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Bacterial species pluralism in the light of medicine and endosymbiosis*

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ABSTRACT: This paper offers a new argument in defence of bacterial species pluralism. To do this, initially I present particular issues derived from the conflict between the non-theoretical understanding of species as units of classification and the theoretical comprehension of them as units of evolution. Secondly, the necessity of the concept of species for the bacterial world is justified; I show how both medicine and endosymbiosis research make use of concepts of bacterial species linked to their distinctive purposes which do not conjoin with the other available concepts. Finally, I argue that these examples provide a new defence for the philosophical thesis of pluralism.

Keywords: bacterial species - endosymbiosis research - pluralism - species concept - unit of classification - unit of evolution.

RESUMEN: Este trabajo ofrece un nuevo argumento a favor del pluralismo de especies en bacterias. Para ello, presento los conflictos derivados de la consideración de las especies de modo no teórico, como unidades de clasificación, frente a su tratamiento teórico como unidades de evolución. Después, justifico la necesidad de un concepto de especie para las bacterias; muestro el modo en que tanto la medicina como la investigación sobre endosimbiosis emplean distintos conceptos de especie bacteriana ligados a sus diferentes propósitos que no son coherentes con el resto de conceptos existentes. Por último, argumento que estos dos ejemplos proveen nueva evidencia en favor del pluralismo filosófico.

Palabras clave: especies bacterianas - investigación endosimbótica - pluralismo - concepto de especie - unidades de clasificación - unidad de evolución.

Introduction

The ontological status of bacterial species is far from clear. In recent years, several definitions have been offered, but none has been capable of monopolizing the debate and a vast amount of literature continues to be published on the issue. Neither biologists nor philosophers agree on one particular concept and when a specific one is proposed, many problems arise, concerning both its limits of application and its theoretical strength. It seems as if *a single* concept cannot be found, and we can only propose ideas and yield to criticism. For these reasons, the category of species, especially when applied to bacteria, is highly problem-

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atic and deserves to be revisited from a philosophical perspective. To do this, here I adopt a pluralistic perspective, similar to the views defended by Dupré (1981, 1996, 2001, 2012), Ereshefsky (1992, 1998) and Reydon (2005). I argue, following their theses, that all the different bacterial species concepts reflect different extant properties of the prokaryotic reality and thus none of them should be abandoned. Moreover, I defend the notion that there is no conflict between approaches; any such perceived conflict arises from our desire to find *the right notion*: the *monopolistic* definition of bacterial species. Finally, I suggest that more research is necessary in order to develop new concepts of bacterial species in medicine and endosymbiosis theory.

To achieve this, the paper is divided in six sections. In section 1, I present the particular issues that stem from the conflict between the methods used to recognize and classify species. Those methods are usually either based on structural properties of canonical individuals or they are theory-laden methods used when considering species as units of evolution. The issues that arise from this disjunction are common to both the eukaryotic and the prokaryotic realms: they are inherent to the very idea of species itself. To continue, in sections 2, 3 and 4, I discuss the necessity of the concept of species as applied to the bacterial world, and I show that medicine and endosymbiosis research require different concepts of bacterial species, due to their different goals and ontological commitments. These examples are particularly intriguing because they reflect the fact that certain classifications work much better than others depending on whether we are trying to discover a particular pathogen symbiont or commensal or the best treatment for a specific disease. The election of the field of endosymbiosis research is due to the recent discoveries of endosymbiotic organisms, which demonstrate the necessity for a new concept of species for prokaryotes, insofar as bacteria are almost always involved in those organisms. Finally, in section 5, I argue that only a pluralist and pragmatic perspective can shed light on the bacterial species problem, and thereby guide both current and future research. Particularly, I defend the notion that the examples presented here show how we might carve the same the reality differently depending on our purposes, without generating any conflict between approaches¹. The idea will be that the expression “bacterial species” should be seen as a homonymic collection: despite using the same term, the distinct concepts reflect different properties of the bacterial world and reveal the ways in which those properties are akin to each other. Furthermore, those different concepts do not clash, since they are applied to separate sets of properties of the same reality in accordance with distinct scientific discourses. Any possible confusion among them would be a category mistake, resulting as a consequence of the homonymic character of the term “species”. Therefore, this paper provides a new defence of bacterial species pluralism and the more general philosophical position of pluralism.

¹ When I refer to “the same reality” or “one and the same reality” I am not attempting to defend an ingenuous form of realism, as might be supposed. I use this term in an explanatory sense and it must be understood, as Quine suggests to understand Quinean ontological relativity: “If you take the total scattered portion of the spatiotemporal world that is made up of rabbits, and that which is made up of undetached rabbit parts, and that which is made up of rabbit stages, you come up *with the same scattered portion of the world* each of the three times. *The only difference is how you slice it*” (1971, 32, emphasis added). The way you slice it, I suggest, will have ontological import; and this is thus a form of promiscuous realism (Dupré 1996). I am indebted to Luis Valdés for this helpful comment and the relevant reference to Quine, which I hope will help avoid misunderstandings of my work.

1. *Species: units of classification or units of evolution?*

As has long been known, the idea of “species” is one of the most problematical ideas in biology and it is far from clear what a species might be. According to Mayden (1997), at least twenty-two different definitions have been proposed since 1940, when Mayr first defended the so-called “biological species concept” (BSC). Some years later, Wilkins counted twenty-six (2009)². In the current literature, many definitions can be found which leave the two main issues concerning the “species problem” unresolved: On the one hand, there is conflict between the theoretical constraints imposed by certain proposed concepts and the actual operational methods used in the identification of different species. On the other hand, there exists a dichotomy: species can be considered either as *units of evolution* or as *units of classification* of the biological world (Kitcher 1984; Hull 1997). As Jody Hey has recently recognized: “the species problem is caused by two conflicting motivations: the drive to devise and deploy categories [units of classification] and the more modern wish to recognize and understand evolutionary groups [units of evolution]” (2001, 329).

The first problem can easily be related to the second; in general, when referring to species as units of evolution, we are considering them from a theoretical perspective: the perspective that comes from evolutionary theory. For this reason, the definitions offered are usually theory-laden, and theories constrain the methods that can legitimately be used (Laudan 1984). So, those definitions do not seem to be very operational, and therefore the taxonomist faces serious difficulties when attempting to apply them. In addition, if the taxonomist is a palaeontologist trying to shed some light on extinct species which appear in the fossil record, the problem is even more acute, because many of the characteristics or properties that are said to be shared by the individuals that belong to the same species cannot be put to the test. Think, for instance, of the extremely common BSC, according to which individuals belong to the same species if they form groups of interbreeding isolated populations (Mayr 1940). How can a palaeontologist identify the existence of reproductive isolation? In many cases, this goal is simply unachievable, and other concepts are required.

It is worth mentioning here, concerning the treatment of species as units of evolution, the pioneering work of Willi Hennig (1966), who proposed treating species as monophyletic groups, whereby all the descendants from a common ancestor are treated as members of the same species. Despite the controversies that it generated among biologists, Hennig’s idea of species inaugurated the cladistics treatment of species and had a major impact on subsequent research on systematics, more specifically on phylogenetic research, mainly oriented towards evolutionary theory.

In contrast, operational methods are those that are usually applied and required if we are dealing with problems of classification; that is to say, if we are trying to classify species according to the distinguishable properties they have and which can be easily recognized. The best known example of an operational non-theoretical concept used to classify species is the *phenetic species concept* (PSC) defended by Sneath and Sokal in the 1970s (Sokal & Sneath 1963). This concept relates species to phenetic clusters of individuals, in such a way that two individuals would not belong to the same species unless they shared a large

² For a good summary of the main species concepts in use in biology today see Torretti (2010).

number of traits which are considered to be relevant. This definition is extremely useful if we are interested in recognizing some of the most common features of individuals belonging to a defined species; so species are considered as units of classification of the biological world. Furthermore, such a definition can easily be applied to many forms of life. However, it is usually argued that this definition is too fuzzy, because no specific criteria are established for signalling out the relevant traits. In fact, this concept was soon abandoned by geneticists and evolutionists, since the characters used in it to classify species are not evolutionary ones. Although I will not argue the point here, because it goes beyond the scope of the paper, I do not believe this to be problematic: if we are not guided by evolutionary theory and what we want is to recognize what kinds of beings there are in the world, we need specific methods of recognition which are free from theoretical requirements, the latter being undesirable –obviously, we are freed of these requirements in a *broad sense* because, as S. Leonelli (2013) has recently pointed out, classificatory activities generate their own theories.

The literature concerning species clearly reflects this issue and the perception of conflict appears in many different works. Sometimes a theoretical definition is preferred and species are said to be exclusively units of evolution; and the focus is on their role in evolutionary theory (Ereshefsky 1992, 1998; de Queiroz 2005, 2007). On other occasions, attention is focused on the role of species as units of classification which can be recognized in the biological world. One example of this latter approach would be the following: if we say “A is a *Leucophaeus scoresbii*” (or, in short, a seagull, depending on our personal interests in a particular classification), we are allowed to infer that A must have wings and that it must be able to fly. Dupré (1999, 2001) has usually advocated such a thesis and he maintains that the term “species” should continue to refer to the kind of entities it has always; that is to say, to units of classification. In his opinion, when we are referring to units of evolution we should use the term “lineage”; lineages, not species, are the entities which evolve.

Keeping all this in mind, I will defend the usefulness of both concepts of “species” in biological theory. As Dupré argues, for a long time species been seen as the minimal units of classification of the biological world, and they have served their job, so it would be useless and irrational to abandon such a well-established term. Classifying species and being able to determine certain features of individuals belonging to those groups is very important in our daily lives, with reference to both biological and non-biological matters (Dupré 1981, 1996, chap. 2). Distinguishing, for instance, between poisonous and non-poisonous snakes, or between pine and fir trees could make the difference between life and death, or between good and bad furniture.

It is nonetheless also true, however, that Darwin, though not claiming to know what species might actually be (*Origin*, chap. 2), entitled his most important book *On the origin of species*; signalling that his theory was about how new species emerge and how they change over time. So species were supposed to be what changed through time; that is to say, the units on which the many forces of evolution act. Their role in evolution does not, therefore, seem disputable. Many philosophers have argued that if we only consider species as units of evolution we will pave the way to solving the species problem (Ghiselin 1974; Hull 1976, 1978). However, as I have attempted to justify and I will try to reinforce, we need to consider species both as units of classification and as units of evolution, and then to try to cope with the problems that arise.

2. *Is the concept of species necessary for our understanding of the bacterial world?*

The application of the idea of species to the bacterial world has for a long time seemed highly problematic. Many authors deny the existence of bacterial species; they consider that bacteria do not form differentiated species and that such an idea is either exclusive of the eukaryotic world (Margulis & Sagan 2002) or simply misleading (Ereshefsky 2010). The main problem is posed by horizontal gene transfer, also called lateral gene transfer (LGT): the mechanism by which bacteria transfer genes freely. LGT is said to be infrequent and promiscuous (it takes place between relatively extremely genetically distant strains of bacteria, sometimes sharing no more than 75% of their genes). LGT is responsible for the high rate of mutation among prokaryotes and their features, such as the capacity to develop resistance to antibiotics (Cohan 2001, 2002; Franklin 2007; Doolittle & Zhaxybayeva 2009; Baptiste et al. 2009). So, LGT complicates the species concept for the prokaryotic realm.

The more traditional species concepts, the 70% DNA-DNA hybridization criterion and 97% 16S rRNA approach, were merely morphological concepts that failed to capture important bacterial features other than the rate of hybridization of their DNA or their 16S rRNA (Gevers et al. 2005). These concepts are not useful for predicting either the sexual characteristics of bacteria or their most significant features, such as their degree of virulence, their reaction to particular antibiotics or the kinds of alterations that they cause in the reproductive behaviour of the organisms which they interact with. In addition, LGT complicates the development of new concepts and new methods of recognition of bacterial species. Taking those issues into account, while I think that the idea of species must be applied to both the eukaryotic and the prokaryotic world, I recognize that much work remains in this field and we need to develop new methods and concepts. I will argue that these new concepts should be applied to bacteria considered both as units of evolution and as units of classification of the biological world. So the concept of species must be understood in a broad ontological sense; it must be capable of including and emphasizing different properties, depending on the reasons why it is coined. As noted above, this application will always be problematic, because the methods used to classify bacteria are not always in harmony with the methods that evolutionary theory requires when bacterial species are being considered as units of evolution. Nevertheless, conflict arises from the alleged interest that biologists manifest in developing *the* bacterial species concept, denying the complexity of the prokaryotic world and the many different properties that should be (and normally are) emphasized in particular domains. Normally, such an interest in determining *the* bacterial species concept is defended on the basis of coherence. However, allowing for the existence of complexity and the necessary plurality that this would show those disputes to be empty: different scientists are ultimately talking about different things, conditioned by the peculiar requirements of their particular fields of inquiry, and thus no real conflict exist. This philosophical position is not hermetic against the possibility that biologists might one day find properties that would be necessary and sufficient to define bacterial species, and which would be equally applicable to all fields of inquiry (genetics, ecology, medicine, endosymbiosis, etc.). However, it is based on the data provided by present-day science, which suggest that such a unified concept (*the* bacterial species concept) has not yet been found, and all our current knowledge argues against its existence.

To support my pluralist position, I will next consider the ways in which, on the one hand, medical practitioners and on the other, endosymbiosis researchers talk about species in different ways (stressing different properties) that are ultimately in accord with the internal structure of their disciplines.

3. *Bacterial species as units of classification: the case of medicine*

The example to be considered here is the role that bacterial species play in the medical environment and the way in which a particular concept might be needed or at least prove very helpful. As is well-known, bacteria were first discovered as pathogens in the medical researches of Louis Pasteur. Bacteria cause many diseases among humans, some of which are lethal and even catastrophic. Given their importance as originators of disease, doctors study many features of bacteria that do not coincide with the characteristics that are of main importance to geneticists (DNA-DNA hybridization, 16S rRNA, etc.), ecologists (Cohen's definition) or evolutionary biologists (the phylo-phenetic species concept or polyphasic species concept). This allows for a medical classification of bacterial species which, I will argue, is equally valuable, but mostly different from the classifications provided by other scientists³. In order to prove my argument I will first use a real example and later a thought experiment specially designed to strengthen the ideas I put forward.

To begin with, consider *Yersinia pestis*, formerly called *Pasteurella pestis*, a Gram-negative bacterium which in humans causes the horrific and lethal disease of plague. *Y. pestis* is responsible for three different kinds of plague, each one classified according to the part of the body infected: pneumonic plague, bubonic plague and septicaemic plague. The first infects human lungs and is said to be the most virulent and unusual. Bubonic plague mainly attacks the lymphatic system and was responsible for the unfortunately very well-known Black Death that reduced European population by one-third in the fourteenth century. Finally, septicaemic plague affects the blood stream, although it quickly disseminates and infects the whole body. From a genetic, ecological or evolutionary point of view, the mere idea of thinking about classifying *Y. pestis* as three different species would be undesirable: the bacteria causing these three different infections are so genetically, ecologically and evolutionary similar that such a division would only complicate our research in a most unproductive way. However, from a medical perspective, it seems important to distinguish between the three types of plague for many pragmatic reasons.

First of all, not only the location in the body, but also the transmission vector is different depending on the kind of infection that one has. Septicaemic plague, for instance, is not only passed on by the bite of a flea, as usually occurs with bubonic plague; the person is usually infected as a result of an open wound in the skin. Pneumonic plague, in contrast,

³ My defence of the need for an alternative medical classification is not trivial; in the medical literature there are such cases. One particularly interesting example is that of *Treponema pallidum*, the bacteria responsible of syphilis. While biologists refer only to *T. pallidum*, doctors are forced to distinguish different species: *T. pertenue*, which causes yaws (also called pian or framboesia); *T. endemicus*, responsible of bejel (endemic syphilis); and *T. carateum*, which produces the famous pinta disease. While there is no genetic basis for such a classification, medical reasons are pressing enough to sustain it (Perine 1984; Antal et al. 2002; Cjeková et al. 2012; Giacani & Lukehart 2014).

is almost always transmitted from human to human by simple inhalation of contaminated droplets. The different vectors of transmission involved in the different diseases can require highly diverse medical procedures in order to avoid new infections, while important and very useful generalizations can be made. These generalizations can provide us with the grounds to enact only procedures that are necessary and can result in a saving of money or the prevention of avoidable alarm.

Secondly, the symptoms do not coincide: in many instances of septicaemic disease, symptoms never appear and patients die before knowing they are infected. In contrast, bubonic plague is easily recognizable by means of large blisters situated near the affected lymphatic area. Lastly, pneumonic plague normally causes pains in the patient's chest; a symptom that is very helpful to differentiate this type of plague from the others.

Finally, the evolution and mortality rates are also very different depending on the disease, which prompts the following assertion: if we differentiate three bacterial species, then we will be able to make different generalizations which can be very useful and practical in dealing with current and future cases of infection. What is more, such a differentiation of three species would be grounded on, first, the peculiarities of the disease in question (according to an accepted theory of diseases) and second, medical theory concerning pathogens and their responsibilities in disease.⁴

Now let us consider a thought experiment which I believe is very illuminating. Suppose the following be the case: we have two bacterial strains, A and B, which produce a particular disease (C) when they are inoculated into humans. The symptoms of C (high fever, vomiting and a strong pain in the hands), its treatment and immunological response and the vectors of transmission (dog scratch) are the same, regardless of the strain that caused it.⁵ When a sufferer goes to the doctor to find out what disease they are suffering from that causes such terrible pain in their hands, the doctor says, irrespective of the particular strain that could have caused the disease: "You have C, and this is the best treatment for it; also, take precautions with your dog, because it was the infectious agent". If the patient is interested in knowing what will happen in the following weeks, the doctor will tell them, again irrespective of the particular strain that has infected the unfortunate patient, what the expected immunological response and evolution of his disease will be, and will encourage them to come back if they do not feel better.

Now imagine that a geneticist, interested in classifying bacterial species, obtains a pure culture of the two strains, A and B, and determines the rates of DNA-DNA hybridization and of 16S rRNA divergence among them. The geneticist shows that this rate is lower than the conventionally required 70% and 97% respectively, so classifies them as two different species. To strengthen this assumption, suppose that an ecologist, using Cohan's cohesion concept according to which two bacterial species are different when "they reach the point that they can survive each other's periodic selection events" (2002, 463) also determines that the strains are two different species. Finally, suppose that another scientist, using the so called phylo-phenetic approach which defines bacterial species as "a group of strains that

⁴ All the information concerning *Y. pestis* and the plagues is extracted from Madigan (2004, 918-20).

⁵ I take this as being the most common marker of bacterial diseases and as a possible way of classifying bacterial species from a medical point of view, following Rolain et al. (2004, 1921-1922). Some other aspects that could also have been taken into account, such as the rate of antibiotic resistance, have been ignored in order to facilitate the exposition of the argument.

show a high degree of overall similarity and differ considerably from related strain groups with respect to many independent characteristics” (Rosselló-Mora & Amann 2001, 53), also determines that they are two different species. Therefore, a consensus is reached between biologists and through the application different criteria; this kind of consensus is not usually the rule, but the exception, because normally, diverse criteria cross-classify the bacterial world (Franklin 2007; Ereshefsky 2010). Hence, it would seem reasonable to define strains A and B as different bacterial species.

The question now, however, is: Should doctors be interested in such a classification and require, for instance, a blood test of all patients with the common symptoms of C? I certainly do not think so; what is more, I believe it would be useless, and could well be harmful and counterproductive. What doctors are interested in are diseases, their processes of evolution, their degree of virulence and the extant treatments. So, they do not need to change their definitions or procedural methods in order to accommodate the criteria of geneticists, ecologists or systematists. Doctors may and should have their own criteria for defining bacterial species, and these criteria, though they sometimes *seem* to clash with those established in other branches of science, do not really clash, because they are applied from a different perspective; from different fields of inquiry which can legitimately divide up reality (indeed, *the same* reality) in different ways. In other words: our aims and goals in different disciplines can lead to cross-classification of the extant entities in the world. Although this cross-classification may seem to drive us to a disordered world, or to a new Babel (Hull 1999), this is not actually the case, because the cross-classifications are applied to different areas of interest in which we emphasize certain properties to the detriment of others. As I believe these examples clearly show, different and alternative classifications, one highlighting certain properties (genetic, ecological, evolutionary, etc.), and the other emphasizing others (medical), can lead us to different classifications of the world with significant beneficial and pragmatic results. Thus, the disputes between ecologists, geneticists and doctors regarding the classification of *Y. pestis* or the hypothetical disease C must be seen as empty; different properties are emphasized and therefore different cross-classifications (in this particular case, in the form of more “fine-grained” classifications) can exist in perfect harmony.

One could, of course, acknowledge my argument but at the same time point out that classifications in biology are orthogonal to the classifications made by doctors: while the former try to classify bacteria, the latter classify *diseases*, and diseases and bacteria are not the same thing. Although I recognize that this point can be made, I think it is unfair to the kind of work that many doctors do; many doctors are researchers who in fact do try to classify the extant species of bacteria (cf. Madigan et al. 2004; Prescott 2004). The fact that these classifications are goal-oriented towards practical results (the development of vaccines, antibiotics, avoiding certain forms of propagation, etc.) does not change the pretensions of the classifications themselves. Doctors, like geneticists, do classify bacteria; the only difference between them is the goal which guides their different classifications.

4. *Bacterial species as units of evolution: the case of endosymbiotic theory*

The issue of bacterial species and the different ways of classifying prokaryotes acquires a particularly interesting dimension from the point of view of researchers working on endo-

symbiosis (cf. Booth 2014; Suárez 2015). Endosymbiosis is a biological phenomenon which consists of two different organisms belonging to distinct species, called “endosymbionts”, living together; host and symbiont are distinguished with the symbiont living inside the cells of its host⁶. Furthermore, as a kind of symbiotic interaction, endosymbiosis encompasses three different kinds of interactions: *mutualistic* interactions, from which both host and symbiont benefit; *commensalism*, which is neutral for both; and *parasitism*, from which the symbiont is benefitted to the detriment of the host. Finally, among endosymbiotic relationships it is useful to distinguish two different ways in which the symbionts might be transmitted from progenitors to offspring: transmission may be *vertical*, if the progenitors pass on their own symbionts to their progeny during reproduction; or *horizontal*, if they do not, and the symbionts are acquired from the environment (Moran 2006).

My concern with endosymbiosis research here and its relevance for my arguments on bacterial classification are threefold: To begin with, endosymbiosis, in spite of what had commonly been believed until recently, should not be seen as a rare phenomenon in nature, but as something quite widespread (Moya et al. 2008). Secondly, bacteria are normally involved in endosymbiotic interactions, since the hosts usually develop special organs called “bacteriocytes”, which are highly susceptible to having bacteria live in them (Margulis 1998; Margulis & Sagan 2002). Finally, as many authors have noted, such bacterial consortiums constitute “a mechanism for rapid speciation” (Carrapiço 2010, 136), since they frequently cause certain kinds of reproductive isolation in their hosts⁷. These three reasons lead endosymbiotic biologists to worry about prokaryotes and, as I will argue, to develop new notions of bacterial species that do not necessarily match either intensionally or extensionally with the classifications made by ecologists, geneticists or other protistologists. In my argument, I will present the real case of the bacterium *Wolbachia pipientis* to show how the criteria provided by endosymbiosis researchers to classify bacteria do not necessarily generate classifications that are extensionally equivalent to those used by other biologists.

The case of *W. pipientis* is particularly renowned among endosymbiosis researchers and it is considered a standard for the research in the field. *Wolbachia* belong to the order *Rickettsia*, as do many other important endosymbionts, and are considered to constitute a separate monophyletic group. What is outstanding about *W. pipientis* is its extension: it is widespread and according to recent research, present in approximately 65% of insects species (Hilgenboecker et al., 2008). Furthermore, its symbiotic effects are very diverse, ranging from many distinct form of reproductive parasitism in arthropods to mutualism, in the case of its relationship with some nematodes. Another very interesting feature of *Wolbachia* is the fact that their phylogeny does not concord with the phylogeny of their hosts;

⁶ It should be noted here that in endosymbiotic relationships, in contrast to other kinds of symbiotic relationships (ectosymbiosis), the symbiont lives *inside* the cells of the host. This definition excludes relationships such as that extant between plovers and crocodiles or *Escherichia coli* and the human gut which are symbiotic relationships, but do not constitute endosymbiosis (Sapp 1994; Archibald 2014, chap. 2).

⁷ The best known (and most scientifically accepted) case is the origin of eukaryotic cells as a result of two previously extant prokaryotic organisms merging and thus giving rise to mitochondria and chloroplasts (Sagan 1967). However, there are many more cases, such as the consortium aphid-*Buchnera aphidicola* (Latorre & Moya 2013) or the origin of *Paracatenula* (Gruber-Vodicka et al. 2011).

this suggests “extensive lateral movement of *Wolbachia* between host species” (Werren et al. 2008, 741)⁸. However, despite their lack of concordance with the phylogeny of their hosts, *Wolbachia* cannot be cultured outside them, which suggests their long-term participation in symbiotic relationships. Currently, there is no phylogenetic basis for distinguishing different species of *Wolbachia*, but biologists have distinguished eight different strains (Casiraghi et al. 2005). All these features render *W. pipientis* very interesting both from a phylogenetic and from an endosymbiotic point of view.

From an endosymbiotic point of view the most important features of *W. pipientis* are: the fact that it may interact mutualistically with nematodes, whereas it is parasitic in its relationship with arthropods; and the variety of reproductive alterations which it causes in its parasitic hosts. Four different kinds of reproductive alterations have been reported: cytoplasmic incompatibility (CI), parthenogenesis induction (PI), feminization of genetic males (FGM) and male killing (MK). All these alterations are considered to be mechanisms for rapid speciation and are very important for many other practical purposes and applications, such as control of disease vectors or pests. Let us first consider the parasitic effects that *W. pipientis* may have; later I will turn to the mutualistic effects.

CI is the most common alteration that *Wolbachia* cause in their hosts. It of infected males not being capable of successfully mating with uninfected females (unidirectional incompatibility) or with infected females that do not harbour the same *Wolbachia* strain (bidirectional incompatibility). CI is due to the modifications that *W. pipientis* causes to the sperm of its hosts, modifications which are “rescued” when the host mates with a suitable female. CI thus tends to generate reproductive isolation.

PI consists of the asexual reproduction of females which generates new females infected by the same strain of *Wolbachia* as the progenitors. This phenomenon has only been documented in mites, some wasps and thrips; species in which males develop from unfertilized eggs. PI thus tends to eliminate males from the population.

FGM is the process by which genetic males develop as females as a consequence of a *Wolbachia*-induced hypertrophy of the androgenic gland, which inhibits its function. It has been documented in isopods and some insects, such as some Lepidoptera (*Eurema hecabe*) and some Hemiptera (*Zyginidia pullula*). The importance of FGM lies in the fact that it might lead to the appearance of new systems of sex determination, such as male heterogamety.

Finally, MK has been observed in certain Coleoptera, Diptera, Lepidoptera and Pseudoscorpiones. It consists of the killing of males during embryogenesis, to the benefit of females, which can directly transmit the bacteria. MK is interesting in as much as it can lead to the fixation of female populations, to the detriment of the males.

Such a classification of mechanisms induced by *Wolbachia* that affect reproduction is of major importance for endosymbiosis research since “closely related [phylogeneti-

⁸ It is very important to note that, when a bacterium participates in an endosymbiotic relationship for a long time, its phylogeny usually matches the phylogeny of its host. A canonical example is the phylogeny of *Buchnera aphidicola*, which is completely dependent on the phylogeny of the aphids (Brucker & Bordenstein 2012; Latorre & Moya 2013). This is why *Wolbachia* are so interesting from a phylogenetic point of view.

cally] *Wolbachia* bacteria can cause quite different effects on their hosts” (Stouthamer et al. 1999). Indeed, this fact is still more striking, since there have been documented cases in which the same strain of *Wolbachia* induced different reproductive alterations in different hosts. For instance, the same strain of *W. pipientis* induces CI in *Drosophila recens* and MK in *D. subquinaria* (Jaenike 2007). This fact means that endosymbiosis researchers, interested as they are in the evolutionary character of *Wolbachia* (inso-far as it acts as rapid speciation mechanism in their host), may classify the parasitic *W. pipientis* into four different categories, depending on the effects it originates in its hosts. Such a classification would be different and independent from the classifications made by phylogeneticists, who are interested in different features of the bacteria (mainly genetic); or those made by ecologists (Cohan 2002) or by authors following the phylo-phenetic approach (Rosselló-Mora & Amann 2001). Indeed, the same phylogenetic, ecological and phylo-phenetic strain of *W. pipientis* would be classified as two different species by endosymbiosis researchers, depending on the possibility of it causing MK in *D. subquinaria* and CI in *D. recens*. So, where all biologists would distinguish one species belonging to one strain, endosymbiosis researchers would distinguish two species.

In contrast, when attending to the possible mutualistic effects of certain strains of *W. pipientis*, endosymbiosis researchers would tend to classify different strains (strains C and D) as one species, since they are only found in mutualistic relationships in filarial nematodes. Therefore, where some biologists would find two species (for example, adopting Cohan’s approach) and others would distinguish two strains within the same species (phylogenetically, as I said, there is only one species: *W. pipientis*), endosymbiosis researchers would recognize just one species⁹.

In conclusion, endosymbiosis researchers share common practices and are concerned, on the one hand, with the distinction between mutualistic and parasitic effects and, on the other, with the different reproductive modifications that bacteria induce in their hosts. As a consequence, they would classify bacterial species differently from other biologists. However, as happens in the case of medical classification, the fact that researchers classify bacterial species differently should not be seen as a clash with standard methods. Rather, it reflects the intrinsic plurality of the world and the fact that different theories generate distinct classifications of the same reality, depending on the particular properties and arrangements of properties that those theories emphasize. Again, as happened in the case of doctors, cross-classifications only show that different scientific discourses may require distinct ways of carving up the world.

5. *The road to pluralism*

What philosophical morals follow from the examples I have explored above? How should we carve up the bacterial or prokaryotic world? I believe that there is not one particular preferred way of dividing up the prokaryotic world, but many equally worthy divisions.

⁹ Most of the information that I use concerning *W. pipientis* comes from the excellent review by Werren et al. (2008). The particularities of CI, PI, FGM and MK come partially from Werren (1997), Stouthamer et al. (1999) and Zimmer (2001).

Furthermore, the different classifications we might build are not really in conflict with each other, but only apparently so, due to the idea that there is one and only one correct way of carving up the world. The problem with the “species” notion, when it is applied to bacteria according to the different criteria cited above, is that there is not one unique way of dividing up the prokaryotic reality, but many; and the particular division that we chose on a particular occasion will (and should) depend on our interests. Moreover, the different notions are not *synonyms*, but *homonyms*, that is to say: there are different concepts in the arena that we give the same name to (Reydon 2005). This suggests the possibility of conflict and that one of the particular definitions may be more important than others. But the evidence suggests just the opposite: the different concepts stress different properties of one and the same reality (the bacterial world) and, according to the different properties stressed, different kinds of relations are discovered and different generalizations are formulated, so no one concept is more important than the others. Thus, the recognition of the existence of different concepts is linked to the recognition of the existence of different properties, which can be singled out in different fashions with an important pragmatic import.

Clearly, a new and important question now arises: How is it possible that one and the same reality (the bacterial world) can be divided up into different classes? If there is one reality, then there should only be one possible classification of it. As Plato observed in *Phaedrus* and in the *Sophist*, nature must be carved at its natural joints, and scientists have to discover these joints. So maybe an as yet undiscovered concept will be the key to disentangling the complexities of the bacterial world; a concept through which all the different features highlighted by different specialists converge. Once this concept is discovered, none of the problems posed by the classification of bacterial species will remain. We will have found the natural way of carving the world and no confusion will remain. However, the arguments in this paper seem to demonstrate that this does not seem possible; the actual evidence from medicine and endosymbiosis research suggests just the opposite. Doctors and evolutionary biologists, on the one hand, and endosymbiosis researchers and phylogenetic biologists, on the other, emphasize very different features and it seems very implausible that we will find a new characteristic within which they all converge. The traditional and optimistic assumption within the history of science according to which there is one correct manner of dividing up the world seems wrong; the manner in which we carve up nature depends on our interests and one and the same range of objects may be carved up in distinct manners depending on those interests and on the scientific discourses that we are using (Dupré 1996; Cartwright 2005).

Furthermore, I have argued that the divisions presented here are pragmatically valuable from different standards, and thus they are necessary and helpful; there is no reason to eliminate them. With respect to the idea of a cross-classification of reality, I have indicated that cross-classification is neither problematic (because different classifications are recognized for different purposes), nor conflictive (because both doctors and endosymbiosis researchers know and easily recognize the criterion that is being used). So, should we prefer one particular classification over the others? I do not think so: different purposes lead us to distinguish different properties. Those properties are akin in different manners and thus they lead us to different classificatory schemes. That said, two criteria will be required for a cross-classification of reality to be valid: the different classifications must be motivated by different goals (say, for instance, discovering diverse regularities); and they must be proved

to be pragmatically valuable. The examples presented here fulfil these requirements, and hence the classifications are legitimate.¹⁰

6. *Concluding remarks: medical and endosymbiotic bacterial classifications as a new argument for pluralism*

In this paper, I have presented the bacterial species problem from the point of view of the distinction between species as units of evolution and species as units of classification. I have justified the necessity of the species concept for the bacterial world and I have shown how medicine and endosymbiosis research give raise to different classificatory systems of the bacterial world from those presented in other areas of biology (ecology, phylogenetic, etc.). Finally, I have argued that these examples show that different scientific discourses generate different classificatory systems depending on the particular interest of the researchers and of the field. Moreover all those classifications reflect extant properties of the bacterial world and allow researchers to make interesting inferences, which shows that a pluralist and a pragmatic attitude concerning the bacterial species problem is the most adequate in the current situation.

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¹⁰ These are brief and very schematic criteria which are only necessary. Giving precise criteria for a useful classification is, again, beyond the scope of this paper. Some useful and brief remarks on this issue can be found in Ereshefsky (1992, 682-4) and in Dupré (1999, 209-12).

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