Chapter 10

Darwin's Species Concept Revisited

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1. Introduction

What did Darwin *really* mean by "species"? There are different ways of answering this question, different ways of doing history, and they need not converge on the same answer.

One way is to look at Darwin's definitions of the term "species" and to use a comparative method analogous to the comparative method in biology, comparing and contrasting Darwin's definitions with those of his contemporaries, with his predecessors, and with definitions today. This is the method favoured typically by philosophers of biology and biologists who are concerned with history, and it might be called the *pure history of ideas approach*.

One problem with this approach is that it assumes that Darwin meant what he said in his definitions. But why would one assume that? Darwin was a great scientist, to be sure, as well as a wonderful husband and father and an upstanding member of society, but he was also a human being and human beings do not always mean what they say, either intentionally or unintentionally. Why should a scientist be exempt from this general truth about humans, especially when there already exist examples of dissimulation, even radical dissimulation, among leading intellectuals? (I shall turn to some famous cases at the end of this chapter.) To think otherwise of Darwin, to place him on a pedestal above human nature, is to descend to the level of religious iconography.

Another way to approach what Darwin really meant by "species" is to deal with Darwin's writings in the context of his time, not just the scientific context but the personal, social, cultural, economic, and political contexts as well. As Bernard Lightman [1] puts it in his Introduction to an anthology devoted to contextualist analyses of Victorian science, "The hallmark of contextualist studies is their emphasis on the way scientific ideas are embedded in material culture such that there are no insides or outsides of science." This, he says, "allowed historians to avoid the false analytical distinction between science and society (or base and superstructure), dissolve the categories external and internal, and begin to tran-

scend the science/society dualism" (p. 7). For at least the past two decades now, this is the method of doing history of science that seems most favored by professional historians of science, epitomized by the books by Desmond and Moore [2, 3], and may be called the *pure contextualist approach*.

This approach suffers from a number of difficulties, however, not the least of which is that, as Lightman [1] points out, these historians need not always agree on the same matter because "there are many different kinds of contexts" (p. 7). A much greater difficulty, arguably the biggest, concerns the background assumptions of the approach, such as what Lightman calls "the false analytical distinction between science and society." That the distinction is a false one might be the conclusion of a massive process of induction, and hence synthetic, even an inference to the best explanation. But if historians of this persuasion are not open to the possibility that a scientist can have an idea or theory that is not the product of his or her time, then the approach is dogmatic and this way of doing history takes on the character of an ideology. There is also the problem of a self-referential paradox, in that one has to wonder how these historians have managed to transcend their cultural milieu and arrive at objective, accurate causal explanations but not natural scientists. Surely a more balanced approach would be to allow that many scientific ideas and practices are to some extent products of their environment but not necessarily all. So then we are back to what Darwin really meant by "species," and whether what he meant was a product of his time or something unique, something that one would not have been able to predict (let alone retrodict).

What I have called the *pure contextualist approach* to history of science is not the only way of doing contextualist history. Another kind of contextualist history involves a careful consideration of the writings of an author within the author's environmental context *so as better to understand what the author meant*. There is no assumption here that the ideas of the author were purely the product of their context so that the author could not have had ideas that were contrary to his or her environment. There is no assumption even that the author could not have had ideas that were ahead of his or her own time. Richard Ashcraft [4] uses this approach (though not purely) to better understand Locke's political philosophy as given in his *Two Treatises of Government*, in contrast to the approach to Locke typically found in philosophy, which considers his writings almost in a Platonic heaven and examines them for validity and soundness. As Ashcraft puts it, his approach is "to raise questions concerning the meaning of a particular political theory that are referable to the actor's social life-world, the nature of the intended audience, and the purposes for which the political theory were formulated" (p. 6). Hence his focus is on the radical political movement of which Locke was a part, headed by Shaftesbury, involving former Levellers, secret codes, and plots to kill the King such as the Rye House Plot, rather than on the rise of capitalism, mercantilism, the scientific revolution, and so on.

But this approach is not necessarily preferable when it comes to Darwin on "species." Darwin was the head of a scientific revolution, to be sure, which today goes by his name, but one cannot assume that he wrote in a specific manner that only his followers would have fully understood. He might have, but the parallel with Locke is highly strained at best. In the case of Darwin, unlike with Locke, we have to be open to the possibility that he some-

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times wrote in a manner that was aimed at manipulating his followers along with the rest of his readers in ways they might not have recognized. But how could one ever hope to find that out if true?

This brings us to the method of doing history that seems to me perfectly suited to the present purpose. It is taken from philosophy of language, from Ludwig Wittgenstein to be specific, and is employed in a manner which he might not have agreed with or even imagined but which follows from his theory of meaning. In short (and I shall have more to say about his theory in the third section), what I shall do in this chapter is go beyond Darwin's *definitions* of "species" in his writings and pay careful attention to his *use*. In the famous words of Wittgenstein which I here paraphrase, when it comes to what a word means in a language community *don't ask for the meaning, ask for the use*. The same principle can also be applied to the writings of a single author, not only to a particular work but to the entire corpus, viewed in much the same way as a palaeontologist looks at strata. In the case of Darwin on "species," I hope to show in the present chapter the enormous power of this method and some of its fruits. The method, moreover, should not be viewed as incompatible with history of ideas approaches, or with contextualist approaches either, but in the case of Darwin it should be seen that the approach is best suited as the preliminary one to any further investigations.

2. Survey of the current state of scholarship

Before we begin by applying a Wittgensteinian approach to Darwin on "species," it is important to take a brief survey of the current state of scholarship on Darwin's species concept. What is utterly remarkable is the near total state of confusion. After all the years since Darwin first published *On the Origin of Species* [5], one would naturally have expected better.

What is perhaps most surprising is the paucity of attention that contextualist historians of science have given to Darwin's species concept, in stark contrast to the amount of effort they have given to other key concepts and theories of his, notably natural selection, divergence, adaptation, and the Tree of Life. For example, in his book devoted to the development of Darwin's theory of evolution by natural selection from 1838–1859, Dov Ospovat [6] makes much of the influence of British natural theology and biological theories of progress, including the influence of particular naturalists such as Owen and von Baer, but he nowhere deals with Darwin's species concept. Granted, the work was seminal, and this important young historian could not be expected to do everything in his book (especially since he did not live long enough to see it in print). As Adrian Desmond points out in his Foreword to the book, Ospovat "wanted to make Darwin less of a seer, standing out of time, and more a man of his day" (p. ix), with the consequence that "Dov set many hares running, and we all chased them" (p. xi). It is therefore all the more surprising that none of the contextualists seem to have bothered to chase Darwin's "species" hare, or to even have noticed that it needed (or was worth) catching. Desmond and Moore's *Darwin* [2], as a prime example, "seeks to portray the scientific expert as a product of his time" (p. xviii), and they "want to understand

how his theories and strategies were embedded in a reforming Whig society" (p. xix), but one looks in vain in their book for a contextualist analysis of what Darwin meant by "species." The same holds true for their latest book on Darwin [3], which they claim "is the untold story of how Darwin's abhorrence of slavery led to our modern understanding of evolution" (p. xxi). This is especially surprising given that Darwin categorized all the humans races as members of the same species.

When we turn to philosophers of biology and biologists devoted to a historical understanding of Darwin, we find an entirely opposite situation, marked by lots of publications on Darwin's species concept and lots of different answers. In order to indicate the current state of scholarship on this topic, what may be called *the problem situation*, I want to confine myself to a summary of five publications from the past few years. The methodology they share is basically the history of ideas approach, but clearly something else is going on, much of it arguably not history in any sense of the term.

We begin with a book by the philosopher John Wilkins [7], which is devoted entirely to a detailed examination of the history of the concept of biological species. His book explicitly is not an example of contextualist history of science but instead is written in the tradition of history of ideas, and hence is "a conceptual history" (p. ix). His purpose, moreover, is not simply to do history for the sake of history but to make a contribution to the present debate on "species" in biology and philosophy of biology. In the very least, he says, "Knowing the past may also help scientists to avoid repeating it unnecessarily" (p. 7). He recognizes that "Darwin acts as a focal point" (p. 5) in the history of the debate, not only because Darwin did have something to say about the nature of species but because the *Origin* "changed *every* scientist's way of looking at species thereafter" (p. 130). Accordingly Wilkins devotes an entire chapter to "Darwin and the Darwinians." Here, through roughly twenty pages of analysis of Darwin's writings from his mature period, we find that Darwin "presents species as real," that he thought that species as "*groupings*" of organisms exist in nature and are not necessarily arbitrary like constellations, but that he did not think of species "as a formal and fixed rank" (p. 144). The claim seems to be the same as that developed by John Beatty [8], who in this respect followed the original claim of Michael Ghiselin [9], which is that Darwin was a species taxa realist but not a species category realist and accordingly did not have a species concept. Wilkins [7] tels us that "Darwin was not a cladist, but he was pretty close to it" (p. 153), that Darwin was "not a nominalist but a pluralist with regard to what makes a species distinct" (p. 158)—elsewhere he states that "he was a pluralist as to the degree of difference between, and causes of, species" (p. 230)—and that "in the end, Darwin proposed a 'snowflake' theory of species: all members are alike in some ways, but they are also unique individuals" (p. 158). In the last few pages of his book, in his summary, Wilkins states that Darwin's work was "perhaps the first and most complete attempt to deal with the implications of the transmutation of species" (p. 231) and he seems to add that Darwin got it basically right. This is because "the standard stories and assumptions from the architects of the modern synthesis are often simply incorrect" (p. 233), such that "We might stop trying to overgeneralize species concept(ion)s or species mechanisms to all species" (p. 234).

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Second in our list is a chapter on Darwin on "species" by the philosopher Phillip Sloan [10]. In his chapter Sloan is mainly concerned with historical influences which he believes impacted on Darwin's species concept. Linnaeus crystallized what Sloan calls the "species$_L$" approach to species, which was logical and classificatory, based on necessary and sufficient criteria for class membership, while Buffon crystallized the "species$_H$" approach, which was historical and ontological. Immanuel Kant attempted to systematize the distinction, Charles Lyell framed the question about the reality of species in terms of species$_L$, whereas Johann Jacob Bernhardi framed the question about the reality of species in terms of species$_H$. Darwin, it is then argued by Sloan, employed and "synthesized" both traditions in *Natural Selection* and then in *Origin*, the species$_L$ tradition in characterizing species as "tolerably well-defined" at "any one period" and the species$_H$ tradition when he "interprets species and varieties as genealogical lineages that display varying degrees of historical relationship" (p. 79).

Third on our list is a paper by the biologists Mark Ellis and Paul Wolf [11]. The paper is devoted to the proper teaching of the concept of species to biology students, which they consider fundamental to the understanding of evolution. Much of their paper is devoted to the history of the concept of species, with Darwin as the hero of the story: "Charles Darwin would finally provide the keys to understanding and accepting the reality of evolving species, breaking the millennial stranglehold" (p. 92). But no actual species concept is explicitly attributed to Darwin. The species concept that they themselves subscribe to, however, and which they imply Darwin would have accepted had he known of it, is the ecumenical species concept developed by the biologist R.L. Mayden [12], his "overarching nonoperational species concept" as they [11] put it (p. 94), which takes most modern competing species concepts as operational only and incorporates them into a hierarchical concept. The proper concept of species, in short, according to these two authors, is that of "organisms in one or more populations that together form a cohesive, reproductive unit—a separate lineage on its own evolutionary trajectory" (p. 90). Mayden himself [12] places the diachronic evolutionary species concept of G.G. Simpson on top of the hierarchy, as the "primary concept" (p. 419), with "all of the other concepts," reckoned as being at least 21 concepts, serving as secondary, operational concepts "at some level" (p. 417).

In a paper devoted to examining why Darwin's view on species was rejected by most twentieth-century biologists, the biologist James Mallet [13] spends some effort in examining those passages in the *Origin* which Ernst Mayr especially (and the many who followed him) made much of, passages which Mallet maintains were either misunderstood in themselves or because they were not taken in their textual context. According to Mallet, in short, Darwin was not confused about species nor was he a species nominalist. Instead, "Darwin had a good idea of what he was talking about after all" (p. 498), which was that species taxa are delimited by "gaps in morphology in nature" (p. 499). "He believed," adds Mallet, "that species existed, but that they were not 'fundamentally' different from varieties, and that they did not have essences." Hence varieties for Darwin were "incipient species" and in explaining the origin of varieties and species Darwin also explained why "borderline cases" are to be expected. In all of this, Mallet adds still further, "we appear to be returning to more

Darwinian views on species, and to a fuller appreciation of what Darwin meant" (p. 498). This is because "Today, genetic markers are available and widely used to delimit species, for example using assignment tests: genetics has replaced a Darwinian reliance on morphology for detecting gaps between species" (p. 497). Again: "Darwin's view of species as clusters of similar individuals separated by gaps remains relevant today. Species are multilocus genotypic clusters that retain identity when in sympatry with close relatives" (p. 502). Darwin, then, according to Mallet, was not only right to focus on morphological gaps in delimiting real species in nature but should be viewed as the father of the genetic marker approach to species and speciation.

Finally, in a paper devoted to examining "Darwin's solution to the species problem," the philosopher Marc Ereshefsky [14] explicitly follows Ghiselin [9] and Beatty [8] in interpreting Darwin as a species taxa but not species category realist: Darwin's "skepticism of the species category did not extend to taxa, and in particular those taxa called 'species'" (p. 409). Ereshefsky also follows Beatty in holding that Darwin maintained the reference of the species taxa so designated by his fellow naturalists and that he did this for "pragmatic reasons" (p. 421). But Ereshefsky goes beyond Ghiselin and Beatty when he argues that Darwin was basically right. According to Ereshefsky, different modern species concepts pick out different real taxa and modern biology requires a pluralism of species concepts in order to adequately capture the diversity of life. Darwin, says Ereshefsky, rejected the reality of the species category "based on his skepticism of the species/variety distinction," whereas modern biology "implies that Darwin's skepticism of the species category is correct" (p. 425) because it has uncovered a heterogeneous lot of real taxa in the world called "species" (reproductively isolated, phylogenetic, ecological, asexual, etc.), taxa that are equally meaningful in terms of information, prediction, and explanation. Given that this is so, given that disagreement over the definition of "species" has actually increased in biology, and given the enormous impracticality of removing the term "species" from the biological lexicon, Ereshefsky concludes that "Current biological theory confirms Darwin's solution to the species problem" (p. 410).

3. Problems with the current state of scholarship

One thing that is remarkable about the five recent publications summarized above is how different their understandings are of what Darwin meant by "species." After decades of research and publications on what Darwin meant by one of the central terms in what is now called "the Darwinian revolution," there is still no consensus on what Darwin meant by "species," and little of what might be called progress on the matter. To be sure, few if any accuse Darwin any longer of being an outright species taxa nominalist, but there is no consensus on where Darwin stood concerning the binary categories that virtually define the modern species problem: category monism or pluralism, speciation monism or pluralism, taxa as primarily horizontal or vertical, taxa as process or pattern/product entities, taxa as classes or individuals (or something else), taxa as monophyletic or polyphyletic.

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There is something further that is striking about the publications examined in the previous section. With the exception of Sloan, each of the other authors remind me of a phenomenon Albert Schweitzer observed over a hundred years ago in his *The Quest of the Historical Jesus*, first published in German in 1906. Examining many biographies of Jesus, Schweitzer found that each author of a *Life* tended to infuse into the teachings of Jesus his or her own theological beliefs, liberal or otherwise, instead of remaining neutral and objective. As Schweitzer put it in his autobiography [15], speaking of the individuals in the field collectively, "we managed to interpret Jesus' teaching as if it were in agreement with our own worldview" (p. 55). Here surely is a research project for a bright young graduate student, the quest of Darwin's species concept from 1859 to the present.

The fundamental point is that if we really want to get to the history of the matter, if we really believe it is possible to reconstruct to a significant degree what was going on inside Darwin's head when he wrote about species (taxa and category), the first thing we have to do is to completely put aside our preferred solutions to the species problem. In short, what we have to do is make a serious effort to avoid the evil that historians calls *presentism*, which is reading the present (whether personal or collective) into the past, in this case reading into Darwin's writings what we think species are.

The second thing we have to do is to look beyond Darwin's various definitions of "species." Looking to the *Origin* [5] alone, it is very easy to conclude that Darwin was a species nominalist, that he thought that the species category (as it is now called) is completely manmade and that the designation of organisms into species taxa is likewise manmade. In the final chapter, for example, he says, "systematists will have only to decide (not that this will be easy) whether any form be sufficiently constant and distinct from other forms, to be capable of definition; and if definable, whether the differences be sufficiently important to deserve a specific name" (p. 484). Again, "In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience.... we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species" (p. 485). Or one could go outside the *Origin* and focus on its predecessor, Darwin's unfinished *Natural Selection* [16], as the historian Gordon McOuat [17] does, which he says provides Darwin's "only one clear definition of species in any of his work" (p. 4n10), which is: "In the following pages I mean by species, those collections of individuals, which have commonly been so designated by naturalists" (p. 98).

To say that we should "look beyond" Darwin's definitions is not to say that we should ignore them. But it is to say that we have to look deeper. At this point a famous injunction of Wittgenstein comes strongly to mind, as found in his *Philosophical Investigations* [18]. I am not a "Wittgensteinian," a philosopher who believes that philosophy should be confined to conceptual elucidation, but Wittgenstein described part of the elephant of meaning when we wrote that "For a *large* class of cases... the meaning of a word is its use in the language" (§43). Hence his repeated injunction when trying to figure out the meaning of a word: "don't think, but look!," "*look and see*" (§66). This is the motto that should guide research into Darwin's species concept, given the collective muddle of conflicting claims

over what Darwin meant by "species." In other words, one should be willing to "do a Wittgenstein" on Darwin.

What this means is that we have to look beyond and get over what Darwin *says* about species, whether about the term or about species taxa in general. That information might prove to be important at some point (I believe it is important), but it would be none but a superficial analysis to leave it at that. To really be able to see whether Darwin had a species concept, and what it was if he had one, we have to turn mainly to his *use*, to what he *does* with particular species designations. This will be no easy matter, as the writings Darwin left us are enormous. But it is what we must do if we want to determine whether Darwin actually employed a species *concept* throughout his writings. To have a concept, of course, does not necessarily mean that one has a definition (although one might). But if one repeatedly and consistently applies a term in a variety of contexts, then it is legitimate to suppose that a concept is in operation, with rules for its use, involving a meaning. It might be a "family resemblance" concept, as Wittgenstein claimed is the case for the term "game," or it might be a concept where every example of its use has features "common to them all." The only way to know is to "look and see."

In the case of Darwin on "species," many have thought and continue to think that in his early period he employed something like the modern biological species concept, which is based on reproductive isolation. But that is not the period in his life that should mainly concern us. Instead, if we want to speak of "Darwin's species concept," we should want to focus on his *mature* period as an evolutionist, which should probably include his barnacle work given its role in the redevelopment of his theory of evolution and that it immediately preceded his work on *Natural Selection*, which he intended to be his scientific case for evolution to the world.

The catalyst for my own research on this topic [19, 20] was John Beatty's often-cited paper [8]. At the core of his thesis is the claim that

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His species concept was therefore interestingly minimal: species were, for Darwin, just what expert naturalists called "species." By trying to talk about the same things that his contemporaries were talking about, he hoped his language would conform satisfactorily enough for him to communicate his position to them. [p. 266]

In all of this Beatty was taking the thesis of Michael Ghiselin [9] a step further, who argued, again, that Darwin was a species taxa realist but not a species category realist. What is remarkable, as I point out in my book, is how many biologists, philosophers of biology, and even historians of biology followed Beatty in his central claim. No one, as far as I could find, ever thought to test Beatty's thesis empirically. Scientists routinely think of ways to test novel and even established theories, but this habit of thinking is typically missing in the humanities.

The point of it all is that Beatty's theory can indeed be tested. And the way to test is to "do a Wittgenstein" on Darwin's writings, focusing on his mature period. What this means is that

we need to go through Darwin's writings much as a paleontologist goes through strata, looking for patterns that perhaps everyone else has missed. In the case of Darwin this means going through not only his books, such as *Origin* and *The Descent of Man*, but also his articles, letters, and marginalia. This is no small task, given the enormous amount of writings that Darwin left to us, but the effort is richly rewarding. What follows is a representative sample of my own efforts in this regard, some from the larger sample in my book but noticeably improved, and some entirely new.

In looking at these examples, it should become apparent that Darwin did not simply follow the species designations of his fellow naturalists. But what is especially significant is why Darwin deviated when he deviated from the species designations of his fellow naturalists. This is in fact the key to unlocking the door to what Darwin really meant by "species." In what follows, what is required on the part of the reader to fully grasp this key and to see what is behind the door is not only a considerable degree of patience, but also a strong ability to perceive a recurring pattern, what may rightly be called a kind of *scientific imagination*.

4. Evidence from Darwin's barnacle work

As a preliminary, we need first to juxtapose two claims made by Darwin in the *Origin* [5]. The first is that, "To sum up, I believe that species come to be tolerably well-defined objects, and do not at any one period present an inextricable chaos of varying and intermediate links" (p. 177). The second is that, "Lastly, looking not at any one time, but to all time, if my theory be true, numberless intermediate varieties, linking most closely all the species of the same group together, must assuredly have existed" (p. 179). From these passages alone, it should be clear that Darwin, to use modern terminology, thought of species taxa as real and that their reality is primarily horizontal or synchronic. This is not to say that he excluded the extension of the reality of species taxa over long stretches of time. What he has to say about "living fossils" (pp. 107, 486), along with the fact that he capitalizes species E and F in his one and only diagram in the *Origin*, species "either unaltered or altered only in a slight degree" (p. 124), indicates that he allowed a vertical or diachronic reality to species taxa. But the reality of species taxa was for him still primarily horizontal or synchronic—evidenced alone by the fact that he twice calls species F^{14} a "new species" (pp. 117, 124).

The above should make it clear that Darwin was not a cladist, or a proto-cladist, or that he anticipated the theory of punctuated equilibria. Nevertheless, what Darwin often said about the "natural system" of classification in his scheme as being primarily genealogical, that "all true classification is genealogical; that community of descent is the hidden bond which naturalists have been unconsciously seeking" (p. 420), has led many to believe otherwise, to believe that Darwin was a proto-cladist, taking genealogy entirely as the basis of classification [21, p. 356], and that he believed species to be spatially limited and temporally extended individuals [9, p. 85]. What Darwin actually did with species designations, however, especially when he went against his fellow naturalists, should make it clear enough that he thought of species taxa as primarily horizontal entities and that he did not

employ a concept of monophyly, in whatever way the latter is defined today, as part of the ontology of species taxa.

But first, did Darwin really believe that at any one time most species are "good species"? To answer this question we need to turn to Darwin's most important contribution to taxonomy, namely, his eight grueling years of work on barnacles from 1846–1854, mainly for which he received the Royal Medal of the Royal Society in 1853. What struck Darwin more than anything else right from the start was the amount of variation in barnacles. As he puts it in his volume on the Balanidae [22], "it is hopeless to find in any species, *which has a wide range, and of which numerous specimens from different districts* are presented for examination, any one part or organ—which from differing in the different species is fitted for offering specific characters—absolutely invariable in form or structure" (p. 155). And yet, when we turn to Darwin's pages devoted to the genus *Balanus*, which for Darwin was the largest genus of barnacles and which he considered to have "an especial amount of variation" (p. 156)—and which accordingly caused him the greatest frustration—we find that of the 45 species he describes, most of the species, once they are "disarticulated," are described as good species: as "quite distinct species," as "well-marked species," as "well-defined species," as "strongly characterized species," and so on. At this point he was almost near the end of his eight years of taxonomic work on barnacles, and Darwin never did formal taxonomy again, so that when he says in the *Origin* that "species come to be tolerably well-defined objects, and do not at any one period present an inextricable chaos of varying and intermediate links," we need to take him at his word.

Darwin, of course, was not with his barnacle work trying to communicate his theory of evolution by natural selection to his fellow naturalists. He had not yet made public his evolutionism, and was still working on preparing his case, which had to be as empirical as possible to be accepted as scientific. So there is no point asking whether he was following his fellow naturalists here in what they *called* "species." What needs to be asked at this point, instead, is on what basis Darwin made his species. Barnacle taxonomy prior to Darwin was an enormous mess, not only because the "book species" and even "book genera" were given different names by different taxonomists, the problem of synonymy, but because barnacle taxonomy had been done based only on external characters. As Darwin puts it in one of his letters at the time, "not one naturalist has ever taken the trouble to open the shell of any species to describe it scientifically" [23, p. 207].

What we need to do, then, is to look and see how Darwin made his "book species" of barnacles. What he did for barnacle taxonomy was entirely new: he focused mainly on the anatomy of the organisms. He found much variability, to be sure, but again, even in the highly variable *Balanus*, Darwin concluded that most organisms divided into good species, as noted above.

But what made a "good species" *good*? If we are to find an origin for Darwin's mature species concept, Darwin's only major taxonomic work would seem the natural place to start. Interestingly, in the same volume in which he deals with *Balanus*, Darwin [22] states quite clearly that "In determining what forms to call varieties, I have followed one common rule: namely, the discovery of such closely allied, intermediate forms, that the application of a

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specific name to any one step in the series, was obviously impossible; or, when such intermediate forms have not actually been found, the knowledge that the differences of structure in question were such as, in *several allied forms*, certainly arose from variation" (p. 156). In other words, Darwin was much more of a lumper than a splitter. And yet in the largest and most variable genus, *Balanus*, Darwin found that most species were good species.

But there is more to the matter. It wasn't simply continuity in traits between barnacle specimens punctuated by gaps that defined species taxa for Darwin. There were "specific or diagnostic characters" that Darwin used to distinguish one barnacle species from another (p. 1). The amount of detail in Darwin's anatomical work is staggering, and it must be kept in mind that the specific functions of many of the internal parts that he studied were either unknown or imperfectly known. Yet Darwin marched on. Confining ourselves to *Balanus*, an instructive example is that of *B. improvisus*, a species hitherto unrecognized by Darwin's fellow naturalists, having been confused with either *B. crenatus* or *B. balanoides* (p. 252), the latter two usually confused together as well (p. 261). Darwin recognizes *improvisus* as a distinct species, not only because of differences in many fine points of anatomy, such as in teeth and thoracic cirri, but mainly because it is adapted to both freshwater and saltwater, and saltwater is a "deadly poison" to most species of the genus (p. 253). *B. balanoides* is indeed not adapted to salt water (p. 272), though with *crenatus* Darwin doesn't say either way. *B crenatus*, however, unlike the other two, has a "great geographical range" (p. 264), from the tropics to the arctic. *B. improvisus* extends from the tropics only northward to Britain. *B. balanoides* is a "tidal species," confined to shallow water apparently for the need of air (p. 272), and is found only along the coasts of the north Atlantic. In all of this, it becomes apparent that the "specific or diagnostic characters" that Darwin is aiming at are ultimately adaptive ones.

This becomes more evident when we look at his designation of varieties for each of the above three species. Only some longitudinal lines distinguish *var. assimilis* from *B. improvisus*, and "it is impossible to consider so trifling a character as specific" (p. 252). *B. crenatus* is not designated any varieties, which is surprising given its great range. *B. balanoides* is given one variety, which Darwin simply calls "the remarkable variety (*a*)," and it is interesting to see why it is not designated as a species by Darwin. He gives four reasons, the two most important of which are: (i) "all the characters by which this variety differs from the common *B. balanoides*, are those which are variable in the latter," and (ii) there are specimens from Ayrshire, located on the shores of south-west Scotland, such that "it was impossible to decide whether to rank the Ayrshire specimen under *var*. (*a*) or under the common form, so that I was compelled to give up *var*. (*a*) as a species" (pp. 270–271). This last reason speaks to Darwin's "one common rule" above, while the former speaks to the lack of a distinguishing adaptation.

The period from 1846, when Darwin began his work on barnacles, to 1856, when he began his big book on species, *Natural Selection*, was one during which Darwin's theory of evolution underwent substantial change. His barnacle work, of course, gave him much of the empirical data that he needed to make his case for evolution by natural selection, specifically, plenty of individual variation. But it also contributed to the development of his "principle of

divergence," his principle of the ecological division of labor, whether it was developed during a period of reflection shortly after his barnacle work [6, pp. 170–184] or was brewing during his barnacle work [24, pp. 101–108]. A further issue concerns Ospovat's [6] claim that even to the end of his barnacle work Darwin retained the belief in perfect adaptation, inherited from British natural theology, which he combined with intermittent selection, and only changed it shortly thereafter to relative or imperfect adaptation combined with the constancy of natural selection and the principle of divergence, all of which makes its first appearance in *Natural Selection* [pp. 2–3, 205–207]. Throughout all of this the temptation is to think that Darwin's species concept, assuming for the moment that he had one, might also have undergone a change. I have argued nevertheless that in Darwin's barnacle work it is already possible to discern a species concept that distinguishes species primarily by different adaptations. What I shall now argue is that, when we turn to Darwin's *Origin* and beyond, this picture becomes much clearer, such that it becomes possible to speak confidently of "Darwin's mature species concept." (We could also begin with *Natural Selection*, but the nature of the *Origin* as an "Abstract" of the former makes it the more desirable choice.)

5. Evidence from the *Origin* and beyond

Beginning with the *Origin* [5], then, what proves especially instructive is when we look at the particular cases where Darwin went *against* the species designations of his fellow naturalists, the cases that empirically falsify Beatty's central claim. The striking fact is not only that there are plenty of examples, but that in example after example there is a recurring pattern, which not only indicates that a species concept on Darwin's part was in operation, and a consistent one at that, but that it is possible to actually reconstruct his species concept, especially if we pay close attention to the details and do some cross-referencing.

A good example to begin with is Darwin on primroses and cowslips. In the *Origin* Darwin tells us that primroses and cowslips are "united by many intermediate links" (p. 50) and so are "generally acknowledged to be merely varieties" (p. 485), which Darwin on the latter page states as a matter of principle: "for differences, however slight, between any two forms, if not blended by intermediate gradations, are looked at by most naturalists as sufficient to raise both forms to the rank of species." But intermediate links was not the fundamental linking principle. Instead it was the creationist principle of common descent, which in the minds of many naturalists allowed for the production of varieties by secondary laws. As Darwin puts it, returning specifically to the case of primroses and cowslips, "every naturalist has indeed brought descent into his classification.... He who believes that the cowslip is descended from the primrose, or conversely, ranks them together as a single species, and gives a single definition" (p. 424). Darwin himself believed that primroses and cowslips "descend from common parents" (p. 50), by which he meant a common parental species, but nevertheless he did not follow his fellow naturalists and call primroses and cowslips merely varieties. He tells us that "it is very doubtful whether these [intermediate] links are hybrids." But more importantly, he tells us that "These plants differ considerably in appearance; they have a different flavor and emit a different odour; they flower at slightly different

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periods; they grow in somewhat different stations; they ascend mountains to different heights; they have different geographical ranges; and lastly, according to numerous experiments made during several years by that most careful observer Gärtner, they can only be crossed with much difficulty. We could hardly wish for better evidence of the two forms being specifically distinct" (pp. 49–50).

The last reason in the list above was apparently thrown in by Darwin for rhetorical effect. For a start, Darwin argues later in the *Origin*, against the majority of his fellow naturalists including Kölreuter and Gärtner, that "neither sterility nor fertility affords any clear distinction between species and varieties" (p. 248). Secondly, unlike the other differences between primroses and cowslips that Darwin lists above, sterility between species was not believed by Darwin to be a product of natural selection, only a byproduct, and so not an adaptation. As he puts it in the *Origin*, the sterility (of whatever degree) "of first crosses and of hybrids... is not a special endowment, but is incidental on slowly acquired modifications, more especially in the reproductive systems of the forms which are crossed" (p. 272). This was to remain Darwin's view, with a brief possible exception occurring in late 1862, during which he toyed with the idea that sterility between species might possibly be selected [25, pp. 700–711]. Third and finally, as we examine more cases of where Darwin went against his fellow naturalists in calling a form a "species" or not, it will become apparent that he was amazingly consistent—either explicitly or implicitly—in appealing only to adaptations produced by natural selection.

Darwin, of course, knew of what today are called "sibling species," species so outwardly identical that biologists confused them as one species until innate reproductive isolation was discovered between them. As he puts it in the *Origin* [5], "many species there are, which, though resembling each other most closely, are utterly sterile when intercrossed" (p. 268). But it should not be assumed that reproductive isolation was part of his own species concept. A case in point is willow wrens, which Darwin refers to in a number of places in his writings. As he puts it in *Natural Selection* [16], they are "so close that the most experienced ornithologists can hardly distinguish them," especially given that they "inhabit the same country [? county]," and yet they are "undoubted species." But Darwin never mentions reproductive isolation in any sense, only adaptive characters, such as differences in "their voice, & the materials with which they line their nests" (p. 99).

Returning to the case of primroses and cowslips, what needs to be noticed is that the rest of Darwin's reasons for distinguishing them as two species speak to adaptation by natural selection, especially his phrase "different stations," which is borrowed from the distinction between "stations" and "habitations" emphasized by Charles Lyell [26, p. 69], and which today would be translated as "niches" and "habitats." That Darwin does not explicitly appeal to differences in adaptation between primroses and cowslips in the passage we examined above is possibly because his chapter on natural selection was not to come for another two chapters. But that Darwin's real focus was exclusively on adaptations produced by natural selection will become abundantly evident as we look at more examples.

We are not quite finished, however, with primroses and cowslips. At the end of the *Origin* [5] Darwin repeats that in classifying primroses and cowslips as two species instead of one

he is going against his fellow naturalists. He says, "It is quite possible that forms now generally acknowledged to be merely varieties may hereafter be thought worthy of specific names, as with the primrose and cowslip; and in this case scientific and common language will come into accordance" (p. 485). In using the word "generally" Darwin might possibly have misunderstood, misremembered, or even misrepresented botanists in the classification of primroses and cowslips. As Darwin's friend the botanist H.C. Watson [27] pointed out many years earlier, Linnaeus had indeed classified primroses as one species with cowslips as a "subordinate" variety, but, says Watson, "This view will scarce find favour in the eyes of those botanists who labour under the 'species-splitting' monomania" (p. 219). Linneaus himself had complained of the mania for splitting among his fellow botanists, the making of species out of mere varieties, as had Lamarck after him and not only Watson but J.D. Hooker in Darwin's day. But even worse, in a companion paper published in the same issue, which Darwin refers to in his correspondence and in *Natural Selection*, Watson [28] states that the "prevailing opinion" (p. 145), the "majority" view among naturalists (p. 161), is that primroses and cowslips are "truly distinct species." Then again, Darwin might simply have been confused about the situation, since in the *Origin* [5] he actually misnames the common primrose and the common cowslip "Primulaveris and elatior" (p. 49), a point corrected by Watson in a letter to Darwin shortly after the publication of the *Origin* [29, p. 408]—it should have been *Primula vulgaris* and *Primula veris*, a matter of naming he had previously gotten right in *Natural Selection* [16, p. 128], in which he concludes that "common practice & common language is right in giving to the primrose & cowslip distinct names" (p. 133). But no matter. In all of this the point still stands: Darwin in the *Origin*, if we take him at his word, believed that he was going *against* the classification of primroses and cowslips by his fellow naturalists, and it is important to see why.

Darwin's reasons for going against his fellow naturalists (assuming such) are remarkably similar to his position on the races of man in *The Descent of Man* [30]. The big debate, of course, was over whether the races of man are subspecific (monogenism) or specific (polygenism). Darwin defended monogenism, the view that the human races (whatever their number) are all of one species, and it is important to see why. Darwin readily acknowledges, as he puts it in his concluding chapter, that some of the races of man, "for instance the Negro and European, are so distinct that, if specimens had been brought to a naturalist without any further information, they would undoubtedly have been considered by him as good and true species" (p. 388). And yet in his chapter on the races of man, Darwin argues that "Those naturalists, on the other hand, who admit the principle of evolution,... will feel no doubt that all the races of man are descended from a single primitive stock" (p. 229). This was because of "a close agreement in numerous small details," all suggesting descent "from a common stock" (p. 233). Darwin takes it, however, that "the most weighty of all the arguments against treating the races of man as distinct species, is that they graduate into each other, independently in many cases, as far as we can judge, of their having intercrossed" (p. 226).

As we have seen, Darwin also argued that primroses and cowslips descended from a common stock and had between them numerous intermediate links, which he did not think were the result of intercrossing, and yet he went against his fellow naturalists (or so in the

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Origin he apparently thought) and classified primroses and cowslips as separate species. But when it comes to the races of man he does not classify them as separate species, and once again it is quite informative to see why.

It was not because he thought the human races are interfertile. Darwin was well aware that there were naturalists who claimed empirically that some of the human races had a low degree of fertility between them, and that the children of mixed parentage were either low in fertility or low in vitality. He rejected the evidence as being "almost valueless" (p. 220). But what is important is his claim that even if he was proved right, even if "it should hereafter be proved that all the races of men were perfectly fertile together," nevertheless "fertility and sterility are not safe criterions of specific distinctness" (p. 222), a claim, as we have seen above, that he had made earlier in the *Origin*.

Darwin's reasons were different, even though he recognized that geographically there is a "considerable amount of divergence of character in the several races" (p. 234). For a start, he claims that "as far as we are enabled to judge (although always liable to error on this head) not one of the external differences between the races of man are of any direct or special service to him" (pp. 248–249). In other words, Darwin does not believe that the external differences used to distinguish human races, such as skin color, hair, and the shape of the nose, are adaptations, and so he does not believe that they were produced by natural selection. Instead he thinks that they were produced by "Sexual Selection" (pp. 249–250), and as a simple matter of varying concepts of beauty between the races (pp. 338–384). Consequently he does not think of external racial differences as adaptations at all.

And what of internal characters, particularly social, moral, and intellectual faculties such as reason and language? Here again, although Darwin does not refrain from ranking human races as higher and lower, in the very least as more civilized and less civilized, with the superstition and cannibalism of the Fuegians among the lowest, he nowhere argues that the differences are a matter of different adaptations, but instead treats them only as a matter of degree. As Darwin puts it in a characteristic passage, "The American aborigines, Negroes and Europeans differ as much from each other in mind as any three races can be named; yet I was incessantly struck, whilst living with the Fuegians on board the 'Beagle,' with the many little traits of character, shewing how similar their minds were to ours; and so it was with a full-blooded negro with whom I happened once to be intimate" (p. 232). And it is surely significant that a year prior to when he began writing *Descent*, when Darwin was only planning "a little essay on the Origin of Mankind," he would write in a letter to Wallace that "I still strongly think... that sexual selection has been the main agent in forming the races of Man" [31, p. 109].

Of further significance are the differences Darwin [30] drew between natural selection and sexual selection. Even though he states that "in most cases it is scarcely possible to distinguish between the effects of natural selection and sexual selection" (p. 257), he also states that sexual selection "acts in a less rigorous manner than natural selection" (p. 278), since natural selection is a matter of "life or death at all ages" and sexual selection rarely results in death and only begins its operation at the age of reproduction. In addition, sexual selection has no limits to the process unless when checked by natural selection, so that the products of

natural selection, which are about "the external conditions of life," are "rather more perfect" (p. 279) and sexual selection will be "dominated by natural selection for the general welfare of the species" (p. 296). This is not to say that sexual selection cannot produce genuine adaptations in Darwin's view; it can, but they are not the kind of adaptations that would distinguish species, not only because, as he puts it in the *Origin* [5], "no one dreams of separating them [the two sexes]" (p. 424), given that male and female are not separate populational entities and sexual dimorphism is inherited from common parents, but because modifications produced by sexual selection, at best, are adaptations only in a secondary sense, since they do not (or generally do not) contribute to the survival of the organism and its fit in what Darwin repeatedly calls "places" in "the economy of nature" (e.g., pp. 81, 315).

This brings us to a process related to natural and sexual selection and a case related to Darwin on the races of man, namely, Darwin on domestic pigeons. In the *Origin* [5] Darwin states that "Altogether at least a score of pigeons might be chosen, which if shown to an ornithologist, and he were told that they were wild birds, would certainly, I think, be ranked by him as well-defined species. Moreover, I do not believe that any ornithologist would place the English carrier, the short-faced tumbler, the runt, the barb, pouter, and fantail in the same genus" (pp. 22–23). This is similar to Darwin's statement above on what a non-evolutionary naturalist would conclude about the races of man based on specimens "without any further information," that he would conclude that they represented "good and true species." But the case of pigeon breeds introduces some interesting differences, and not only that it was not a hot-button politically-charged topic.

In response to a request from T.H. Huxley for written sources on domestic breeding so as better to defend Darwin in a lecture he was preparing, Darwin in his first reply letter states that he knows of "no one Book" and that he "found it important associating with fanciers & breeders" [29, p. 404]. Less than three weeks later he wrote Huxley again supplying an "enclosure" containing some direct quotations from two books on pigeon breeding by John Matthews Eaton, a prize-winning pigeon breeder and also a friend of Darwin's. In those quotations Eaton refers to the different breeds of domestic pigeons as different "species" (p. 429). Darwin remarks in his letter that if Huxley could see the drawings which Darwin himself has, then Huxley "would have grand display of extremes of diversity" (p. 428). Darwin therefore had a good reason to follow Eaton and others and designate the different breeds of pigeons as different species. But he did not do this. Instead, both in his letter to Huxley and in the *Origin* [5], Darwin repeatedly refers to the different breeds as all one "species" (pp. 20–28), a practice he would continue in *Variation* [32 I, chs. V and VI].

The reason for this cannot simply have been that Darwin [5] thought that all the domestic breeds were derived from a common stock, the rock pigeon, *Columba livia* (p. 23). If that were his reason then he also would have had to designate primroses and cowslips as a single species, because, as we have seen above, he thought they were all derived from a common stock, too. The reason, it turns out, is because primroses and cowslips were evolved by natural selection whereas domestic pigeons were evolved by artificial selection, and there is a substantial difference in product between the two processes. As Darwin puts it in the *Origin* (pp. 83–86), natural selection acts "on every shade of constitutional difference" and pro-

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duces adaptations, which are for "the good of the being," whereas artificial selection acts only on "external and visible characters," and "only" for the good of the breeder. Moreover nature has tens of thousands and ultimately millions of years for the operation of natural selection, whereas the wishes and efforts of man are "fleeting," his time is "short," so that "how poor will his products be, compared with those accumulated by nature during whole geological periods." Thus, for Darwin, "nature's productions should be far 'truer' in character than man's productions" and "should be infinitely better adapted to the most complex conditions of life." Elsewhere in the *Origin* he states that natural selection "is as immeasurably superior to man's feeble efforts, as the works of Nature are to those of Art" (p. 61). Similarly in *Variation* [32 I], just before summarizing his two chapters on pigeons, Darwin states that "It is not likely that characters selected by the caprice of man should resemble differences preserved under natural conditions either from being of direct service to each species, or from standing in correlation with other modified and serviceable structures" (p. 233). In short, Darwin did not call different pigeon breeds different "species," although it clearly would have aided his argument for evolution in the eyes of many, because he did not want to equivocate on the term "adaptation." Natural selection, and natural selection alone, produces genuine, real adaptations—based on the original meaning of the term in natural history as a possessive, namely, a complex (not simple) heritable trait or behavior that benefits the organism that has it in what Darwin [5] calls the "struggle for life" or "struggle for existence" (pp. 61–62).[1] Artificial selection, on the other hand, does not produce real adaptations (although it could in principle), which is why primroses and cowslips are different species in Darwin's view but not the different breeds of domestic pigeon.

Sports or monstrosities provide another interesting test category, cases of saltation (sudden origin), which some of Darwin's fellow naturalists classified as new species but which in every case Darwin refused to accept as such. In *Variation* [32 I] he discusses the Himalayan breed of rabbit, which is born albino but develops brownish-black ears, nose, feet, and upper tail, and which if kept separate breeds true. Darwin, however, rejects the status of *Lepus nigripes* as a distinct species, arguing that its distinctive characters are a matter of "reversion, supervening at different periods of growth and in different degrees, either to the original black or to the original albino parent variety" (p. 115).

Another example is the "'japanned' or 'black-shouldered'" form of peafowl, of which there were a number of cases in Great Britain, which bred true, and at least one "high authority" named it a distinct species, *Pavo nigripennis*. In *Variation* [32 I], however, Darwin refuses to call it a "species," but instead a "strongly marked variety or 'sport', which tends at all times and in many places to reappear" (p. 307). In a letter written a number of years earlier, Darwin wagers that it will "prove a variety,—hardly more surprising in its origin, than the so-called Himalayan rabbit" [25, p. 193].

1 Darwin's concept of adaptation included two important additions. One is that an organism can have an adaptation that benefits it very little or not at all but that fully benefitted its ancestors. He calls these structures and organs "rudimentary" (pp. 450–456). The other important addition is that in social animals some adaptations do not benefit the organism that has it but instead the social group, the "community," of which the organism is a part (pp. 87, 202–203).

A similar case is a variant of *Begonia frigida* that had arisen by saltation in the Royal Botanic Gardens at Kew. William Henry Harvey, the professor of botany at Trinity College, Dublin, wrote about it as a case against Darwin, not only as a distinct species but, if it had been discovered in nature, as possibly the type of a distinct order. In his letters on the topic, Darwin refers to such monstrosities as distinct "forms" [33, p. 102] but never as "species." As he puts it in a letter to Asa Gray on the topic of adaptation by sudden variation, "There seems to me in almost every case too much, too complex, & too beautiful adaptation in every structure to believe in its sudden production" (p. 317). The "almost every case" only indicates that Darwin was not dogmatic on the topic. The same view was elaborated by Darwin a few years earlier in *Natural Selection* [16]: "I cannot believe that in a state of nature new species arise from changes of structure in old species so great & sudden as to deserve to be called monstrosities.... Nor can I believe that structures could arise from any sudden & great change of structure (excepting possibly in rarest instances) so beautifully adapted as we know them to be, to the extraordinarily complex conditions of existence against which every species has to struggle" (p. 319). In all of this the connection between species and adaptations should not be lost, regardless of whether Darwin thought it *possible* that a genuine adaptation could arise by saltation instead of by natural selection.

A related test category for Darwin on species is speciation by hybridization. In the *Origin* [5] Darwin tells us that "The view generally entertained by naturalists is that species, when intercrossed, have been specially endowed with the quality of sterility, in order to prevent the confusion of all organic forms" (p. 245). We should therefore not expect to find naturalists among Darwin's contemporaries who claimed that a new species had arisen by hybridization. And yet there were some who accepted fertility between species, in various degrees, and who even called distinct hybrids "good species" if they bred true. The most famous case prior to Darwin's time is that of Linnaeus, whose experiences with what he named *Peloria*, a new genus which he believed was produced in nature by hybridization, changed his view on species and spawned among his fellow naturalists the purported discovery of a large number of hybrid species [34, p. 148]. They were not contemporaries of Darwin, and yet there were new purported cases of hybrid species in Darwin's day. Perhaps the most famous was the exceedingly beautiful *Bryanthus erectus*, an intergeneric hybrid originally produced by the Scottish nurseryman James Cunningham in 1841. The plant was regularly cultivated in British gardens within the decade, and Cunningham's discovery was mentioned in the commemoration of his death in 1851 in *Gardeners' Chronicle and Agricultural Gazette* of the same year, a journal to which Darwin had long subscribed. Two of Darwin's correspondents during 1863 and 1864 wrote to Darwin about their experiments in breeding the hybrid [35, pp. 18, 79, 81, 98, 353–354, 386; 36, pp. 82, 94]. Darwin did indeed include the name of the purported species in his list of plants for his planned "hothouse" at Down for "experimental purposes" [35, p. 747], which was built in February of 1863. But as Burkhardt *et al.* [36] note, Darwin in one of his reply letters "evidently expressed doubt about Scott's reference to *Bryanthus* as a bigeneric hybrid" (p. 84n11). The species name is not to be found in any of Darwin's published writings, and except for his "hothouse" list it is not to be found in any of his extant correspondence. At any rate, from what we have already seen, it would be surprising to find

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Darwin claim, or accept, that a new species had arisen by hybridization. In fact we should not be able to find a single case, given his belief in the origin of species by means of natural selection.

The above is a case of negative evidence, but the theory itself can be tested, as all theories of history can be tested, namely, retrodictively, by making predictions against the past. My prediction was and continues to be that one cannot find anywhere in Darwin's writings where he calls a hybrid form a new species. I was therefore shocked when Ghiselin [9] states that Darwin, in one of his later papers [37], calls a hybrid form a new species. As Ghiselin puts it, Darwin in his paper on primroses and cowslips "demonstrates that the intermediate form, or oxlip, is a sterile hybrid, and supports this inference by showing that the oxlip occurs where the parent species are present, but not otherwise. The third species is shown to be sterile when crossed with the others, and to be distinct in morphology and in geographical range" (p. 100). If Ghiselin is right, I thought, that Darwin called the oxlip a "species," then my whole theory on Darwin on species is shot to pieces! The paper by Darwin was not one I had read, since it was not included in the collection of Darwin's papers by Barrett [38]. Upon examining the actual paper [37], however, I was relieved, for I found that nowhere in that paper did Darwin call the oxlip a "species." The three species Darwin in that paper refers to are not the primrose, cowslip, and oxlip, but rather the common primrose (*Primula vulgaris*), the common cowslip (*Primula veris*), and the Bardfield oxlip (*Primula elatior*), the latter which Darwin argues "is not a hybrid," and he adds that all three "have as good a right to receive distinct specific names as have, for instance, the ass, quagga, and zebra" (p. 451). The common oxlip Darwin simply refers to as a "hybrid," a taxonomic practice which Darwin continues, along with the three named "true species" above, in his *Different Forms of Flowers* [39, ch. II].

Our final example is taken from Darwin's *Orchids* [40]. In that book Darwin states that "The object of the following work is to show that the contrivances by which orchids are fertilized, are as varied and almost as perfect as any of the most beautiful adaptations in the animal kingdom" (p. 1). In this work Darwin also does not always follow what his fellow naturalists called "species." A case in point is *Habernaria chlorantha*, which the distinguished botanist George Bentham, President of the Linnean Society from 1861 to 1874, had classified as a variety of *H. bifolia* in his *Handbook of British Flora*, published in 1858. In a letter Darwin wrote in 1861 to Bentham, he states that "I must think you are mistaken in ranking Hab. chlorantha as a var. of H. bifolia: the pollen-masses & stigma differ more than in most of the best species of Orchis" [41, p. 185]. In *Orchids* [40] Darwin mentions that Bentham "and some other botanists" rank *H. chlorantha* as a mere variety (p. 73), but Darwin explicitly calls it a "species," not only because it is among "the most wonderful cases of adaptation which has ever been recorded" (p. 44), but also because it is distinguished from *H. bifolia* in "the stations inhabited," and no matter if "these two forms be hereafter proved to graduate into each other" (p. 73).

6. Darwin's species concept and its implications

The modern entomologist Hugh Paterson thought he found in Darwin a precursor of his own species concept, which he called the Recognition Species Concept and which he based on distinct fertilization mechanisms evolved by natural selection. Looking to the first line of Darwin's *Orchids*, which I quoted above, Paterson [42] claims that Darwin there "expresses a view in perfect agreement with the recognition concept" (p. 25). And a few years earlier he would write [43], looking now at Darwin's *Origin*, that "Although Darwin's views were inadequate in detail, for he did not realize that species and varieties were qualitatively distinct, I, nevertheless, accept that they are philosophically ancestral to the recognition concept" (p. 275). Paterson, unfortunately, by a selectivity of evidence, missed seeing that Darwin did not distinguish species only by fertilization mechanisms produced by natural selection but by any and all adaptations produced by natural selection.

Many years earlier the pioneering geneticist T.H. Morgan [44], in a paper devoted to the topic of adaptations, complained that "to-day, accepting evolution,... it is notorious that, by systematists, specific distinctions rest in many cases on differences that have no adaptive significance whatever" (p. 203). Morgan himself says, "from this time forward when I speak of the origin of species I mean the origin of the adaptive characters of species" (p. 204). Surprisingly, both of these statements are taken in the context of a discussion on Darwin's *Origin*, not just on Darwin's theory of natural selection operating on chance variations (Morgan was now over his anti-Darwinism phase), but also on the meaning of the title of Darwin's book. As Morgan puts it, "Darwin's famous book is entitled 'The Origin of *Species*' but his theory of natural selection explains the *adaptations* of living things." What is remarkable is that Morgan failed to realize that his own species concept in his paper comes from Darwin's *Origin*.

Morgan and Paterson are examples of scholars who, unlike the scholars whose very recent works were examined in the second section above, "came close but no cigar," to use a common metaphor. It is time at last for the cigar, for Darwin's species concept, and what we have seen in the previous two sections should give us sufficient confidence that we now have it. Accordingly, using modern language, we may express Darwin's species concept as: *A species is a primarily horizontal population of organisms in the Tree of Life united by common descent and distinguished from other species by at least one organismic or group adaptation*.

Of course, it is not enough to simply have the cigar. We should not simply want to look at it, we should want to smoke it, too. Or to use a better metaphor, we should want to see if "light will be thrown" on Darwin's related activities. I shall now argue that Darwin's species concept, as understood above, reveals a wider consistency (though not perfect) with Darwin's writings than hitherto realized.

For a start, light is thrown on the title of Darwin's most famous book, *On the Origin of Species by Means of Natural Selection*. It was not misnamed such that it should have been "*On the Unreality of Species as Shown by Natural Selection*" [45, p. 143]. The book was properly named because, according to Darwin, (i) natural selection is the one and only process that produces

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those wonders of biology rightly called "adaptations," and (ii) adaptations rightly distinguish one species from another.

Nor can one turn to Darwin's original title for the *Origin* in order to obfuscate the matter, which was *An Abstract of An Essay on the Origin of Species and Varieties Through Natural Selection* [29, p. 270]. The title certainly does not imply that varieties are basically the same as species, for if natural selection and only natural selection produces adaptations it does not follow that natural selection does nothing else. The title is simply consistent with Darwin's view that varieties are "incipient species" and that, as we have seen above, only species are distinguished by adaptations. And it is certainly significant that in a letter to John Murray, dated September 10, 1859, Darwin wrote that he wanted to omit the word "Varieties" from the title, mainly because of an objection raised by "a friend," and added that "The case of Species is the real important point" (p. 331).

In a related matter, light is also thrown on a curious passage that comes at the end of the Introduction to the *Origin* [5], a passage that has misled many, in which Darwin says he is "convinced that Natural Selection has been the main but not exclusive means of modification" (p. 6). "Modification" simply means heritable change. Darwin allowed for many processes which "modify" a species, not only natural selection but also use and disuse, the direct effects of climate, and correlation of growth. But that does not mean he was not a good Darwinian. The latter three causes (along with some others) are discussed together in a chapter Darwin titled "Laws of Variation" (ch. V), not "Laws of Adaptation." But just as important, it needs to be recognized that adaptation is a much narrower concept than modification, and it is a recurring theme in Darwin's writings that only natural selection produces adaptations. All throughout the *Origin* it is clear that the job of natural selection is to explain, not merely the modification of species, but, as he puts it in the Introduction, "that perfection of structure and coadaptation which most justly excites our admiration" (p. 3). Darwin's project, after all, was basically the same as Paley's *Natural Theology*, which Darwin read and greatly admired back when he was a student at Cambridge, a point he emphasizes in his correspondence [29, p. 338] and much later in his *Autobiography* [46, p. 59]. But it was the adaptations themselves, not Paley, that really mattered. As Darwin puts it in his *Autobiography*, "I had always been much struck by such adaptations, and until these could be explained it seemed to me almost useless to endeavour to prove by indirect evidence that species have been modified" (p. 119). The fundamental point is that nowhere in the *Origin* does Darwin credit any explanation for adaptations other than the process of natural selection.

It should also now be clear that Darwin did not really believe that species and varieties were basically the same, even though he made statements in the *Origin* [5] that have the contrary appearance, such as that "there is no essential [or 'fundamental'] distinction between species and varieties" (pp. 276, 278), passages that have fooled many. What is clear from Darwin's *practice* is that species in his view, but not varieties, are distinguished by adaptations. And what makes a variety an "incipient species" is whether any part of it is being worked on by natural selection in the direction of an adaptation. The key is heritable variation. As Darwin puts it in a letter to Hooker, "if a variation be not inherited, it is of no significance to us" [29, p. 297].[2] One might base a variety on a variation that is incapable of being inherited (or if so

capable, that is not profitable to the organism), but it would not be an "incipient species" in Darwin's view (let alone a species).

The focus on adaptations also explains "borderline cases" in Darwin's writings. Varieties, as he repeatedly puts it in the *Origin* [5], are "incipient species" (e.g., pp. 52, 111), and given that the evolution of an adaptation is a very slow process, one taking hundreds if not thousands of generations, borderline cases at any horizontal level in the Tree are only to be expected, cases where expert naturalists—Darwinians at that—cannot determine whether closely allied forms should be classified as varieties or as species. But this should not take away from the fact that for Darwin there are clear cases when an organismic structure or behavior is an adaptation and when it is not.

Darwin's focus on adaptations also throws light on what he says about genealogy and classification, that, as we have seen above from the *Origin* [5], "all true classification is genealogical; that community of descent is the hidden bond which naturalists have been unconsciously seeking" (p. 420). Darwin does not say this because he was a proto-cladist, motivated by producing an objective *method* of classification, one without an appeal to similarity, nor does he say this because he was motivated by the *logic* of individuals as opposed to classes. His motive, instead, was *biological*, based on the fact (as he understood it) that adaptations do not arise in organisms spontaneously but are only transmitted by generation, by the reproduction of one organism by another. It is logically and biologically possible that the same adaptation could arise independently in different lineages, but it still for Darwin is the case that it is mainly by descent that adaptations get shared, even more so that a suite of adaptations get shared. The *origin* of adaptations, of course, is by slow, gradual, cumulative natural selection according to Darwin, but the *transmission* of adaptations is only by reproduction.[3] Hence, given that species are the basal units of taxonomy and that it is only the adaptations in organisms that rightly distinguish for Darwin one species from another, the only legitimate conclusion for Darwin was that classification must be "genealogical." But it would not be exclusively genealogical, for if a species acquires a new adaptation in its evolution (or loses one) without any branching, it would not be numerically the *same* species, a consequence that would make its way up the various taxonomic (manmade) ranks. All of this, and this alone, explains why Darwin in the *Origin* uses the phrase "the *vera causa* of community of descent" (p. 159).

The term *vera causa*, meaning "true cause," brings us to another important point. The science of Darwin's time was based on the *vera causa* ideal, both for scientific explanation and for scientific classification. This was made especially evident in Sir John Herschel's *Preliminary Discourse on the Study of Natural Philosophy* [47], which Darwin had read at least twice (shortly before his *Beagle* voyage and then again shortly after his first reading of Malthus) and which he highly regarded along with its author, who many considered the greatest scientist

2 The point is likewise made in the Origin [5]: "Any variation which is not inherited is unimportant for us" (p. 12). To this should be added a further point that is made: "unless profitable variations do occur, natural selection can do nothing" (p. 82).

3 As Darwin loosely puts in the Origin [5], "the chief part of the organisation of every being is simply due to inheritance" (p. 199).

and philosopher of science of his time [48]. The principal aim of natural science, Herschel argues, is to discover laws of nature, which themselves are the effects of real forces in nature, which Herschel [47] following Newton calls "*vera causæ*" (esp. pp. 18, 76, 91, 104–105, 144). According to Herschel it is only laws of nature that scientifically explain natural phenomena. But Herschel also argues that scientific classification is based on laws. He devotes an entire chapter to scientific classification, in which he distinguishes between "artificial and natural systems of classification in general" (p. 143n). Two of the fields he discusses are botany and mineralogy, each notorious for their "artificial systems" of lumpers and splitters, and it was surely not lost on Darwin that Herschel throughout his book elaborates on the case of mineralogy, which did not have *real* "mineral species" and hence scientific classification until the discovery of the "laws of crystallography" (pp. 123, 139–140, 183, 239–243, 290–296). Accordingly, although Darwin in the *Origin* [5], surprisingly, does not explicitly call natural selection a *vera causa*, he does nevertheless call it a "power" (pp. 61, 109, 205, 454) and a "law" (pp. 244, 472, 489–490), and he clearly expresses his belief that the evolution of species by natural selection is a true theory (pp. 457–458, 481). Little wonder, then, that Darwin would stress in his correspondence following the publication of the *Origin* that he thought of natural selection as a "veracausa" because of its power to explain a variety of phenomena [33, pp. 76, 84, 102, 123]. And little wonder also that Darwin felt it a "great blow & discouragement" when he heard that Herschel had rejected his theory as "the law of higgledy-piggledy" [29, p. 423]. In arguing for *the origin of species by means of natural selection*, Darwin in the *Origin* [5] had attempted to solve "that mystery of mysteries, as it has been called by one of our greatest philosophers [Herschel]" (p. 1) by bringing *both* the origin *and* the classification of species into the scientific domain. Arguing for evolution by natural selection, therefore, did not involve in his mind simply following what his fellow naturalists *called* "species."

7. Deeper implications of Darwin's species concept

Further questions still remain, questions that are more controversial. First, was Darwin a species category realist? Well if he in fact had a realist species concept then it would probably make more sense to categorize him as a species category realist than not. It all depends on what one means by "species category realist." Having a realist species concept might not be a sufficient condition, but I would certainly think it is a necessary one. What is interesting is that if we use Ereshefsky's [14] "minimum threshold" (p. 413) for species category realism, then Darwin as understood in the present chapter would have to be categorized as a species category realist. First, for Darwin not only most but *all* of the taxa *clearly* categorized by him as species share a common feature, namely, a distinguishing organismic or group adaptation (presumably also he would accept a unique set of adaptations). Second, that feature helps us to understand the nature of the members of the category, in that adaptations are not produced spontaneously but only over many generations by the process of natural selection and are transmitted only via reproduction. Third and finally, the feature that distinguishes members of the species category, viz., adaptations, distinguishes those members

from members of other categories, such as the members of genera (the species that make up a genus are not distinguished by *species* adaptations) or the members of ecological categories (members of the predator category, for example, are not distinguished by one or more adaptations that define "predator").

This raises a further question: Is Darwin's species concept seriously flawed because it is parasitic on the concept of adaptation? Some might think so. As Gregory Radick [49] points out, "Now historians have thrown doubt on the naturalness of the Darwinian kind 'adaptation'" (p. 162). They take it to be a social construction—"inseparable from Britain in the age of complex machines and counter-revolutionary theology" (pp. 153–154)—and nothing more. I suspect that most if not all modern biologists would reject this view, not just a few such as Richard Dawkins. (Radick himself makes Darwin's theorizing on species parasitic on the *vera causa* ideal embodied in Whig ambitions for British science and society.) As touched upon in the opening section, I find this kind of contextualist history of science, epitomized by the books by Desmond and Moore [2, 3], not only more suggestive than substantive, but more argumentation by an ideologically-driven cloud of detail than argumentation by logic and evidence including inference to the best explanation. The work ethic is not in dispute here, only the philosophy behind it. The problem is not simply the self-imposed problem found in history of science in general, what the historian Mary Winsor [50] calls the "Taboo Problem," the reluctance to deal with the evidence itself for whether any of the science they study is true (pp. 240–241). The problem, more specifically, is the dogmatic allegiance to a kind of deterministic reasoning that in logic is known as *cum hoc ergo propter hoc*. No scientist is a genius, according to this kind of contextualist history of science, no scientist is ahead of his or her time in anything, no scientist really sees into nature. But these historians themselves somehow manage to transcend their milieu and see into the nature of science and scientists!

What should be disturbing is not that Darwin's species concept is based on the concept of adaptation, but that Darwin's species concept is not at all compatible with some of what he explicitly says about species *per se*, such as that "It is really laughable to see what different ideas are prominent in various naturalists minds, when they speak of 'species'.... It all comes, I believe, from trying to define the indefinable" [51, p. 309] and that "we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species" [5, p. 485]. Other passages on species in the *Origin* alone [5], such as those on "amount of difference" (pp. 57, 485), on characters "constant and distinct" (pp. 47, 484), and on "well-marked and permanent varieties" (p. 133) or "strongly marked and fixed varieties" (p. 155), can perhaps be harmonized with Darwin's species concept elucidated in this chapter. But not the other passages above, the passages, most interestingly, that have gained for Darwin the longstanding reputation of being a species nominalist.

The time would seem ripe, then, for proceeding to the (in itself) undesirable terrain of *dissimulation hypotheses* for Darwin, possibly even *radical* dissimulation. The phrase "dissimulation hypothesis" comes from scholarship on "the father of modern philosophy," René Descartes. There is strong evidence suggesting, for example, that Descartes was not sincere with his proofs of the existence of God [52], and that he was deceptive in the ordering of his

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three proofs of God's existence [53]. But science, too, has its fair share of dissimulation, ranging from the manipulation of data in the pursuit of truth to outright fraud in the pursuit of self-aggrandizement. Sir Isaac Newton, for example, in the second edition of his *Principia*, claimed greater mathematical precision for his work on gravity, sound, and the precession of the equinoxes than his work warranted, while his attack on Leibniz for plagiarizing calculus verged on the neurotic [54]. Robert Millikan, who received a Nobel Prize in 1923 for his discovery of the unit amount of charge in an electron, selectively edited data for his published reports as shown in his private notebooks [55]. Much more recently, the groundbreaking work of Woo Suk Hwang and colleagues on the creation of human embryonic stem cell lines was shown to be largely fabricated, resulting not only in retracted articles by *Science* but in legal charges [56]. Examples abound [57], though clearly one should not want to throw out the proverbial baby with the bathwater.

In the case of Darwin, assuming that the analysis presented in this chapter is basically correct, we can only speculate as to his motive or motives for withholding his real species concept. Perhaps it was because he thought that an explicit nominalistic definition would help to either break through or bypass the psychological barrier of what Wollaston [58], in characterizing the core of the "general" concept of species, called the "axiom" of special creation and non-transmutation (p. 133). Or perhaps Darwin chose to bypass defining "species" for mainly linguistic rather than psychological reasons, simply in order to better communicate his theory of evolution [8, p. 266]. And then perhaps Darwin felt that he would be lowering himself by adding to what he called the "really laughable" babble of species concepts among "systematic naturalists," something he complained about in the letter to Hooker quoted from above [51, p. 309] and repeated in *Natural Selection* [16, p. 98].

And then perhaps his motive changed with time and circumstances. In the years following the publication of the *Origin*, the *evolution* of species became widely accepted in scientific circles, but not his proposed *mechanism*, natural selection. As time passed he might then have viewed bringing out his species concept as pointless. Revealing is his statement, written in 1863, that "Whether the naturalist believes in the views given by Lamarck, or Geoffroy St.-Hillaire, by the author of the 'Vestiges,' by Mr. Wallace and myself, or in any other such view, signifies extremely little in comparison with the admission that species have descended from other species and have not been created immutable" [38 II, p. 81]. The same point is found in his letters of the same year [35, pp. 36, 40]. Darwin himself, no doubt, continued to believe in the truth of his theory of natural selection, but perhaps what mattered more to him now was the acceptance of the evolution of species *per se* than the evolution of species *by means of* natural selection. This is a remarkable thought. What it means for our topic is that if establishing the product (evolution) had become primary and the process (natural selection) secondary, then making the primary proof (for evolution) hinge on a questionable species concept, which depended on the secondary proof (for natural selection), might not have seemed wise. And certainly with regard to natural selection Darwin was prescient, since even as *a* mechanism of species evolution natural selection was not generally accepted in his lifetime and only began to achieve wide acceptance in biology in the 1930s [59].

8. Conclusion

We shall probably never have a convincing theory on Darwin's motive. But no matter. For the great many, myself included, who admire Darwin as one of the greatest scientists of all time, and also as an English gentleman, the idea that he might have intentionally misrepresented his species concept (whatever his motive) "may not be a cheering prospect," but the evidence must be followed wherever it leads, no less in history of science than in natural science. That Darwin did intentionally mislead in this matter does not take away from his scientific accomplishments, but it does bring him down from the heights of the virtuous gods of knowledge and makes him appear much more human, even as a scientist.

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