem at all, since we can use the concept of game (or species) in practice very effectively: "But this is not ignorance. We do not know the boundaries because none have been drawn. . . . We can draw a boundary for a special purpose. Does it take that to make the concept usable? Not at all! " (§69). For our purposes as biologists, we can draw on one set of threads or another to work with particular species, depending on what taxonomic group we are considering. For example, in separating clonal or parthenogenetic taxa, the biological species concept's reliance on reproductive isolation is pretty much useless, while the same criterion is particularly appropriate for obligate

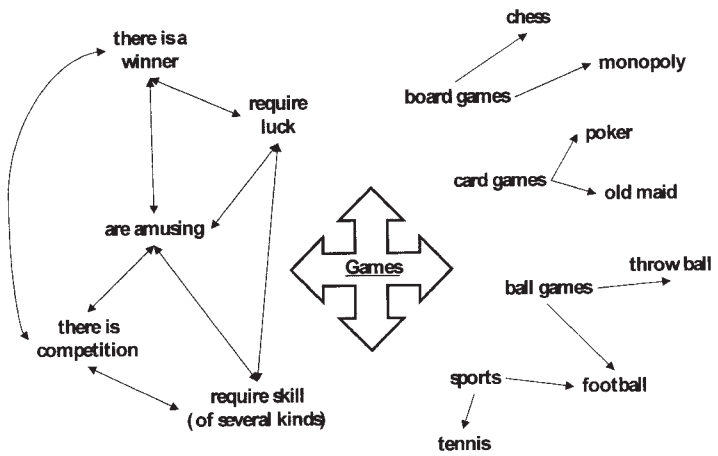

Figure 1. The idea of "game" as a family resemblance, or cluster, concept. On the left, some of the many characteristics we associate with games (the arrows signify that some of these characteristics are linked in the definition of particular games; not all possible relationships are visualized). On the right, types of games and some representative examples.

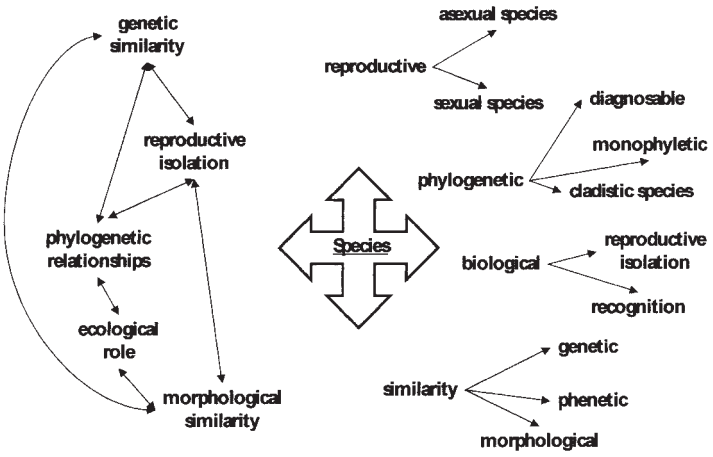

Figure 2. The idea of "species" as a family resemblance, or cluster, concept. On the left, some of the many characteristics we associate with species. The arrows represent the idea that more than one of these traits may enter into the appropriate characterization of any particular group of species (not all possible relationships are explicitly drawn). On the right, categories of species concepts based on different kinds of properties defining them.

outcrossers. In both cases there will be a phylogenetic component, but it will be easier to determine in the second than the first instance, and so on.

What, then, are species, and why do we care?

My suggestion here then is that species is a family resemblance concept whose underpinning is to be found in a series of characteristics such as phylogenetic relationships, genetic similarity, reproductive compatibility and ecological characteristics. These traits take on more or less relevance depending on the specific group one is interested as a function of the particular biology of that group.

Adopting Wittgenstein's approach solves several problems at once, both on the biological and philosophical side of the species problem. To wit:

- We can now move from our historical obsession with Platonic "essentialist" views of species to a cluster concept view that is more nuanced and realistic. This is a philosophical shift, although it is informed by the wealth of empirical information that we have on species: our understanding of cluster concepts depends on our experience of them.
- Wittgenstein's family resemblance idea, when applied to species, is actually compatible with Hey's[10] suggestion, discussed above, that part of the problem may be in a mismatch between the categories recognized by the human brain (and hence language, Wittgenstein's main focus of interest) and whatever natural categories are really "out there."
- Wittgenstein's suggestion (and Simon's elaboration of it, Ref. 35) that we may draw boundaries on subsets of family resemblance concepts for practical purposes at once erases the need for endless squabbles among biologists on what *the* best species concept is. The concept is fluid (but not arbitrary!) and gains enough flexibility to be applicable to the variety of real biological cases, which should be a welcome feature for whoever is accustomed to appreciate the extent of variation in the biological world. While scientists tend to be uncomfortable with fuzzy concepts, this is simply a philosophical prejudice: just because we cannot draw a precise line somewhere, it doesn't mean that there are no distinctions and that everything can be accommodated. Cluster concepts are not at all about abandoning the search for definitions, but they do force our mind to be less rigid about it.

It is important to note that what I am suggesting here is conceptually very different from the idea of pluralism of species concepts advocated by Mishler, Donoghue, Kitcher, and Dupré (toward which I am also sympathetic, I think without falling into a contradiction with my present proposal). The pluralist suggestion is that there are equally legitimate, *conceptually independent*, species concepts that can be used depending on the interest of the investigator. So, if a biologist's focus is on phylogenetic relationships, then a species concept that involves phylogeny is useful. If, however, the interest veers toward functional ecology, then a mixture of biological and ecological species concepts will be more appropriate. What I am saying here, on the other hand, is that species represent one large cluster of natural entities, quite independently of the interests of human observers. This cluster, however, is a loose one, with its members connected by a dense series of threads, not all of which go through every single instantiation of the concept. Among the species concepts listed in Table 1, Templeton's "cohesion" concept[37,38] comes close to the idea of family resemblance, especially if a phylogenetic component is appropriately factored into it.

Biologists can benefit from the adoption of a cluster concept of species in a variety of ways. First, they can stop wasting their time by trying to empirically solve a problem that has philosophical components that cannot be settled by the accumulation of new data. Second, however, they should not therefore

draw the conclusion that the solution of the problem is irrelevant to their aims and "just" a matter for philosophers to quibble about. On the contrary, the lesson to be drawn was encapsulated in what philosopher of science Daniel Dennett[39] warned about in a different context: "There is no such thing as philosophy-free science; there is only science whose philosophical baggage is taken on board without examination."

Indeed, the latter two points represent in my opinion the best model of the relationship between science and philosophy: on the one hand some philosophical problems do require empirical input and hence have to use information from science; on the other hand, science proceeds on the basis of philosophical assumptions and, at least occasionally, it pays to be aware of such assumptions. In practice, biologists will go about their business of identifying and classifying species in the usual way, but thanks to philosophy they should now feel liberated from a philosophical burden that they are not trained to deal with.

Acknowledgments

I wish to thank Jonathan Kaplan and Paula Kover for careful readings of previous versions of this manuscript. A long discussion on the concept of species with Roberta Mason-Gamer, following a presidential address (about species concepts) by Kevin de Queiroz at the 2002 Evolution meetings in Urbana-Champaign, helped me focus on the subject matter of this essay. I also wish to heartily thank Kevin and Adam Wilkins for an extended correspondence concerning this paper, which certainly improved my understanding of the species problem and, hopefully, the clarity of ideas as presented here.

References

1. Hey J. The mind of the species problem. Trends Ecol Evol 2001;16:326–327.
2. van Valen LM. Species, sets, and the derivative nature of philosophy. Biology and Philosophy 1988;3:49–66.
3. Ridley M. The cladistic solution to the species problem. Biology and Philosophy 1989;4:1–16.
4. Mayr E. What is a Species, and What Is Not? Philosophy of Science 1996;63:262–277.
5. De Queiroz K. Phylogenetic Definitions and Taxonomic Philosophy. Biology and Philosophy 1992;7:295–313.
6. de Queiroz K. The general lineage concept of species and the defining properties of the species category. In: Wilson RA, editor. Species: New Interdisciplinary Essays. Cambridge, MA: MIT Press; 1999. 49–89.
7. Wittgenstein L. Philosophical Investigations. New York, NY: Macmillan; 1953/1973.
8. Hull D. The effect of essentialism on taxonomy—Two thousand years of stasis. British Journal for the Philosophy of Science 1965;15;16:314–326.
9. Otte D, Endler JA. Speciation and its Consequences. Sinauer, Sunderland, MA; 1989.
10. Hey J. Genes, Categories and Species. Oxford, England: Oxford University Press; 2001.
11. Claridge MF, Dawah HA, Wilson MR. Species: the units of biodiversity. London: Chapman & Hall; 1997. pp. 439.
12. Howard DJ, Berlocher SH. Endless Forms: Species and Speciation. Oxford, England: Oxford University Press; 1998. pp. 470.
13. Grant V. Evolution of the species concept. Biol Zent bl 1994;113:401–415.
14. Gleason JM, Griffith EC, Powell JR. A molecular phylogeny of the *Drosophila willistoni* group: conflicts between species concepts? Evolution 1998;52:1093–1103.
15. Mayden RL. A hierarchy of species concepts: the denouement in the saga of the species problem. In: al MFCe, editor. Species: the Units of Biodiversity. Chapman & Hall; 1997. 381–424.
16. Noor MAF. Is the biological species concept showing its age? Trends Ecol Evol 2002;17:153–154.
17. Pigliucci M. Are ecology and evolutionary biology "soft" sciences? Annales Zoologici Finnici 2002;39:87–98.
18. de Queiroz K. The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. In: Howard DJ, Berlocher SH, editors. Endless Forms: Species and Speciation. Oxford, England: Oxford University Press; 1998. 57–75.
19. Ruse M. Definitions of species in biology. Br J Philosophy of Sci 1969; 20:97–119.
20. Giray E. An integrated biological approach to the species problem. British J Philosophy of Science 1976;27:317–328.
21. Mishler BD, Brandon RN. Individuality, pluralism, and the phylogenetic species concept. Biology and Philosophy 1987;2:397–414.
22. Stanley SM. A theory of evolution above the species level. Proc Nal Acad Science USA 1975;72:646–650.
23. Gould SJ. The Structure of Evolutionary Theory. Cambridge, MA: Harvard University Press; 2002.
24. Horvath CD. Phylogenetic Species Concept: Pluralism, Monism, and History. Biology and Philosophy 1997;12:225–232.
25. Sterelny K. The Nature of Species. Philosophical Books 1994;35:9–20.
26. Kitcher P. Species. Philosophy of Science 1984;51:308–333.
27. Splitter LJ. Species and identity. Philosophy of Science 1988;55:323–348.
28. Mishler BD, Donoghue MJ. Species concepts: a case for pluralism. Systematic Zoology 1982;31:491–503.
29. Dupré J. The Disorder of Things: Metaphysical Foundations of the Disunity of Science. Cambridge, MA: Harvard University Press; 1993.
30. Sorell T. Scientism: Philosophy and the Infatuation with Science. London: Routledge; 1991.
31. Levitt N. Why professors believe weird things: sex, race, and the trials of the new left. Skeptic 1998;6(3): pp. 28–35.
32. Weinberg S. Against philosophy; Dreams of a Final Theory. New York: Pantheon; 1992. 166–190.
33. Gazzaniga MS. Cerebral specialization and interhemispheric communication. Does the corpus callosum enable the human condition? Brain 2000;123:1293–1326.
34. Armstrong D. What is consciousness? In: Block N, Flanegan O, Guzeldere G, editors. The Nature of Consciousness. Cambridge, MA: MIT Press; 1997. 721–728.
35. Simon MA. When is a resemblance a family resemblance? Mind 1969;78: 408–416.
36. Sneath PHA, Sokal RR. Numerical taxonomy. San Francisco: W.H. Freeman & Co.; 1973.
37. Templeton AR. The meaning of species and speciation: a genetic perspective. In: Endler DOaJA, editor. Speciation and its consequences. 1989. 3–27.
38. Templeton AR, Maskas SD, Cruzan MB. Gene trees: a powerful tool for exploring the evolutionary biology of species and speciation. Plant Species Biology 2000;15:211–222.
39. Dennett D. Darwin's Dangerous Idea. New York, NY: Simon & Schuster; 1995.