The origins of species concepts

History, characters, modes, and synapomorphies

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Abstract

The longstanding species problem in biology has a history that suggests a solution, and that history is not the received history found in many texts written by biologists or philosophers. The notion of species as the division into subordinate groups of any generic predicate was the staple of logic from Aristotle through the middle ages until quite recently. However, the biological species concept during the same period was at first subtly and then overtly different. Unlike the logic sense, which relied on definitions of the essence of both genus and species, biological species from the time of Epicurus were consistently considered to involve a reproductive element: in short, living species relied not on essential definitions, but on the generative cause, which might not be definable. I term this the *generative conception of species*: species were the generation by reproduction of form. This undercuts the claim that species before Darwin were essentialist, and divorces the notion of a *type* from that of *essence*. In fact, as late as the end of the nineteenth century, logicians explicitly treated biological "species" as a homonym only of logical essentialist species, and permitted considerable deviation from the type or form. At every point, species in logic were thought to be a subset, in effect, of some more general notion. I sketch a history of both philosophical and biological traditions of the species concept, before turning to the current conceptions. These are reconsidered in the light of this history, and in particular Mayr's changing views are shown to be somewhat Whiggish, historiographically. Of the many touted biological species concepts, only one of which (Mayr's) is called *the* Biological Species Concept, none appears to capture all the relevant facts, intuitions, and operational requirements of biology. Cladistic conceptions, however, have much in common with the older philosophical literature, in that the natural group of cladism is the clade, or monophyletic group. After considering the Individuality Thesis, and the metaphysics of species, we see that species are the most particular terminal taxa in a clade, and that they are "defined" in terms of the particular synapomorphies, or evolved characters, that are causally responsible for keeping the lineages that organisms form distinct from one another. In this way, we can remain within the generative conception of species that has been in play for over two millennia, and yet avoid the pitfalls of prior attempts to find a universal conception of species.

Declaration

This is to certify that

(i) the thesis comprises only my original work towards the PhD except where indicated in the Preface,

(ii) due acknowledgement has been made in the text to all other material used,

(iii) the thesis is less than 100,000 words in length, exclusive of tables, maps, bibliographies and appendices.

[Complex ideas] have their union and combination only from the understanding which unites them under one name: but, uniting them without any rule or pattern, it cannot be but that the signification of the name that stands for such voluntary collections should be often various in the minds of different men, who have scarce any standing rule to regulate themselves and their notions by, in such arbitrary ideas.

John Locke, *Essay on Human Understanding* III ix 8

Dedication

To my wife Paula and children Alice and John Nathaniel, who endure my obsessions with grace and resignation; and to David Hull and the late David Rindos, who both encouraged me.

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Preface

The history of research into the philosophy of language is full of *men* (who are rational and mortal animals), *bachelors* (who are unmarried adult males), and *tigers* (though it is not clear whether we should define them as feline animals or big cats with a yellow coat and black stripes).

Umberto Eco, (1999 p9)

'What sort of insects do you rejoice in, where *you* come from?' the Gnat inquired.

'I don't *rejoice* in insects at all,' Alice explained, 'because I'm rather afraid of them – at least the large kinds. But I can tell you the names of some of them.'

'Of course they answer to their names?' the Gnat remarked carelessly.

'I never knew them do it.'

'What's the use of their having names,' the Gnat said, 'if they won't answer to them?'

'No use to *them*,' said Alice; 'but it's useful to the people that name them, I suppose. If not, why do things have names at all?'

'I can't say,' the Gnat replied. 'Further on, in the wood down there, they've got no names …'

Lewis Carroll, (1962 p225)

Juliet asked, "What's in a word?" and went on to note that "a rose by any other word would smell as sweet".[1] What, indeed, is in a word, particularly in this case the word *species*?[2] Definitions of that word abound – it is even more defined than that other hot term of biology, *gene*. This is the purpose of this review – to see what, if anything, is in the word *species* and why it should matter.

A while ago, an Australian journalist objecting to the views of geneticist David T. Suzuki on the perils of genetically modified (G.M.) food, castigated him for saying there was a danger that modified genes in G.M. canola might escape into wild plants. Suzuki, declared the worthy scribe, had his facts wrong. Everybody knows that could not happen – and why? Because the wild plants and canola are **different species** and do not interbreed. Suzuki, he declared, must be a very poor scientist if he could make **that** simple mistake. Of course, like most of his profession when it comes to assessing

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[1] I am indebted to Elizabeth Hubbell for pointing out that the reading, "What's in a name" is incorrect and was popularised by the Cambridge and Globe editions of the nineteenth century. The Second Quarto, apparently from the original manuscript, reads

> Whats in a word, that which we call a rose
> By any other word would smell as sweete,

The common reading is taken from the First Folio, which is a reconstruction from the performances.

[2] Bold is used throughout for emphasis, and italic represents a word that is mentioned, rather than used. When *species* is given, the concept or term is referred to. Roman text indicates the things themselves.

scientific judgements the journalist was ignorant of the facts; for example, that around half of all flowering plants and nearly all ferns and fern allies happen to be hybrids, often between relatively unrelated species (within families, but not necessarily the same genera). Moreover, genes can cross genera, class, phylum or even kingdom divisions through viral transcription, and Suzuki is, of course well aware of these facts. **His** concern lies in the risk assessment, and that is an open empirical question, one that critics of G.M. often overstate. However, this minor farce exposes the public and scientific significance of the concept of a species.

We **use** species concepts to do things. At the most trivial we use them to arrange our data and specimens, and to talk to one another. More importantly, we use them to predict the behaviour and properties of organisms in medical research, and in ecological, conservation, pharmacological, commercial or even evolutionary contexts (Nelson 1989). In conservation law in the United States, for example, a species concept is written into the legislation (Allendorf et al. 2001; Cracraft 1997; Crandall et al. 2000; Linder 1995). Species concepts are far from being mere abstractions of interest only to specialists.

What good is a **philosophical** review of species concepts? The traditional philosophical speculation and analysis of scientific concepts, and particularly of taxonomic concepts, has often rested on a naive and intuitive understanding of scientific practices and methodologies. In recent years, there have been exceptions, but generally, the philosophical aspects of the debate have been driven more by taxonomists themselves than by philosophers.

Philosophers have tended to adopt several recurring approaches towards taxonomy. By far the most common is to assume that the generic knowledge and ordinary language of a linguistic community is sufficient to commence ruminations on the fundamental categories of classification. John Stuart Mill, whose *System of Logic* was written well in advance of the work of Darwin, Hooker and the extensive systematic biological work of the twentieth century, at least had an excuse, although his examples are nevertheless surprisingly sophisticated.[3] But twentieth century analytic and linguistic philosophers have been quite naïve – the usual philosophical examples of a "natural kind", so far as biological examples are given at all, are "cats", "the tiger" or "man" or even, "the unicorn".[4] Knowledge of intraspecific variation, problems with

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[3] Cf. Bk IV, ch VII, §2 (Mill 1930).

[4] E.g., the essentialists of the 1980s (Putnam 1981: 25f, 43ff; Kripke 1980). See Hull (1984a) for a discussion.

dichotomous key diagnosis or genus membership are apparently beneath the purity of philosophical reflective equilibrium.

A second common strategy is to accept a given species concept – for example, Mayr's concept of reproductive isolation (biospecies) – and to elaborate on this. So far from being the end-result of a wide reflective equilibrium using philosophical methods, this approach takes as a given the categories of at least one influential working biologist. In as much as it is, this is a virtue – at least the explanandum is science. But the philosopher inherits whatever confusions the biologist suffers from, and is in effect just cheering from the sidelines. Hence, philosophers who take this line either become biology partisans or have nothing much to contribute to the debate. **Biologists** who adopt one concept from a precursor and then philosophically elaborate it are doing some kind of biology, but mostly what philosophy and history of science they do is constrained more by their theoretical concerns (and, of course, their detailed knowledge of at least one group of organisms) than by their philosophical methods. Philosophers, however, are not constrained in this way and the opportunity to overdraw generalisations is usually taken up enthusiastically.

A third and far less common reaction is for the philosopher to become *au fait* with the biology (or, more commonly, a biologist to become proficient with the philosophy). This is far more desirable than either imposing the standards of a philosophical tradition or the implicit meanings of ordinary language upon the science, or blindly following as authoritative the pronouncements of a few partisans in the ongoing battle. However, it is difficult, and there is the constant danger that the subject matter will become so intrinsically interesting to the philosopher that the philosophical morals are never drawn.

I have fallen prey at different times to all these errors, and in overcoming the confusions that resulted, I have tried to balance the philosophical, historical, theoretic and methodological issues evenly, so that in all probability, I have done none of them as well or deeply as I might, and may indeed still be bemired. Nevertheless, in not making metaphysics, or advocacy for a singular scientific view my motivation, perhaps I can contribute something to the subject.

I will not attempt a full sociological or political analysis of the debate over what species are. This is not because that analysis would be uninteresting or wrong-headed, but because it would not be **philosophy** or **history** of biology, and this is what I wish to do here. I do hope that one day some interested and competent social historian or sociologist will review the 250 years or so of debate in an attempt to correlate profession, country, context, and study organisms. A start has been made by some (e.g., McOuat 2001). More needs to be done.[5]

So, what is the point of this review, and what is it intended to achieve? It seems to me that the prescriptive elements of the philosophy of science must rest upon the **actual** historical development of the concepts, theories and issues of the science under review. Lakatosian "rational reconstruction" of a historical sequence satisfies nobody except as an exercise in narrative explication of some ideally rational or "correct" scientific philosophy. This work aims to address one categorical concept – species – in the context of the wider concerns of systematics since the slow birth of modern biology, to see if some general notion can incorporate most of those specific concepts that have been formulated. Some quite general considerations will provide an umbrella concept that does situate many of the existing varieties, but it will also, for reasons of principle, exclude several as well. This is a sign that it is doing some work, even if only trimming the undergrowth.

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[5] Gordon McOuat, in fact, is undertaking a contextual history of the species concept at the time of writing (pers. comm.).

Kim Sterelny, editor, and an anonymous referee, of *Biology and Philosophy* made comments and suggestions that I hope helped me improve the argument.

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Therefore, in the light of this gracious assistance from so many people, all misunderstandings, errors and incoherencies that remain are my own fault.

Chapter 1. Philosophy and the species problem

1.1. Ideal Species Concept

What is it we want the category *species* to do? The answers to this question are legion, and so we had better list the criteria we would prefer in an Ideal Species Concept. For a start, it would be universal to all living things – it would apply equally well to plants, fungi, lichens and bacteria, to animals, and to asexual as well as sexual organisms. It would apply to single-celled, colonial and multicellular organisms. It would cover existing and extinct organisms, Recent and fossil organisms, and groups of organisms that live together (in sympatry and synchrony[6]) as well as those that live apart (in allopatry) and those separated in time (allochrony). This amazing concept would also deal with the natural differences and similarities of organisms rather than those differences that depend upon the conventional, social, or cognitive features of specialists of one particular kind of organism at one particular moment in history. (For convenience, concepts that fit the second class will be referred to in this work as "artificial".) It would mark out interesting and important properties of organisms. Assigning organisms to different species should be the outcome of learning facts about the organisms. And since this is a shopping list for the conceptual delicatessen in Plato's Heaven, this ideal concept would be operationally employable. It would be something we could *use* in each particular case.

Can we get to this state of theoretical grace? Is an Ideal Species Concept possible? Probably not (Hull 1997). Many think it is a chimera, a messy hybrid, and propose chimeric and messy but realistic alternatives. I will not present the Ideal Concept in this work, but a philosopher's reach should exceed his grasp, or what's a Platonic Heaven for? Even if we cannot deliver the Ideal, striving for it may advance matters. Rather than restrict species concepts to some manageable small domain of life, or to allow for a radical anarchism in which a thousand concepts bloom, I choose to attempt as complete a reconciliation of the plurality of concepts now in play as I can. And there **are** facts to be accommodated. Species evolve, the criteria used for differentiation or for grouping species are not universally met for practically every concept, and several

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[6] For non-biologically-trained readers, I will define technical terms as they are used. Allopatry is the state of two populations living apart geographically. Sympatry is the state of two populations living in the same geographical region. Speciation that occurs in each state is called allopatric speciation or sympatric speciation respectively. In cases where speciation occurs in a peripheral population of a broadly distributed species, it is called peripatric speciation (Mayr 1963). Synchrony and allochrony are obviously chronological states.

concepts provide unstable and subjective classifications. So this reconciliation must avoid subjectivity and simultaneously must admit as broad a class of facts as possible.

Whatever else may be said of species – that they are the "units of evolution" or the outcome of it, that they grade insensibly into each other or are separated by bridgeless gaps – species play a central role in classification. They are, in short, the children's blocks from which all classifications are constructed. Like children's blocks, they are not atomic. They have internal structures and are composed (at least) of organisms, but classification is not achieved by counting organisms but by sorting them into groups and identifying the kinds those groups belong to. "Species" is what Locke called a *sortal* concept (*Essay* Bk III, ch III §15), the obverse of a general concept. They are the most distinguishable kind of thing within some more general class (a *genus*), as we shall see in the history given in the following chapters.

The task of a classification can be many things. It may have a functional role in a society. Buffon, for example, wanted to classify according to the immediate usefulness to humanity (and 18th century French humanity at that, cf. Roger 1997, beginning with the Horse). Normally, classification in biology is an attempt to organise knowledge, so that research into a natural group will transfer to other groups and all members of the group. What we learn about squid nervous systems applies to human nervous systems, for example, just to the extent that squids are related to humans. Still, there are competing goals of classification. They also include communicability, tractability of data, convenience of information storage and retrieval, inductive generalisability and pragmatic utility. Some of these goals are more relative to the behaviour of the classifiers and their clients than to the properties of objects classified. To take only one example, classifications of commercial plants for sale to domestic gardeners are organised around the functional properties of the plants, to be sure, but these properties are exogenous – grows well in sandy soil, is capable of withstanding pruning, flowers when other plants are out of bloom etc. The properties are significant in the classifications because they relate to the goals and interests of gardeners and the economy that caters to them. A **natural** classification[7] is one that reflects the properties that are significant to the organisms themselves in the absence of observers

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[7] Traditionally, a natural classification is contrasted to an artificial one. At the time of Linnaeus and Buffon, a natural classification was an ideal – using all characters rather than a few (Stafleu 1971; Panchen 1992; Nelson et al. 1981). It was held to be unobtainable. An artificial classification gave some weight to an arbitrarily chosen few characters. In later times, a natural classification was one that was "forced" by the inherent distributions of the characters themselves, and it was in this sense that the so-called "phenetic" school of numerical taxonomy was founded (Sokal et al. 1963; Sneath et al. 1973). Its failure in this regard led to its general abandonment in favour of cladistics later on (Hull 1988c).

and their goals and interests (cf. Maynard Smith 1993 p223). Of course, this introduces a fundamental tension: the classification aimed at by naturalists is one that is based upon the absence of the naturalists themselves in the phenomena. The natural order is observer-independent, but can be expressed only by observers. This tension means that a purely natural classification is seemingly a contradiction in terms – in order to have the classification, observers have to be in some relation to the things being classified, and yet this implies that the classification is at least in part relative to the interests and goals of the observers.

1.2. Natural and artificial

Much of this debate turns on the meaning of such terms as “arbitrary”, “conventional”, “subjective” and “circular”. A convention, the dictionary tells us, is an agreement. An arbitrary choice is one that might as well have been different. According to Lewis (1969 p70), any “convention is arbitrary because there is an alternative regularity that could have been our convention instead” while **non-arbitrary** conventions, if they existed, would simply be the best thing to choose – a unique coordination equilibrium for example. One thing Lewis does not discuss in that work is that there may be a restricted range of alternatives, so that choices are partially forced, but not uniquely. This often happens in taxonomy; that there are only a few feasible choices but none is uniquely determined by the data. So, conventions can be adopted in a relatively non-arbitrary manner. Of course, this is a matter of degree rather than kind; conventions are still to some extent arbitrary even if that extent is restricted.

Subjectivity in science is usually held to be a Bad Thing. Taxonomy, at various times, has been held to be a science or an art, and occasionally both[8] but overall the ideal or goal has been to develop real or true classifications. Systematists often speak of the “One True Phylogenetic Tree” (only sometimes in jest). The problem with subjective classifications is that it makes an appeal to a person or personal authority, not to the evidence or facts of the matter as such. With the effective rejection of phenetics, some “objective” method was sought and found, it was claimed, in cladistics.

The currently proposed alternatives in the species concept literature are of several flavours. Objectivists tend to predominate, but there are some whose views might be

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[8] Cf. G. G. Simpson’s (1961 p107) comment cited in Panchen (1992 p126):

> Taxonomy is a science, but its application to classification involves a great deal of human contrivance and ingenuity, in short, of art. In this art there is a leeway for personal taste, even foibles, but there are also canons that help to make some classifications better, more meaningful, more useful than others.

appropriately called Conventionalism. These views are often related to the emphasis placed on evolution, or more accurately upon gradualistic evolution. One is John Maynard Smith, who thinks that the main role of taxonomic concepts is to facilitate communication between specialists, and that so long as they agree on the way organisms are named, it does not matter very much what we call species or otherwise.[9] That there is a conventional element (in the sense of being convenient to specialists) to taxonomy is undoubted – the question remains whether that is *all* we want of our taxonomic concepts. While the objectivists, particularly in the process cladist tradition, sometimes do overstate their case for the objectivity that follows from the application of cladistic methodologies, the "best" species concept will be one that marks out real differences in the biological world. This is, after all, the reason why the reproductive isolation concepts we shall soon discuss are known as *biological* species concepts, in preference to the older arbitrary concepts based on dichotomous morphological keys.

In this review and discussion, many cladistic terms, ideas and methods will be used, but this should not be thought to make me an ardent cladist, with a commitment to all views (especially epistemological ones) that often travel under the rubric. It is evolution, not cladism, that provides my unifying concept, but the terms Hennig and his followers invented, and the theoretical considerations Hennig developed with respect to phylogenetics, are useful and unambiguous when discussing evolution, as all systematists bar a few now generally admit, irrespective of their overall views on cladistic philosophy. We will therefore use terms like *apomorphies* and *plesiomorphies*, *monophyletic*, *paraphyletic* and *polyphyletic* groups, *clades* and so forth.[10] It is the task

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[9] Personal communication. See also (Hey 2001a; 2001b). Joe Felsenstein dubbed this the It Doesn't Matter Very Much (IDMVM) school of systematics in connection with cladistic versus evolutionary systematic methodologies (on the sci.bio.paleontology Usenet group, January 2001).

Systematics and taxonomy are almost, but not quite, the same thing. The usual definition (Ornduff 1969) is

> Taxonomy: classification of taxa (units of classification) in a system that expresses their relationships
>
> Systematics: comparative studies of a systematic unit (i.e., a group of organisms or species and higher), the fact-finding field of taxonomy

These seem inverted – systematics **ought** to be the relationships between taxa, and taxonomy **ought** to be the fact-finding (i.e., descriptive) side of it. But the terms were introduced that way (by A. P. de Candolle for *taxonomy*, 1813, Lindley for *systematics,* 1830), that's how it got established. Simpson (1961 p7–11) more sensibly treats taxonomy as the principles and rules of classification (as metaclassification, as it were) and systematics as the study of kinds and diversity of organisms and their relationships, but it seems his view was not consciously adopted by many.

[10] *Plesiomorphies* are the ancestral or underived traits of organisms. *Apomorphies* are derived or evolved characters. Shared ancestral characters are *symplesiomorphies*. Shared derived characters are *synapomorphies*. Traits that are unique to a taxon are *autapomorphies* of that taxon relative to its sister taxa. A *clade* (Greek for "branch") is a phylogenetic lineage or group of lineages that share a common

of systematics and the concepts of biology to mark out objective rather than subjective, natural rather than conventional, and theory-problematic rather than theory-dependent differences in the biological world. If anyone wishes to label this “cladism”, they are welcome to. Those who attack or defend cladism against the inaptly-named “evolutionary” systematics resemble philosophers in the heat of emotion to which the combatants are prone. In particular, they resemble disputants in the philosophy of mind over whether consciousness or some other phenomenological category is physical or not. And like them, the terminology and techniques of one camp is tending to sharpen the arguments and ideas of the others. Without declaring myself for a “Popperian” philosophy like many systematists (see Smith 1994), there is enough common ground in phylogenetic systematics to get us started. In my resolution of the debate, I will declare in favour of a controversial aspect of classical cladism, but I have my own justifications for it, owing more to Nelson Goodman (1973) than Karl Popper.

Since what follows relies heavily upon cladistic categories and argument, a few words are due about why I take cladism so seriously. A lot of taxonomists do not. One has to start somewhere, though, and one primary virtue of cladistics is that it is clear in what it asserts. Given that Hennig (1950; 1966) founded it in part on the set-theoretic ideas of Woodger (1937, with no less than Tarski’s imprimatur in the form of an appendix by him), this is understandable. More to the point, cladistic taxa, including species, do not require that there is some prior theoretical model; they are formed by aggregating empirical types of organisms and restricting the resulting groups to proper sets and subsets. If one requires that species meet some kind of model of populations, gene flow, adaptation, ecological niche occupancy or whatever, then there is no point in further debate. “Species” has been defined by fiat. Hence, I prefer to adopt the cladistic sense of naturalness; at least it allows for an open mind as to what it is that forms particular taxonomic groups. It may turn out that the mechanisms that do this are the same ones proposed by the biospecies, or some other, definition; if so, then that model is supported by empirical data. But given that an indefinite number of (more or less viable) models can be proposed, we need to test them somehow; cladistics is a way to do this, and so its notion of a natural group is conceptually prior to those of the models.

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ancestral node in a phylogenetic tree, and which no other lineages also share, which is the cladistic definition of monophyly. *Cladograms* are trees formed by comparing character distributions, and taxonomy that depends upon cladogram construction is often called cladistics, or more properly, phylogenetic systematics. *Monophyly* is the state of being all taxa in a cladograms that are separated from the rest of a cladograms by a single cut. In short, it is a branch (Greek: *klados*). Any branch that is incomplete is *paraphyletic*. Any group formed from more several incomplete branches is *polyphyletic*.

A conceptual problem in science is often a sign that the discipline has not been able to resolve the limits of its domain. This is not the case with species in biology. Usually, with some exceptions (every general rule in biology has exceptions, including this one), systematists can recognise species, and can tell where the biology (or at any rate their specialisation within it) leaves off and convention begins. No biologist these days thinks that mineral species and biological species are instances of a general categorical concept, as Linnaeus did. The difficulty had with *species* is, rather, one of cross-speciality commensurability. This is clearest in practical matters, as in conservation questions – in what sense is a taxon of eucalypt or bacteria the "same" as a taxon of insect or mammal? If species evolve, then we must expect that there will be problem cases where differences arise to varying degrees. However, species *in statu nascendi* (the standard systematic phrase for "in the state of being born") are not the main difficulty. The main problem is how to compare a kind of plant with a kind of mammal in order to decide how much biodiversity to attempt to save, and why (Waples 1991; Mallet 1995). Which contributes most to a total measure of biodiversity – a small flowering plant, which is one of a large family of occasional hybridising species in a family of plants or the last species of a genus of birds? This is only one of the issues and practical questions that species occasion. Within a genus, issues can arise, as when two varieties of coyote or dingo exist, one of which is threatened. Is saving the other variety enough? And so on. Quite apart from the technical issues in biology, species concepts and their commensurability affect practical matters in medical and pharmacological research, agriculture and horticulture, and public policy regarding genetically modified foods, animal rights, pest control and epidemiology.

1.3. Species realism

Why be a species realist? Why be a realist of any kind? The antirealism of Putnam (1981), van Fraassen (1980) and others suggests that it is acceptable to some merely to have an operational scientific concept in order to proceed with the science. Some, such as Ereshefsky (2000; 1992), take this approach to the species category: *species* is just a concept of convenience and there is no biological reality attached to it. I cannot argue this in detail here, but several considerations lead me to think that species are real things, and that the term has a purchase in dealing with these things.

For a start, biologists and non-biologists alike recognise much the same sorts of base level taxa in the natural world. This might be an artifact of human cognitive propensities (Hey 2001a; 2001b), but as in the famous case of the *Rana pipiens* complex of frog in the southern United States, the organisms **themselves** recognise these differences even if humans do not (Littlejohn et al. 1968; Littlejohn 1969), in this case based on differing mating calls, and the taxonomy followed suit once these differences were recognised by taxonomists. Sometimes the taxonomic identity of groups is something recognised by parasites (e.g., the malaria parasite and the *Anopheles* mosquitoes of southern Europe). These are not artifacts of human cognition; indeed, the human cognition follows the discovery of acts of specific recognition by nonhuman organisms. If species – these particular species – are not real, then the phenomena are hard to explain. This is not conclusive, but it is enough to suggest that at least some species have a good claim to being real.

Species realism has usually been cast in terms of "natural kind" terms (cf. Boyd 1999; Kitts et al. 1979). On this account, a species is real *iff* the name denotes some class of organisms. Such essentialism sits poorly with evolutionary thinking, leading some authors, arguably including Darwin, to reject the notion of real species. Despite attempts (e.g., Kitcher 1984; Ruse 1987; 1998) to make an account of species in terms of sets and classes, no convincing account of species as classical natural kind terms has been forthcoming. So it may seem that to be a species realist is to hold to a conception of species that has historically and biologically failed. Species realism entails taxonomic reality but no essentialism apart from monophyly (a view argued by Griffiths 1999). However, that individual species are real seems to me the "default" view, given that biologists themselves are forced to adopt it, at least operationally. Perhaps most biologists are wrong. If so, then it is up to biologists to show this in practice, not philosophers to legislate against a category so fundamental to biological practice. So if realism does not involve essentialism, what could it involve?

I believe it does **not** involve the idea that there is a single commensurate universal rank in taxonomy that is privileged over all others. Whatever species are, there is no need for them to all be of the same structure or ontological standing. The main claim of this work is, in fact, that they are not. What they **are**, however, are groups of organisms that share something biologically important that they do not share with other organisms. Prior to the publication of the *Origin*, the reality of species had less to do with them being natural kinds as such than it did with species being reproductively isolated; of hybrids being sterile, a view that goes back to Buffon, later shared by Lyell, Darwin in the Notebooks, and most other naturalists of the day. Something is a real species on this account if it has some isolating mechanisms. Darwin and Wallace even noted that there are no fixed amounts of difference that makes for species, and yet both held that species are (temporarily) real (Kitcher 1984; Kottler 1978). If we recast the issue of the reality of species "in nature" as Lyell put it, as whether species that are named, the groups, exist, instead of whether species are real classes or natural kinds, then we have a better case to make. In short, of course, this is the question whether species as individuals (as groups, that is, not as ranks) are real. The question we are addressing here, then, is what makes an individual group a species.

Returning briefly to the antirealism debate; in addition to the absolute realist view and the antirealist view, Putnam suggested internal realism – the idea that the reality of a scientific entity is the assertion in that theory that such entities exist: "… *what objects does the world consist of?* is a question that only makes sense to ask *within* a theory or description" (Putnam 1981 p49). In the context of modern biology, and in particular evolutionary theory, species exist as terminal taxa in the tree of life. These taxa exist; they are real, at least in Putnam's sense. It is enough for now – *species* is a concept that has a fundamental role in a theoretical context or several, and to that extent species are real, no matter whether realism is restricted to the insides of a theory or not. So long as species play that necessary role in evolutionary, ecological, developmental and other biological theories, there can be a presumption they are real, or as real as anything in a theory can be.

Like electrons, which as Hacking (1983 p36) noted were once the paradigm of an unobservable theoretical entity but are now manipulable and which make a difference to objects (such as those in a scanning electron microscope), species are also entities that make a difference. But this is an argument from the "pragmatic virtues" (see Clarke 2001). A merely pragmatic argument will not deliver us the sort of realism that biologists – most of them, at any rate – want for species and other theoretical terms. What they typically want at a minimum is the "entity realism" that Clarke situates between full-blown scientific realism and the anti-realist or internal realist position. This is the sort of realism one gets by taking scientifically required entities to be real even if there is no global theory in which they are described universally. Species pass this muster.

1.4. Three species problems

The species problem is actually a number of problems that biologists have had ever since the term was first applied to biological organisms by Aristotle. The three main problems are *the grouping problem*, *the ranking problem*, and *the commensurability problem*.[11] It will pay us to distinguish these clearly at the beginning of our discussion

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[11] Jody Hey (Hey 2001a; Wilkins 2002a) has a different but related division: the *count creep* problem, the *concept conflict* problem, and the *fuzzy species* problem. The first is the classic lumping and splitting debate, with a tendency to split rather than lump (lumpers tend to be reformers); the second is definitional (which is the right definition for biologists to use in everyday biology), and the third a question of vagueness and incomplete differentiation, such as is to be expected under an evolutionary account of species.

and to bear them in mind as we consider the history of and current discussions about species.

1.4.1. Grouping problem

Our first problem is: How are members of species to be grouped together and excluded from other groups? No matter whether species are constructs and arbitrary or natural and objective, the issue remains how we can include some organisms and exclude others from a species. As we shall see in the historical review, prior to the term being exclusively a biological one (in use by biologists, at any rate), the notions of *differentiae* and *relata* were brought to bear. A species was differentiated by characters, and those that marked organisms in some relevant way enabled classifiers to exclude some organisms from a species. Likewise, a character that related organisms was thought to be sufficient to include organisms within species despite their individual differences. In short, the grouping problem is one primarily of operationality. But not entirely – organisms can be seen as **self-classifiers**, especially in the reproductive isolation concepts of sexual species. So long as organisms are able, it is said, to differentiate between themselves and find related enough organisms to mate with, then they form species even if we humans might not be able to identify what it is about them that the organisms themselves find salient in the process. Maynard Smith, for example (1975), notes that one reason why we have so little trouble identifying some groups of species (e.g., birds) is that they are of the same general size as we are, and use much the same criteria in self-differentiating: sound, appearance and behaviour. It follows, some think, that other groups that are equally salient to us must also have some causally significant differentiae and relata. Likewise, it follows that organisms that are (reproductively) distinct, but are otherwise indistinguishable by us, must have some differentiae and relata that we do not recognise (e.g., biochemical differences) without specialist equipment. So our grouping problem reduces to the issue of what is appropriately seen (by us or by organisms themselves) as grounds for distinguishing some and grouping others into species.

1.4.2. The ranking problem

Is *species* a fixed, that is to say, absolute, rank in taxonomy (in contrast to the so-called "artificial" higher taxa)? Arguments about whether some or all taxonomic ranks are natural or not go back a very long way. Linnaeus clearly thought that species and genera were natural ranks,[12] while Buffon felt that they were not (arguably – see the

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[12] Arguably, Linnaeus thought that genera were more likely to be natural than species.

historical review), and some “species deniers” even today (Ereshefsky 1992; 1999; 2000; Pleijel et al. 2000; Vrana et al. 1992) present alternative views that species themselves are not natural, but only individuals or presently terminal taxa are. Much of the species debate has been over what it is that species are that makes them a natural (that is, a real) rank. Discussions of reproductive isolating mechanisms, for example, or ecological niches, geographic replaceability, and so forth, take it for granted that there does exist a real rank of taxa, that it is appropriate to call that rank the species-level, and that what we all disagree about is what to use to define that level, or rather what it is that makes some taxon that level. Other problematic cases, such as ring species, well-defined geographic races, facultatively interfertile species, superspecies, sympatric species swarms, and of course asexuals, both quasispecies and secondarily asexual taxa, lead some to think that the notion of species is a homonym for many distinct concepts. Moreover, species seem to be constituted in different ways in different groups of organisms. Many plant species are formed, for example, by hybridisation, a process that is often ignored or glossed over when discussing animal species. Some fungi have multiple sexual morphs instead of the regulation two, and so reproductive isolation becomes a much harder concept to qualify for them than animals.

Consequently, if we are trying to compose a general concept of species that applies to all living things, or to compare and contrast the concepts that are relevant only to particular cases, two questions arise. One is whether there *is* indeed a rank of species in all taxonomic hierarchies, or whether it is relative to the discriminating criteria used in a given group of taxa; the other is whether a species level is required at all.

1.4.3. The commensurability problem

The most common and popularly known species concept is, of course, the biological species concept championed by Mayr (1942). It is typically the definition taught to undergraduate zoology students, although often only one of many taught to botany students. It is not taught, however, to bacteriology students or virologists, nor is it the preferred definition of lichenologists. Taxa that are formed by most bacteria and viruses do not rely on constant sexual reproduction if any, and lichens are obligate symbionts formed by a mutualistic association between cyanobacteria and fungi. Immediately the commensurability problem rears its head. Species among animals are not commensurate with species among many single-celled organisms, or species among symbionts. Some, such as Dobzhansky, simply deny that asexual organisms form species (since by definition reproductive isolation is what makes species, and every asexual individual is reproductively isolated). This is surely putting the definitional cart before the evolutionary horse. If species are outcomes of evolution, and asexual taxa – forms, morphs, types, niche occupiers, whatever – are the outcome of evolution, then we need to be able to justify the special status of taxonomic units like species over other taxonomic units. Simple familiarity through tradition and acquaintance in one domain of biology, or definitional stipulation, is insufficient – zoological hegemony has been a tendency in evolutionary and taxonomic theory for most of the 20th century. In part, the species problem arises because categorical concepts that applied well in zoology failed to generalise outside it, or even those that applied well to some particular group such as birds, mammals or insects failed to generalise even to other animals, let alone plants, fungi, lichens, algae, and so on. Perhaps, some biologists and philosophers suggest, *species* is a trashcan categorical, and should be replaced altogether. At least one major group of polychaete worms has been described recently without mention of species, except to explain why species aren't mentioned (Pleijel 1999). Perhaps *taxon* is sufficient. This will be discussed later.

With these topics in mind, let us look through the history of the concepts of species, in both the original logical and philosophical traditions, and in the period of biological definitions that followed, and developed alongside in some cases, before we return to the modern debates and concepts, and then to the philosophical issues. It transpires that a good many of the ideas of today have been visited before, and that many of the biological problems have philosophical ancestors.

Chapter 2. A philosophical history of the species concept

> Progress, far from consisting in change, depends on retentiveness. Those who cannot remember the past are condemned to repeat it.
>
> George Santayana[13]

> We call a species, first, the shape of anything... We also call a species what is under the genus of the sort presented...
>
> Porphyry the Phonecian, *Isagoge*, §2 (Porphyry et al. 2003 p5) c.270CE[14]

> … The homonymy between Aristotle's terms and ours should not fool us.
>
> Pierre Pellegrin (1986 p194n142)

2.1. Received History

There is a Received History of the species concept that is largely the result of work published by biologists themselves.[15] It appears in fragmentary form throughout a number of publications, and we shall look at three examples.

George Gaylord Simpson was perhaps the greatest of the paleontological evolutionary theorists of the twentieth century. His influential text on animal taxonomy (Simpson 1961) included a chapter entitled "The development of modern taxonomy". According to Simpson, Scholastic logic, based on Aristotle, relied on the "essence" of a "species", which consists of its "genus" plus its "differentia", which was a logical relationship (p36f). It was this that Linnaeus adopted (p38), and it has several serious faults: one is

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[13] In *Life of Reason* (1905–6) vol I ch. xii. *Flux and Constancy in Human Nature*. I cannot find a copy to verify it. The *Oxford Dictionary of Quotations*, second edition, from which the citation is taken, has the second last word as "fulfil", but I am told this transcription error is fixed in the subsequent edition.

[14] I shall use the convention of CE for Common Era and BCE for Before Common Era for dates where necessary. Throughout the quotations from historical sources, I have replaced the orthographical convention of an unspaced long dash (an "em-dash" in compositor's terms), which was used by most English language typesetters of earlier times, with a spaced shorter dash (an "en dash") to match modern styles.

[15] After I had written the first draft of this chapter, I came in contact with Polly Winsor, who has investigated this subject in much greater detail (Winsor 2003). Winsor traces the origin of the Received History to Arthur Cain's (1958) reliance on a 1916 misinterpretation of Aristotle (Joseph 1916; cf. Winsor 2001) and subsequent writings on the history of taxonomy (Cain 1958; 1959c; 1959b). These influenced both Simpson and Hull, and also Mayr's later development of the story. Similar conclusions were also reached by Amundson on typology (Amundson 1998) – transendentalism and idealism were less essentialistic than the received view indicated, a view in part revised by Hull himself (Hull 1983b).

There is a tendency in the philosophy of science to refer to an older viewpoint or school of thought as the "Received View". The Semantic Conception of Theories presented by Suppe (1977; 1988) is contraposed to a Received View. Hull himself contrasts his evolutionary view to the Received View of Popper and Hanson (Hull 1988c p484). I do run the risk of falling into the mistake of assuming a global hegemony of views against the "radical" nature of my own, I know. However, I truly think that until recently this view of species has indeed universally been received even by those who *want* to defend essentialism (such as Ruse 1987; 1998).

that "properties" and "accidents" (these are Simpson's scare quotation marks) are excluded from the "essence" **and therefore the definition** (my emphasis) of the species. Another is that this method produces a classification of **characters** not **organisms** (his emphasis). From Linnaeus to Darwin there was an increasing emphasis on empirical rather than a priori classification.

According to Simpson, there was a typological tradition stemming from Plato and coming via Aristotle, Neo-Platonic, scholastic and Thomist philosophy into biological taxonomy (p47). He writes:

> The basic concept of typology is this: every natural group of organisms, hence every natural taxon in classification, has an invariant, generalized or idealized pattern shared by all members of the group. The pattern of the lower taxon is superimposed upon that of the higher taxon to which it belongs, without essentially modifying the higher pattern. … Numerous different terms have been given to these idealized patterns, often simply "type" but also "archetype," "Bauplan" or "structural plan," "Morphotypus" or "morphotype," "plan" and others.

In contrast, modern taxonomy relies on common descent (pp52-54), statistical properties of populations (p65) and biological relationships. Simpson took his historical information on this subject from a paper by A. J. Cain (Cain 1958; cf. Winsor 2001). Cain, following the interpretation of Aristotle and the later logicians of H. W. B. Joseph (1916), had said that Linnaeus based his conception of species on Aristotelian definition of essences, on "*a priori* principles agreeable to the rules of logic" (p147, quoted by Winsor 2001 p249). He later reversed this position after retirement and time to properly read Linnaeus and Ray (e.g., in Cain 1993; 1994; 1999a; 1999b). Nevertheless, his earlier papers (Cain 1958; 1959a; 1959b) became the foundation for the Received History.

Ernst Mayr is someone with whose ideas and narratives we will deal later in some detail. He has often put forward a narrative history of species concepts, and it is his ideas that are most widely known and accepted. According to him, the species concept begins in biology with Linnaeus (Mayr 1957 p2f) since before then, apart from Ray, nobody believed species were stable entities. Later, Darwin held that species were fluid (p4), but in the intervening period, there was a tendency of various writers like Cuvier, De Candolle, Godron[16] and von Baer to treat them as real and definite entities, united, as van Baer says, by common descent from original stock. The realisation that species exhibited a "supraindividualistic bond" (p8) and that members of species reproduce only with each other came slowly. The older view was "typological" and it is "the

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[16] D. A. Godron, a French botanist (1807–1880). According to Mayr (1982 p649), his major interest was in the nature of species.

simplest and most widely held species concept" (p11). Typology, according to Mayr, as for Simpson, is due to the influence of Plato, and those who follow him are trying to define a species in terms of "typical" or "essential" attributes:

> Typological thinking finds it easy to reconcile the observed variability of the individuals of a species with the dogma of the constancy of species because the variability does not affect the essence of the eidos [the Greek term translated as "species"] which is absolute and constant. Since the eidos is an abstraction derived from human sense impressions, and a product of the human mind, according to this school, its members feel justified in regarding a species "a figment of the imagination," an idea. [p12]

In contrast, a species today is regarded as a gene pool rather than a class of objects.

Mayr presents this history in more detail in his *The Growth of Biological Thought* (Mayr 1982 p254–279). Here again, the source of essentialism is Plato, via Aristotle to John Ray and Linnaeus. Again, it is only with the increasing emphasis on empiricism and the development first of evolution and then of genetics that naturalists begin to realise that species are gene pools, reproductively isolated from each other. In the end, the biological species concept is triumphant.

A third history, for contrast, is that provided by David Hull, who became perhaps the leading philosopher of biology of his generation. He has made it a point to focus on the actual history and biology of his subjects rather than on a "rational reconstruction" or textbook history, as was sometimes the practice of prior philosophical scholarship of science. In his seminal paper "The effect of essentialism on taxonomy – two thousand years of stasis" (Hull 1965), he presented the Received View, in part relying on Joseph's book,[17] in part on Mayr and Simpson. The foundations of classification rest on Aristotle's notion of definition (318f), while a contrary tradition, beginning with Adanson, treated taxa as disjuncts, which themselves became the essence of a species in classical Aristotelian form. The moderns – Simpson, Dobzhansky, Mayr – moved to a reproductive isolation conception, founded on evolution. In a much later work (Hull 1988c), he devoted a chapter (chapter 3, "Up from Aristotle") in which the Received History is expanded and in many ways revised: Plato is relegated to the background and Aristotelians offered a view of species as types from which deviations

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[17] Hull, pers. comm. As Hull's ideas have been so influential, it should be noted that he also about this time (Hull 1967) published a brief history in which he went into more detail, and which cites Joseph in note 3. In it, he notes that the observation that things do not always breed true was made by Aristotle and Theophrastus, and that therefore species **do** allow variation and divergence from the type. I should like to have given Theophrastus a treatment in this work, but space and time forbade it. Even so, Hull still skips from Aristotle to Cesalpino, with only a short allusion to the Great Chain of Being, and while he refers to neo-Platonism, it is the neo-Platonism of the late eighteenth, not the classical and renaissance, centuries.

were possible. After Aristotle, we reach Linnaeus, then Buffon, Lamarck, Cuvier, Geoffroy and then the ideal morphologists until we meet Darwin, followed by the New Systematics group – Dobzhansky, Mayr, Julian Huxley, and so forth.

In each of these, and others (e.g., Wiley 1981 p70–72, to take one example at random) the Received History runs roughly thus:

*Plato defined Form (*eidos*) as something that had an essence, and Aristotle set up a way of dividing genera (*gene*) into species (*eide*) so that each species shared the essence of the genus, and each individual in the species shared the essence of the species. Linnaeus took this idea and made species constant and essentialistic types. Darwin overcame this essentialism. Later naturalists, under the influence of genetics, discovered the biological species concept, in which species are found to be populations without essences, but with common ancestry. Population thinking replaces typological essentialism.*[18]

My original problem with this history was that between Aristotle (*d*322 BCE) and Linnaeus's first works on classification (*fl*1750 CE) lies a two-thousand-year gap. What happened in that intervening period? It was a period of active philosophy, as it includes the bulk of the classical period, not to mention the high period of Arab science and scholarship, the medieval debates, and the Renaissance. Are we to think that there was *no* change or development in these ideas in that time? Therefore, I undertook to investigate this gap and to see what I could see, expecting no more than a continuous narrative supporting the Received History. The results were surprising. In most respects, I found the Received History to be incorrect, seriously incomplete, or simply false. Effectively every philosophical issue raised in the modern period was raised in one form or another during this interregnum. Moreover, the crucial mediate link between Aristotle and modern biology was not Linnaeus, nor even Aristotle's own writings. It was the late classical Neo-Platonists, rediscovered by the Cambridge Platonists (themselves properly considered to be neo-Platonists after Plotinus and Porphyry, to whose works they had direct access), by way of their influence on John Ray, John Locke, and various other seventeenth century notables. In effect, the species problem is a neo-Platonist plot, not an Aristotelian one.

Further, the Received History has tended to ignore the Great Chain of Being and the universals debates, which are of great importance in the way later writers such as Cusa deal with the notion of essence and definition. It is *not* the case that typology and essentialism were bound together, and in many ways typology as it was actually

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[18] A term introduced by Mayr (Mayr 1959; quoted in Mayr 1963 p5f).

discussed is more in line with Mayr's "population thinking" than he has ever admitted.[19]

Few truly novel **formal, conceptual**, elements of species concepts have arisen since the eighteenth century. Biologists and philosophers have been dealing from the same deck of conceptual cards ever since. In fact, I cannot find any generic **biological** concepts later than Alphonse de Candolle (1806–1893), who stressed the observable variational nature of species, although new philosophical interpretations have arisen, and there are many modern eclectic concepts that mix various alternatives that were in play at the time of Lamarck. Of course, many **technical** concepts are novel – for example Templeton's genetic concept (Templeton 1989) relies upon Mendelian genetics, and Wu's genic concept (Wu 2001) relies on molecular genetics, both of which are much later additions to the repertoire of biology.[20]

Despite what we might expect, Darwin and his successors did not add much to the species debate except to raise in sharp relief problems brought about by speciation and the mutability of classifications. Nevertheless, Darwin acts as a focal point for what follows, and even the formalists had to address his conceptions. Since the "Modern Synthesis" of the 1930s, the only truly novel philosophical ideas about species have been the theses of the individuality thesis and the refinement of notions of class inclusion and hierarchies, which themselves rest on prior work. So far as I can tell, there are precursors for everything else, at least in the loose sense of some formal resemblance, if not direct and demonstrated descent. It is often the case that these ideas are continually reinvented, especially by biologists. Equally, however, it is often the case that these modern alternatives are not directly descended from the precursors, although there is evidence of indirect descent. For example, Jody Hey's views (2001a; 2001b), which depend extensively upon Quine's philosophy of language in *Word and Object* (Quine 1960), are a reinvention in some respects of John Locke's conventionalism (Wilkins 2002a). Quine is of course dealing with the same issues of the empiricist, linguistically-directed, philosophical tradition that Locke began, and knows his Locke very well, but Hey, who is a geneticist and can be excused from not

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[19] Winsor (2003) refers to the typological conception as the "method of exemplars", which we shall see is a much better characterisation. See also Amundson (1998). Challenges to the typological/essentialist account begin, so far as I can see, with Farber, Platnick and Nelson, and Panchen in the period from 1970 to 1985 (references cited below and in the next chapter).

[20] I am indebted to Kim Sterelny for this observation. It is open to doubt that ideas that are merely formally similar are in fact "the same" ideas as later ones. But the similarities are themselves instructive; if an older debate dealing with formally similar notions is resolved into a few opposing viewpoints, we may learn from them what to expect of modern debates.

knowing the detailed history of an abstruse episode in philosophy, seems unaware of it. This pattern is repeated even when the originator of a view, for instance Hennig, **is** aware of his philosophical precursors (in this case Woodger and Gregg) – later followers of that initial account often do not realise that there ever was such a prior history. For this reason it is important to at least sketch some of the main pre-biology and early biology historical accounts of species, and this of course means beginning in the western tradition with Plato and Aristotle. I seek excuse for this western bias, despite much interesting literature in Persian and Asian cultures on classification of organisms, because it is from the western tradition and not the others that the modern species problem derives, and on which it depends. For the same reason, I will pass over the work of cultural anthropologists on classification in non-western indigenous cultures (Atran 1999; 1998; 1995; 1990; 1985; Bulmer 1967; Ellen 1993).

Likewise, I shall not attend to the work done on the developmental and psychological origins of taxonomic concepts (Eco 1999; Estes 1994; Gil-White 2001; Griffiths 1997; Hey 2001a; Keil 1995; Sperber et al. 1986; Sperber et al. 1995; Millikan 1984).[21] I assume here that scientific concepts, whatever their etiology in biological substrates, are subject primarily to change due to the institutions and culture of science and cultural influences such as philosophy. We all share whatever psychological and cognitive foundations there are of classification and categorical notions; but the scientific debate has gone its own way, and so we may take it that biological biases are not determinants of such categories. It is my view that cultural evolution, including the evolution of science (Hull 1988c), has its own dynamics, perhaps biased by psychology and evolutionary adaptations and heritage, but it is usually decoupled from them (Toulmin 1970; Campbell 1965).

This chapter and the next form an essay in the history of ideas (although I prefer the term *conceptual history*), and in particular of the ideas that came before and might be demonstrated or fairly thought to have contributed to the ideas in play in biological thought about species and classification. "History of ideas" has become rare and somewhat disparaged by professional historians, and this is understandable given the whiggish, presentist, bias much of it exhibits. I am well aware of the problems faced by the historian of ideas, as described by John Greene:

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[21] Despite its title, Ghiselin's paper "On psychologism in the logic of taxonomic controversies" (Ghiselin 1966) does not address the psychological origins of taxa, but the introduction into taxonomy of epistemological conventionalism.

> Of all histories the history of ideas is the most difficult and elusive. Unlike things, ideas canot be handled, weighed, and measured. They exert a powerful force in human history, but a force difficult to estimate.
>
> (Greene 1963 p11)

But history of ideas is necessary if we are to understand why ideas are as they are in internal terms; that is, in terms of the **content** of the ideas. There is also a need for an externalist history of ideas, of the **context**, but this is much harder to do, and in any event cannot be done without at least some awareness of the internal history. Without defending this further, the history of ideas is at least intrinsically interesting for those seeking to explain current scientific ideas, given that science, as an intellectual set of traditions, relies on the notions of the past as a starting point in the way it develops them further. Knowing the past may also help scientists to avoid repeating it unnecessarily.[22]

We shall not refer much to the usual labels and banners applied to the various thinkers; terms such as *idealist*, *transcendentalist*, *empiricist* and so on. This is because it is my experience that such absolute distinctions ride roughshod over the complexities and similarities of these thinkers. Calling somebody a "transcendentalist" implies they were interested only in Platonic ideas. In the case of a Cuvier or an Agassiz, that is a hard claim to sustain – they attended closely to empirical evidence, and for all their shortcomings, neither merely made inferences *sub specie aeternitatis*, as Plato did. And in abandoning these hard distinctions I have found, I believe, a similarity of conception that runs through most, if not all, non-Darwinian thinkers and researchers on the topic of *species*, and which is found even in them, as well. As Amundson notes (1998 p159), we have a "conceptual tangle" when we attend to the actual history of concepts.

As always in the history of ideas, much of the earlier material must be drawn in terms of resemblance and succession. Because one author – say Porphyry – discusses ideas similar to another's – say Aristotle – is not in itself reason to believe either that there is a direct relationship of intellectual ancestry or even an indirect relationship unless the one cites or refers to the other (as Porphyry does Aristotle). Prior to the "biological problem" of species beginning with Bauhin, Cesalpino and John Ray (next chapter),

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[22] I am influenced by David Hull's evolutionary conception of science (Hull 1973; 1983a; 1984b; 1984d; 1984c; 1988c; 1988a; 1988b; 1990; 1992a), and have tried to present my own evolutionary account of science and culture in this vein before (Wilkins 1998; 2001; 2002b). If there is a difference now, it is that I no longer expect ideas to be subjected to selection – that is to say, memes, like genes, drift (Wilkins 1999).

this lineal descendency must be taken as an approximation. With that caveat, let us proceed.

The history of the species concept can be divided into a pre-biological and a post-biological history, which is how the Received History has always treated it. But the two histories overlap substantially, and it is much better to consider instead the history of the species idea that applies to any objects of classification – the period of universal taxonomy and philosophical logic – and independently the particular history of the species idea that applies solely to biological organisms. Even though, for example, Linnaeus famously applied the notion *species* to minerals as well as organisms, his biological definition included elements not included in the mineralogical case. Hence, we will distinguish between universal and biological taxonomic notions of *species*.[23]

The modern and medieval word "species" is a Latin translation of the classical Greek word εἶδος (*eidos*), sometimes translated as "idea" or "form" (see Table 1). Other significant terms are also translations of Greek terms: *genus* from γένος (*genos*), *differentia* from διαφορά (*diaphora*). Liddell and Scott (1888) tell us that εἶδος means "form", and is derived from the root word "to see", and γένος means "kind" and is derived from the root word "to be born of". We still find these senses in the English words "specify", "special", "spectacle", and "generation", "gene" and "genesis". Διαίρεσις (*diairesis*) is an interesting term that will play a major role later in our story. Another term that is later adopted by the Latins is συναγωγὴ (*synagoge*), or in Latin "*relatum*". *Relata* are those features by which things group together.

Table 1: Some Greek terms and their translations

Greek word, plural form	*Classical meaning (Liddell et al. 1888)*	*Latin translation*	*English words*
εἶδος, εἶδη [*eidos, eide*]	That which is seen, form, shape, figure; a class, kind or sort.	*Species, forma*	Species, idea, kind, sort (Locke), form
γένος, γένη [*genos, gene*]	Race, stock, family. A generation.	*Genus (pl. genera)*	Genus, kind
διαφορά [*diaphora*]	Difference, distinction, variance, disagreement	*Differentia (pl. differentiae)*	Difference
διαίρεσις [*diairesis*]	A dividing, division	*Divisio*	Division
συναγωγὴ [*synagoge*]	A bringing together; a conclusion	*Relatum (pl. relata)*	Relation, affinity

Hereafter, we shall transliterate the Greek alphabet.

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[23] This account owes its outline and many details to Nelson and Platnick (1981) and Panchen (1992).

However, another caution must be made at the beginning. Merely because words derive their etymology from older uses of terms, or translate words in other languages, does not immediately mean that they are the same terms with the same intension or extension. By *eidos* and *species*, for example, different authors have meant *forms*, *kinds*, *sorts*, *species* (in the logical sense of non-predicables, Ross 1949 p57), *biological species*, *classes*, *individuals*, and *collections*, both arbitrary and artificial, or natural and objective. In particular, *species* has meant varieties of ideas and sense impressions, *species intelligibilis*, (Spruit 1994-1995) and the material form of the elements of the sacraments in the Roman Catholic tradition.[24] This must be borne in mind, or it will cause confusions when we consider the views of different authors. This is an instance of a more general problem, called "incommensurability" after Kuhn's thesis that terms in scientific theories can have different referents in the shift from one theory to another; Sankey (1998) has called this particular problem "taxonomic incommensurability". We should not make too much of this, but the terms used in classification shift in subtle and major ways that sometimes obscure the views each author is presenting. This chapter is primarily concerned with the tradition outside biology that **has** impacted on the biological notions and usage.

2.2. Universal taxonomy

We can distinguish between two kinds of taxonomy. There is the *universal taxonomy* that is largely the philosophical tradition from Plato to Locke (but which continues through to the considerations of sensory impressions, or *qualia*, by the logical positivist tradition[25]) and in which species are any distinguishable or naturally distinguished categories with an essence or definition. Then there is the *biological taxonomy* that develops from this tradition as biology itself develops from the broader field known as "natural history".[26] These biological notions of species do not

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[24] The English plural of "species" singular is "species". The word "specie" refers to small coinage. However, in Latin there is a singular (*species*) and plural form (*speciei*), which is signified in one text (Porphyry 1975) by italicising the ending thus: spec*ies*. Here I follow the rule of the biological writers of the past century and refer to "the" species or italicise the entire word for the concept, and leave the term unqualified for number except by context.

[25] The general philosophical tradition of considering classification to be an indispensable aspect of science seems to end with Mill and Whewell (a point noted by Hull, pers. comm.), and the revivification of taxonomy in philosophy of science in recent decades appears, with one exception (Woodger 1937) to be driven by biological systematics itself rather than through philosophy motivating biology. As a result, the philosophical foundations of taxonomy are critically incomplete and rely upon philosophers who disregard the matter almost entirely, like Popper (who only mentions it dismissively in Popper 1957b §27; Popper 1959 p65; as noted by Hull 1988c p252).

[26] "History" is, in this older sense, the Greek word ἱστοϱια (*historia*), which means an inquiry or investigation, which derives from the title, or rather the opening words, of Herodotus' *History*. Later it comes to mean "knowledge" or "learning".

necessarily refer to reproductive communities, nor do they in the medical definitions of species of diseases of the period (Cain 1999b), but we do need to recognise that "species" develops a uniquely biological flavour in the seventeenth century. [27]

2.2.1. Plato

The problem of how to classify things, including living things, is first recorded to be dealt with in detail by Plato in the *Sophist* (219a–221a). Plato proposed a method of binary division until the object being classified was reached; this was known as the *diairesis* (division, or as we would now call it, dichotomy). For example, he somewhat whimsically defined fly-fishing (Jowett's translation) as a model for all such classification. He has the Stranger of the dialogue ask leading questions, such as:

> STRANGER: Let us begin by asking whether he is a man having art or not having art, but some other power.
>
> THEAETETUS: He is clearly a man of art.
>
> STRANGER: And of arts there are two kinds?
>
> THEAETETUS: What are they?
>
> STRANGER: There is agriculture, and the tending of mortal creatures, and the art of constructing or moulding vessels, and there is the art of imitation—all these may be appropriately called by a single name.

and

> STRANGER: Next follows the whole class of learning and cognition; then comes trade, fighting, hunting. And since none of these produces anything, but is only engaged in conquering by word or deed, or in preventing others from conquering, things which exist and have been already produced—in each and all of these branches there appears to be an art which may be called acquisitive.

resulting in the following "final" definition:

> STRANGER: Then now you and I have come to an understanding not only about the name of the angler's art, but about the definition of the thing itself. One half of all art was acquisitive—half of the acquisitive art was conquest or taking by force, half of this was hunting, and half of hunting was hunting animals, half of this was hunting water animals—of this again, the under half was fishing, half of fishing was striking; a part of striking was fishing with a barb, and one half of this again, being the kind which strikes with a hook and draws the fish from below upwards, is the art which we have been seeking, and which from the nature of the operation is denoted angling or drawing up (*aspalieutike, anaspasthai*).

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[27] An excellent treatment of many of the themes discussed in this chapter, and a good aid to understanding the historical contexts, can be found in Mary Slaughter's wonderful book (1982); a broader and more liberal treatment, but one that suffers from over-theorising, is Michel Foucault's *The Order of Things (Les Mots et les Choses)* (Foucault 1970), particularly chapter 5.

As Oldroyd says (1986: 42) "Hence, angling is a coercive, acquisitive art, carried out in secret, in which live animals living in water are hunted during the day by blows that strike upwards from below!" (see figure 1). In addition to division, Plato also classified by grouping (*synagoge*), so that he divided things and grouped them according to their differences and similarities (Pellegrin 1986). Plato's classification style here is clearly arbitrary. In order to force the division into dichotomies, he (through his "Stranger") selects the "right" connections for the next differentia, but nothing is obvious about these steps, and it is clear that he knows ahead of time what he wants to deliver. In short, this is question-begging. Aristotle saw this clearly.[28]

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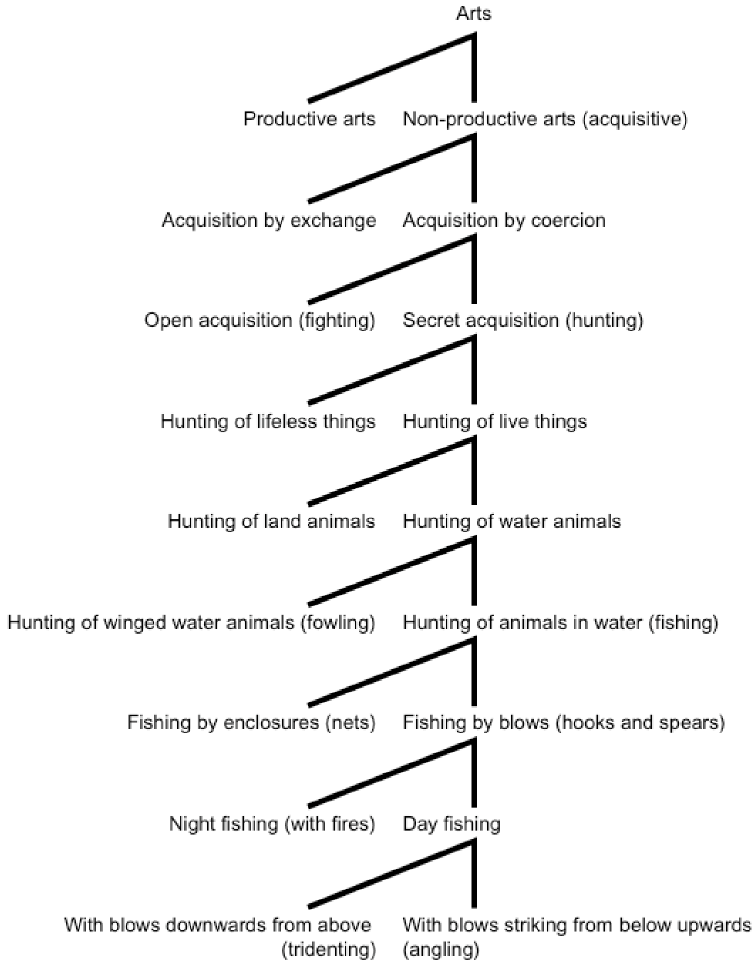
[28] Clearly, there is considerable detail to Plato's views that I have passed over that are relevant to the notion of Form, or Idea (*eidos*), but as this is a well-understood field of history of philosophy, and entirely outside the scope of the present treatment, I am forced to avoid it. A good technical introduction to the received opinion on Plato's theory of Forms is provided by Windelband (1900, §35) and a more updated treatment is found in the introduction to Matthews (1972), and in chapter 1 of Oldroyd (1986). For Plato the *ideai* were metaphysical or ontological realities that were neither changeable nor in the transitory world, and which were preconditions for knowledge. This is the commencement point for the later tradition of forms as the basis for classification we find in Aristotle. Hull asked in correspondence why we don't begin with Socrates. I wonder why we don't begin with the Presocratics. The answer is that basically the biological tradition began with Plato, or with Plato's Socrates – for instance the famous "carve nature at its joints" passage in the *Phaedrus* 265d-266a

> Soc. The second principle is that of division into species according to the natural formation, where the joint is, not breaking any part as a bad carver might.

using Jowett's translation. Socrates then says he is a great lover of division and generalisation, and follows anyone who can see a "One and the Many" in nature. Note, however, that Socrates includes human society in the term "nature" here.

Nelson and Platnick (1981 p67f) quote a passage from Plato's *The Statesman* (262d) in which Plato presents an argument against incomplete groups that is similar in many ways to Aristotle's argument against privative groups below, but we are not discussing Plato's logic here. As Hull (Hull 1967 p312) observes, Plato's **direct** influence on biology is late, not until the eighteenth century. Indirectly, though, is another matter, as I will argue below.

Figure 1 – Plato's classification of angling



2.2.2. Aristotle

If, as Whitehead said, western thought is a series of footnotes to Plato, then biological thought is a series of footnotes to Aristotle.[29] He wrote several works of a biological nature, the most prominent for our purposes being *On the Parts of Animals*, *The History of Animals*, and *On the Generation of Animals*. In these works he employed the logical notions *genos* (genus), *eidos* (species), and *diaphora* (differentia) (Pellegrin 1986). These were not initially special biological notions; in fact, they were part of his

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[29] A point also made by Darwin shortly before his death, when, in a letter to William Ogle thanking him for a copy of his translation of Aristotle's *Parts of Animals* on 22 February 1882, he wrote,

> From quotations which I had seen I had a high notion of Aristotle's merits, but I had not the most remote notion what a wonderful man he was. Linnaeus and Cuvier have been my two gods, though in very different ways, but they were mere school-boys to Aristotle. I never realized before reading your book to what an enormous summation of labor we owe even our common knowledge.

Quoted from Francis Darwin's *Life and letters*, vol 2, p427 by Depew and Weber (1995 p43) wider classificatory logic, outlined in the *Metaphysics*, the *Categories*, and the *Posterior Analytics*. Aristotle was quick to point out a problem with the simple Platonic method of dichotomous classification, although it is not true that he rejected the idea of division as such (Pellegrin 1982; 1986). Many of the categories used in a Platonic diairetic classification were what Aristotle called "privative" categories – defined in terms of what they were *not*, rather than what they were. He proposed instead a method of the decomposition of broader categories into parts on the basis of how the parts differed, but he did not require that each division be a dichotomy as Plato and the Academicians had: there could be many parts in each category. In the *Posterior Analytics*, bk. II, chap. 13 (96b15–24), he says[30]

> The authors of a hand-book on a subject that is a generic whole should divide the genus into its first *infimae species* – number e.g,. into triad and dyad – and then endeavour to seize their definitions by the method we have described … . After that, having established what the category is to which the subaltern genus belongs – quantity or quality, for instance – he should examine the properties 'peculiar' to the species, working through the proximate common differentiae. He should proceed thus because the attributes of the genera compounded of the *infimae species* will be clearly given by the definitions of the species; since the basic element of them all [note: *sc.* genera and species] is the definition, i.e. the simple *infimae species*, and the attributes inhere essentially in the simple *infimae species*, in genera only in virtue of these. (McKeon 1941)

This method came to be known in the late middle ages as *per genus et differentiam*[31] – by the general and the differences. Something that was differentiable within a *genus* was known under the influence of the late neo-Platonist transmitters of Aristotle's work to the western tradition as a *species*. In scholastic philosophy, *species* represented a range of things we would now call propositions, sense impressions, and so forth, and this usage persisted through Leibniz to the philosophical discussions of Kant, Mill and Russell. However, initially a species was merely something that could be differentiated out of a more general concept.[32]

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[30] Using G. R. G. Mure's older translation for emphasis of the terms genus and species. A more recent translation (Barnes 1984) is less clear, using the terms "atomic", "primitive" and "simple" in preference to "infimae species". As an interpretation of the intent of Aristotle himself, the Barnes edition is probably better, but Aristotle has been mediated to the modern (post-medieval) tradition via the sorts of interpretation embedded in the Mure translation.

[31] More fully, as *per genus proximum et differentiam specificam*.

[32] In the *Topics* (101b16–25) Aristotle defines four "predicables" (that which is predicated of things): definition (*horos*), property (*idion*), genus and accident (*symbebekos*). Species (*eidos*) is not, in Aristotle's list, a predicable, because it is only true of individuals. We shall see this come to prominence briefly in the late middle ages.

He extends his discussion of this in the *Metaphysics* in book Z, chapter 12 (1037b–1038a, Aristotle 1998), by asking what it is that makes *man* (the logical species) a unity instead of a "plurality" such as *animal* and *two-footed*. He says,

> … differentiae do not pertain to a genus [qua genus]. The reason for this assumption is that, if they did, and given that the differentiae that differentiate a genus are opposites, opposites would pertain to the same thing. And even if differentiae do pertain to a genus, the same reasoning will apply whenever there is more than one differentiae pertaining to the same species, e.g., apteric bipedal pedestrian. What makes this lot a unity, not a plurality? It cannot be the mere fact of the compresence in a single genus, on pain of collapsing all the differentiae of that genus into a single entity.

In short, he is saying that the differentiae of a genus can lead to its including species which are polar opposites in their specific differences, but that, with respect to the genus itself, there is no differentiation. This makes sense only if each genus is divided further in terms other than the predicates that define the genus. Further, he rejects Plato's dichotomous approach:

> … it makes in general no difference whether the specification is by many or few differentia, neither does it whether that specification is by a few or by just two…

Therefore, he asks whether the genus exists "over and above the specific forms constitutive of it", and answers that it doesn't matter, because the definition is "the account derived just from the differentiae". In the end, we reach the "form and the substance", the last differentia, unless we use accidental features, in which case we will find that we have an incorrect division as evidenced by the differentiae being "equinumerous with the cuts". In short, a species is the form and the substance of the genera, when we reach the last differentia.

In the *History of Animals*, Aristotle discusses why privative terms are not proper to classification (book I, chapter 3):

> … privative terms inevitably form one branch of dichotomous division, as we see in the proposed dichotomies. But privative terms in their character of privatives admit of no subdivision. For there can be no specific forms of a negation, of Featherless for instance or of Footless, as there are of Feathered and of Footed. Yet a generic differentia must be subdivisible; for otherwise what is there that makes it generic rather than specific? There are to be found generic, that is specifically subdivisible, differentiae; Feathered for instance and Footed. For feathers are divisible into Barbed and Unbarbed, and feet into Manycleft, and Twocleft, like those of animals with bifid hoofs, and Uncleft or Undivided, like those of animals with solid hoofs. Now even with differentiae capable of this specific subdivision it is difficult enough so to make the classification, as that each animal shall be comprehended in some one subdivision and in not more than one; but far more difficult, nay impossible, is it to do this, if we start with a dichotomy into two contradictories. (Suppose for instance we start with the two contradictories, Feathered and Unfeathered; we shall find that the ant, the glow-worm, and some other animals fall under both divisions.) For each differentia must be

> presented by some species. There must be some species, therefore, under the privative heading. Now specifically distinct animals cannot present in their essence a common undifferentiated element, but any apparently common element must really be differentiated. (Bird and Man for instance are both Two-footed, but their two-footedness is diverse and differentiated. So any two sanguineous groups must have some difference in their blood, if their blood is part of their essence.) From this it follows that a privative term, being insusceptible of differentiation, cannot be a generic differentia; for, if it were, there would be a common undifferentiated element in two different groups.

Classifications, according to Aristotle, must say something direct and clear. Dividing the world into things that are, and aren't, describable by some predicate, is at best only a partial classification, and the taxa that result are not good divisions of the broader genus. Some things that fall under a privative term must be species, but there is no genus out of which those species can be differentiated, and so the privative "genus" is illusory. Plato's mistake was, he thought, to assume that classifications must be made in terms of polar opposites.[33]

> Again, if the species are ultimate indivisible groups, that is, are groups with indivisible differentiae, and if no differentia be common to several groups, the number of differentiae must be equal to the number of species. If a differentia though not divisible could yet be common to several groups, then it is plain that in virtue of that common differentia specifically distinct animals would fall into the same division. It is necessary then, if the differentiae, under which are ranged all the ultimate and indivisible groups, are specific characters, that none of them shall be common; for otherwise, as already said, specifically distinct animals will come into one and the same division. But this would violate one of the requisite conditions, which are as follows. No ultimate group must be included in more than a single division; different groups must not be included in the same division; and every group must be found in some division. It is plain then that we cannot get at the ultimate specific forms of the animal, or any other, kingdom by bifurcate division. If we could, the number of ultimate differentiae would equal the number of ultimate animal forms. For assume an order of beings whose prime differentiae are White and Black. Each of these branches will bifurcate, and their branches again, and so on till we reach the ultimate differentiae, whose number will be four or some other power of two, and will also be the number of the ultimate species comprehended in the order.

Before the formulation of set theory, Aristotle was saying that classification must always be in terms of proper sets and subsets. Partial inclusion is not legitimate in a good classification, in effect, because it does not make complete sets.

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[33] Balme says that in *Parts of Animals* 1.2-4 (Balme 1987b p19):

> … Aristotle concludes that diairesis can grasp the form if it is not used dichotomously as Plato used it but by applying all the relevant differentiae to the genus simultaneously; after that he explains the ways in which animal features should be compared so as to set up differentiae – by analogy between kinds (genē), by the more-or-less as between forms comprised within a kind (eidē).

It is traditionally held that Aristotle was inconsistent in the way he used γένος and εἶδος between the logical and the biological writings (e.g., Mandelbaum 1957) but recent work by Pellegrin, Balme and Lennox has shown otherwise (Balme 1987a; Lennox 1987; Lennox 1993; 1994; 2001; Pellegrin 1986; 1987). In part, the problem arises because the common view rests mainly on the medieval concepts that, we shall see, are derived out of the later neo-Platonic reinterpretation of Aristotelian logic. Aristotle is only inconsistent if understood to use the term εἶδος in the same way that Porphyry and others later use the term *species*. Pellegrin says that Aristotle was not producing a biological taxonomy in *History of Animals.* Instead, he was producing general classifications, and animals happened to be one domain in which he applied that method. What Aristotle treats as genera and species do not answer exactly to the modern, post-Linnaean, conceptions of species, although this has sometimes been the default interpretation. A species is for him a group that is formed by differentiating a prior group formed by a generic concept. Genera have essential predicates (definitions), and so do species. Infimae species happen to be indivisible, that's all. In this respect, biological species are no different to any other kind. Pellegrin (p110) says,

> Aristotle thus conveys by the term *genos* the transmissible type that in our eyes characterises the species, and by *eidos* the model that is actually transmitted in generation. It would be necessary for these two terms to converge and become superimposed for the modern concept of a species to be born. For Aristotle, the species did not yet exist.

Pellegrin argues that Aristotle's disagreement with Plato is not that classification by division is wrong, but that one should not proceed by dichotomous division into groups that are defined by a differentia and its contrary. He notes (p 48), "Although Aristotle condemns dichotomy as used in the Academy, and does so in all the relevant texts, he does not reject division." For Aristotle, he says, the species is a group, and is merely the least divisible group, or, in other words, the least inclusive classification. However, in the later tradition from which Ray and Linnaeus and others took their systematic ranks, the smallest **group** category was the genus[34]. *Homo* was a species because all present men (women being included) were descendants of a single pair, Adam and Eve. Linnaeus' binomial nomenclature of the genus name and species epithet, as in *Homo sapiens*, was intended, like a personal name, to give the group (the surname, as it were) and a uniquely referring name of that individual parental pair (and their descendants).

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[34] A point made by Hugo De Vries in 1904 (in De Vries 1912), intriguingly, although one might dispute his detailed claims about the genus being natural and not the species in Linnaeus' works. See the discussion below on the medieval debates over the predicables.

Aristotle's biological works and those of his student Theophrastus also strongly influenced the later development of biology, and in particular of early botany, but one particular doctrine was most influential – the doctrine of the souls of living things in *De Anima*. Soul (*psyche*, φυχή) here means something like "motivating force" – plants have only a "nutritive soul" (413a21–35, 414a30), animals also have a "sensitive soul" capable of sensation (413b4–9, 414b3), and hence they must have an "appetitive soul", as do all organisms capable of sensation, because they must have some desire (413b21–24, 414b1–15). Some animals have in addition a "locomotory soul" (413b3, 414b17, 415a7) and one of those, Man, alone also has the power of rational thought, or a "rational soul" (415a7-12). Soul is the source of movement and growth, and it is the final cause of those faculties (415b9–27), that for which things are generated. This forms the foundation for the later Great Chain of Being tradition, as we shall see, and was the foundation for the initial classifications and explanations of Cesalpino and Bauhin (Sachs 1890).

2.2.3. Epicureanism

But the Aristotelian and Platonic traditions were not the only ones in the classical period that dealt with species. The atomists, and in particular the Epicurean tradition, also had an account of why forms are as they are. Epicurus' (341–270 BCE) own writings are largely lost, in particular his *On Nature*. However, we have a full account of the Epicurean doctrines in the work *On the Nature of Things* by Lucretius, a first century BCE Roman disciple of Epicurus. Lucretius tied specific natures of things to the ways in which they came to be:

> If things could be created out of nothing, any kind of things could be produced from any source. In the first place, men could spring from the sea, squamous fish from the ground, and birds could be hatched from the sky; cattle and other farm animals, and every kind of wild beast, would bear young of unpredictable species, and would make their home in cultivated and barren parts without discrimination. Moreover, the same fruits would not invariably grow on the same trees, but would change: any tree could bear any fruit. Seeing that there would be no elements with the capacity to generate each kind of thing, how could creatures constantly have a fixed mother? But, as it is, because all are formed from fixed seeds, each is born and issues out into the shores of light only from a source where the right ultimate particles exist. And this explains why all things cannot be produced from all things: any given thing possesses a distinct creative capacity. (Lucretius 1969 p38, Book I. 155-191)

It is commonly understood that Lucretius gives a more or less faithful exposition in Latin of Epicurus' ideas expressed in Greek some two centuries earlier, in the period following Aristotle of the fourth century BCE. This being so, we can suppose that something resembling the biospecies concept existed by the fourth century BCE. The Epicurean view of species (which is not restricted to biological species – like

Aristotle's, it applies to elemental forms of all things, but is here illustrated in terms of living things) relies upon the potential nature of the composite parts of things. It is, if you will, a kind of *generative view of species*. He goes on to say that things grow at the right season and are able to live because only then are the right "ultimate particles" (i.e., atoms) available to promote growth. Otherwise, everything could happen, such as children and trees maturing in an instant:

> But it is evident that none of these things happens, since in every case growth is a gradual process, as one would expect, from a fixed seed, and, as things grow, they preserve their specific character; so you may be sure that each thing increases its bulk and derives its sustenance from its own special substance.
>
> (*loc. cit.*)

We shall see the generative notion of species being struck upon repeatedly in the history of the concept, both before and after the term attains a technical sense in biology (for example in both Cusa before it and Buffon after).

Lucretius further expounds the nature of species in the generalised sense of classification of all things in terms of the natures of the atoms that comprise those things, in I. 584–598. Again he appeals to the natures *in potentia* of the constituents as determining the limits of a species.

> Furthermore, since in the case of each species, a fixed limit of growth and the tenure of life has been established, and since the powers of each have been defined by solemn decree in accordance with the ordinances of nature, and since, so far from any species being susceptible of variation, each is so constant that from generation to generation all the variegated birds display on their bodies the distinctive markings of their kind, it is evident that their bodies must consist of unchanging substance. For, if the primary elements of things [i.e., atoms] could be overpowered and changed by any means, it would be impossible to determine what can arise and what cannot, and again by law each thing has its scope restricted and its deeply implanted boundary-stone; and it would be equally impossible for the generations within each species to conform so consistently to the nature, habits, mode of life, and movements of their parents. (Lucretius 1969 p49)

> ... every species that you see breathing the breath of life has been protected and preserved from the beginning of its existence either by cunning or by courage or by speed. (Lucretius 1969 p191)

Intriguingly, and famously, Lucretius (5. 837–877) and the Epicureans have an "evolutionary myth" of the origins of living species, and in it they suppose that these generative natures were not fixed in the initial period of life. The mixtures of the elemental particles were random, and so all kinds of organisms and monsters were born. Eventually, only those that could propagate remained in existence, and the others died out. It is sometimes held that Lucretius and the Epicureans therefore held a natural selection view of adaptation (the classical locus being Osborn 1894), but in fact they suppose that the species are as they originally were formed by chance, and are kept to the limits of their generative potential. This is not selection as Darwin and Wallace proposed it – there is no variation except in the different but unchanging natures of the characters that by chance form the species themselves, not within the species.

The Epicureans therefore differed from Aristotle, who held that species were forms that are imposed upon the substance of things, instead holding that species are forms generated by the natures of their substances. For Aristotle, material substance is malleable. For Epicureans, it is deterministic of the nature of the things it comprises. Of course, Aristotle, too, held that the four elements he proposed in the *Physics* contribute through the "material cause" to the nature of the objects, but he also allowed for formal, efficient, and final causes. Epicurus and his disciples seem not to allow for any determination of natures other than by the material atoms, which in this context function somewhat like genes.

This explains a comment made in Boëthius' *Second Commentary* on Porphyry's *Introduction* (*Isagoge*) to Aristotle's *Categories* some four centuries later, and which is crucial to the transmission of the species problem to the medieval universals debate, and thence to the modern era:

> "It is clear... that this happened to him [Epicurus], and to others, because they thought, through inexperience in logical argument, that everything they comprehended in reasoning occurred also in things themselves. This is surely a great error; for in reasoning it is not as in numbers. For in numbers whatever has come out in computing the digits correctly, must without doubt also eventuate in the things themselves, so that if by calculation there should happen to be a hundred, there must also be a hundred things subject to that number. But this does not hold equally in argumentation; nor, in fact, is everything which the evolution of words may have discovered held fixed in nature too."
>
> *Second commentary on Porphyry's Isagoge*, Bk I, sect 2 (McKeon 1929 p73)

Boëthius is complaining that the Epicureans and the "others" have presumed that because they have been able to construct a coherent account, that what is said must be true of the things being spoken of. Aristotelians, and the neo-Platonists that followed, held that the physics of Aristotle was based upon observable features of the world, while Epicurus' atoms are mere speculations, and hence so are the things that depend upon them for their natures, such as species. This is somewhat ironic, given the clearly theoretical nature of the quintessence in Aristotle's cosmology, and even more so given the merely logical role that genus and species plays in Aristotle's categorical logic. Aristotelian essence is, in effect, exactly the kind of reification to which Boëthius, who thinks he is defending Aristotle, objects. Although Aristotle's essence concept was not then considered to be an inappropriately abstracted notion (what Whitehead 1938 later called the Fallacy of Misplaced Concreteness) when Boëthius wrote, the issue had been raised by Porphyry himself as to whether species exist merely as abstract mental objects.

2.2.4. The Hermetic tradition

Around 100CE, a text was written under the pseudonym of Hermes Trismegistus, today known as *Asclepius* I (Scott 1924). This tradition in part is the direct descendent of Plato and the Academy, with a strong veneer of mysticism and *gnosis*. In this text, nature is the matter that nourishes the forms (*species*) that are imposed on it by God (3c), and in the manner of Plato's souls in *The Republic*, different kinds (*species*) are realised according to the source. The god-kind produces gods, the daemon-kind produces daemons, and the man-kind produces men (4). Unlike Plato, however, the author allows that individuals might partake in many kinds:

> ... though all individuals exactly resemble the type of their kind, yet individuals of each kind intermingle [*miscentur*] with all other kinds.

A later scribe has interposed the comment that organic bodies receive their kinds by the fiat of the gods, and individual things receive form by the ministration of daemons.

In *Asclepius* II (c150–270CE), matter is considered "ungenerated" (15) but to have a "generative power" and to be creative, reiterated also in book II (c270CE). The Hermetic tradition is thought to be strongly influenced by the Stoics.

2.2.5. The neo-Platonists

Aristotelian categories strongly influenced the neo-Platonists, who in turn influenced the medieval scholastics from whom Linnaeus drew his ranking categories. A clear example is the fourth or fifth century writer Martianus (or Felix) Capella. In Martianus' scheme, which is representative of the tradition, genus is the higher grouping and species are the members of the genus. What is a genus with respect to one predicate can be a species with respect to another. Martianus, who was by tradition a farmer in 5th century CE Africa, but more probably was a wealthy landowner, did not explicitly deal with the classification of living things, but effectively repeated the abstract position of Aristotle's chapter 13 of the *Categories*. His text, whimsically entitled *The Marriage of Philology and Mercury*, was used as a major textbook of the medieval educational program that came to be known as the Quadrivium and the Trivium, for over a thousand years, surely a record for a purpose-written instructional textbook. It is significant in this context as defining what Franz Stafleu (1971) called the "classificatory philosophy" of Linnaeus and his predecessor

John Ray, through whom the notion of biological species entered the modern context. Martianus wrote:

> Genus is an assemblage of many forms under one name, as, animal: and of a particular species, as: man, horse, lion, and so on. But sometimes some species are so subordinate to the genus that they, too, having other species subordinate to them, can be a genus, as the genus of man, that is a species in regard to animals, and a genus in respect of foreigners and Romans. The genus may extend to the point where, after division of its species, an indivisible point is reached: …
>
> We also call species forms. Forms are those things that, subordinate to the genus, have its name and definition, as: man, horse, lion: since they are forms of animal: and man horse, and lion can be called animal and a body participating in life. The term and definition of genus are thus determined.[35]

The interesting thing about this is that there is no necessity that a species should not be further decomposable (see below in Whatley's *Logic* of the 19th century). That is, a species can be a genus on its own, with differentiating characters (the *differentia*, or the *diaphora*) that allow the classifier to distinguish further species within that genus. Later Scholastic philosophy allowed for the existence of species that could not be further differentiated. The characters that were the "same" or which related members of the infimae species were the *relata*. Also noteworthy is that the examples used here are biological ones. This tradition began early.

In the neo-Platonic interpretation of Aristotle, mediated to medieval Christianity by Martianus and Porphyry in the *Isagoge,* via Boëthius in the *Commentaries*, a species was a member of a broader group – a genus – that was formed by a predicate. There was no necessity for any object to be a member of a single genus, and a species might be, with respect to some other predicate a genus in its own right. In short, species were predicate-relative individuals. However, they were not individuals in either the nominalist sense – name-bearing particulars – or the Strawsonian sense (Strawson 1964 chapter 8) – historically and geographically delimited objects. They were whatever was differentiable out of the genus. This gave rise to Porphyry's dichotomous notion of classification, although the terminology and many of the concepts were derived from Aristotle's *Posterior Analytics.* Porphyry syncretised Plato's dichotomous method with Aristotle's logical division of predicables. Aristotle's conception of the *infimae species* was primarily a matter of logical analysis. Porphyry combined this and Plato's method of classification in the *Sophist* to produce what has become known as *Porphyry's comb* or *tree*, which is topologically the same as a cladogram (see figure 2). But a major distinction between a phylogenetic tree and Porphyry's comb is that the

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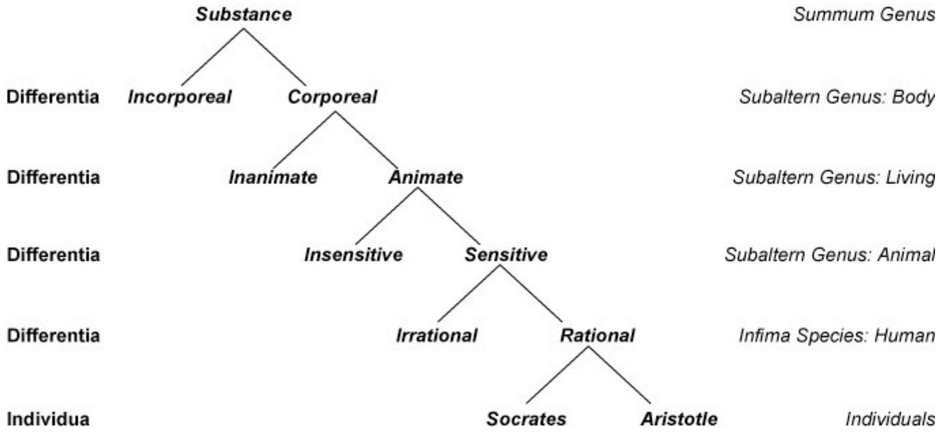
[35] From the section "On rhetoric" in book I, translation by H E Wedeck, from (Runes 1962 p211-212).

former is derived from history, while the latter is derived from diagnosis (Nelson et al. 1981).

Porphyry treated species slightly differently to Aristotle. In place of the four predicables, Porphyry had five: genus, difference, species, property and accident (cf. Barnes' commentary §0 in Porphyry et al. 2003 p26–32; also see Joseph 1916, chapter IV), replacing *definition* with *species*.[36] In the later middle ages, this tetrad was much debated (Green-Pedersen 1984 p118–121). While Porphyry's tetrad was not exactly followed by all, there was debate over whether species should be considered "predicate-types", because, as Green-Pedersen says, the species "can only be predicated about individuals, and there can be no science about individuals", a view held consistently through the middle ages (p120). In the fourteenth, and increasingly in the fifteenth, century, though, the suggestion is made in the commentaries that the species is an addition (*annexum*) to the genus. This, in effect, would make *species* into a class concept like *genus*, which it was not in the earlier logic.

Figure 2 – Porphyry's Tree



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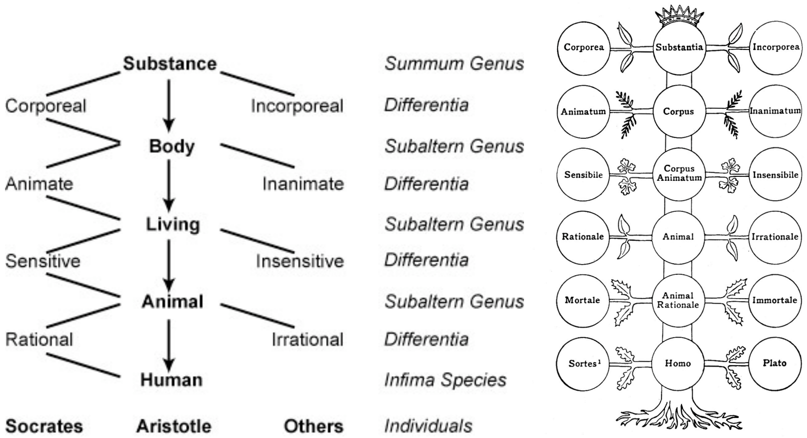
[36] As noted above, Joseph's book has been implicated in the adoption by Cain and Hull of the idea that pre-evolutionary species are timeless and static entities defined by their essences. It should be noted that Joseph is presenting a formal account of the pre-set theoretic logics from Aristotle until his day, and he does, in several places (pp 53n, 92–96), note the differences between Aristotle and Porphyry, but it would not have been obvious to anyone not familiar with the technical aspects of the medieval commentaries on Porphyry. It is actually a very good late example of the treatment of logic in the Aristotelian tradition, surviving into the post-Darwinian era but aware of it. Hull (1967 p310n313) cites a passage from Joseph in which Joseph notes that the evolution of species is not thought through by biologists in the logical sense.



The top version has been adapted from (Oldroyd 1983 p29) to make the logical isomorphism with a cladogram clearer – the traditional form of Porphyry's tree is more like the one Oldroyd presents (below left), an example of which, from Nelson and Platnick 1981, p74, is shown at right, where "Socrates" has ironically been corrupted as "Sortes". See also the discussion by Barnes in (Porphyry et al. 2003 p109f), who locates the earliest such tree in the middle ages, not in Porphyry's own text. The terms used are those of the late medieval scholastic tradition

As Nelson and Platnick note, the tree is strongly reminiscent of the later apomorphy/plesiomorphy distinction of Hennig (1966; 1950). Hennig distinguished between derived and underived states in taxonomy. *Plesiomorphic* characters are those in a monophyletic group (a clade) from which the transformations begin, and *apomorphies* are those derived from them in evolution (p. 89). An apomorphy of a group can be a plesiomorphy of a clade contained within that group. It follows that in both the neo-Platonic and Hennig's classificatory schemes that genus/plesiomorphy and species/apomorphy are not absolute ranks, but are relative. They are relative to the differentiae, the predicates and the properties those predicates denote which make the differences between taxa. Hennig, like Martianus, has no system of absolute taxonomic levels. There are just taxa, and they are arrayed in a flexible local hierarchy (Nelson 1989). The base-level taxonomic rank – the infimae species – was a taxic entity that was not itself the genus of any other species and which contained only individuals. Likewise, Hennig has terminal taxa, and these he calls species, following Linnaean tradition. Where the infimae species and the Hennigian species differ from the Linnaean species, however, is that the former are derived from the general group being sequentially divided into subgroups on the basis of characters shared (a single dichotomous key in the medieval conception, on a parsimony criterion of many characters for Hennig), while Linnaeus assumed fixed taxon ranks. Linnaean species are an absolute rank, and so also are the higher taxa they comprise, as we shall see.

Boëthius reported that Porphyry had raised the issue of whether species and genera exist only in the mind, some 1400 years before Locke addressed the same issue (see below), and indeed well before the nominalists of the fourteenth century:

> As for genera and species, [Porphyry] says, I shall decline for the present to say (1) whether they subsist or are posited in bare [acts of] understanding only, (2) whether, if they subsist, they are corporeal or incorporeal, and (3) whether [they are] separated from sensibles or posited in sensibles and agree with them. For that is a most noble matter, and requires a longer investigation.[37]

This began what we now know as the "Universals" debate and led, fairly directly, to the position that came to be known as nominalism. Why did Porphyry even raise this question? It seems to come out of nowhere. Aristotle had no doubt that the *eidos* was real – it was the form of the thing that existed as a material object. Plato had no such doubt either – to him **only** Ideas were real.[38] I suspect that Porphyry was responding to the debates over atomism that bridge the period of Aristotle and the Epicureans, and his day, around 500 years' duration. Plotinus had addressed the arguments of the Gnostics in his *Enneads*, which Porphyry edited. It is possible that the topic had indeed been raised by the Roman Epicureans, who discussed the nature of sensation extensively, and that the Aristotelians in the person of Porphyry are attempting to defend the essentialist account against the atomistic substantist one.[39]

We must now consider some of the leading ideas and thinkers in the post-medieval period. This is not because the medievals were unimportant – very far from it. The revival of the universals debate in the late eleventh century, by Roscelin, Abelard and

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[37] The passage is translated from *Anicii Manlii Severini Boethii In Isagogen Porphyrii commenta*, editio 2a, lib. I, ca. 10-11, Samuel Brandt, ed., p. 159 line 3 – p. 167 line 20. Translation by Paul Spade, unpublished. Barnes' direct translation of Porphyry (Porphyry et al. 2003 p3, lines 10–15) reads:

> For example, about genera and species – whether they subsist, whether they actually depend on bare thoughts alone, whether if they actually subsist they are bodies or incorporeal and whether they are separable or are in perceptible items and subsist about them – these matters I shall decline to discuss, such a subject being very deep and demanding another and a larger investigation.

[38] And interestingly, until late in the seventeenth century, "Realism" denoted a realism about ideas; what we would consider Idealism today (Blackmore 1979).

[39] Barnes agrees (Porphyry et al. 2003 p312-317), with more warrant than I have, that the traditional claim of Stoic influence has no basis in fact, and conjectures (pp356–358) that there are many "Epicurean touches" in Porphyry. Preus (2002) notes that Plotinus, Porphyry's teacher, had made some passing comments on form (*eidos*) in the *Enneads* (V.9.6) which gives an Epicurean-style generative account of species, in which *logoi* are the generative powers "in the seed" and of every part of an organism. He says

> Some call this power in the seeds 'nature,' which was driven thence from those prior to it, as light from fire, and it turns and enforms the matter, not relying on the help of those much-discussed mechanisms (levers), but by imparting the *logoi*. [Preus' translation, p46]

eventually the nominalist school, was critical in bringing the notion of genera and species to the forefront of western thinking (Leff 1958). Once there the idea was taken up by the nascent biological sciences in the 17th century, but so far as I can tell, nominalism did not directly influence biological practice. Albert the Great (Albertus Magnus) for example, held that species were quite mutable, although not in an evolutionary way, a view abandoned from the beginning of the modern botanical tradition (Arber 1938 p5). Even his student Thomas Aquinas' discussion in the *Summa* (Bk I, Q. 86) does not materially advance the matter and can be treated for our purposes here as straight transmission of the earlier Scholastic logic.

2.3. Post-medieval period

2.3.1. Nicholas of Cusa

Nicholas of Cusa (1401–1464) in his *On learned ignorance* (c1440, cf. Hopkins 1981) represents a bridge between the medievals, who were rediscovering Aristotle but using the categories bequeathed to them by the neo-Platonists, and the Renaissance era. He was an eclectic, and his comments on categories show an influence from Pythagorean as well as neo-Platonic sources. He held, for example, that ten is the supreme number, and that all unity is found in it (Book II chapter 6, §123). He thus justifies the Aristotelian ten *topoi* (Categories), and says,

> And so, we see that the universe is contracted in each particular through three grades. Therefore, the universe is, as it were, all of the ten categories *[generalissima],* then the genera, and then the species. And so, these are universal according to their respective degrees; they exist with degrees and prior, by a certain order of nature, to the thing which actually contracts them. And since the universe is contracted, it is not found except as unfolded in genera; and genera are found only in species. [§124]

Cusa is naturally aware of the nominalist debate, and takes a pretty standard Aristotelian view of the matter:

> But individuals exist actually; in them all things exist contractedly. Through these considerations we see that universals exist actually only in a contracted manner. And in this way the Peripatetics speak the truth [when they say that] universals do not actually exist independently of things. For only what is particular exists actually. In the particular, universals are contractedly the particular. [§124]

In effect, he is saying that species are particulars (individuals). All general things, such as universals, and indeed the entire universe, only actually exist "in a contracted way" [§125], as particulars, although things of the same species share in a specific nature:

> For example, dogs and the other animals of the same species are united by virtue of the common specific nature which is in them. This nature would be contracted in them even if

> Plato's intellect had not, from a comparison of likenesses, formed for itself a species. Therefore, with respect to its own operation, understanding follows being and living; for [merely] through its own operation understanding can bestow neither being nor living nor understanding. [§126]

Cusa thus answers Porphyry's question: the understanding gathers species and genera together through comparison, so that these universals are likenesses of nature. Genera and species exist both in the mind and in nature.

> Therefore, in understanding, it unfolds, by resembling signs and characters, a certain resembling world, which is contracted in it. [§126][40]

Later, in Book III, Cusa defines the universe as existing "contractedly in plurality", unlike God, who is "the Oneness of the Maximum" existing "absolutely in itself" (§182).

> Now, the many things in which the universe is actually contracted cannot at all agree in supreme equality; for then they would cease being many. Therefore, it is necessary that all things differ from one another – either (*1*) in genus, species, and number or *(2)* in species and number or *(3)* in number-so that each thing exists in its own number, weight, and measure. Hence, all things are distinguished from one another by degrees, so that no thing coincides with another. Accordingly, no contracted thing can participate precisely in the degree of contraction of another thing, so that, necessarily, any given thing is comparatively greater or lesser than any other given thing. Therefore, all contracted things exist between a maximum and a minimum, so that there can be posited a greater and a lesser degree of contraction than [that of] any given thing. [p124]

No individual member of a species, since it would be a contracted thing, can therefore exhibit or instantiate all the features of the species, and so there is in the actual organisms of a species (or any non-biological species) variation in the degree to which they participate in the specific essence. According to Cusa, then, there is variation both within and between taxa. Here we see the beginnings of the "type" concept – while the type itself is definable in terms of some necessary and sufficient conditions, "members" of the type can diverge from it or not instantiate it fully. The only limit "of species, of genera, or of the universe" is "the Center, the Circumference, and the Union of all things" [§185]. Here we see also the underlying assumption of the Great Chain of Being. Cusa's subsequent discussion bears quoting at length:

> And among the different species there is such an order of combination that the highest species of the one genus coincides with the lowest [species] of the immediately higher [genus], so that there is one continuous and perfect universe. However, every union is by degrees; and we do

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[40] This brings to mind Donne's much later use of the phrase, "the world's contracted thus" in his poem "The Sunne Rising" (c1605). Donne was a one for lamenting the loss of the older medieval categories of thought, famously complaining in his "Anatomy of the World" (1611) that all coherence was gone with the loss of Aristotelian physics and astronomy (Kuhn 1959 p194).

> not arrive at a maximum union, because that is God. Therefore, the different species of a lower and a higher genus are not united in something indivisible which does not admit of greater and lesser degree; rather, [they are united] in a third species, whose individuals differ by degrees, so that no one [of them] participates equally in both [the higher and the lower species], as if this individual were a composite of these [two species]. Instead, [the individual of the third species] contracts, in its own degree, the one nature of its own species. As related to the other species this [third] species is seen to be composed of the lower and of the higher [species], though not equally, since no thing can be composed of precise equals; and this third species, which falls between the other two, necessarily has a preponderant conformity to one of them – i.e., to the higher or to the lower. In the books of the philosophers examples of this are found with regard to oysters, sea mussels, and other things.
>
> Therefore, no species descends to the point that it is the minimum species of some genus, for before it reaches the minimum it is changed into another species; and a similar thing holds true of the [would-be] maximum species, which is changed into another species before it becomes a maximum species. When in the genus *animal* the human species endeavors to reach a higher gradation among perceptible things, it is caught up into a mingling with the intellectual nature; nevertheless, the lower part, in accordance with which man is called an animal, prevails. Now, presumably, there are other spirits. … And because of a certain nature which is capable of perception they are said, in an extended sense, to be of the genus *animal.* But since the intellectual nature in them prevails over the other nature, they are called spirits rather than animals, although the Platonists believe that they are intellectual animals. Accordingly, it is evident that species are like a number series which progresses sequentially and which, necessarily, is finite, so that there is order, harmony, and proportion in diversity... [§§185–187]

The gradualism of the Great Chain is evident, as also is the influence of the neo-Platonic view of classification. Of particular note is that Cusa's examples are biological ones.

2.3.2. Marsilio Ficino

Ficino (1433–1499) was responsible for a number of neo-Platonic texts being translated and published under Cosimo de Medici. Among other texts, he oversaw texts by Porphyry, Proclus, Plotinus and Dionysius the Areopagite; all source texts for the neo-Platonic philosophy (Cassirer et al. 1948 p185). In his discussion of the genus–species distinction, he is at pains to view the logical progression of Aristotle as being a description of the actual progression of things, and God, of course, is the source of all things. In his *Five Questions Concerning the Mind*, Ficino writes (Cassirer et al. 1948 p194):

> The motion of each of all the natural species proceeds according to a certain principle. Different species are moved in different ways, and each species always preserves the same course in its motion so that it proceeds from this place to that place and, in turn, recedes from the latter to the former, in a certain most harmonious manner.

Here we have again the generative notion of species that we saw in Lucretius. However, unlike the materialist account of Lucretius, Ficino's view is based upon the essence of the species and of the *primum* of a genus (the ontological principle *primum in aliquo genere*). Each genus has what later came to be thought of as a *type species*, a first and highest example of the kind, according to Ficino (Cassirer et al. 1948 p189), the primum, which is the species that is purely of the genus, with no defining essences other than those of the genus. God is, of course, the primum of the genus Being, and from him all being flows, in the standard neo-Platonic way. Things do what they do because they share the limits of their species and are constrained by the end of that genus. The primum does it best of all.

With elements, plants and "brutes", Ficino gives the Aristotelian accounts – the elements have heaviness and so they fall. Plants and animals have a nutritional and generative power (compare Aristotle's nutritive faculty, *De anima* 413a20-33, and the discussion of reproduction in *De generatione animalium*). Species are perpetuated because they have an end, or rather, because to be a species is to have an end. Ficino presents this as a prelude to discussions of the mind that do not concern us here.

2.4. Great Chain of Being

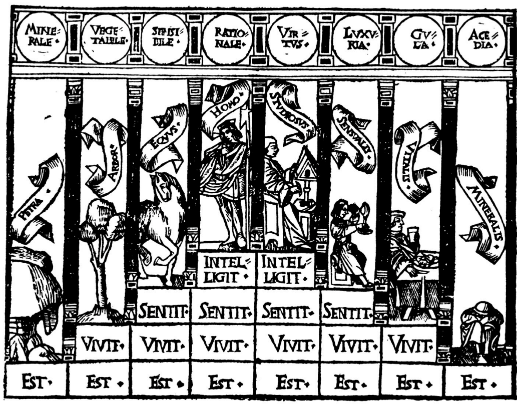
That the philosophical view deriving from the neo-Platonists had reached popular culture is evidenced in Alexander Pope's *Essay on Man* (1733), sect VII:

Vast chain of being! Which from God began;
Natures ethereal, human, angel, man,
Beast, bird, fish, insect, who no eye can see,
No glass can reach; from infinite to thee;
From thee to nothing.—On superior powers
Were we to press, inferior might on ours;
Or in the full creation leave a void,
Where, one step broken, the great scale's destroy'd:
From Nature's chain whatever link you like,
Tenth, or ten thousandth, breaks the chain alike.

This view is known as the *Great Chain of Being* (Lovejoy 1936), and it has a history that arises from Aristotelian concepts, through the neo-Platonists, into the middle ages and the revival of Aristotle in the 14th through to the 16th centuries (Kuntz et al. 1988). The predicables that defined organismic species were an ascending scale of increasingly "perfect" features: from being, to growth, to animation, to rationality. Raymond Lull is perhaps the exemplar of this view. In his view, around 1512, the chain of being was a series of steps in a staircase to heaven (figure 3).

Figure 3 – Representations of the Great Chain

A. Raymond Lull's chain of being conception as a stairway to heaven. The steps are: stone, flame, plant, animal, man, heaven, angel, God.



B. Shortly before Lull, Bovillus illustrated a slightly simpler, and more morally-directed, scale: as one adds predicates (being, vitality, sensibility, rationality) one ascends the scale from minerals, vegetables, sensible animals, and rational beings. Humans can morally decline down that scale too, as they lose their intellectual function (virtue), their sensibility (luxury), their life (appetite) and motion, leaving only bare existence. The properties here answer to Aristotle's "souls".

(Figures from Kuntz et al. 1988)

The Great Chain view consisted of a number of related theses held in varying ways by its adherents. One of these, named by Lovejoy (1936 p52) *the principle of plenitude*, has it that the world is as full of all the things it could be, or, as Lovejoy himself stated it,

> … the universe is a *plenum formarum* in which the range of conceivable diversity of *kinds* of living things is exhaustively exemplified, but also any other deductions from the assumption that no genuine potentiality of being can remain unfulfilled, that the extent and abundance of the creation must be as great as the possibility of existence and commensurate with the productive capacity of a 'perfect' and inexhaustible Source, and that the world is better, the more things it contains.

In short, everything that can be, is, and the world is made to be everything it can be. This is where Leibniz's doctrine of the *lex completio* came from, that Voltaire so wickedly caricatured in his *Candide* as the teachings of Dr Pangloss. It is found in

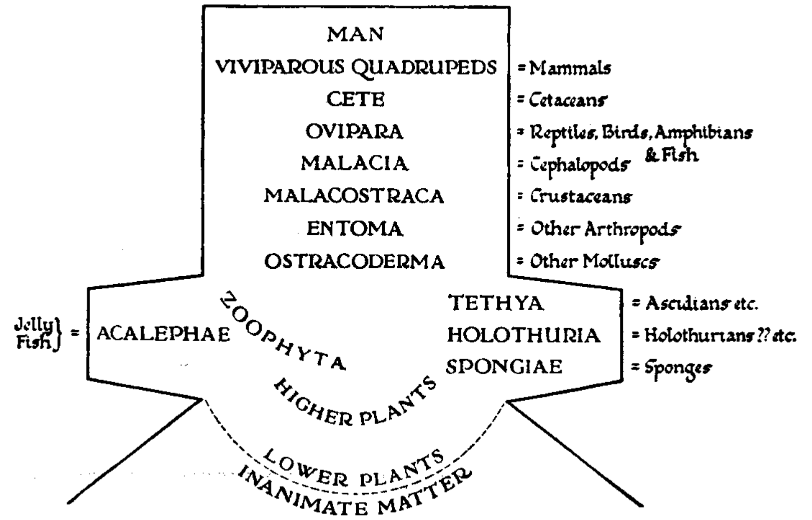
Plato's writings, but not in Aristotle: who famously wrote in the *Metaphysics* (II, 1003a 2, and XI, 1071b 13), "it is not necessary that everything that is possible should exist in actuality", and "it is possible for that which has a potency not to realize it" (quoted by Lovejoy 1936 p55). However, the second plank of the great chain is the law of continuity (Leibniz calls it the *lex continui*) – that all qualities must be continuous, not discrete. While Aristotle did not make all things linear, arranged in a single ascending series, he did require that there be no sudden "jumps", from which the medieval claim *natura non facit saltus* (nature does not make leaps) came, which we shall meet again. Aristotle's version did not itself insist that one would classify a single living being in one and only one series, nor that an organism that is graded as superior in one respect must be superior in all (Lovejoy 1936 p56f) but that became the general impression later. Lovejoy says

> It will be seen that there was an essential opposition between two aspects of Aristotle's influence on subsequent thought, and especially upon the logical method not merely of science but of everyday reasoning. ... He is oftenest regarded, I suppose, as the great representative of a logic which rests which rests upon the assumption of the possibility of clear divisions and rigorous classification. Speaking of what he terms Aristotle's "doctrine of fixed genera and indivisible species", Mr. W. D. Ross has remarked that this was a conclusion to which he was led mainly by his "close absorption in observed facts." Not only in biological species but in geometrical forms – ... he had evidence of rigid classification in the nature of things. But this is only half of the story about Aristotle; and it is questionable whether it is the more important half. For it is equally true that he first suggested the limitations and dangers of classification, and the non-conformity of nature to those sharp divisions which are so indispensable for language and so convenient for our ordinary mental operations. ...
>
> From the Platonic principle of plenitude the principle of continuity could be directly deduced. If there is between two given natural species a theoretically possible intermediate type, that type must be realized – and so on *ad indefinitum*; otherwise there would be gaps in the universe, the creation would not be as "full" as it might be, and this would imply the inadmissible consequence that its Source or Author was not "good," in the sense which that adjective has in the *Timaeus*. [p57f]

From Aristotle's notion of an ontological scale – the higher beings were less potential and more determinate (God, the *ens perfectissimum*, could not be otherwise than he is), and "all individual things may be graded according to the degree to which they are infected with [mere] potentiality" (Ross 1949 p178, after a discussion of the Metaphysics, quoted by Lovejoy on p159). It is perhaps arguable if this idea really does exist in Aristotle's writings, or that he intended it; but whether or not he did, this is the idea that was formulated by the Neo-Platonists (Lovejoy 1936 p61–66, on Plotinus' construction of the chain), and various passages in his works led to a serial classification of organisms (Singer 1950 p40–41). This philosophy influenced many biologists, especially in this context, Bonnet, as we shall discuss in the next chapter. Later, in the late eighteenth century, at first in Buffon, then his pupil Lamarck and

Erasmus Darwin in England, but also in Maupertuis, Robinet, Diderot, Holbach and Kant, the great chain became temporalised. The ladder became a pathway.

Figure 4 – Aristotle's Scale



Singer's representation of Aristotle's "version" of the great chain (Singer 1950 p40).

The *lex completio*, and the *lex continui*, taken together do not allow for temporal change. Leibniz could not allow that there could be more monads later than earlier (Lovejoy 1936 p256–258). Others, most famously Voltaire, rejected the gradation scale for the same reason. Things did change, and they weren't always for the best. One or the other had to go. As we shall see with Lamarck, the *lex completio* was the first of the two major planks of the great chain to be rejected in biology.

2.5. Universal Language Project

Towards the end of the Renaissance, neo-Platonism was revived, particularly at Cambridge University under the general leadership of Ralph Cudworth and the later title of the "Cambridge Platonists". This movement was instrumental in the establishment of seventeenth century science in England in particular, and Bishop John Wilkins among others began discussion groups to review recent experiments and results.

Mary Slaughter (1982) has discussed the universal language project at length, and she traces the influence of this approach from the medieval herbalists and the heritage of Aristotle. She noted

> The sixteenth and seventeenth centuries were heirs to a worldview that is essentially Aristotelian and that worldview had repercussions in the study of language; it created the way in which people thought about language and in turn provided the model for the way in which they analyzed language. [p87]

The theory of language that developed is founded on the epistemology of Aristotelian scholasticism – based on analytic differentiation of the *topoi*, the Categories. The "universal grammarians" Vossius, Caramuel and Campanella of the sixteenth century in turn gave way to the "universal language projectors" of the seventeenth. These began with the work of Francis Bacon's, *The Advancement of Learning* (1605), in which, Slaughter says, he systematically

> described, analyzed and classified Renaissance provinces of knowledge, dividing learning into the arts of imagination, memory and reason ... . Among the subdivisions of the arts of reason was rhetoric; among its parts Bacon included the Art of Transmission, or communication. [p89]

Bacon argued that letters of the Latin alphabet are conventional signs, but the Chinese characters were "real characters, not nominal" which he said

> represent neither letters nor words, but things and notions; insomuch that a number of nations whose languages are altogether different, but who agree in the use of such characters ... communicate with each other in writing; to an extent that indeed any book written in characters of this kind can be read off by each nation in their own language. [quoted on p90]

Words are signs that can represent the world, or they can be false and misleading, which he called "Idols of the Marketplace", "idols which have crept into the understanding through the alliances of words and names" (*Novum Organum,* 1620, I.lix quoted on p91). Slaughter comments (p92):

> While Bacon criticizes words here [in a quoted passage from *Novum Organum* I.lx], it is clear in his later works that linguistic problems merely reflect conceptual problems ... "There is no soundness in our notions whether logical or physical. Substance, Quality, Passion, Essence itself, are not sound notions; much less are Heavy, Light, Dense, Rare, Moist, Dry, Generation, Corruption, Attraction, Repulsion, Element, Matter, Form and the like; but all are fantastical and ill defined." [quoting from *Novum Organum* I.xv]

Bacon goes on to say that we can be pretty sure that words for animal species and simple sensory perceptions are accurate enough:

> Our notions of less general species, as Man, Dog, Dove and of the immediate perceptions of the sense, as Hot, Cold, Black, White, do not materially mislead us; yet even these are sometimes confused by the flux and alteration of matter and mixing of one thing with another. All the others which men have adopted are but wanderings, not being abstracted and formed by proper methods. [*Novum Organum* I.xvi]

So, there is a method (*organon*) one must adopt to do this properly, says Bacon:

> There are and can be only two ways of searching into and discovering truth. The one flies from the senses and particulars to the most general axioms, and from these principles, the truth of which it takes for settled and immovable, proceeds to judgment and to the discovery of middle axioms. And this way is now in fashion. The other derives axioms from the senses and

> particulars, rising by a gradual and unbroken ascent, so it arrives at the most general axioms last of all. This is the true way, but as yet untried. [*Novum Organum* I.xix]

Bacon, in effect, treats science as a bottom-up process of generalisation, in opposition to the top-down classification practised by the Aristotelians. As Slaughter comments,

> Enumeration was to be followed by classification, the critical operation in the discovery and the definition of the essences of things. Natures could be properly defined only when instances were properly classified into 'the true divisions' of nature. [p93]

In short, real science meant that the labels of things were correct representations or signs of the way the world was, and that essences were found as axioms, or generalisations, made step by step from empirical inductions.

Bacon recognised that organisms and other things could deviate from the type. There is no necessity for things to be constrained by their species' essences:

> Among Prerogative Instances I will put in eighth place *Deviating Instances*, that is, errors, vagaries, and prodigies of nature, wherein nature deviates and turns aside from her ordinary course. Errors of nature differ from singular instances in this, that the latter are prodigies of species, the former of individuals. Their use is pretty much the same, for they correct the erroneous impressions suggested to the understanding by ordinary phenomena, and reveal common forms. …
>
> … we have to make a collection or particular natural history of all prodigies and monstrous births of nature; of everything in short that is in nature new, rare, and unusual.

Bacon also thinks it worthwhile to discover which things are a mixture of species (§30); but it is clear that he considers the term in a much broader manner than the modern sense, and his notion of hybrids in the final phrase is quite arbitrary:

> … I will put in the ninth place *Bordering Instances*, which I will also call *Participles*. They are those which exhibit species of bodies which seem to be composed of two species, or to be rudiments between one species and another. …
>
> Examples of these are: moss, which holds a place between putrescence and a plant; some comets, between stars and fiery meteors; flying fish, between birds and fish; bats, between birds and quadrupeds; also the ape, between man and beast—
>
> Simia quam similes turpissima bestia nobis;[41]
>
> Likewise the biformed births of animals, mixed of different species, and the like.
>
> (Bacon 1960 pp178f)

He was followed by Descartes, who proposed that an artificial language could be constructed on the true divisions of nature (in his letters), but the work of the linguist

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[41] "How like us is that very ugly beast, the monkey", Ennius (239-169?BCE) as quoted in Cicero's "On the Nature of the Gods". Thanks to Tom Scharle for the reference and translation.

Comenius in *Janua linguarum researata* (1631) and *Janua linguarum researata vestibulum* (1633) made a start at a universal language answering to all things. In later work he expanded the scope of this project, and he had unrealised plans for

> an inductive history in which all things all things, which have ever been exactly observed and proved beyond all possibility of mistake to be true, are faithfully collected and set before our eyes; so that by an adequate examination of each one and by comparison of one with another the Universal Laws themselves of Nature may be brought within our knowledge."
>
> (Quoted by Slaughter, p102f)

He tried, unsuccessfully, to engage the botanist and polymath Joachim Jung in editing his works.

Other universal language projectors included Samuel Hartlib, Theodore Haak, Francis Lodowyck, Cave Beck, Francis Van Helmont, George Dalgarno, Athanasius Kircher, Johann Joachim Becher, Seth Ward, and various others involved in the nascent Royal Society at Cambridge. One contributor, one might say the zenith, of the universal language project was Bishop John Wilkins (1614–1672). My namesake was the brother-in-law of Oliver Cromwell and is widely regarded as the founder of the Royal Society (Slaughter 1982; Wilkins 1970; Wright Henderson 1910) of which he was the first Secretary. He produced *An Essay Towards a Real Character and a* philosophical language (1668), the only longstanding influence of which is to have been the foundation of the scheme for Roget's *Thesaurus* (and the occasion for a Borges essay). In fact, Wilkins' scheme was not so much a universal language as a kind of indexical classification of concepts of his time (which, in typical style for the time and since, he thought to be universally true of the entire human condition), where words were actually unique keys to each conceptual "address". He managed to engage (for money) a naturalist by the name of John Ray to produce a table of species according to his own a priori categories. Ray felt that this a priori scheme was too constrictive, but according to Raven (1986 p182f, 192) it did provide him with a motivation to do better in his later publications (see next chapter).

2.6. Death of essentialism

2.6.1. Locke and Leibniz –real and nominal essence

> For the natural tendency of the mind being towards knowledge; and finding that, if it should proceed by and dwell upon only particular things, its progress would be very slow, and its work endless; therefore, to shorten its way to knowledge, and make each perception more comprehensive, the first thing it does, as the foundation of the easier enlarging its knowledge, either by contemplation of the things themselves that it would know, or conference with others about them, is to bind them into bundles, and rank them so into sorts, that what knowledge it gets of any of them it may thereby with assurance extend to all of that sort; and so

advance by larger steps in that which is its great business, knowledge. This, as I have elsewhere shown, is the reason why we collect things under comprehensive ideas, with names annexed to them, into genera and species; i.e. into kinds and sorts.

Locke, *Essay on human understanding*, Bk II, chap. 32, §6

A friend of the Cambridge Platonists and universal language projectors was John Locke. But Locke was also a friend of Robert Boyle, the atomistic ("corpuscularean") chemist, whose philosophy demoted sensory perceptions from immediate empirical experiences of things to secondary qualities, since we do not observe the corpuscles of which things are composed. Locke followed Boyle rather than Bacon in this, and so our knowledge of things must be nominal rather than essential (Slaughter 1982 p193–207). Locke is sometimes called a nominalist, and there is a sense in which this is true, but it relates to his views about names, and not about the underlying things the names refer to. Names denote abstractions, and some names denote the essences of ideas. But Locke does not deny that there are what he calls "real essences", only that the essences of kinds, or "sortals", as he calls them, agree to anything else but "nominal essences".

Locke is not particularly remembered by biologists for his contribution to the species debate, but he should be (Cain 1997). His views, expressed especially in chapters 3 to 7 of Book 3 of the *Essay* are the first statement of a position one may call *species conventionalism*, and which is held today even by those who reject his essentialistic notion of names (e.g., Jody Hey). He triggered a response by Leibniz that was influential on French naturalists, including Buffon and Lamarck.

The learning and disputes of the schools having been much busied about genus and species, the word essence has almost lost its primary signification: and, instead of the real constitution of things, has been almost wholly applied to the artificial constitution of genus and species. It is true, there is ordinarily supposed a real constitution of the sorts of things; and it is past doubt there must be some real constitution, on which any collection of simple ideas co-existing must depend. But, it being evident that things are ranked under names into sorts or species, only as they agree to certain abstract ideas, to which we have annexed those names, the essence of each genus, or sort, comes to be nothing but that abstract idea which the general, or sortal (if I may have leave so to call it from sort, as I do general from genus), name stands for. And this we shall find to be that which the word essence imports in its most familiar use. [Bk III, chap. III, §15]

Locke considers "species" to be merely the Latinised version of the good English word "sort" or "kind" (Bk III, chap. I §6), and held that species are conventional names used mainly for specialists to communicate. In fact, most of the then-current species names were based on what we would now call "folk taxonomy":

This shows Species to be made for Communication.—The reason why I take so particular notice of this is, that we may not be mistaken about *genera* and *species*, and their *essences*, as if they

> were things regularly and constantly made by nature, and had a real existence in things; when they appear, upon a more wary survey, to be nothing else but an artifice of the understanding, for the easier signifying such collections of *ideas* as it should often have occasion to communicate by one general term; under which divers particulars, as far forth as they agreed to that abstract *idea*, might be comprehended. And if the doubtful signification of the word *species* may make it sound harsh to some, that I say the species of mixed modes are "made by the understanding"; yet, I think, it can by nobody be denied that it is the mind makes those abstract complex *ideas* to which specific names are given. And if it be true, as it is, that the mind makes the patterns for sorting and naming of things, I leave it to be considered who makes the boundaries of the sort or *species*; since with me *species* and *sort* have no other difference than that of a Latin and English *idiom*. [Bk III, chap. V, §9]
>
> But supposing that the *real essences* of substances were discoverable by those that would severely apply themselves to that inquiry, yet we could not reasonably think that the *ranking of things under general names was regulated by* those internal real constitutions, or anything else but *their obvious appearances*; since languages, in all countries, have been established long before sciences. So that they have not been philosophers or logicians, or such who have troubled themselves about *forms* and *essences*, that have made the general names that are in use amongst the several nations of men: but those more or less comprehensive terms have, for the most part, in all languages, received their birth and signification from ignorant and illiterate people, who sorted and denominated things by those sensible qualities they found in them; thereby to signify them, when absent, to others, whether they had an occasion to mention a sort or a particular thing. [Bk III, chap. 6, §25]

Locke here recognises a distinction between folk taxonomy and a proper (philosophical) enquiry into the scientific issues. Leibniz in the *New Essay on Human Understanding* (1996, p319) paraphrases this more succinctly (Philolethes is Locke, Theophilus is Leibniz):

> PHIL. **§25**. Languages were established before sciences, and things were put into species by ignorant and illiterate people.

To which he responds,

> THEO. This is true, but the people who study a subject-matter correct popular notions. Assayers have found precise methods for identifying and separating metals, botanists have marvelously extended our knowledge of plants, and experiments have been made on insects that have given us new routes into the knowledge of animals. However, we are still far short of halfway along our journey.

Leibniz is more of an optimist about the causal powers that form species being available to investigators than Locke, who seems to propose a permanent conventionalism based on the current inability to define species according to their "internal real constitutions". Nevertheless, Leibniz held to a view that species were not real as discrete objects. He was an adherent of the *scala naturae* or the Great Chain of Being, and popularised the *lex completio* – the view that there could be no incompleteness in the world as made by a beneficent God.

Locke discussed, rather interestingly, the presence in species of divergences from the type (Book II, chap. VI, §§16–17, 26–27). In this he was preceded by Cusa, as we have seen, and also by Francis Bacon (New Organon, Book II, §29, cf. Glass 1959a p36), but Locke's discussion is surprisingly modern in a way that Bacon's is recognisably medieval. He greatly influenced, among others, Buffon, through the writings of French admirers of Locke's empiricism and new way of ideas (here again, the appearance of εἶδος). He is often thought to be solely a species nominalist, as Buffon transitorily was, but it seems more accurate to say that he believed our ideas and associated names were conventional, but that, as Bacon thought, there was some underlying essence that was likely to remain out of our reach. This idea was famously given its canonical expression in the doctrine of the *noumenal* and the *phenomenal* of Kant.

2.6.2. Immanuel Kant and the continuity of species

Kant's views on biological species are interesting primarily because they influenced the work of Blumenbach (Lenoir 1980) whose own work, published in 1781, established the notion of races as distinct subspecific ranks within the human species (Osborne 1971 p164) and later the *Naturphilosophen* (Amundson 1998; Nyhart 1995). While Blumenbach worked mainly with skull morphology, his views on teleology were influenced deeply by Kant, and Kant regarded him as the scientist who best understood his ideas. So we may consider Kant's view to be influential on some aspects of his contemporary biology (Moss 2003 p10–12), and also on later biology through Goethe and Oken.

The *Critique of Pure Reason* was first published in the same year as Blumenbach's race work. A second edition[42] followed in 1787, and it is this version (pages B679–690) that we will follow here (Kant 1933). In the context of discussion if a fundamental power exists which unites the things of understanding, Kant asks whether reason derives the unity of things by transcendental employment of understanding; in other words, if parsimony is a law of nature as well as of reason. He answers that unity is a necessity, for otherwise we would have no reason at all, and launches into a standard account of genera and species:

> That the manifold respects in which individual things differ do not exclude identity of species, that the various species must be regarded merely as different determinations of a few genera, and these, in turn, of still higher genera, and so on; in short that we must seek for a certain systematic unity of all possible empirical concepts, in so far as they can be deduced from

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[42] The page numbers of which are conventionally preceded by the letter B, and of the first edition, by the letter A.

> higher and more general concepts – this is a logical principle, a rule of the Schools, without which there can be no employment of reason. [B679f]

Kant equivocates here, it seems. On the one hand he wants to adopt the classical process of differentiation from the *summum genera* employed by the Scholastics. On the other, he wants to derive unity from empirical data, that is, to classify from the bottom up. Parsimony is an advance, as when chemists reduce all salts to acids and alkalis (B680),

> … but not content with this, they are unable to banish the thought that behind these varieties there is but one genus, nay, that there might even be a common principle for the earth and the salts. [B681]

Parsimony is due to the need for the understanding to reduce multiplicities into unities. This is exactly what the scholastics would have sought. But he then continues:

> The logical principle of genera, which postulates identity, is balanced by another principle, namely that of *species*, which calls for manifoldness and diversity in things, notwithstanding their agreement as coming under the same genus, and which prescribes to the understanding that it attend to the diversity no less than to the identity. [B682]

Observation of things must discriminate, he says, as much as the "faculty of wit" must find the appropriate universal. This differs from the scholastic account, and in some ways is more like Cusa's contraction in species. Here, observation allows us to group diversity of species under general predicates, he says, for if

> … there were no *lower* concepts, there could not be *higher* concepts. Now the understanding can have knowledge only through concepts, and therefore, however far it carries the process of division, never through mere intuition, but always again through *lower* concepts. The knowledge of appearances in their complete determination, which is possible only through the understanding, demands an endless progress in the specification of our concepts, and an advance to yet other remaining differences, from which we have made an abstraction in the concept of the species, and still more so in that of the genus. [B684]

Kant has it both ways after all – we abstract our more general categories from empirical observation, and understanding divides categories logically so that reason can deal with them (B695f). But species border each other – there is a logical continuum, "admitting of no transition from one to another *per saltum,* but only through all the smaller degrees of difference between them." (B687) This he calls the logical law of the *continuum specierum,* a version of the transcendental law of *lex continui in natura*, which is Leibniz's law of continuity. While this applies to the realm of possible concepts, though, Kant rejects it in nature.

> For in the first place, the species in nature are actually divided, and must therefore constitute a *quantum discretum*. … And further, in the second place, we could not make any determinate empirical use of this law, since it instructs us only in quite general terms that we are to seek for

> grades of affinity, and yields no criterion whatsoever as to how far, and in what manner, we are to prosecute the search for them. [B689]

He wants species to be useful in reason and understanding – if there were no gaps in nature, then we could not make sense of it; the fact that things actually *are* divided by gaps is therefore fortuitous.

There is no biological discussion in this critique, but he does provide one in the *Critique of Judgement* in 1790 (second edition in 1793: Kant 1951). In section 64, he states:

> In order to see that a thing is only possible as a purpose, that is to be forced to seek the causality of its origin, not in the mechanism of nature, but in a cause whose faculty of action is determined through concepts, it is requisite that its form be not possible according to mere natural laws… The *contingency* of its form in all empirical natural laws in reference to reason affords a ground for regarding its causality as possible only through reason.

It seems Kant is saying that contingent forms (i.e., species) can be understood not as the determinate outcome of mechanisms, but rather as the result of conceptual necessity. Eco discusses this at length (Eco 1999 p89–96) and concludes that the platypus discovered, and displayed in Europe, shortly after Kant's death would have given Kant trouble unless he was able to subsume it under existing conceptual categories (such as "water mole"). While the platypus, or to use Kant's own example, a tree, is there and as a natural purpose produces itself as both cause and effect, generically, our ideas of it depend on our knowing the purpose or goal of such organised things (§65). Kant says in §67 of the *Judgement*,

> Hence it is only so far as matter is organized that it necessarily carries with it the concept of a natural purpose, because this its specific form is at the same time a product of nature. …
>
> If we have once discovered in nature a faculty of bringing forth products that can only be thought by us in accordance with the concept of final causes, we go further still. We venture to judge that things belong to a system of purposes which yet do not (either in themselves or in their purposive relations) necessitate our seeking for any principle of their possibility beyond the mechanisms of causes working blindly. For the first idea, as concerns its ground, already brings us beyond the world of sense, since the unity of this supersensible principle must be regarded as valid in this way, not merely for certain species of natural beings, but for the whole of nature as a system.

Kant's teleology is too far afield from our topic, but it is important to see that he saw species as the outcome of self-generative organisation in nature, as well as things which we needed to think of as goal-directed in order to understand them. Again, here is the philosophical current of the generative notion of species in play. Famously, Kant was influential on Goethe, and through him, Oken, and the ideal morphologists that followed him (see below, on Owen and Agassiz).

2.6.3. Nineteenth century logic

Early in the nineteenth century, in 1826, an influential text on logic was published by Archbishop Richard Whatley (1875, my edition being the ninth). In this book, Whatley describes *species* as *essences*, as *heads of predicables*, and as that of which genera are parts (and not species being parts of genera, since the genus partakes of the essence, or definition, of the species, Bk II, ch. 5 §3, p85). But, in the ninth edition, at any rate, he also notes that **this** sense of "species" is quite distinct from the sense in which **naturalists** use it of "organized beings" (Bk IV, ch. 5 §1), for they are real things, "unalterable and independent of our thoughts" (p183):

> ... if anyone utters such a proposition as ... "Argus was a mastiff," to what head of Predicables would such a Predicate be referred? Surely our logical principles would lead us to answer, that it is the *Species*; since it could hardly be called an Accident, and is manifestly no other Predicable. And yet every Naturalist would at once pronounce that Mastiff, is no distinct Species, but is only a *variety* of the Species Dog. ...
>
> ... the solution of the difficulty is to be found in the peculiar technical sense ... of the word "Species" when applied to *organized Beings*: in which case it is always applied (when we are speaking strictly, as naturalists) to individuals as are supposed to be *descended from a common stock*, or which *might* have so descended; *viz.* which resemble one another (to use M. Cuvier's expression) as much as those of the same stock do.

Whatley expressly exempts species concepts in biology, then, from the strictures of logical notions, and that, it must be observed, includes essential characters. He notes

> [The fact of two organisms being the same species] being one which can seldom be *directly* known, the consequence is, that the *marks* by which any Species of Animal or Plant is *known*, are not the very *Differentia* which *constitutes* that Species. [p184f]

So well prior to Darwin, and in a logical context, we find that the *species* of biology and the *species* of logic are understood to be different concepts. However, Whatley expects there **will** be diagnostic "marks".

By the middle of the nineteenth century, despite the arguments naturalists were now having over the meaning of the term *species*, the "genera plus differentia" definition remained widely accepted by logicians until, under the weight of the new set theory and the biological pre-eminence of the use of the term, the older logic was relegated to specialists in metaphysics and medievalists. Here, for example, is the definition of a widely-used dictionary of science and the arts in 1852:

> SPE'CIES. (Lat.) In Logic, a predicable which is considered as expressing the whole essence of the individuals of which it is affirmed. The essence of an individual is said to consist of two parts: 1. The material part, or genus; 2. The formal or distinctive part, or difference. The genus and difference together make up, in logical language, the species: e.g. a "biped" is compounded of the genus "animal," and the difference "having two legs." It is obvious that the names *species* and *genus* are merely relative; and that the same common terms may, in once case, be the

> species which is predicated of an individual, and, in another case the individual of which a species is predicated: e.g. the individual, Cæsar, belongs to the species man; but man, again, may be said to belong to the species animal, &c., as we contemplate higher and more comprehensive terms. A species, in short, when predicated of individuals, stands in the same relation to them as the genus to the species; and when predicated of other lower species, it is then, in respect of these, a genus, while it is a species in respect of a higher genus. Such a term is called a subaltern species or genus; while the highest term of all, of which nothing can be predicated, is the "summum genus;" the lowest of all, which can be predicated of nothing, the "infimæ species." The difference which, together with the genus, makes up the species, is termed the "specific difference."
>
> (Brande et al. 1853 p1137)

By the third edition in 1859, the discussion had been rewritten by Richard Owen to include the biological meaning, but this is as succinct a summary of the traditional conception as one will find. However, we should note that it follows Aristotle in rejecting binary diairesis in favour of multiple species per genus, each of which carries its own special differentiae ("specific differences").

However, this view was not necessarily the view held by the leading philosophers of the day. Mill and Whewell in particular had tried to accommodate the current facts of natural history into the notion of a classification (Hull 2003). In his *System of Logic* (1843, Mill 1930), Mill showed considerable knowledge of botanical classification conventions and awareness of variation within species. The discussion in Bk I, chap. VII, especially §3–4, is well-informed as to scholastic *and* biological conventions, and attempts a reconciliation of the two, without much success.

In Book I, chap VIII, §4, he discusses the Cuvierian use of the term "Man" as the scientific definition, "Man is a mammiferous animal having two hands". This defines Man by giving "the place which the species ought to occupy in that particular [scientific] classification". He notes the Aristotelian use of *per genus et differentiam,* which he seems not to challenge. It is significant not for its resolution of the topic, but because we see here a philosopher taking pains to use as many biological examples as possible, although we also see elements and minerals appearing in the *exemplia gratia*. He defines species, at least in the sense used by naturalists (Book I, chap. VII, §3), as

> not, of course, the class in the sense of each individual of the class, but the individuals collectively, considered as an aggregate whole... .

Mill clearly is treating the species of the naturalist in a different sense, a "popular acceptation" more general and less logical than the sense of the logician. Nevertheless, both he and Whewell treated species as "natural classes", as Whewell stated it (Hull 2003 p184f), with essences, and in his response to Darwin's *Origin*, Whewell was dismissive of the idea that these classes could change. Hull quotes him as saying:

> … a natural class is neither more nor less than the observed steady association of certain properties, structures, and analogies, in several species and genera.
>
> (Whewell 1831; quoted in Hull 2003 p185)

Whewell's Humean associationist psychology is evident here, but also the Lockean idea of general terms as creations of the mind to collate past experiences. It is unclear if this was, as Hull suggests, the core of his objections to Darwin's theory of evolution, but at the least his philosophical adherence to logical essentialism certainly played a part in it.

Interestingly, **after** Darwin, a kind of essentialism regarding species was espoused by Jevons (1887 p710–713), but he is clear that this refers to diagnostic species; that is, to classes of definitions of objects. He states that in a "natural" system of classification, all

> arrangements which serve any purpose at all must be more or less natural, because, if closely enough scrutinised, they will involve more resemblances than those whereby the class was defined [p680}

and thus they are inductive groups, based, in living beings, on "inherited resemblances", such that the

> *arrangement … would display the genealogical descent of every form from the original life germ.* [*loc. cit.,* italics original]

Therefore, diagnostic essences are correlations that are causally important. Jevons follows Porphyry in treating Species as a predicable (p698).

The use of the notions of *genus* and *species* in logical discussions seems to have petered out with the introduction of set theory by Venn, Cantor, Peirce, Frege and others towards the end of the 19th century, especially around 1870–1878 in the case of Cantor. Where the inclusion of a species in a genus and of lower species in that species was the mainstay of classificatory logic prior to this development, now the talk was of sets and subsets. Moreover, the introduction of set theory itself seemed to over-ride the older approach of diairesis, or top-down division. Sets could be defined from larger sets by division, or by aggregation of smaller sets. Even more radical was the distinction between intensional and extensional definitions of sets.[43] A species in the older logic had to be definable from the larger genus. A set could be described *or* defined. An extensionally defined set is treated as isomorphic with another set, or, as Quine (1970 p67) expresses it, "the *law of extensionality*, which identifies sets whose members are the same"; intensions (which Quine abhors) are specified by predicates,

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[43] The terms "intension" and "extension" are apparently medieval, according to Joseph. Mill's *Logic* introduced the terms "connotation" and "denotation" (Joseph 1916 p14-142).

which "have attributes as their 'intensions' or meanings". Under the Aristotelian account, all species were intensionally defined – this was the point of defining them by their essences. Now we had aggregates that could be treated as synonymous merely by sharing all members, irrespective of their essences. It was not immediately clear how this might apply to the biological species problem, and it indeed took some time for it to be applied.

Even so, some continued to use the older logical terminology and the Aristotelian conceptions that underlay it, even if there were some concessions to the new set theory. Husserl, for example, writing in 1913 (Husserl 1931), writes in section 12 of his *Ideas*,

> Every essence, whether it has content or is empty (and therefore purely logical), has its proper place in a graded series of essences, in a graded series of *generality* and *specificity*. The series necessarily possesses two limits that never coalesce. Moving downwards, we reach the *lowest specific differences* or, as we also say, the *eidetic singularities*; and we move upwards through the essences of genus and species to a *highest genus*. Eidetic singularities are essences, which indeed have necessarily "more general" essences as their genera, but no further specifications in relation to which they themselves might be genera (proximate or mediate, higher genera). Likewise that genus is the highest which no longer has any genus above it.

More interestingly, and influentially on the subsequent debate, H. W. B. Joseph's *Introduction to Logic* (first edition 1906, second 1916) allowed that the evolutionary species of Darwin and Spencer were a different notion to that of the logical species of definitions. He goes so far as to note that species in biology cannot be defined, and that instead one must describe a type, from which individuals can diverge:

> The difficulty of determining what attributes are essential to a substance, and therefore of discriminating between essence and property, does not however arise entirely from the seeming disconnexion of the attributes of a kind. It arises also, in the case at least of the organic, from the great variation to which a species is liable in divers individuals. Extreme instances of such variation are sometimes known as border varieties, or border specimens; and these border varieties give great trouble to naturalists, when they endeavour to arrange all individuals in a number of mutually exclusive species. For a long time the doctrine of the fixity of species, supported as well by the authority of Aristotle and of Genesis, as by the lack of evidence for any other theory, encouraged men to hope that there was a stable character common to all members of a species, and untouched by variation; and the strangest deviations from the type, excluded under the title of monstrosities or unnatural births, were not allowed to disturb the symmetry of the theory. Moreover, a working test by which to determine whether individuals were of different species, was furnished, as is well known, by the fertility of offspring; it being assumed that a cross between different species would always be infertile, as in the case of the mule, and that when a cross was uniformly infertile, the species were different. But now that the theory of organic evolution has reduced the distinction between varietal and specific difference to one of degree, the task of settling what is the essence of a species becomes theoretically impossible. ...

> If [biological] species were fixed: if there were in each a certain nucleus of characters, that must belong to the members of any species either not at all or all in all: if it were only upon condition of exhibiting at least such a specific nucleus of characters that the functions of life could go on in the individual at all; then this nucleus would form the essence of the kind. But such is not the case. The conformity of an individual to the type of a particular species depends on the fulfilment of an infinity of conditions, and implies the exhibition of an infinity of correlated peculiarites, structural and functional, many of which, so far as we can see ... have no connexion one with another. There may be deviation from the type, to a greater or less degree, in endless directions; and we cannot fix by any hard and fast rule the amount of deviation consistent with being of the species... Hence for definition, such as we have it in geometry, we must substitute classification ... A classification attempts to establish types...
>
> (Joseph 1916 p81f, 88f)

Joseph continues in the tradition that Whatley adopts, of separating logical species defined by essence and biological species described by types. Even at this late stage, types and essences are held to be different notions.

Until Woodger introduces set theory to biology (Woodger 1937; 1952), such issues are not discussed except by a declining number of philosophers; and then of course in the context both of cladism and the individuality thesis we shall consider later.

2.7. Summary and conclusions

We see that from Aristotle through to the end of the middle ages and the Renaissance, the notion of species has not remained static; Aristotle's conventions and notions have been modified. Mostly, they were modified by the neo-Platonists and especially by Porphyry, who made Aristotle's top-down classification scheme dichotomous after the manner of Plato. Aristotle had opposed "privative" classification, classifying in terms of what things are **not**, although the grander schemes of later writers up to Lamarck had little problem with this, and happily classified groups such as Invertebrata.

In the medieval scheme, the notion of genus and species did not involve fixed ranks; a species might in turn be a genus on its own. The only "absolute" ranks were the *summum genera,* which represented in the Aristotelian tradition the universal categories (or *topoi*) from which all things were to be divided. The nominalist issue whether these general terms were merely aspects of mental categories or were real was alive and active well into the scientific period.

We find in the Epicureans a *generative notion of species* as early as the fourth century BCE, and this recurs throughout the remaining discussions until the biological tradition begins in the seventeenth century. Essences, on the whole, were not themselves necessary and sufficient criteria for membership in species, and all writers admitted that there were deviations from the type. The classical scheme was, however, almost always based on a top-down classification with a large admission of apriorism, until the collapse of the Universal Language Project, and the rise of corpuscular philosophy, which rendered species secondary qualities, or unknowable.

The Great Chain of Being meant that, depending on what emphasis was given to the principle of plentitude and the principle of continuity, species were arbitrary divisions in a plenum, sometimes logical, sometimes substantial and actual. The specific nature of a member of a species was thought by Cusa to be a contraction of the essence in that individual, but the ultimate reality, according to Cusa, is the individual. A continuing battle between nominalists and realists (idealists in modern terms) meant that there was a field of alternate opinions. Variation is recognised to be a fact within taxa from the fifteenth century onwards. Some, such as Ficino, held that there was a species that was most representative of a genus, since other species within the genus could play on variations of the generic theme, as it were.

With Bacon we move from an immediate generalisation of the universals from observed instances, and a subsequent top-down division of things, to the inductive construction of increasingly broader generalisations. He too allows for deviations and variations in species and other taxa; and Locke proposes not only that there is biological variation, but that species (sorts) themselves are conventional names we use to communicate easily. Nevertheless, he did allow for a real essence; only it is one that cannot be defined or even discovered. Leibniz was more optimistic; Kant even more pessimistic.

Kant rejects Leibniz’s view of the law of completion (principle of plenitude) and argues that nature is discretely divided; and he too uses a generative conception of species. Although the traditional logic survives until the institution of set theory in the nineteenth century, even Mill is able to twist it to serve biological realities. Both the logical tradition before Darwin and after, in his own country, allow for a difference between essentialist logical species and typological biological ones.

There is everywhere a remarkable lack of the sort of essentialism that Mayr and others believe permeates this period and its philosophy. While we see typology, when it comes to dealing with biological organisms, most of the time there is no insistence upon essences, and sometimes there is an explicit exemption for biological species of any knowable essence.

Chapter 3. Biological Taxonomy

Species the lowest (taxonomic) grouping of animals or plants that, at least potentially, forms an interbreeding array of populations unable to breed freely with other sorts of animals or plants. The species is the only natural unit (taxon) of CLASSIFICATION. It is usually recognized on the basis of morphological characters (a MORPHOSPECIES), but different species can be morphologically identical (*sibling species*), for example, *Drosophila pseudobscura* and *D. persimilis* exhibit behavioral differences leading to REPRODUCTIVE ISOLATION. See BINOMIAL NOMENCLATURE.

(Hale et al. 1991)[44]

3.1. Beginnings

Out of the neo-Platonic resources of the Cambridge Platonists and the Universal Language Project, the transition was begun to an autonomous program of biological classification. This heritage had two opposing aspects. First, as we have seen, there was the history of species as the sharp categories of a top-down classification. The other, via Descartes and Leibniz, was the Great Chain of Being notion of continuous gradation from simpler forms to more complex. Ironically, both of these develop ideas nascent or explicit in Aristotle's writings. Lovejoy (1936) writes:

> The first [aspect] made for sharp divisions, clear-cut differentiations, among natural objects, especially among living beings. To range animals and plants in well-defined species, presumably (since the Platonic dualism of realms of being was still influential) corresponding to the distinctness of Eternal Ideas, was the first business of the student of the organic world, The other tended to make the whole notion of species appear a convenient but artificial setting-up of divisions having no counterpart in nature. It was, on the whole, the former tendency that prevailed in early modern biology. [p227]

In the tension between sharp classification and gradual variation from one form to another in the Great Chain, we see the early stages of species realism, based on typological definitions, and species nominalism, based on the unreality of any divisions between them. Much of the early biological debate over species is an attempt to deal with this tension, and indeed it continues to the present day. This is made more complicated by the second main developing tradition of the distinction between "natural" and "artificial" classification.

3.1.1. Cesalpino and Bauhin – the beginnings

According to Lovejoy, the Florentine Andreas Cesalpino (1519–1603) was an enthusiast of Aristotelian classification, and Lovejoy notes that it was the fresh study of

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[44] Intriguingly, the title dedication reads: "For Professor Arthur J. Cain who told us both what a species is!"

Aristotelian writings that set Cesalpino to producing his *De Plantis* (1583).[45] In this and his *Peripatetic Problems* (1588, under the Latin title Quaestionum peripateticarum, libri V, Nordenskiöld 1929 p113) he worked on strict Aristotelian lines: "exhaustive comparative analysis of the forms, concisely worded theoretical definitions, and, based on these, abstract conclusions" (Nordenskiöld 1929 p192). Sachs (1890 p52) quotes him saying in chapter 13:

> That according to the law of nature like always produces like and that which is of the same species with itself.

In chapter 14, Cesalpino stated:

> We seek similarities and dissimilarities of form, in which the essence ('substantia') of plants consists, but not of things which are merely accidents of them ('quae accidunt ipsis').
>
> [quoted in *loc. cit.*]

Cesalpino therefore seems to be the mediate source of both the idea that species are fixed, and that species have an underlying essence, or substance in the Latin, that is distinct from other characters that may vary accidentally.

Independently of Cesalpino, Caspar (or Kaspar) Bauhin of Switzerland (1550–1624) organised known scientific names and descriptions of plants into two works (*Prodromus* and *Pinax theatri botanici*), in which the genus–species arrangement was used. However, he did not necessarily use it consistently as Linnaeus did (although Sachs thinks he was quite consistent, 1890 p33–35, and is dismissive of Linnaeus's "dry systematising manner", p40). Even so, Bauhin used the common likeness of plant forms as his basis for classification, unlike Cesalpino's artificial system, which was based on the special characters of what he considered the "soul" or heart of the plants (hearkening to Aristotle's *De Anima*). In his *Phytopinax* (1596), Bauhin states in the preface that he has applied one name to each plant for clarity (Arber 1938 p168). Cesalpino tended, according to Nördenskiold (p 193f), to focus on the fruits of plants in his classifications, a decision that also later influenced Linnaeus. Both Cesalpino and Bauhin were transitional between the older herbals tradition in which classification was either by alphabet or by utility in medicine and cooking (Arber 1938).

The formal distinction into genera and species in botany arises in the work of Konrad Gesner, according to Arber (p166), when he employs the practice of giving genera

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[45] Arber (1938 p142f) gives the full title as *De plantis libri xvi* and notes that Linnaeus' personal copy is heavily annotated. She comments that "Cesalpino's strength lay in the fact that he approached his subject with a trained mind; he had learned the lesson which Greek thought had then, and has now, to offer to the scientific worker – the lesson of how to think."

substantive names, and Arber considers him the earliest to do so. However his work was not widely known, and Arber instead considers Fabius Columna, in his *Ekphrasis* (1616), under the influence of Cesalpino, to publish the first views on the nature of genera in botany, relying on flower and seed rather than the older morphologies of leaf and stem to distinguish them.[46]

3.1.2. John Ray – propagation from seed

John Ray (1627–1705) was a seventeenth century naturalist who, in conjunction with Francis Willughby (1635–1672), prepared the first systematic flora for a region – at first of Cambridgeshire, and later of Britain (Raven 1986). In the *Historia plantarum* (1686–1704), he and Willughby attempted to describe all known species of plants. He also collaborated with Willughby, before his untimely death, on a treatment of insects, animals and fishes. To this end, he needed to define "species", and he was the first to do so entirely in a biological context. This strongly influenced Linnaeus' conceptions of species and other ranks.

In the *Historia plantarum*, in the volume published in 1686, Ray defined a species thus:

> In order that an inventory of plants may be begun and a classification of them correctly established, we must try to discover criteria of some sort for distinguishing what are called "species". After long and considerable investigation, no surer criterion for determining species has occurred to me than the distinguishing features that perpetuate themselves in propagation from seed. Thus, no matter what variations occur in the individuals or the species, if they spring from the seed of one and the same plant, they are accidental variations and not such as to distinguish a species … Animals likewise that differ specifically preserve their distinct species permanently; one species never springs from the seed of another nor vice versa.
>
> (Quoted in Mayr 1982 p256)

Mayr notes, "Here was a splendid compromise between the practical experience of the naturalist, who can observe in nature what belongs to a species, and the essentialist definition, which demands an underlying shared essence" (Mayr 1982 p257). However, one wonders if the influence of the generative conception is not more apparent here. Ray is dealing with the Aristotelian problem of accidental variation – like Locke he believes there must be a real essence, and not merely a nominal one. He

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[46] Arber herself, a botanist in the ideal morphology tradition, is a species "nominalist", writing:

> The progression from the vague concepts of the early writers to the sharp definition of genera and species to which we are now accustomed, has been in some ways a doubtful blessing.. There is to-day, as a recent writer has pointed out, a tendency to treat these units as if they possessed concrete reality, whereas they are merely convenient abstractions, which make it easier for the human mind to cope with the endless multiplicity of living things. [p168f]

The "recent writer" may be G. Senn (1925), whom she cites in her Appendix III (p306).

conjectures that it is, or rather defines it to be, based upon descent. But in most cases, as many have observed since (see below, Buffon), descent is *not* observable; and he clearly did not observe the fact that one species never springs from the seed of another. In fact, he wrote, in the *Methodus plantarum* of 1682:

> … I would not have my readers expect something perfect or complete; something which would divide all plants so exactly as to include in positions anomalous or peculiar; something which would so define each genus by its own characteristics that no species be left, so to speak, homeless or be found common to many genera. Nature does not permit anything of the sort. Nature, as the saying goes, makes no jumps and passes from extreme to extreme only through a mean. She always produces species intermediate between higher and lower types, species of doubtful classification linking one type with another and having something common with both – as for example the so-called zoophytes between plants and animals.
>
> (quoted in Glass 1959a p35)[47]

According to Glass, Ray did allow some limited transmutation between related species, especially hybridisation, a problem that Linnaeus later also had to accommodate.

Sometimes called the originator of the British natural theology tradition – he wrote the book *Wisdom of God Manifested in the Works of the Creation* (1691, Gould 1993 p140) – Ray also had a problem with extinction. It was not that he did not find it an operational concept; it was ruled out in terms of the principle of plenitude (Bowler 1989a). Initially he thought that fossil forms would be found alive elsewhere, but later he was forced into denying that fossils were even the remnants of living forms, but had instead grown within the rocks.

Ray is responsible for the first entirely **biological** notion of species, but this is not the same as saying that he presented what we would now consider a Biological Species Concept. For him, this was a sense of "species" that applied to reproducing **forms**, i.e., living things. It was the first time a concept was proposed that applied **only** to the classification of living things – prior to this, all such concepts were general-duty

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[47] I am curious about the provenance of the saying Ray adopts here: *natura non facit saltum*. Usually associated with Linnaeus (see below), it can be found also in Leibniz and even, in a form, in Albertus Magnus: "nature does not make [animal] kinds separate without making something intermediate between them, for nature does not pass from extreme to extreme *nisi per medium*" (quoted in Lovejoy 1936 p79). The idea can be traced back to the views of Plotinus and Porphyry, and probably also to the Gnostic idea of emanation. Ray also used similar phrases: *Natura nihil facit frustra* (nature makes nothing in vain) and *Natura non abundant in superfluis, nec deficit in necessarius* (Nature abounds not in what is superfluous, neither is [it] deficient in necessaries) – in the *Wisdom of God* (quoted in Cain 1999a p233). This saying, adopted much later by Darwin, is also found in a similar form in Leibniz's *New Essays*: "In nature everything happens by degrees, and nothing by jumps", (Leibniz 1996 Bk IV, ch xvi, p473).

concepts of classification that were then applied equally to, say, books or rocks as to life.

Ray clearly saw his classificatory logic as the continuation of the Aristotelian, scholastic, tradition, but his adherence to the Great Chain of Being, its neo-Platonist heritage, and to the idea that there needed to be a real essence, led him to propose not so much an operational concept as Mayr would have it, but a metaphysical one. As mentioned above, Ray had prepared a table of species before the *Historia* for Bishop John Wilkins' magnum opus *Essay Toward a Real Character and Philosophical Language*, published by the Royal Society in 1668. As we have seen, Wilkins was one of the so-called "Cambridge Platonists", a neo-Platonic school that was directly and indirectly responsible for much scientific work done in Britain at the time, and from whom the Royal Society sprang. He, like Ray, was influenced by Ralph Cudworth, whose ideas deliberately continued those of Plotinus and Porphyry. In addition, Ray had received the standard *Trivium* education (Grammar, Logic, and Rhetoric) that was presented at the grammar schools of the time, and which at sixteen and a half he began also to receive from Cambridge. With his friend and mentor Henry More, Ray was thoroughly inculcated in the techniques and terminology of the older scholastic logic. As a result, he opposed the material possibility of extinction or transmutation, although he admitted to its formal possibility, and documented some problematic cases for the fixity of species. Nevertheless, these were not fatal anomalies for him – he maintained his *scala naturae* views and his belief in the fixity of species since creation, a view that he bequeathed to Linnaeus.

3.1.3. Carl Linnaeus – species as the Creator made them

Whether or not the texts of the neo-Platonists Martianus and Porphyry, or of Boëthius, were ever used to teach a Swedish student who later became interested in botany, the medieval method and logic *was* taught to Carl Linnaeus.[48] Born in 1707, Linnaeus died in 1770, the most celebrated Swede of his day. His birth name was Carl (Charles) Linnaeus. In 1761, he was knighted with the vernacular name Carl von Linné, and took the Latinised name Carolus Linnaeus.

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[48] I am informed by Staffan Müller-Wille (pers. comm.) that Linnaeus, being from a relatively poor district of Sweden, Småland, known (presumably by an Englishman) as the "Scotland of Sweden", was taught from old standard textbooks, and not out of the neo-Platonists early or late, as far as is recorded (see also Frangsmyr et al. 1983; Koerner 1999; Goerke 1973). According to Hagberg (1952 p44ff), he was greatly influenced by Aristotle's *Historia Animalium* as a young student.

Linnaeus was a botanist, and trained in Holland where he published his first botanical works. Before Linnaeus, species were given all kinds of descriptive names, usually in Latin, up to ten words or so long. Each author made up their own terms, and there was no real convention for referring to species. On Linnaeus' account, both species and genera were fixed, real and known by definitions. He apparently believed that the genus was more real that species, and he allowed late in life that species may occasionally arise, but only within genera, through hybridisation. Some (e.g., Stafleu 1971; Mayr 1969; 1982) consider Linnaeus to be an essentialist regarding species. This was due to the fact that, unlike the medieval conception, for Linnaeus all species (at least in botany, zoology and mineralogy) were infimae species. He attempted to provide a diagnaostic definition for each species, although his practice and adopted motto "*In scientia naturali principia veritatis observationibus confirmari debent*" (in natural science, the principles of truth ought to be confirmed by observation, Stafleu 1971) suggests that he was not firmly wedded to a priori essentialism.

In the *Systema Naturae* (10th edn, 1759, p7) Linnaeus proposed a system of five ranks:

Regnum (Kingdom),
  Classis (Class),
        Ordo (Order),
          Genus,
              Species,

the last four of which corresponded to the logical ranks of *genus summum, genus intermedium, genus proximam,* and *species*. He also added a subspecific category of *Varietas*, which was the logical *individuum*.

Later taxonomic conventions added the ranks of *Phylum* between Kingdom and Class, and *Family* between Order and Genus, giving seven ranks.[49] The philosophical notion of species was not entirely helpful in botany, so Linnaeus changed it a little. Instead of there being any number of subaltern genera, he made the scale of classes absolute, and instead of working downwards, he started in the middle (at the genus). Linnaeus' ranks began at species, and these existed in genera. Hence, to name a species you needed to give the generic name and the species name. Humans are members of the

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[49] According to the *Oxford English Dictionary*, *phylum* is a term first coined by Cuvier, in *Regne Animal* (1817), to cover his four *embranchements. Family* is most probably Adanson's term (Judd et al. 1999 p40). I have not been able to trace the introduction of these terms to Linnaean classification, but Agassiz in the *Essay on Classification* in 1857 was talking about the rank of family being real (Panchen 1992 p15). Thanks to Gary Nelson for help tracking this down.

genus *Homo* (or Man; according to Linnaeus, one of several[50]) and our species is called *sapiens* (the wise one). So in Latin our "name" is "the wise man". Humans, under his initial system, are:

Animals (*Regnum Animale*),
  Mammals (*Classis Mammalia*),
    Primates (*Ordo Primates*),
      Man (*Genus Homo*),
        Wise or rational *(Species sapiens).*

What Linneaus did was to make species and genera fixed ranks. He established this universal system for the naming and classification of all organisms. There were, for example, various kingdoms – plants (Plantae) and animals (Animalia). Each species had a street address (its generic name, or *genus*) and a street number (its species name, or *epithet*).[51] Now, taxonomists (those who classify taxa, or groups of organisms[52]) could use a single and relatively simple system for their organisms, and all could agree on how to name them, and what to name.

Linnaeus was a special creationist – that is, he believed that each species was created specially by God. He wrote:

"There are as many species as the Infinite Being produced diverse forms in the beginning."(*Species tot sunt diversae quot diversas formas ab initio creavit infinitum Ens, Fundamenta botanica* No. 157, 1736).

However, in 1744 he was forced to allow that some species are the result of hybridisation, at least in plants, because he observed it happening. A species of plant he placed in a genus *Peloria* (from the Greek *pelor*, meaning monstrosity) was in stem

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[50] Huxley describes the initial history of hominoid classification, and notes that while there had been some excellent descriptions of orangutans and chimpanzees in the 18th century, Linnaeus relied on second-hand sources, and classified four species under the genus Homo: Under the specific epithet of *troglodytes*, he combined the prior "species" of *Homo sylvestris* (probably a juvenile chimp), and *Homo nocturnus* (a badly-represented orangutan) (cf. Huxley 1906 p10–13) in the 1858 (tenth edition) *Systema naturae* (p25), apart from *Homo sapiens*. Huxley also lists *Homo caudatus* (a cat tailed ape, either mythical or a misunderstanding of a description of a baboon), but by the tenth edition at least, this was no longer in evidence. It is occasionally noted that by the established rules of nomenclatural priority, chimpanzees should therefore be included in *Homo* on Linnaean grounds as well as on cladistic grounds (which is argued in, for instance, Diamond 1991). However, *troglodytes* explicitly mentions the Orangutan in the *Systema Naturae*, while the chimp is more likely to be *Simia satyrus*, in another genus altogether (p25).

[51] Incidentally, in modern practice, the genus name is always capitalised and the species epithet is always lower case, and both are always italicised. Other taxonomic ranks are capitalised but not italicised.

[52] According to Mayr (1982 p870n), the term *taxon* was proposed in 1926 by Meyer-Abich. Hence in this context it is an anachronism. Stafleu notes that Linnaeus' own general term for taxa was *phalanx*, but that it did not catch on.

and leaf structure part of the *Linaria* genus, but the flower was clearly different (Hagberg 1952 p196f; Glass 1959b). Still, he thought that genera were real and the possibilities for change limited. According to Larson (1967), Linnaeus imagined in the *Fundamenta fructifications* "that God created one species for each natural order of plants differing in habit and fructification from all others. These species, mutually fertile, gave birth to as many genera as there were different parents, their fructification somewhat changed" (p317).

In the *Pralectiones* (1744), Linnaeus went further:

> The principle being accepted that all species of one genus have arisen from one mother through different fathers, it must be assumed:
>
> 1) That in the beginning the Creator created each natural order only with one plant with reproductive power.
> 2) That by their various mixings different plants have arisen which belong to the mother's natural order as they are similar to the mother with regard to their fructifications, and are, as it were, species of the order, i.e., genera.
> 3) We may assume that plants have arisen within the orders, i.e. by genera of one order, may mix with each other. In this way there will arise species that should be referred to the mother's genus as her daughters. [quoted in Larson, *loc. cit.*]

Linnaeus thus employed the Great Chain of Being in a rather unusual way. Most "chainists" accepted what was later called the Principle of Plenitude (the *lex completio*), which stated that God would create everything that could be created, since he would not make an incomplete creation (Lovejoy 1936; Glass 1959b). This usually meant that species graded into each other is a series of varieties. Linnaeus instead represented species using the metaphor of countries adjoining each other (in the *Philosophia botanica* §77). In his early writing, all the territory is pretty much filled – as he said, nature does not make jumps – but the countries are discrete and distinct from one another. In the later work, this strict fixism of the first edition of the *Systema naturae* has been modified. All hybrids did was fill in a rare empty bit of territory in God's time and plan. The borders were set by the genera, and all genera arose from a single species created by God. At the end of the 1750s, says Hagberg (1952 p199), Linnaeus was in a state of perplexity with respect to species. In 1755, he published *Metamorphosis plantarum*, dealing primarily with the development of plants, but also with monstrosities and varieties. Such later hybrids he called the "children of time" in an anonymous entry in a competition at St Petersburg in 1759 (Hagberg 1952 p201f). Hagberg says, "Linnaeus never succeeded in pin-pointing his new conception of species. But the old one, that formed the basis of *Systema Naturae*, was utterly and irrevocably abandoned." But these ideas of his were not influential.

When Linnaeus was working, European trade and exploration was limited. Linnaeus himself classified around 6,000 species of mainly Mediterranean and northern European plants, and later animals (Stafleu 1971). This was more than had been done before, but still it was a fraction of what we know today. He didn't expect to find many more. His own students proved him wrong, by sending him specimens from around the world. Linnaeus hoped that his system would enable taxonomists to list all actual species, but he knew that his system was artificial – that is, not the result of studying the actual characters of organisms, but imposing an a priori scheme on them for convenience. He hoped there would be a "natural" scheme developed on the basis of an aggregation of characters, but he was never able to do more than a partial sketch of one. In his later work, he set up a "rational" system that allowed for there to be 3,600 genera in plants, each of which could generate species through hybridisation. Although this was supposed to be a "natural" system (one based on the closeness of resemblance of **all** traits of the organisms and not just a single character), in fact he chose just three features of plants and restricted the varieties to 60 types of each (hence 60^3 = 216,000 maximum of plant species). However, this was fragmentary and in an appendix, and not developed further.

In summary, Linnaeus proposed a five rank taxonomic system, and there were only a set number of species possible, although later he was forced by various observations, including his own, to accept that new species could be created through hybridisation. All that remains of his taxonomy are the names and general ranks of his system, but even this has been dramatically modified, with such groups as tribes, sub-families, and so on being added to deal with the massive increase in species discovered since.

Linnaeus distinguished between the diagnostic characters (*characters*) and actual traits (*notae*) of organisms, but it seems not much came of this distinction. He appears to have despaired of a natural system in his foreseeable future, and so promoted a purely diagnostic and hence conventional taxonomy, even though he believed that species were themselves natural, along with genera. This tension underlies much of later taxonomy.

3.1.4. Buffon – degeneration, mules, and individuals

Georges-Louis Leclerc, Comte de Buffon (1707–1788), referred to simply as Buffon, was one of the last naturalists with an encyclopaedic knowledge of all biology. Indeed, he effectively defined that discipline. He was a French aristocrat (a count) who superintended the "King's Garden" (*Le Jardin du Roi*, later *Le Jardin des Plantes*). His pupil and later associate was the famous early evolutionist Lamarck, but Buffon was not what we would understand to be an evolutionist himself.

Buffon strongly disapproved of Linnaeus' binomial system and particularly of his use of sexual characters in discriminating plants. As a result, he and his followers were often in argument and political manoeuvrings against the Linnaeans. He was the primary author of the 44 volume *Natural History, with particular reference to the Cabinet of the King (Histoire naturelle,* 1749–1789) of which he issued 36 volumes and in the course of this stylistically elegant but often confusing and sometimes contradictory series he made a number of passing comments regarding species.

Buffon was a relatively standard adherent to the Great Chain – he adopted the "law of continuity" (*lex continua*) of Leibniz and his followers, but he did not necessarily accept the Principle of Plenitude, and so did not expect that every possible kind of species would necessarily exist. He wrote that it was an error in metaphysics trying to find a natural definition of species.

> The error consists in a failure to understand nature's processes (*marche*), which always take place by gradations (*nuances*). ... It is possible to descend by almost insensible degrees from the most perfect creature to the most formless matter. ... These imperceptible shadings are the great work of nature; they are to be found not only in the sizes and forms, but also in the movements, the generations and the successions of every species. ... [Thus] nature, proceeding by unknown gradations, cannot wholly lend herself to these divisions [into genera and species]. ... There will be found a great number of intermediate species, and of objects belonging half in one class and half in another. Objects of this sort, to which it is impossible to assign a place, necessarily render vain the attempt at a universal system. ...
>
> In general, the more one increases the number of one's divisions, in the case of the products of nature, the nearer one comes to the truth; since in reality individuals alone exist in nature.
>
> [*Histoire naturelle*, (1749), p12, p13, p20, p38 (quoted in Lovejoy 1936 p230)]

In his opinion, the boundaries between species were arbitrarily drawn– species grade into each other (Farber 1971; Eddy 1994; Roger 1997; Sloan 1979). However, this was not a statement about transmutation. He merely thought that the variation between species was continuous, not that species continuously arose from prior species. That idea was left to his student Lamarck to elaborate (although Darwin's grandfather Erasmus independently trumped Lamarck by several years with the same idea).

Buffon did allow that some change was possible. He thought that there were "types" of organisms roughly equivalent to Linnaeus' genera. The original type was the "true" form, and various species could degrade from that type to become a kind of "monster". Again, the influence of Aristotle is apparent, but there were limits to the sort of change species could undergo.

Two animals are of the same species, he wrote in the second volume of the *Histoire naturelle* (Lovejoy 1959 p93f),

> … if, by means of copulation, they can perpetuate themselves and the likeness of the species; and we should regard them as belonging to different species if they are incapable of producing progeny by the same means. Thus the fox will be known to be a different species from the dog if it proves to be a fact that from the mating of a male and female of these two kinds of animals no offspring is born; and even if there should result a hybrid offspring, a sort of mule, this would suffice to prove that fox and dog are not of the same species – inasmuch as this mule would be sterile (*ne produirait rien*). For we have assumed that, in order that a species might be constituted, there was necessary a continuous, perpetual and unvarying reproduction (*une production continue, perpétuelle, invariable*) – similar, in a word, to that of other animals.

Intriguingly, Mayr (1982 p334) omits the last sentence, perhaps from a desire to find forerunners for his own biological species concept. Here, we again find in Buffon the generative notion of species that, like Ray and Linnaeus and others before and after, includes both form and reproduction.

Buffon had a story for what kept organisms reproducing according to type – it involved what he called the *moule interieur*, or interior mold. This was an epigenetic, but particulate, hereditary factor that was held constant, or at least not deformed too much. It was derived from the *premier souche*, the primary stock from which all species of a type degenerated, and because it was shared, he was convinced that all species within the type were actually one species and interfertile, and he undertook experiments to prove this, with limited success.

His was not the first reproductive concept of species – as noted above, John Ray had said something similar– but he was first to make reproductive isolation the test of whether two organisms should be included in the same species. At other times he seemed to claim that only the organisms themselves were real, and that species were just convenient fictions or names of biologists.[53] Inconsistent in his definitions over the course of the *Natural History*, he had denied that species are real, asserting that only individuals exist (the first example of biological species nominalism). Farber (1971) and Eddy (1994) delimit two stages in Buffon's intellectual development. At first, around 1749, in his "Premier discours" (volume 1 of the *Histoire*) he declared that the reality of species cannot be determined using the artificial methods of naturalists. Later, in 1753,[54] he stated that he considered species to be the "constant succession of similar individuals that reproduce", and that

> [t]he term *species* is itself an abstraction, which in reality corresponds only to the destruction and renewal of beings through time.

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[53] He called them naturalists, of course, because the *term* biology was not coined until the end of the 18th century.

[54] Full citations and page numbers to be found in Eddy (1994 p646n).

In volume 2 of the *Histoire* (1749), Buffon adopted the notion of the *moule interieur*; generation was entirely a physical process akin to Newtonian forces, in many ways similar to Darwin's later pangenesis hypothesis (Darwin 1875). As Eddy recounts the hypothesis, unused molecules in an organism are brought together and reassembled in the form of the organism in the seminal fluids. This notion of form being physical is in itself very Aristotelian, as Sloan (1985) observes, but Buffon is also directly influenced by Leibniz (which Sloan also notes) and so there is a tension in his thought. If species are forms, then forms must be distinct, but if they are arbitrary, and grade into each other, as Leibniz taught the *scala naturae*, then they are not distinct. Eddy (1994 p648n) discusses this and points out that Buffon did not, in his view, propose at this stage a historical or biological conception of species so much as a logical one, but whether one adopts Sloan's or Eddy's view, he later came to both, and it is in this that he most influenced his pupil Lamarck.

In the period of 1764–5, Buffon moved to a temporal and physical conception, beyond question. But he did not think that form changed; it was fixed eternally, and at best change could be a process he came to call degeneration in an essay in 1766 entitled "De la dégénération des animaux". Form could be modified, he thought, by external environmental changes, but should the "species" be brought back into their ancestral environment, those changes would be reversed (Roger 1997). Such change from the *premier souche* was primarily due to damage; Eddy says, "[f]ar from seeing degeneration in terms of organic history, Buffon saw it as the death of the organic past; through degeneration, organisms lose their organic identity, become weak and vitiated, and in extreme cases, have trouble reproducing" (Eddy 1994 p652). Roger reports that Buffon carried out experiments on hybridisation to test this theory, and had surprising success, but that eventually he accepted that some animals, particularly domesticated ones, do not revert to the purity of the wild type.

In his *Histoire naturelle des oiseaux* (1770), Buffon claims that the size of the species of bird directly correlates with the number of species that degenerate from the *premiere souche*:

> A sparrow or warbler has perhaps twenty times as many relatives as an ostrich or a turkey; for by the number of relatives I understand the number of related species that are sufficiently alike among themselves to be considered side branches of the same stem, or at least ramifications of stems that grow so closely together that one can suspect that they have a common root, and can assume that originally they all sprang from this root, of which one is reminded by the large number of their shared similarities; and these related species probably have separated only through the influence of climate, food, and the procession of years, which brings into being every realizable combination and allows every possibility of variation, perfection, alteration, and degeneration to become manifest.

(Stresemann 1975 p56 translating p75 in the original.)

He held at the end the view that species were definite categories, and that one might determine the boundaries by seeing experimentally whether reproduction was possible; he made much in his essay "Mulets" (1776) of the sterility of hybrids as a mark of species boundaries. But what he meant by *espèces* was more like Linnaeus' genera, and he was not fussed about using the Linnaean terminology inconsistently, occasionally shifting from one term to another, perhaps deliberately to annoy the Linnaeans. Local variant forms for him were more geographical varieties than they were species, which was the *premiere souche*. Moreover, he believed that these varieties were closely related to similar forms in the Old as in the New World. It was a kind of vicariance definition of species; Stresemann (*op. cit.* p57) gives the example of Buffon putting shrikes (gen. *Lanius*) into a single species with species from Senegal (*Tchagra senegala*), Madagascar (*Leptopterus madagascarinus*), and Cayenne (*Thamnophilus doliatus*) as climatic variations.

3.1.5. Charles Bonnet and the ideal morphologists

Bonnet (1720–1793) was a Swiss zoologist who was greatly influenced by Leibniz's ideas about the continuity of nature (the *lex continui*) and he produced the classical ladder of nature as a result, first in his *Traité d'insectologie* (1745), and then in his *Contemplation de la nature* (1764, Stresemann 1975 p172). His ladder was envisaged as an artificial system of ranking things in terms of their progression, although he did so, he said, without "presuming to establish the progressive order of Nature". The ladder ran from fish to birds to quadrupeds, and each division itself was further divided; birds into aquatic, amphibious, and terrestrial, etc. (see figure 5).

Figure 5 – Bonnet's Scale

Bonnet's "Chain of natural beings" as presented in his Contemplation de la nature *(1764) was enormously influential, even though it was a reworking of the medieval notions derived originally from Aristotle. It was a static, rather than temporal, ladder, but Lamarck (see below) transformed it into a temporal sequence. (Redrawn from Bowler 1989a p61)*

Bonnet's *échelle des êtres naturels*, as he called it, implied that extant species were the current forms of "extinct" species, but that we can only diagnose the modern forms in terms of their reproduction of like forms. Like the early Buffon, he effectively denied the reality of species considered as essences, and plumped for a nominalistic individualist conception:

> If there are no cleavages in nature, it is evident that our classifications are not hers. Those which we form are purely nominal, and we should regard them as means relative to our needs and to the limitations of our knowledge. Intelligences higher than ours perhaps recognize between two individuals which we place in the same species more varieties than we discover between two individuals of widely separated genera. Thus these intelligences see in the scale of our world as many steps as there are individuals.
>
> (Contemplation de la Nature, 2nd edn, 1769, I, p28, quoted in Lovejoy 1936 pp231)

Lovejoy notes wryly, "[t]hus the general habit of thinking in terms of species, as well as the sense of separation of man from the rest of the animal creation, was beginning to break down in the eighteenth century". However, in the same century in which the notion of *species* had acquired a biological sense distinct from the philosophical and logical tradition, it is highly significant that this nominalism occurs so early, and remains contentious from that day until this.

Donati in 1750 extended this view, says Stresemann, and "therefore conceived the notion that every being is a knot in the web of nature, and its resemblance to other forms may be compared to the threads between the knots" (*op. cit.* p172f), which may have influenced Linnaeus' conception of analogies between orders. Such ideas recur in the work of Johannes Hermann (1783), and Jean Baptiste Robinet (1763), who produced a three-dimensional lattice in which species were nodes in the lattice. Stresemann traces this view through Schelling, Spix, Oken and others through to Swainson (*op. cit.* pp174–177).

Swainson's view on classification led to a particular account of species as platonic ideas. For him, following the ideas of William Macleay published in 1819 (Hull 1988c p92–96), all taxa had to be organised in circles that touched ("osculating circles"). The details are not important here (details of both Macleay's and Swainson's systems can be found in Nelson et al. 1981; see also Hull 1988c; Panchen 1992), except that each circle of taxa had a "type" taxon, which diverged to the periphery. Hence, if a circle represented a genus, there would be a type species for that genus. Variation (that is, diversity) of the species follows the same pattern as variation within the higher groups. There would be a type genus for a family, and so on.

This tradition ended in England with the fallout from Darwin's *Origin*. Stresemann (*op. cit.* p181) notes that in ornithology the end came with the publication of T. C.

Jerdon's *The Birds of India* in 1862, which was the last idealist account. In Oken's native Germany, though, the tradition he had begun continued in the work of Johann Jakob Kaup (1803–1879) who in turn influenced Leopold Fitzinger. Kaup relied on a pentagrammatic system, but otherwise was much in the tradition of Macleay and Swainson (*op. cit.* p178–188).

3.1.6. Essentialism and natural systems

Essentialism and typology are two attributes of "traditional" taxonomy that are often conflated (e.g., by Mayr). But they actually represent two distinct aspects of the old taxonomic categories. Essences are definable, and can be known by refining definitions, and are common to all members of a kind. No member of the kind can **not** have an essential property fully and constantly. Types, on the other hand, although the term is used in various ways (Stevens 1994 chap. 6), are somewhat different. In biological thought, the type of a kind, such as a genus, can be instantiated more or less[55], and can be varied from. They can be abstract – not actually instantiated in any actual member of the kind. **Every** member of a kind must exhibit essences. Types are formal notions, essences are definitional, and while some types may be essential and some essences may be typical, the two concepts are not identical. Even worse, there are several types of types. Stevens (1994 p134) cites Paul Farber's taxonomy of types. According to Farber and Stevens, there are three kinds: collection, classification, and morphological types:

> Collection type concepts were concerned with how the name of an organism can be referred to a particular specimen or individual species. Classification type concepts were those that dealt largely with summarizing or simplifying data, whereas morphological concepts dealt with the order of nature and its laws (although Paul Farber, whose work I am following here, noted that these two were not always sharply distinguishable).

Divergences from the type of a genus were considered *terata*, or monsters. They were less than perfect, and could be individual organisms or even entire species. Hybrids were monsters too, the sense in which Linnaeus classified his hybrids. In somewhat later thought, e.g., for Buffon, (Gayon 1996; Roger 1997; Stamos 1998), prior to the evolutionary period shortly before the nineteenth century, transmutation was conceived of as degradation from the type. By the time Owen proposed his notion of the *Archetype* that was to influence Darwin, the transcendentalists had restored a Platonic view of types as pure forms, as ideas, and as essences (Desmond 1984), but the Aristotelian account allowed only for types as actual forms. In "pure" Aristotelianism,

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[55] This was, in fact, Aristotle's phrase – "the more and the less" – in his writings, as we have seen.

variation from the type was an accidental difference, but as with the Linnaean fixation of the genus-species level, Enlightenment biologists were not always pure Aristotelians. Some of them weren't Aristotelians at all. Linnaeus himself had asserted that "*Natura non facit saltum*", reiterating the principle of plenitude, at least for genera (he apparently crossed this apothegm out in his own copy when he found species doing exactly that in hybrids). This principle owed most to neo-Platonic doctrines of emanation, and also relied upon the providence and benevolence of God, and it insisted upon completeness, and a grading from one form to another, as we have seen (Lovejoy 1936).

At the end of the eighteenth century, classifications were commonly thought to be of three sorts – "artificial", "natural" or biological. I bracket *artificial* and *natural* in quotes because the way these terms are used in the history of systematics is at odds with the meaning of these terms in other fields (and is indeed inconsistent throughout the history of systematics itself).[56] Linnaeus felt that he was promoting an artificial classification – one based upon a **single aspect** of organisms (in plants, the sexual system). This was a dichotomous single key system based on Platonic diairesis – each subordinate taxon is distinguished from others in the ordinate taxon by the possession or non-possession of the key character – winged/non-winged, two-winged/four-winged, etc. This means that many taxa so formed are privative definitions – defined by what they are **not** (Nelson et al. 1981). He did also attempt a fragmentary "natural" system – one that grouped on all available characters – but species remained those groups that shared all of some set of characters. Others, such as Adanson (Croizat 1945; Lawrence 1963; Stafleu 1963), attempted to base classifications on as many characters as could be used, in an attempt to demonstrate natural groups.[57]

3.2. Nineteenth Century – a period of change

> The ordinary naturalist is not sufficiently aware that when dogmatizing on what species are, he is grappling with the whole question of the organic world & its connection with the time past & with Man; that in involves the question of Man & his relation to the brutes, of instinct, intelligence & reason, of Creation, transmutation & progressive improvement or development. Each set of geological questions & of ethnological & zoo. & botan. are parts of the great problem which is always assuming a new aspect.

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[56] See Polly Winsor's discussions (Winsor in press; 2001; 2003) on the distinction between natural and artificial, and essentialist and typological taxonomies. Winsor calls typology the "method of exemplars", which is a good term. Types applied within species, within genera and within higher taxonomic groups.

[57] Stresemann (1975 p52) notes that Linnaeus is *also* attempting a kind of "natural" system even in his "artificial" system, and contrasts it to the prior "classical" system – that is, the Aristotelian system of differentiating by general features such as, in the case of birds, land or water based lifestyles. As we saw, Bonnet retains a large amount of the classical a priorism of the medievals in this respect.

Charles Lyell, 11 February 1857 (Wilson 1970 p164)[58]

3.2.1. Jean Baptiste de Lamarck – unreal species change

At the turn of the nineteenth century, there was a considerable amount of ferment over the notions of taxonomic groups or ranks. For example, Blumenbach had classified the human species into races – Caucasian, Mongolian, Ethiopean, American and Malayan – and yet he still regarded these types as subordinate to the human species, and that all were varieties of that species, (Nordenskiöld 1929 p306; Voegelin 1998), although Buffon had previously denied that the notion of "race" applied to the usual human groupings (Roger 1997). Blumenbach's conception of the species was that it was formed through the action of a formative force, a *nisus formativus*, and so his is also a generative notion of species.

More influentially, Lamarck delivered a transmutationist view of species, and followed his mentor Buffon in supposing that there were no realities attaching to the term. In the *Zoological philosophy* (Lamarck 1809; English translation Lamarck 1914), he writes:

> It is not a futile purpose to decide definitely what we mean by the so-called *species* among living bodies, and to enquire if it is true that species are of absolutely constancy, as old as nature, and have all existed from the beginning just as we see them to-day; or if as a result of changes in their environment, albeit extremely slow, they have not in the course of time changed their characters and shape.
>
> …
>
> Let us first see what is meant by the name of species.
>
> Any collection of like individuals which were produced by others similar to themselves is called a species.
>
> This definition is exact: for every individual possessing life always resembles very closely those from which it sprang; but to this definition is added the allegation that the individuals composing a species never vary in their specific characters, and consequently that species have an absolute constancy in nature.
>
> It is just this allegation that I propose to attack, since clear proofs drawn from observation show that it is ill-founded.
>
> (Lamarck 1914 p35)

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[58] Listed as 1851 in the printed version, but this is out of sequence, and certainly a typographical error. I am deeply indebted to Mike Dunford for drawing my attention to this comment of Lyell's (and noting the date typo), the cited note of Agassiz's, James Dana's paper, and for his conversations with me on the period covered by the "uniformitarian" and "catastrophism" debates in geology. As geology was not, at that time, held to be isolated from any other kind of natural history, Lyell felt, as did Darwin, that the issues raised in the one field (geology) had implications for issues in the other (naturalism). Mike's help has been immense here.

As Gillispie (1959 p271) puts it, "(Lamarck's) position is rather that species do not exist, than that they are mutable." Lamarck reiterates in the *Zoological Philosophy* the early view of Buffon that only individual organisms exist in nature:

> Thus, among living bodies, nature, as I have already said, definitely contains nothing but individuals which succeed one another by reproduction and spring from one another; but the species among them have only a relative constancy and are only invariable temporarily. [p44]

It is interesting to note that here and elsewhere Lamarck explicitly restricts his comments to living bodies. His nominalism with respect to organisms is obvious, and species are not themselves in nature, but, as Locke had said, are made for communication:

> Nevertheless, to facilitate the study and knowledge of so many different bodies it is useful to give the name species to any collection of like individuals perpetuated by reproduction without change, so long as their environment does not alter enough to cause variations in their habits, character and shape. [*loc. cit.*]

The generative conception is again in play, except that Lamarck has added temporality to the mix. In the *Recherches* (Lamarck 1802) Lamarck proposed that there was a "life-fluid" that was a variety of physical energy, a *feu éthéré*, that maintained organisms in their form, and it impelled spontaneous generation out of inanimate matter. Species was a notion that applied to the mineral kingdom as well as the biological, but mineral species differed in that they had no individuality while plants and animals did, and neither did they reproduce. In the *Zoological Philosophy* he added that **all** classifications are arbitrary products of thought, and that in nature there are only individuals. Lamarck did not accept the reality of extinction apart from human agency, but held that fossil species merely transformed into later forms (Nordenskiöld 1929 p325). Gillispie notes that Lamarck was slightly inconsistent on species between 1797 and the statements of 1802 and 1807, but goes on to say (p272),

> … the inconsistency on species (is) trivial. … All he did between 1797 and 1800 was to assimilate the question of animal species – or rather their nonexistence – to that of species in general. For in Lamarck the word has not lost its broader connotations. It still carries the sense of all the forms into which nature casts her manifold productions in all three kingdoms (or rather in both divisions).

Lamarck is still indebted to the medieval notion of species as subsidiary divisions of the *summum genus* (being) through to the infimae species of rational living things in the case of humans. In this respect, he was attempting to classify all things as the outcome of physical molecules and forces, and animal species were just an arbitrary part of that chain of being. Still, his view of these nominalistic species is that they are formed out of the generative properties of the life-fluid, and so this is a generative notion of species in that respect.

As to nomenclature, he accepted Linnaeus' binomial convention, and given there was no fact of the matter, held that an international agreement should be made to make names stable (Nordenskiöld 1929 p326). At this stage, Buffon's objections to the binomial nomenclature have lost the field entirely, when even his own student accepts the practice. Lamarck's view of evolution is basically a temporalisation of the ladder of nature/great chain of being (figure 6, Jordanova 1984; Bowler 1989a; Lovejoy 1936). He treated each species as a single lineage that had its own original spontaneous generation out of non-living material, and which ascended something like Bonnet's ladder, although the ladder could branch, as we see in the famous diagram (figure 7).

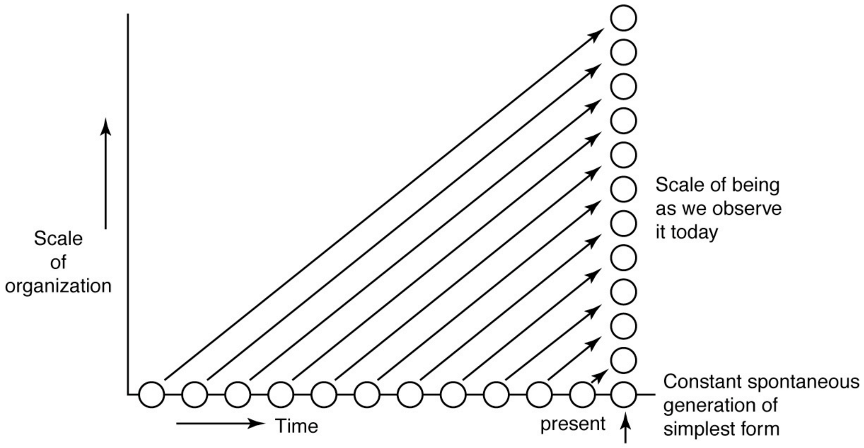

Figure 6 – Lamarck's view of evolution

Lamarck's view of evolution had each species at a given moment as the present level of organisation achieved by a lineage that was not in common descent from any prior lineage. It follows that Lamarck's conception of species necessitated that the entire species evolved simultaneously (redrawn from Bowler 1989a p85; a similar diagram can be found in Panchen 1992 p60).

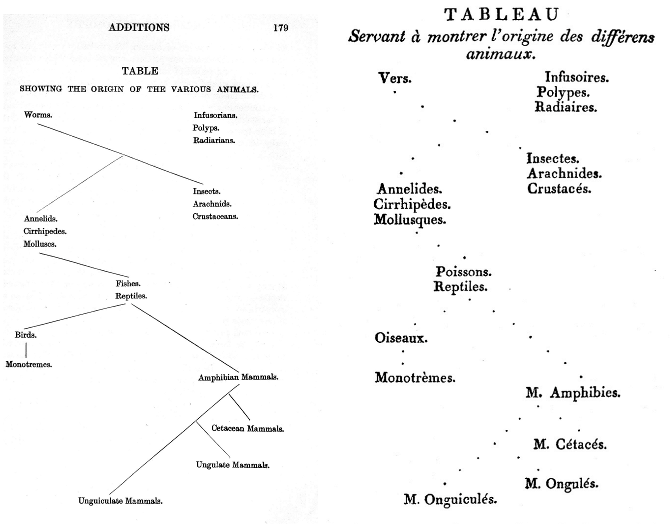

Figure 7 – Lamarck's scale

"Table: showing the origin of the various animals." Left, the 1914 English version, right, Lamarck's original 1809 diagram. The ladder that Lamarck adopted (Lamarck 1914 p179), however, was less direct than Bonnet's. He wrote:

> I do not mean that existing animals form a very simple series, regularly graded throughout; but I do mean they form a branching series, irregularly graded and free from discontinuity, or at least once free from it. [p37]

3.2.2. Cuvier – fixed forms and catastrophes

Lamarck's nemesis, Cuvier, was by contrast a full-blooded species realist. Not only were species real, they did not transmute from one to another. Species were generated in some manner at the time of a catastrophe, and previous forms were obliterated. Nordenskiöld writes

> The immutability of species is to Cuvier's mind an absolute fact; he has not a trace of Linnaeus's hesitation, which he expressed in his old age, in face of the difficulty of drawing a line of demarcation between the species; according to Cuvier's definition, species consist of "those individuals that originate from one another or from common parents and those which resemble them as much as one another." In this definition no mention is made of the creation of the species, which, it will be remembered, Linnaeus took as his starting point, but which, on the whole, Cuvier does not discuss at all.
>
> (Nordenskiöld 1929 p339)

Cuvier's definition is interesting in several respects. Despite the superficial resemblance to Linnaeus' definition given above, Cuvier's more closely resembles John Ray's definition. It is a historical definition, and yet it requires resemblance, presumably to bar monsters. It is, as was Ray's, a generative, and yet still a formalist, definition. For Cuvier, species are created at the beginning of each geological epoch and never vary thereafter. Cuvier's views were very influential on philosophers, as the discussion in Whatley's and Mill's logics shows.

3.2.3. Agassiz – the last fixist

In this opinion, Louis Agassiz, Cuvier's devotee and intellectual successor, concurred. Notwithstanding this, however, Agassiz did not expect that there would be a set of characters unique to all members of a species; resemblance was not itself clear or absolute. In an early short note (Agassiz 1842), he denied that characters gave the species, and instead insisted that while there was a process that underlay the forms of species, there need not be any diagnosable characters that all members of the species exhibited, bringing to mind the Lockean distinction between real and nominal essences. Like Locke, Agassiz was rejecting the nominal and accepting the real essence, and it was a generative notion of real essence at that:

> *… no so-termed character – that is, no observable mark – can be so striking as to indicate an absolute specific distinction; but at the same time, it should never be regarded as so trifling as to point to absolute identity; that characters do not mark off species, but that the combined relations to the external world in all circumstances of life do.* [italics original]

Agassiz's version of the real essence here is the causal relations of the organism throughout its lifecycle to its environment, and he cites the sometime inclusion of the male and female of a species in separate taxa, which was still occurring later in the century. Agassiz explicitly rejected a diagnostic notion of species, and in effect anticipated the later notion of "cryptic species" of Mayr. However, in practice, he was not so exact. He distinguished between eight "species" of Man – Caucasian, Arctic, Mongol, American Indian, Negro, Hottentot, Malayan, and Australian, and claimed that these were all independent creations, not related by descent, each with its own region, flora and fauna. The basis for this was not some generative notion, or reproductive isolation (since it was clear that human "types" could interbreed without trouble), but their clear physical differences (Lurie 1960 p264ff). In short, the characters indicated an absolute specific distinction. Or perhaps Man was different.

Agassiz was not a Lockean, however; he was clearly a variety of Platonist, or at least of idealist. He wrote:

> There is a system in nature … to which the different systems of authors are successive approximations. … This growing co-incidence between our systems and that of nature shows … the identity of the operations of the human and the Divine intellect …
>
> (Agassiz 1859 p31; Lurie 1960)

Lurie calls this Agassiz's "cosmic philosophy", and notes that in his view

> Species, the individual units of identity in nature, were types of thought reflecting an ideal, immaterial inspiration. The same was true of the larger taxonomic categories – genera, families, orders, branches, and kingdoms. All such categories had no real existence in nature. Reality could be discovered only in the character of the individual animals and plants that had inhabited or were now inhabiting the material world. The individual fossil or living from represented on earth the categories of divine thought ranging from species to kingdom and ultimately symbolized a complete identity with the highest concept of being, God.

This would have been completely familiar to Boëthius, Lull or even to an extent, Porphyry. Two years after the publication of his "Essay on Classification", the *Origin of Species* was released, and so it provides a good demarcation point between the traditional view of classification, and the revolution that was to come, even if Agassiz's views were already archaic. In that essay[59], he argued again for the stability of species, although his primary task was to discuss ways in which naturalists could identify and name species, rather than to define them other than as the smallest division of the four great *embranchements* named by Cuvier, which Agassiz called "great types" (Winsor 1979 p97). These were the ways of being, typical plans of nature. Species were the lowest group that could be differentiated out of these plans (which play the role, therefore of Aristotle's summum genera). They had in themselves no identifying morphological character, because that was exhausted in the genus. Winsor notes,

> [h]aving already publicly rejected the criterion of interbreeding, during the debate on the unit of mankind, Agassiz had to ask himself what besides morphological detail and sexual preference enables a biological species to be recognized. His answer was, its mode of reproduction and growth, its geographic distribution and fossil history, and the manifold relations that the individual organism bears to the world around it."
>
> (Winsor 1979 p98)

A species is, it seems, a description of the overall biological features of organisms, for Agassiz gave the individual organism priority, not unlike Buffon. Winsor notes further, "[h]is purpose was … to affirm the reality of all those relationships of similarity that are expressed in a natural classification." She quotes him from the *Essay*:

> Species then exist in nature in the same manner as any other groups, they are quite as ideal in the mode of existence as genera, families, etc., or quite as real. … Now as truly as individuals, while they exist, represent their species for the time being and do not constitute them, so truly do these same individuals represent at the same time their genus, their family, their order, their class, and their type, the characters of which they bear as indelibly as those of the species.

Species exist as ideas, which represent the relations actual individuals bear to the world. They are not things, in the physical sense of the term, so much as what the things represent (but do not comprise). This is very Platonic.

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[59] Published as volume I of the *Contributions to the Natural History of the United States*, 1857 to 1862.

Later, Agassiz attacked "Darwinism" by means of an attack on Haeckel's genealogical classifications in Darwin's name, in a chapter added to a French edition (Agassiz 1869; Morris 1997). Here he attacks the apriorism of the work of Oken and those who follow the ideal morphology school, including Haeckel in that class because he imposes his expectations on the data, which he also accuses Darwin of doing, a point he made in an earlier review of the *Origin*. He rejects the claim of the "Darwinists and their henchmen" that organisms will not reproduce the essential characters of their ancestors. In Morris' translation[60], Agassiz says

> All the observations relative to domestic animals, among which there are so many and so numerous variations, again did not succeed in demonstrating a sufficiently large amplitude in these variations; never did they [the Darwinists] have as a result anything which manifests the indefinite tendency to a changeability without limit…

In short, Agassiz rejected the Darwinian view of species on the grounds that the requisite variation had not been observed. Oddly, as Lurie (1960 p194f) noted, Agassiz was unable to see that there could possibly be more than a certain amount of variation in his own specimens:

> When he had hundreds of fishes spread before him on a work table, these convictions (of the fixity of species) were of such force that even his keen powers of observation and his excellent ability to compare diverse types failed him. He insisted on identifying specimens that seemed even the slightest degree different from one another as separate species rather than as variants. In one analysis alone, for example, he described nine separate "species" of fishes that were in actual fact reducible to four schools of single species.[61]

Agassiz, merciless on taxonomic splitters, was in practice himself a splitter because of his tendency to classify on form alone despite his stated convictions about species in theory. In another, more sinister, respect also, his views led him to excessive splitting. He claimed that Negroes were not of the same species as whites, because, it seems, of the feelings of revulsion he had for them that led him to deny they could be conspecific to whites. This famously meant that he became the leading proponent of multigenism and hence a popular figure in the South before the Civil War (Hunter Dupree 1968 p228f).

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[60] I have amended it slightly for grammar's sake. The original version was accessed on 23 September 2002 at http://www.athro.com/general/atrans.html

[61] According to Mayr, in Lurie's footnote. It would be interesting to see how those species have fared in the molecular period of systematics.

3.2.4. James Dana – a law of creation

But Agassiz was not alone in pressing the Cuvierian view in the period leading up to the *Origin*. His very great admirer James Dana, in an essay in a journal he coedited (Dana 1857), reiterated the old view that "species" applies to all natural things, and that the variable characters of individuals are merely confusing. To this end, he rejected the idea that species are even groups, necessarily. Instead, he wrote

> A *species* corresponds to *a specific amount or condition of concentrated force, defined in the act or law of creation.* [p306. Italics original]

At least in the inorganic world: species are what they were constituted at their creation to be. In the biological world, the idea is the same, leading to the understanding that

> [t]he species is not the adult resultant of growth, nor the initial germ cell, nor its condition at any other point; it comprises the whole history of development. Each species has its own special mode of development as well as ultimate form or result, its serial unfolding, inworking and outflowing; so that the precise nature of the potentiality in each is expressed by the line that historical progress from the germ to the full expansion of its powers, and the realization of the end of its being. We comprehend the type-idea only when we understand the cycle of evolution [*sensu* development – *JSW*] through all its laws of progress, both as regards the living structure under development within, and its successive relations to the external world. [p308]

For Dana, species are the units of the organic world as molecules are the units of the inorganic. He discusses the ranges of infertility of hybrids from the infertile mule to the continuously fertile hybrid, and says that the fully fertile hybrid is not observed in nature, at least among animals; plants are more frequently hybridising. In a rather backhanded manner, he affirms the monogenist position – humans are one species, although non-white races are disappearing

> … like plants beneath those of stronger root and growth, being depressed morally, intellectually and physically, contaminated by new vices, tainted variously by foreign disease, and dwindled in all their hopes and aims and means of progress, through an overshadowing race" [p311]

lest any of his readers get the wrong idea. At least he stood up to Agassiz on monogenism.

Species are not transmutable, for all hybridisation is merely recombination of already extant variation, but there is variation within species – the unfolding of the potentiality inherent within a species according to natural law and changing circumstances (p312). Species are liable to variation as part of the law of a species, and knowledge of the complete type requires knowing all these and how they relate to external circumstances. There is a higher essence, as it were, in the type. Finally, while species are real things, they are not comprehensively covered in any "material or immaterial existence" – in modern parlance, they are types, not tokens[62], and species are both invariant and variant. In short, Dana sees species as the schematic of a developmental cycle and the ways in which it may be perturbed by the environment.

3.2.5. Other fixist views

The view that species were fixed as created was held as late as 1844 by Philip Henry Gosse in his *An Introduction to Zoology*:

> Each order was distributed into subordinate groups, called Genera, and each genus into Species. As this last term is often somewhat vaguely used, it may not be useless to define its acceptation. It is used to signify those distinct forms which are believed to have proceeded direct from the creating hand of God, and on which was impressed a certain individuality, destined to pass down through all succeeding generations, without loss and without confusion. Thus the Horse and the Ass, the Tiger and the Leopard, the Goose and the Duck, though closely allied in form, are believed to have descended from no common parentage, however remote, but to have been primary forms of the original creation. It is often difficult in practice to determine the difference or identity of species; as we know of no fixed principle on which to found our decision, except the great law of nature, by which specific individuality is preserved – that the progeny of mixed species shall not be fertile *inter se*.
>
> (p xv, cited in Simpson 1925 p175)

It is hard not to see Gosse's obdurance as a desperate attempt to maintain the fixity of species even in the face of Buffon's hybridisation experiments, which had a partial success, but in fact there was considerable blindness to variation, as the Agassiz example shows. Another instance cited by J. Y. Simpson (p178f) involves a student of Agassiz, Stimpson, who, when finding intermediate forms of a mollusc he could not decide to place in one species or another,

> "... after he had studied it for a long time, put his heel upon it and grind[ing] it to powder, remarking, "That's the proper way to serve a damned transitional form."
>
> Quoting Nathaniel Southgate Shaler, another student of Agassiz who ended up less disposed to essentialist accounts, from his *Autobiography*, p129

More significantly, for our later story, are the earlier views of Charles Lyell. It is well-known that it was the second volume of Lyell's *Principles of Geology* (1832) that Darwin received on the voyage of the H.M.S. *Beagle* (Kottler 1978 p276-278), which contained the discussion of Lamarck's views, a "book-long refutation of Lamarck", as

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[62] Not *that* modern – the type–token distinction was made by C. S. Peirce (1885; see §§35–37 in Wollheim 1968 for a full discussion of this distinction) only a few decades after Dana wrote. Intruigingly, Peirce's distinction was between *icons*, *indices*, and tokens, and he referred to tokens as *replicas* of symbols (Hookway 1985 p130f).

Desmond and Moore called it (1991 p131). Lyell presented the standard fixist view of species; as Kottler put it,

> Lamarck and Lyell agreed that the 'reality' of species implied their constancy. The words 'real' and 'permanent' were synonymous with respect to species in nature. Thus while Lamarck, the transmutationist, contended species were not real, Lyell, the fixist, argued they were. [p277]

Kottler cites the fifth edition of the *Principles*, published in 1837, which Darwin, upon his return and as he began to consider transmutation and hence the nature of species, heavily underlined and annotated. In this volume, Lyell relies on the infertility of hybrids. According to Lyell, no hybrid could give rise to a new species, unless it was backbred into a pure species. In nature, species had an aversion to interbreeding, which made it "a good test of the distinctness of original stocks, or *species*" (quoted in Kottler 1978 p277 from volume I, p523). He concluded that

> …species have a real existence in nature; and that each was endowed, at the time of its creation, with the attributes and organization by which it is now distinguished.
>
> (quoted in Kottler 1978 p277 from volume I, p528)

While he (reluctantly) changed his mind after the *Origin*, and many discussions with Darwin, his major contribution at this time is to affirm the fixity and reality of species. Mayr (1982 p405) quotes him as saying

> There are fixed limits beyond which the descendants from common parents can never deviate from a common type. … It is idle … to dispute about the abstract possibility of the conversion of one species into another, when there are known causes, so much more active in their nature, which must always intervene and prevent the actual accomplishment of such conversions. [From the 1835, 3rd, edition, vol II, p 162]

Mayr thinks this is an expression of Lyell's essentialism: "each species had its own specific essence and thus it was impossible that it could change or evolve. This, for example, was the cornerstone of Lyell's thought" (*loc. cit.*). But was it really? Lyell seems to be saying not that an **essence** is causing it to remain stable, but that a species is held stable by interbreeding and "known causes". There is typology, to be sure, but overall, Lyell's view is a causal one. Again, we see here hints of a generative notion of species. However, Mayr correctly notes that the *Principles* was Darwin's scientific "bible" (p406) and that he devoted so much time in the *Origin* to refuting special creation largely because of the challenges set by Lyell (p407).

3.2.6. A-P de Candolle and Asa Gray – the Botanical View

A third stream of thought in this period supposes that species are real and that so is variation from the type. This is primarily due to the botanical family, the de Candolles, in particular the elder, Augustin-Pyramus (Candolle 1819). A-P de Candolle stressed the variation of living things, and defined species as

> … the collection of all the individuals who resemble one another more than they resemble others; who are able, by reciprocal fecundation, to produce fertile individuals; and who reproduce by generation, such kind as one may by analogy suppose that all came down originally from one single individual.
>
> (quoted in Hunter Dupree 1968 p54)

So de Candolle's species are groups, in contrast to Cuvierian types, of individual organisms. They are, in the tradition of Ray, both to resemble one another and to generate progeny that are fertile and resemble one another. De Candolle treated variation as the effect of local environments and occasional hybridisation. In this opinion, he was followed closely by the great American botanist, Asa Gray, who was later to become significant in the promotion of Darwinian theory in America against Agassiz (loc. cit). As late as 1846, in a review of the *Vestiges of Natural Creation*, Gray declared that species were created as they are found, and did not transmute (Hunter Dupree 1968 p145–147). His was, by the 1850s, an operational view of species. While creation may have once been of importance, writes his biographer Hunter Dupree (1968 p217), what most concerned Gray was that if species transmuted as Lamarck, Geoffroy and the author of the *Vestiges* declared, then natural history would become meaningless, one presumes because we would be unable to specify the facts about the groups in biology that we encounter. Hunter Dupree says, "it was this inability [of unlike species to breed together – *JSW*] which created the species border, not that he or any other could find this border easily, least of all by referring to an ideal type." Morphology was only a guide to these borders, and relied on the experience of the naturalist and the principles of classification. The Lockean character of this account is manifest. The real essence here is interfertility, not morphology. As a result, Gray worried about hybridisation, and its role in speciation. This had been a concern since Linnaeus' tenth edition of the *Systema Naturae*, and the urgency of the problem was progressively increasing among the naturalists of the period. Gray noted that hybrids would stand a good chance of being fertilised by their parents and asked,

> In such cases they are said to revert to the type of the species of the impregnating parent; but would they return exactly to that type, inheriting as they do a portion of the blood of a cognate species?"

The modern problem of the introgression of genes into a species is foreshadowed here, although Gray relies on a blending inheritance model, of course, causing swamping of the variations.

Gray's other contribution to this topic is in his assertion that humans are a single species. He felt that science in general and his ideas on species and hybridisation in particular pointed to the unity of the human race (p220). It is worth noting here that Gray's rather orthodox Protestantism seems to have had no particular impact on his view of species, as Cuvier's had not. Objections to transmutation appear not to have been founded on orthodox religious doctrine.

3.2.7. Pre-Darwinian evolutionary views of species

… species, the subdivision where intermarriage or breeding is usually considered as natural to animals, and where a resemblance of offspring to parents is generally persevered in.

Vestiges of the History of Creation (Chambers 1844 p263)

In German and French speaking countries prior to the publication of the *Origin*, there were a number of specialists propounding evolutionary views of species. Of note are Bonaparte and Unger.

Prince Charles Lucien Bonaparte (1803–1857), nephew of the famous Napoleon, was an active ornithologist, as his father Lucien had been after he was released from detention by the British in 1814 (Stresemann 1975). Exiled in Leiden by his cousin Louis Napoleon, he became friends with Hermann Schlegel, another famous ornithologist. In 1851 he published the first volume of his *Conspectus generum avium*, a survey of all known species of birds worldwide. In this work, he treated extant species as the descendent forms of prior extinct forms, and in an address to an 1856 convention on "What is a species, particularly in ornithology?" he said:

> We will state with unanimous conviction that the antediluvian crocodiles, elephants and rhinoceroses were the ancestors of those living in our day, and these animals would not have been able to continue to exist without the manifold mutations that their systems produced to adapt themselves to the environment, and that became second nature to their descendants. … If the environment remains the same, so do the species. The stabilizing influence is then by itself all-powerful. The mutating influence can succeed in opposing it only when the whole world surrounding it changes. … But races, however different in characteristics they may be, vanish entirely or at least do not long survive as soon as the environment that produced them ceases to be the same … The transitions between the different races and their type are the best evidence that we can supply to set aside putative species, which are to be relegated to races, with which the painstaking zoologist must nevertheless occupy himself just as earnestly.
>
> Quoted in Stresemann, p166

Of interest in this excerpt is the implication that species are racial groups stabilised by the influence of the environment, somewhat as stabilising selection operates (although there is no reason to suppose Bonaparte thought selection was the reason for the stabilisation). As Darwin later also argued, races are merely species in the making that are not yet made stable. Bonaparte died in 1857, leaving the *Conspectus* unfinished.

Franz Unger, an Austrian botanist at the University of Vienna, published a form of common descent with modification theory in 1852, entitled "Attempt at a History of the Vegetable Realm" (*Versuch einer Geschichte der Planzenwelt*) in which he supposed that all plant life was a single entity that had developed new forms. Unger's theory is often taken to be a forerunner of Darwin (Temkin 1959 p339–342), but he in fact thought that all subsequent development was an expression of the original potentiality of the *Urpflanze*:

> Nothing has been added in this regulated evolutionary process of the vegetal world that had not been previously prepared and indicated, so to speak. Neither genus, nor family, nor class of plants has manifested itself without having become necessary in time.
>
> (Quoted in Temkin 1959 p340)

Temkin notes that Unger held that species themselves do not change, but that some individuals metamorphosed while the old type remained in existence for some time. One year later, Hermann Schaffenhausen published an article "On the Constancy and Transformation of Species" rebutting Unger's ideas on the grounds they indicated man evolved from an orangutan. However, he said in his summary that

> [t]he immutability of species which most scientists regard as natural law is not proved, for there are no definite and unchangeable characteristics of the species, and the borderline between species and subspecies [*Art* and *Abart*] is wavering and uncertain.
>
> (Quoted in Temkin 1959 p342)

It appears then that in the post-Romantic period in Germany and German-speaking countries, naturalists were not so rigid over species as was the Swiss export to America, Agassiz. Unger's conception appears to be an entelechical view – a species was a type that was "in" the plant kingdom from the beginning, in the *Urpflanze*. However, the stasis of the species themselves is due in Unger's book to the generative powers of inner forces. Mayr quotes him saying:

> The lower as well as the higher taxa appear then not as an accidental aggregate, as an arbitrary mental construct but united with each other in a genetic manner and thus form a true intrinsic unit.
>
> (Mayr 1982 p391)

3.3. Darwin's demotion of species

> ... in my own work, I have not felt conscious that disbelieving in the *permanence* of species has made much difference one way or the other; in some few cases (if publishing avowedly on doctrine on non-permanence) I sh^{d}. *not* have affixed names, & in some few cases sh^{d}. have affixed names to remarkable varieties. Certainly I have felt it humiliating, discussing & doubting & examining over & over again, when in my own mind, the only doubt has been, whether the forms varied *today or yesterday* (to put a fine point on it, as Snagsby would say). After describing a set of forms, as distinct species, tearing up my M.S., & then making them

> one again (which has happened to me) I have gnashed my teeth, cursed species, & asked what sin I had committed to be so punished: But I must confess, that perhaps the same thing w^{d}. have happened to me on any scheme of work—...
>
> Darwin to Hooker, 25 September 1853 (Burkhardt 1996 p128-129)

> One of the ironies of the history of biology is that Darwin did not really explain the origin of new species in *The Origin of Species*, because he didn't know how to define a species.
>
> (Futuyma 1983 p152)

Charles Darwin is important not so much for the novelties on the nature of species that he provided – there are only really two of these, failure to breed in nature, and selection as the motive force of specific characters, as we shall see. Rather it is because his book *On the Origin of Species* changed **every** scientist's way of looking at species thereafter. He has been more closely scrutinised than anybody else, and there is a wealth of material available. One thing that we should put out of our minds from the beginning, though: it is *not* true that Darwin did not address the origin of species in *On the Origin of Species* (cf. the epigram at the head of this section). The book is "one long argument" (Mayr 1991) on that very point. Over and again, he discusses why species evolve to be distinct from parental forms, and how they have done so. It is unclear how this idea gained currency.[63]

Darwin's views on species changed over time. In his earlier works he seems to have treated species the same way as his teachers, unsurprisingly, as groups united by some description – that which Mayr refers to as "typological, 'non-dimensional' species of local fauna" (Mayr 1982 p265). Since his views are often misrepresented (see Kottler 1978 for a discussion, particularly p291f) on the basis of comments made in the *Origin*, I will give an extensive and chronological series of quotations from his published works, before continuing to his correspondence and then the Notebooks. While I do not dispute Kottler's analysis, and will rely heavily upon it, some features of Darwin's views that are further developments of the older notions of *species* and some of his comments that are relevant to later debates, particularly over speciation, are to be found in comments not discussed by Kottler or Mayr or Ghiselin (1984).

In his Notebooks, Darwin vacillated between species realism and nominalism. Early on, he was convinced they were real, just as he was convinced they were immutable.

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[63] Possibly it arose from a comment made in 1866 by John Campbell, the Duke of Argyll (Argyll 1884 p240):

> It will be seen, then, that the principle of Natural Selection has no bearing whatever on the Origin of Species, but only on the preservation and distribution of species when they have arisen. I have already pointed out that Mr. Darwin does not always keep this distinction clearly in view…

Later, in the *Origin* in particular, he suggested they were at best transitory and at worst mere conventions, Ghiselin (1984 chapter IV)[64] notes:

> It is not difficult to find passages in Darwin's writing suggesting that he considered species to be purely artificial constructs. For instance: "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. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species."[26] On the basis of statements such as this, Mayr and others have come to the conclusion that Darwin upheld a morphological, as opposed to a biological, species concept.[27] That is, they maintain that he looked upon species as merely classes of organisms having a given degree of similarity and difference in the observed properties of their members.
>
> But there are certain other passages in Darwin's writings which show that the problem is more complicated. In his second notebook on the transmutation of species, Darwin says: "As *species* is real thing with regard to contemporaries – fertility must settle it."[28] The reality of species is affirmed in a letter to Gray written in 1860, in which Darwin severely criticizes some assertions of Louis Agassiz. The following statement is particularly relevant to the question at issue: "How absurd that logical quibble – 'if species do not exist, how can they vary?' As if any one doubted their temporary existence."[29] It appears that there is at least one sense in which species are thought to be real, although it is evident that there is a sense in which they are held to be not real. This being the case, any citation of statements by Darwin in support of his holding one or another point of view must be buttressed by a demonstration of the sense which he intended.[65]

3.3.1. The Notebooks

Kottler (1978) has investigated Darwin's early views on species in the Notebooks B, C, D and E (labelled by Kottler I–IV, which I have relabelled). These are referred to as the "transmutation notebooks" since Darwin started them after he became convinced by Gould's investigations of the finches found on the Galápagos Islands, and the tortoises and mockingbirds backed it up, showed that these were modified descendents of South American colonists (Desmond et al. 1991 p224f). Once he started on the idea, his conjectures came thick and fast: mammalian species were shorter lived than simpler forms because of their complexity, domestic animals were able to revert to the wild forms, or at least live like them, perhaps species had a vital force and a fixed lifespan?

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[64] Text cited from the Lightbinders CD-ROM (*Darwin* 1997).

[65] Ghiselin's footnote references are:

> [26] *Origin*, p. 485.
>
> [27] Mayr, "Isolation."
>
> [28] *Second Notebook*, p. 99. (The view expressed here was later modified.)
>
> [29] Life and Letters, II, 333.

and so on. In the Notebooks, he noted the "repugnance" of species to intercrossing (all quotations from Kottler):

> ... repugnance generally to marriage before domestication, ... marriage never probably excepting from strict domestication, offspring not fertile or at least most rarely and perhaps never fertile. – No offspring: physical impossibility to marriage. [B p 120]
>
> Instinctive feelings against other species for sexual ends ... [B p161]
>
> There is in nature a real repulsion amounting to impossibility holds good in plants between all different forms ... [B p189]
>
> The dislike of two species to each other is evidently an instinct; & this prevents breeding. [B p197]
>
> The existence of wild close species of plants shows there is tendency to prevent the crossing of animals where there is much facility in crossing there comes the impediment of instinct [E p143f]

Kottler observes that at this stage, Darwin agreed with Lyell that intercrossing was forced in domestication, and he made non-interbreeding a test of being a species:

> ... now domestication depends on perversion of instincts ... & therefore the one distinction of species would fail [B p197]
>
> Definition of species: one that remains at large with constant characters, together with beings of very near structure [B p213]
>
> My definition of species has nothing to do with hybridity, is simply, an instinctive impulse to keep separate, which no doubt be overcome, but until it is these animals are distinct species [C p161]
>
> A species as soon as once formed ..., repugnance to intermarriage – settles it [B p24]
>
> Species formed ... keep distinct, two species made; ... [B p82]

Clearly, Darwin is more concerned with the behaviour of organisms in natural conditions, not with the mere possibility of intercrossing. A species is to him an interbreeding group that is kept separate from other groups not only by the possibility of hybridisation, but also by the mating behaviours of each group. Hence, it is not a notion that can be lab-tested. It has to be observed in the field. But there were ways to test species:

> It is daily happening, that naturalists describe animals as species ... There is only two ways [*sic*] of proving to them it is not; one where they can [be] proved descendant [Kottler interpolates: descent from common parents], which of course most rare, or when placed together they will breed. [B p122]

Species are real, according to Darwin here, when they do not interbreed:

> As species is real thing with respect to contemporaries – fertility must settle it [C p 152]
>
> If they [systematists – *JSW*] give up infertility in largest sense as test of species – they must deny species which is absurd. [E p24].

Kottler notes that Darwin is not here using Buffon's 1749 definition of species, as by the phrase "in the largest sense" Darwin is including both sterility and aversion, which Buffon did not – he merely required sterility when crossed. Immediately before the last passage, says Kottler, Darwin had written

> ... one species may have passed through a thousand changes, keep distinct from other, & if a first & last individual were put together, they would not according to all analogy breed together.

Therefore, Darwin takes "being a species" as the **outcome of changes** that lead to a failure of the organisms to interbreed, not as the **outcome of failure to interbreed** first. He is not using a diagnostic notion of species. This is a generative notion, one to be explained by transmutation. In fact, Darwin expects that diagnosis may be nigh on impossible:

> Hence species may be good ones and differ scarcely in any external character [B p213]
>
> ... we do not know what amount of difference prevents breeding ... [B p241]

The Notebooks were completed eight years later, in 1845. In them Darwin developed a notion of speciation as due to adaptation to local conditions, mostly due to geographical isolation, which prevented backcrossing (Kottler 1978 p287f).

3.3.2. Darwin's correspondence

In his correspondence with his scientific friends, Darwin begins to ask questions about species relatively late, around 1855 (Barlow 1967), although Padian (1999 p353) notes that in 1843 he did once ask the museum taxonomist G. R. Waterhouse what he meant by "relationship"; Darwin's query is instructive:

> It has long appeared to me, that the root of the difficulty in settling such questions as yours, – whether the number of species &c &c should enter as an element in settling the value of existence of a group – lies in our ignorance of what we are searching after in our natural classifications. – Linnaeus confesses profound ignorance. – Most authors say it is an endeavour to discover the laws according to which the Creator has willed to produce organized beings – But what empty high-sounding sentences these are – it does not mean order in time of creation, nor propinquity to any one type, as man. – in fact it means just nothing – According to my opinion, (which I give everyone leave to hoot at, like I should have, six years since, hooted at them, for holding like views) classification consists in grouping beings according to their actual *relationship*, ie, their consanguinuity, or descent from common stocks …
>
> 26 July 1843, (Burkhardt 1996 p76)

Waterhouse replied, "by relationship I mean merely resemblance". Darwin, having raised the issue of the number of species (Hey's before-mentioned counting problem) then treats species themselves as a subordinate issue – it is the ways in which **higher** taxa are to be arranged that he is most interested in. Shortly thereafter, he mentions species in passing to Hooker (*op. cit.* p80, 11 January 1844):

> I was so struck with the distributions of Galapagos organisms &c &c & with the character of the American fossil mammifers, &c &c that I determined to collect blindly every sort of fact, which c^{d} bear any way on what are species … At last gleams of light have come, & I am almost convinced (quite contrary to the opinion I started with) that species are not (it is like confessing a murder) immutable.

In 1853, as the epigram at the head of this section shows, Darwin noted to Hooker that his ideas on species had not made all that much difference to his classificatory work.

He asked Henslow several times for an idea of the number of "close species" in botanical genera (27 June, 2 July, 7 July 1855) before he managed to make clear that he was after an impression of how many almost indistinguishable species exist in large genera. Henslow apparently succeeded, for on 21 July 1855 he replied

> I thank you much for attempting to mark the list of dubious species: I was afraid it was a very difficult task, from, as you say, the want of a definition of what a species is. – I think however you were marking exactly what I wanted to know. My wish was derived as follows: I have ascertained, that APPARENTLY (I will not take up time by showing how) there is more variation, a wider geographical range, & probably more individuals, in the species of *large* genera than in the species of *small* genera. These general facts seem to me very curious, & I wanted to ascertain one point more; viz whether the closely allied and dubious forms which are generally considered as species, also belonged on average to large genera.
>
> (Barlow 1967 p182)

In a letter to Asa Gray in 1857 (29 November), Darwin discusses his by-now established opinion that there is no clear distinction between varieties and species, and how there seems under Darwin's evolutionary views to be no easy foundation or set of physical criteria to decide when a variety has earned a specific epithet:

> You speak of species not having any material base to rest on; but is this any greater hardship than deciding what deserves to be called a variety & be designated by a greek letter. When I was at systematic work, I know I longed to have no other difficulty (great enough) than deciding whether the form was distinct enough to deserve a name; & not to be haunted with undefined & unanswerable question whether it was a true species. What a jump it is from a well marked variety, produced by natural cause, to a species produced by the separate act of the Hand of God. But I am running on foolishly. – By the way I met the other day Phillips, the Palaeontologist, & he asked me "how do you define a species?" – I answered "I cannot" Whereupon he said "at last I have found out the only true definition, – 'any form which has ever had a specific name'! …
>
> (Burkhardt 1996 p183)

This anecdote found its way into later mythology in Poulton's essay cited and quoted below, although he dates it a week after the *Origin*. After the *Origin* was published, Darwin had sought Henslow's reaction[66] (11 November 1859):

> If you are *in even so slight a degree* staggered (which I hardly expect) on the immutability of species, then I am convinced with further reflection you will become more and more staggered, for this has been the process through which my mind has gone.

Henslow was staggered enough, it seems. He shortly afterwards wondered at Owen's savage reaction to the views of the *Origin* (5 May 1860):

> … when his own are to a certain extent of the same character. If I understand him, he thinks the "Becoming" of species (I suppose he means the *producing* of species) a somewhat rapid and not a slow process – but he seems to think them *progressive* organised [sic] out of previously organized beings – {analogous (?) to minerals (simple and compound) out of ± 60 Elements}.

And when Sedgwick attacked Darwin in an address, Henslow defended him actively and forthrightly, also saying in his lectures to students, he reported,

> … how frequently Naturalists were at fault in regarding as *species*, forms which had (in some cases) been shown to be varieties, and how legitimately Darwin had deduced his *inferences* from positive experiment.

Letter 10 May 1860 to Hooker, which was then passed on to Darwin.

In correspondence with Huxley before the *Origin*, on 26 September 1853, and 3 October 1853 (Padian 1999 p355), Darwin discussed the "Natural System" of classification: it was merely genealogical; we did not have access to a written record, and thus we had to work it out, but the cause of analogy and homology was genealogy (i.e., descent). Huxley replied that

> Cuvier's definition of the object of Classification seems to me to embody all that is really wanted in Science – it is *to throw the facts of structure into the fewest possible general propositions*" [emphasis original].

Darwin replied

> I knew, of course, of the Cuvierian view of Classification, but I think that most naturalists look for something further, & search for 'the natural system', – 'for the plan on which the Creator has worked' &c &c. – It is this further element which I believe to be simply genealogical.

In summary, his pre-*Origin* correspondence shows him to be rather cautious about showing his hand but he did seek information about what we would now, following Mayr, call "sibling species" and "cryptic species".

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[66] All quotations from Darwin's correspondence with Henslow are taken from Barlow (1967).

3.3.3. Darwin's published comments on species

In his *Journal of Researches* (first published 1839) Darwin makes few comments about species except to note, in the second edition of 1845, eight years after his thinking about transmutation began, that there are checks on the increases of populations.

> Every animal in a state of nature regularly breeds; yet in a species long established, any *great* increase in numbers is obviously impossible, and must be checked by some means. We are, nevertheless, seldom able with certainty to tell in any given species, at what period of life, or at what period of the year, or whether only at long intervals, the check falls; or, again, what is the precise nature of the check. Hence probably it is, that we feel so little surprise at one, of two species closely allied in habits, being rare and the other abundant in the same district; or, again, that one should be abundant in one district, and another, filling the same place in the economy of nature, should be abundant in a neighbouring district, differing very little in its conditions. If asked how this is, one immediately replies that it is determined by some slight difference, in climate, food, or the number of enemies: yet how rarely, if ever, we can point out the precise cause and manner of action of the check! We are, therefore, driven to the conclusion, that causes generally quite inappreciable by us, determine whether a given species shall be abundant or scanty in numbers.
>
> *Journal of Researches*, 1845, Chapter VIII, p167[67]

He also notes the difficulty of defining species in terms of morphology:

> Of the latter [rabbit, a piebald hybrid of black and gray breeds] I now possess a specimen, and it is marked about the head differently from the French specific description. This circumstance shows how cautious naturalists should be in making species; for even Cuvier, on looking at the skull of one of these rabbits, thought it was probably distinct!
>
> Chapter IX, p184

Darwin reports that the Gauchos of South America were able to tell that these were one species because they shared the same territory and interbred, while Cuvier used only morphology. He notes in a footnote:

> The distinction of the rabbit as a species, is taken from peculiarities in the fur, from the shape of the head, and from the shortness of the ears. I may here observe that the difference between the Irish and English hare rests upon nearly similar characters, only more strongly marked. [p184n]

He goes on to say

> I was much struck with the marked difference between the vegetation of these eastern valleys and those on the Chilian side: yet the climate, as well as the kind of soil, is nearly the same, and the difference of longitude very trifling. The same remark holds good with the quadrupeds, and in a lesser degree with the birds and insects. I may instance the mice, of which I obtained thirteen species on the shores of the Atlantic, and five on the Pacific, and not one of them is

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[67] All quotations from Darwin's published works are taken from the Lightbinders electronic edition (*Darwin* 1997) unless otherwise stated.

> identical. We must except all those species, which habitually or occasionally frequent elevated mountains; and certain birds, which range as far south as the Strait of Magellan. This fact is in perfect accordance with the geological history of the Andes; for these mountains have existed as a great barrier since the present races of animals have appeared; and therefore, unless we suppose the same species to have been created in two different places, we ought not to expect any closer similarity between the organic beings on the opposite sides of the Andes than on the opposite shores of the ocean. In both cases, we must leave out of the question those kinds which have been able to cross the barrier, whether of solid rock or salt-water.[5]
>
> [5] This is merely an illustration of the admirable laws, first laid down by Mr. Lyell, on the geographical distribution of animals, as influenced by geological changes. The whole reasoning, of course, is founded on the assumption of the immutability of species; otherwise the difference in the species in the two regions might be considered as superinduced during a length of time.
>
> Chapter XV, p313

Here he is undercutting the widely-held view that species are formed by climate or soil. Instead we have the beginnings of a biogeographic view of species as the result of geological isolation, which we have seen in his Notebooks was a focus of his thinking at this time.

> Besides the several evident causes of destruction, there appears to be some more mysterious agency generally at work. Wherever the European has trod, death seems to pursue the aboriginal. We may look to the wide extent of the Americas, Polynesia, the Cape of Good Hope, and Australia, and we find the same result. Nor is it the white man alone that thus acts the destroyer; the Polynesian of Malay extraction has in parts of the East Indian archipelago, thus driven before him the dark-coloured native. The varieties of man seem to act on each other in the same way as different species of animals – the stronger always extirpating the weaker.
>
> Chapter XIX, p419

Again we can see in hindsight Darwin foreshadowing the idea that better-adapted species will exclude other species in competition with them.

In *Coral Reefs* (1842), Darwin uses the term *species* conventionally, never noting any great problem with corals.[68] In the Monograph on Cirripedia (1851), Darwin describes his taxonomic practice in the Preface:

> In those cases in which a genus includes only a single species, I have followed the practice of some botanists, and given only the generic character, believing it to be impossible, before a second species is discovered, to know which characters will prove of specific, in contradistinction to generic, value.
>
> In accordance with the Rules of the British Association, I have faithfully endeavoured to give to each species the first name attached to it, subsequently to the introduction of the binomial

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[68] Which is odd, since coral species are notoriously difficult to define or delineate (Carlon et al. 2002; Pennisi 2002; Soong et al. 1992; Veron 2001a; 2001b; Vollmer et al. 2002). At this time he might still have been relying on purely morphological criteria, and this is borne out by the way in which he does describe them.

> system, in 1758, in the tenth edition.[1] In accordance with the Rules, I have rejected all names before this date, and all MS. names. In one single instance, for reasons fully assigned in the proper place, I have broken through the great law of priority. I have given much fewer synonyms than is usual in conchological works; this partly arises from my conviction that giving references to works, in which there is not any original matter, or in which the Plates are not of a high order of excellence, is absolutely injurious to the progress of natural history, and partly, from the impossibility of feeling certain to which species the short descriptions given in most works are applicable; – thus, to take the commonest species, the *Lepas anatifera*, I have not found a single description (with the exception of the anatomical description by M. Martin St. Ange) by which this species can be certainly discriminated from the almost equally common *Lepas Hillii*. I have, however, been fortunate in having been permitted to examine a considerable number of authentically named specimens, (to which I have attached the sign (!) used by botanists,) so that several of my synonyms are certainly correct.
>
> [1] In the Rules published by the British Association, the 12th edition, (1766,) is specified, but I am informed by Mr. Strickland that this is an error, and that the binomial method was followed in the 10th edition. of the 'Systema Naturæ.'
>
> Part I, pp ix-x

Darwin is correct in both claims. The Strickland Rules, as they came to be known, did indeed cite the 12th edition, but the 10th was the correct one.

3.3.4. *On the Origin of Species*, on species

In the *Origin* (all quotations and page numbers from the 6th edition[69]), Darwin makes many substantive and theoretical claims about species. In the chapter entitled "Variation under domestication", he makes the following statements intended to convince those who rejected the mutability of species on logical grounds as well as practical ones. He notes that variation is an established fact within species, and that morphology is not a safe guide:

> Indefinite variability is a much more common result of changed conditions than definite variability, and has probably played a more important part in the formation of our domestic races. We see indefinite variability in the endless slight peculiarities which distinguish the individuals of the same species, and which cannot be accounted for by inheritance from either parent or from some more remote ancestor. [p16]
>
> 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 be ranked by him as well-defined species. [p25]
>
> May not those naturalists who, knowing far less of the laws of inheritance than does the breeder, and knowing no more than he does of the intermediate links in the long lines of descent, yet admit that many of our domestic races are descended from the same parents – may they not learn a lesson of caution, when they deride the idea of species in a state of nature being lineal descendants of other species? [p29]

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[69] Darwin's views on species do not seem to have changed much between 1859 and this edition in 1871.

> But what concerns us is that the domestic varieties of the same species differ from each other in almost every character, which man has attended to and selected, more than do the distinct species of the same genera. [p37]

In the subsequent chapter, “Variation under nature”, he says:

> Before applying the principles arrived at in the last chapter to organic beings in a state of nature, we must briefly discuss whether these latter are subject to any variation. To treat this subject properly, a long catalogue of dry facts ought to be given; but these I shall reserve for a future work. Nor shall I here discuss the various definitions which have been given of the term species. No one definition has satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species. Generally the term includes the unknown element of a distinct act of creation. The term “variety” is almost equally difficult to define; but here community of descent is almost universally implied, though it can rarely be proved. We have also what are called monstrosities; but they graduate into varieties. By a monstrosity I presume is meant some considerable deviation of structure, generally injurious, or not useful to the species. Some authors use the term “variation” in a technical sense, as implying a modification directly due to the physical conditions of life; and “variations” in this sense are supposed not to be inherited; but who can say that the dwarfed condition of shells in the brackish waters of the Baltic, or dwarfed plants on Alpine summits, or the thicker fur of an animal from far northwards, would not in some cases be inherited for at least a few generations? And in this case I presume that the form would be called a variety. [p38]

There is a continuum of variation from occasional sports through to well-marked varieties, and some groups of organisms contain within them an enormous amount of variation:

> There is one point connected with individual differences, which is extremely perplexing: I refer to those genera which have been called “protean” or “polymorphic,” in which the species present an inordinate amount of variation. With respect to many of these forms, hardly two naturalists agree whether to rank them as species or as varieties. We may instance Rubus, Rosa, and Hieracium amongst plants, several genera of insects and of Brachiopod shells. In most polymorphic genera some of the species have fixed and definite characters. Genera which are polymorphic in one country, seem to be, with a few exceptions, polymorphic in other countries, and likewise, judging from Brachiopod shells, at former periods of time. These facts are very perplexing, for they seem to show that this kind of variability is independent of the conditions of life. I am inclined to suspect that we see, at least in some of these polymorphic genera, variations which are of no service or disservice to the species, and which consequently have not been seized on and rendered definite by natural selection, as hereafter to be explained. [p40]

Purely morphological notions present difficulties to all naturalists; we find intermediate forms all the time, and inductively, Darwin is suggesting that this does not stop merely within species or between extant forms within genera:

> The forms which possess in some considerable degree the character of species, but which are so closely similar to other forms, or are so closely linked to them by intermediate gradations, that naturalists do not like to rank them as distinct species, are in several respects the most important for us. We have every reason to believe that many of these doubtful and closely

allied forms have permanently retained their characters for a long time; for as long, as far as we know, as have good and true species. Practically, when a naturalist can unite by means of intermediate links any two forms, he treats the one as a variety of the other; ranking the most common, but sometimes the one first described, as the species, and the other as the variety. But cases of great difficulty, which I will not here enumerate, sometimes arise in deciding whether or not to rank one form as a variety of another, even when they are closely connected by intermediate links; nor will the commonly assumed hybrid nature of the intermediate forms always remove the difficulty. In very many cases, however, one form is ranked as a variety of another, not because the intermediate links have actually been found, but because analogy leads the observer to suppose either that they do now somewhere exist, or may formerly have existed; and here a wide door for the entry of doubt and conjecture is opened.

Hence, in determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgment and wide experience seems the only guide to follow. We must, however, in many cases, decide by a majority of naturalists, for few well-marked and well-known varieties can be named which have not been ranked as species by at least some competent judges. [p41]

In short, then, there is often no consensus, and the facts have to be worked out by the most informed majority. Even then, there is often no fact of the matter when a variety is to be distinguished from a species. Darwin is undercutting the intuitions of his audience here.

The geographical races or sub-species are local forms completely fixed and isolated; but as they do not differ from each other by strongly marked and important characters, "There is no possible test but individual opinion to determine which of them shall be considered as species and which as varieties." [Quoting Wallace] Lastly, representative species fill the same place in the natural economy of each island as do the local forms and sub-species; but as they are distinguished from each other by a greater amount of difference than that between the local forms and sub-species, they are almost universally ranked by naturalists as true species. Nevertheless, no certain criterion can possibly be given by which variable forms, local forms, sub-species, and representative species can be recognised. [p42]

In fact, he says, sometimes the distinctness of species is due to the systematist classifying every variant as a distinct species (the splitters of modern taxonomy).

Some few naturalists maintain that animals never present varieties; but then these same naturalists rank the slightest difference as of specific value; and when the same identical form is met with in two distinct countries, or in two geological formations, they believe that two distinct species are hidden under the same dress. The term species thus comes to be a mere useless abstraction, implying and assuming a separate act of creation. It is certain that many forms, considered by highly competent judges to be varieties, resemble species so completely in character, that they have been thus ranked by other highly competent judges. But to discuss whether they ought to be called species or varieties, before any definition of these terms has been generally accepted, is vainly to beat the air. [p43]

I have been struck with the fact, that if any animal or plant in a state of nature be highly useful to man, or from any cause closely attracts his attention, varieties of it will almost universally be found recorded. These varieties, moreover, will often be ranked by some authors as species. Look at the common oak, how closely it has been studied; yet a German author makes more than a dozen species out of forms, which are almost universally considered by other botanists to be varieties; and in this country the highest botanical authorities and practical men can be quoted to show that the sessile and pedunculated oaks are either good and distinct species or mere varieties.

I may here allude to a remarkable memoir lately published by A. [Alphonse] de Candolle, on the oaks of the whole world. No one ever had more ample materials for the discrimination of the species, or could have worked on them with more zeal and sagacity. … De Candolle then goes on to say that he gives the rank of species to the forms that differ by characters never varying on the same tree, and never found connected by intermediate states. After this discussion, the result of so much labour, he emphatically remarks: "They are mistaken, who repeat that the greater part of our species are clearly limited, and that the doubtful species are in a feeble minority. This seemed to be true, so long as a genus was imperfectly known, and its species were founded upon a few specimens, that is to say, were provisional. Just as we come to know them better, intermediate forms flow in, and doubts as to specific limits augment." [p43f]

Intermediates are common, then, and claims of distinctness seem to rely on an *a priori* notion of descent from created parents, rather than be evidence in favour of the idea.

When a young naturalist commences the study of a group of organisms quite unknown to him, he is at first much perplexed in determining what differences to consider as specific, and what as varietal; for he knows nothing of the amount and kind of variation to which the group is subject; and this shows, at least, how very generally there is some variation. But if he confine his attention to one class within one country, he will soon make up his mind how to rank most of the doubtful forms. His general tendency will be to make many species, for he will become impressed, just like the pigeon or poultry fancier before alluded to, with the amount of difference in the forms which he is continually studying; and he has little general knowledge of analogical variation in other groups and in other countries, by which to correct his first impressions. As he extends the range of his observations, he will meet with more cases of difficulty; for he will encounter a greater number of closely allied forms. But if his observations be widely extended, he will in the end generally be able to make up his own mind; but he will succeed in this at the expense of admitting much variation, and the truth of this admission will often be disputed by other naturalists. When he comes to study allied forms brought from countries not now continuous, in which case he cannot hope to find intermediate links, he will be compelled to trust almost entirely to analogy, and his difficulties will rise to a climax.

Certainly no clear line of demarcation has as yet been drawn between species and sub-species – that is, the forms which in the opinion of some naturalists come very near to, but do not quite arrive at, the rank of species: or, again, between sub-species and well-marked varieties, or between lesser varieties and individual differences. These differences blend into each other by an insensible series; and a series impresses the mind with the idea of an actual passage. [p44f]

This passage is most critical – Darwin has moved from the formal variation of groups to the idea that these forms are the result of a temporal sequence. Moreover, the only difference between slight variants, marked variations, and species is a matter of time passed. The difference of **rank** is arbitrary:

From these remarks it will be seen that I look at the term species as one arbitrarily given, for the sake of convenience, to a set of individuals closely resembling each other, and that it does

> not essentially differ from the term variety, which is given to less distinct and more fluctuating forms. The term variety, again, in comparison with mere individual differences, is also applied arbitrarily, for convenience' sake. [p46]

We should be cautious here. It does not seem to me that Darwin is saying that the **groupings** are arbitrary, and the Notebook comment that species are real to their contemporaries backs up the claim that he thinks the groups are natural. What he thinks is arbitrary is where the distinction between the ranks of *species* and *variety* is to be drawn. And genera are the result of the age since common parenthood; some are larger than others and have more variation because the conditions that cause species to form have remained favourable for a long time:

> From looking at species as only strongly marked and well-defined varieties, I was led to anticipate that the species of the larger genera in each country would oftener present varieties, than the species of the smaller genera; for wherever many closely related species (i.e., species of the same genus) have been formed, many varieties or incipient species ought, as a general rule, to be now forming. Where many large trees grow, we expect to find saplings. Where many species of a genus have been formed through variation, circumstances have been favourable for variation; and hence we might expect that the circumstances would generally be still favourable to variation. On the other hand, if we look at each species as a special act of creation, there is no apparent reason why more varieties should occur in a group having many species, than in one having few. [p47]
>
> Moreover, the species of the larger genera are related to each other in the same manner as the varieties of any one species are related to each other. No naturalist pretends that all the species of a genus are equally distinct from each other; they may generally be divided into sub-genera, or sections, or lesser groups. As Fries has well remarked, little groups of species are generally clustered like satellites around other species. And what are varieties but groups of forms, unequally related to each other, and clustered round certain forms – that is, round their parent-species? Undoubtedly there is one most important point of difference between varieties and species; namely, that the amount of difference between varieties, when compared with each other or with their parent-species, is much less than that between the species of the same genus. [p49]

So Darwin presents species as real, but not as a formal and fixed rank. Genera are like species and varieties in that they are the result of groupings of variation. They too do not seem to be a fixed rank, commensurate across all genera. He summarises the argument in this chapter thus:

> Finally, varieties cannot be distinguished from species, – except, first, by the discovery of intermediate linking forms; and, secondly, by a certain indefinite amount of difference between them; for two forms, if differing very little, are generally ranked as varieties, notwithstanding that they cannot be closely connected; but the amount of difference considered necessary to give to any two forms the rank of species cannot be defined. In genera having more than the average number of species in any country, the species of these genera have more than the average number of varieties. In large genera the species are apt to be closely, but unequally, allied together, forming little clusters round other species. Species very closely allied to other species apparently have restricted ranges. In all these respects the species

> of large genera present a strong analogy with varieties. And we can clearly understand these analogies, if species once existed as varieties, and thus originated; whereas, these analogies are utterly inexplicable if species are independent creations. [p49f]

Darwin had no doubt that species were formed through selection on varietial forms, and this provides the missing mechanism for how conditions of life can give rise to varieties:

> Again, it may be asked, how is it that varieties, which I have called incipient species, become ultimately converted into good and distinct species, which in most cases obviously differ from each other far more than do the varieties of the same species? How do those groups of species, which constitute what are called distinct genera, and which differ from each other more than do the species of the same genus, arise? All these results, as we shall more fully see in the next chapter, follow from the struggle for life. Owing to this struggle, variations, however slight and from whatever cause proceeding, if they be in any degree profitable to the individuals of a species, in their infinitely complex relations to other organic beings and to their physical conditions of life, will tend to the preservation of such individuals, and will generally be inherited by the offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive. I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection, in order to mark its relation to man's power of selection. [Chapter III, p51f]

Selection is for Darwin intraspecific, interspecific or even merely a matter of simple survival:

> Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. [p53]
>
> But the struggle will almost invariably be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers. In the case of varieties of the same species, the struggle will generally be almost equally severe, and we sometimes see the contest soon decided… [p60]

And in chapter IV, he notes

> In order that any great amount of modification should be effected in a species, a variety, when once formed, must again, perhaps after a long interval of time, vary or present individual differences of the same favourable nature as before; and these must be again preserved, and so onward, step by step. [p66]

Darwin had no trouble finding links between asexuals and self-fertilising species, and it is clear that he did not exclude asexuals from **being** species, as we see:

> It must have struck most naturalists as a strange anomaly that, both with animals and plants, some species of the same family and even of the same genus, though agreeing closely with each other in their whole organisation, are hermaphrodites, and some unisexual. But if, in fact, all hermaphrodites do occasionally intercross, the difference between them and unisexual species is, as far as function is concerned, very small. [p77f]

Darwin defined the processes that keep species distinct in even occasionally sexual organisms as the result of intercrossing. The benefits of sexual reproduction include "vigour and fertility", both germane to selection (although he doesn't explain exactly why, which resulted in extensive and ongoing debates in the following century on the evolutionary benefits of sex). But equally interesting here is that, contrary to many 20th century Darwinians, Darwin himself has no problem explaining asexual species, and even explains them, as we shall later see Eigen does, as the result of natural selection entirely.

> Intercrossing plays a very important part in nature by keeping the individuals of the same species, or of the same variety, true and uniform in character. It will obviously thus act far more efficiently with those animals which unite for each birth; but, as already stated, we have reason to believe that occasional intercrosses take place with all animals and plants. Even if these take place only at long intervals of time, the young thus produced will gain so much in vigour and fertility over the offspring from long-continued self-fertilisation, that they will have a better chance of surviving and propagating their kind; and thus in the long run the influence of crosses, even at rare intervals, will be great. With respect to organic beings extremely low in the scale, which do not propagate sexually, nor conjugate, and which cannot possibly intercross, uniformity of character can be retained by them under the same conditions of life, only through the principle of inheritance, and through natural selection which will destroy any individuals departing from the proper type. If the conditions of life change and the form undergoes modification, uniformity of character can be given to the modified offspring, solely by natural selection preserving similar favourable variations.[p79]

Darwin at the time of the sixth edition thought that the formation of species did not rely on isolation and here he takes Moritz Wagner's view to task (see below). Isolation does, he thought, make species formation easier, but he cannot agree it is required, as Wagner thought. And if the isolated population is **too** small, then isolation can in fact **prevent** speciation from occurring due to a lack of variation. The founder effect or drift through biased sampling has not occurred to him, as it later did to Weismann (see below).

> Isolation, also, is an important element in the modification of species through natural selection. In a confined or isolated area, if not very large, the organic and inorganic conditions of life will generally be almost uniform; so that natural selection will tend to modify all the varying individuals of the same species in the same manner. Intercrossing with the inhabitants of the surrounding districts will, also, be thus prevented. Moritz Wagner has lately published an interesting essay on this subject, and has shown that the service rendered by isolation in preventing crosses between newly-formed varieties is probably greater even than I supposed. But from reasons already assigned I can by no means agree with this naturalist, that migration and isolation are necessary elements for the formation of new species. The importance of isolation is likewise great in preventing, after any physical change in the conditions such as of climate, elevation of the land, &c., the immigration of better adapted organisms; and thus new places in the natural economy of the district will be left open to be filled up by the modification of the old inhabitants. Lastly, isolation will give time for a new variety to be improved at a slow rate; and this may sometimes be of much importance. If, however, an

> isolated area be very small, either from being surrounded by barriers, or from having very peculiar physical conditions, the total number of the inhabitants will be small; and this will retard the production of new species through natural selection, by decreasing the chances of favourable variations arising. [p79f]
>
> Although isolation is of great importance in the production of new species, on the whole I am inclined to believe that largeness of area is still more important, especially for the production of species which shall prove capable of enduring for a long period, and of spreading widely. Throughout a great and open area, not only will there be a better chance of favourable variations, arising from the large number of individuals of the same species there supported, but the conditions of life are much more complex from the large number of already existing species; and if some of these many species become modified and improved, others will have to be improved in a corresponding degree, or they will be exterminated. Each new form, also, as soon as it has been much improved, will be able to spread over the open and continuous area, and will thus come into competition with many other forms. Moreover, great areas, though now continuous, will often, owing to former oscillations of level, have existed in a broken condition; so that the good effects of isolation will generally, to a certain extent, have concurred. Finally, I conclude that, although small isolated areas have been in some respects highly favourable for the production of new species, yet that the course of modification will generally have been more rapid on large areas; and what is more important, that the new forms produced on large areas, which already have been victorious over many competitors, will be those that will spread most widely, and will give rise to the greatest number of new varieties and species. They will thus play a more important part in the changing history of the organic world. [p80f]

Ironically, as Kottler (1978 p285–288) noted, Darwin in the Notebooks believed that isolation **was** a *sine qua non* for speciation, in part following the views of Leopold von Buch. By this later stage, Darwin appears to have made Natural Selection the primary cause of species, requiring that variation needs to occur *in situ* as it were, and so needing larger populations to give it opportunity to do so.

Darwin notes that the structures that are useful in classifying species are often not of any adaptive value:

> Hence modifications of structure, viewed by systematists as of high value, may be wholly due to the laws of variation and correlation, without being, as far as we can judge, of the slightest service to the species. [p110]

Considering the traditional logical notions of generic and specific characters (*per genus et differentiam*), it is interesting to note that Darwin expects the specific characters to vary more than the generic, and moreover that if a character is variable in the genus between closely allied species, it is also more variable in the individual species as well (p115):

> … on the view that species are only strongly marked and fixed varieties, we might expect often to find them still continuing to vary in those parts of their structure which have varied within a moderately recent period, and which have thus come to differ. Or to state the case in another manner: the points in which all the species of a genus resemble each other, and in which they

> differ from allied genera, are called generic characters; and these characters may be attributed to inheritance from a common progenitor, for it can rarely have happened that natural selection will have modified several distinct species, fitted to more or less widely different habits, in exactly the same manner: – and as these so-called generic characters have been inherited from before the period when the several species first branched off from their common progenitor, and subsequently have not varied or come to differ in any degree, or only in a slight degree, it is not probable that they should vary at the present day. On the other hand, the points in which species differ from other species of the same genus are called specific characters; and as these specific characters have varied and come to differ since the period when the species branched off from a common progenitor, it is probable that they should still often be in some degree variable, – at least more variable than those parts of the organisation which have for a very long period remained constant. [p115]

Asking in effect why the *lex completio* does not result in no species being seen at all but rather one variable mass, Darwin replies,

> 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" [p127]

due to

(i) the fact that variation and selection take time, and may not have yet occurred;

(ii) when smaller isolated populations spread out, selection exterminates the older intermediate forms (in modern terms, when in sympatry, allopatric variations exclude the less fit older forms;

(iii) intermediates are subject to accidental extinction because they are less widely spread; and

(iv) "numberless intermediate varieties, linking closely together all the species of the same group, must assuredly have existed; but the very process of natural selection constantly tends, as has been so often remarked, to exterminate the parent-forms and the intermediate links" (p128).

When reading the *Origin* one is struck by Darwin's repeated locutions, "to the benefit of the species" or "of advantage to the species". Darwin seems to be making the classical blunder of group selectionism. However, as one reads these examples it becomes clear that Darwin is using a circumlocution for "of advantage to the members of the species that carry this trait." It is clear that he thinks that selection occurs, in the main, through competition between varieties (and of course species are just well-marked varieties as he has said above), increasing or decreasing in relative numbers as they carry beneficial or unbeneficial traits. In this usage, *species* is just a way of marking the variety that is subjected to selection, or has been so subjected and gone to fixation; it is roughly equivalent, therefore, in Darwin's mind, to the sum total of what G. C. Williams (1966) later called "evolutionary genes" – those hereditable variations that are selectable.

Darwin did not think that selection **caused** sterility and hence species, but that selection incidentally resulted in forms that were unable to breed together:

> The view commonly entertained by naturalists is that species, when intercrossed, have been specially endowed with sterility, in order to prevent their confusion. This view certainly seems at first highly probable, for species living together could hardly have been kept distinct had they been capable of freely crossing. The subject is in many ways important for us, more especially as the sterility of species when first crossed, and that of their hybrid offspring, cannot have been acquired, as I shall show, by the preservation of successive profitable degrees of sterility. It is an incidental result of differences in the reproductive systems of the parent-species. [p209]
>
> The fertility of varieties, that is of the forms known or believed to be descended from common parents, when crossed, and likewise the fertility of their mongrel offspring, is, with reference to my theory, of equal importance with the sterility of species; for it seems to make a broad and clear distinction between varieties and species. [p209f]

However, on examination, he does not think this holds generally true:

> It is certain, on the one hand, that the sterility of various species when crossed is so different in degree and graduates away so insensibly, and, on the other hand, that the fertility of pure species is so easily affected by various circumstances, that for all practical purposes it is most difficult to say where perfect fertility ends and sterility begins. I think no better evidence of this can be required than that the two most experienced observers who have ever lived, namely Kölreuter and Gärtner, arrived at diametrically opposite conclusions in regard to some of the very same forms. It is also most instructive to compare – but I have not space here to enter into details – the evidence advanced by our best botanists on the question whether certain doubtful forms should be ranked as species or varieties, with the evidence from fertility adduced by different hybridisers, or by the same observer from experiments made during different years. It can thus be shown that neither sterility nor fertility affords any certain distinction between species and varieties. The evidence from this source graduates away, and is doubtful in the same degree as is the evidence derived from other constitutional and structural differences. [p210f]

And also

> By the term systematic affinity is meant, the general resemblance between species in structure and constitution. Now the fertility of first crosses, and of the hybrids produced from them, is largely governed by their systematic affinity. This is clearly shown by hybrids never having been raised between species ranked by systematists in distinct families; and on the other hand, by very closely allied species generally uniting with facility. But the correspondence between systematic affinity and the facility of crossing is by no means strict. A multitude of cases could be given of very closely allied species which will not unite, or only with extreme difficulty; and on the other hand of very distinct species which unite with the utmost facility. …

And, reiterating the comment in the Notebook:

> No one has been able to point out what kind or what amount of difference, in any recognisable character, is sufficient to prevent two species crossing. [p215f]

Darwin notes that species are almost always intersterile, but that this is often due to the fact that as soon as this intersterility is noticed, taxonomists will rank these varieties as species:

> It may be urged, as an overwhelming argument, that there must be some essential distinction between species and varieties, inasmuch as the latter, however much they may differ from each other in external appearance, cross with perfect facility, and yield perfectly fertile offspring. With some exceptions, presently to be given, I fully admit that this is the rule. But the subject is surrounded by difficulties, for, looking to varieties produced under nature, if two forms hitherto reputed to be varieties be found in any degree sterile together, they are at once ranked by most naturalists as species. [p226]

Anyway, some obvious varieties within species are sterile together, even though they are able to breed with mutual races:

> From these facts it can no longer be maintained that varieties when crossed are invariably quite fertile. From the great difficulty of ascertaining the infertility of varieties in a state of nature, for a supposed variety, if proved to be infertile in any degree, would almost universally be ranked as a species; – from man attending only to external characters in his domestic varieties, and from such varieties not having been exposed for very long periods to uniform conditions of life; – from these several considerations we may conclude that fertility does not constitute a fundamental distinction between varieties and species when crossed. The general sterility of crossed species may safely be looked at, not as a special acquirement or endowment, but as incidental on changes of an unknown nature in their sexual elements. [p229]

So in the end, Darwin refuses to make sterility a test of species, nor even to expect that sterility will correlate with systematic affinity, summarising the arguments in that chapter thus:

> First crosses between forms, sufficiently distinct to be ranked as species, and their hybrids, are very generally, but not universally, sterile. The sterility is of all degrees, and is often so slight that the most careful experimentalists have arrived at diametrically opposite conclusions in ranking forms by this test. The sterility is innately variable in individuals of the same species, and is eminently susceptible to the action of favourable and unfavourable conditions. The degree of sterility does not strictly follow systematic affinity, but is governed by several curious and complex laws. It is generally different, and sometimes widely different in reciprocal crosses between the same two species. It is not always equal in degree in a first cross and in the hybrids produced from this cross.
>
> In the same manner as in grafting trees, the capacity in one species or variety to take on another, is incidental on differences, generally of an unknown nature, in their vegetative systems, so in crossing, the greater or less facility of one species to unite with another is incidental on unknown differences in their reproductive systems. There is no more reason to think that species have been specially endowed with various degrees of sterility to prevent their crossing and blending in nature, than to think that trees have been specially endowed with various and somewhat analogous degrees of difficulty in being grafted together in order to prevent their inarching in our forests. [p233]

In the chapter on classification, Darwin attended to the problems that this view brings with it for working naturalists, but also the problems it solves, especially in understanding the reason for the systematic affinities:

> Naturalists, as we have seen, try to arrange the species, genera, and families in each class, on what is called the Natural System. But what is meant by this system? Some authors look at it merely as a scheme for arranging together those living objects which are most alike, and for separating those which are most unlike; or as an artificial method of enunciating, as briefly as possible, general propositions, – that is, by one sentence to give the characters common, for instance, to all mammals, by another those common to all carnivora, by another those common to the dog-genus, and then, by adding a single sentence, a full description is given of each kind of dog. The ingenuity and utility of this system are indisputable. But many naturalists think that something more is meant by the Natural System; they believe that it reveals the plan of the Creator; that unless it be specified whether order in time or space, or both, or what else is meant by the plan of the Creator, it seems to me that nothing is thus added to our knowledge. Expressions such as that famous one by Linnæus, which we often meet with in a more or less concealed form, namely, that the characters do not make the genus, but that the genus gives the characters, seem to imply that some deeper bond is included in our classifications than mere resemblance. I believe that this is the case, and that community of descent – the one known cause of close similarity in organic beings – is the bond, which though observed by various degrees of modification, is partially revealed to us by our classifications. [p319f]
>
> The importance, for classification, of trifling characters, mainly depends on their being correlated with many other characters of more or less importance. The value indeed of an aggregate of characters is very evident in natural history. Hence, as has often been remarked, a species may depart from its allies in several characters, both of high physiological importance, and of almost universal prevalence, and yet leave us in no doubt where it should be ranked. Hence, also, it has been found that a classification founded on any single character, however important that may be, has always failed; for no part of the organisation is invariably constant. The importance of an aggregate of characters, even when none are important, alone explains the aphorism enunciated by Linnæus, namely, that the characters do not give the genus, but the genus gives the characters; for this seems founded on the appreciation of many trifling points of resemblance, to slight to be defined. [p321]
>
> All the foregoing rules and aids and difficulties in classification may be explained, if I do not greatly deceive myself, on the view that the Natural System is founded on descent with modification; – that the characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent, all true classification being genealogical; – that community of descent is the hidden bond which naturalists have been unconsciously seeking, and not some unknown plan of creation, or the enunciation of general propositions, and the mere putting together and separating objects more or less alike.
>
> But I must explain my meaning more fully. I believe that the *arrangement* of the groups within each class, in due subordination and relation to each other, must be strictly genealogical in order to be natural; but that the *amount* of difference in the several branches or groups, though allied in the same degree in blood to their common progenitor, may differ greatly, being due to the different degrees of modification which they have undergone; and this is

> expressed by the forms being ranked under different genera, families, sections, or orders. [p323]

Given that there is some continuing dispute over whether or not Darwin was a cladist (Mayr 1982 p209–213; 1994), it is worth noting here that Padian (1999) is right – for Darwin in this last passage classification is necessarily natural only if it matches genealogy; but it may also be represented as well in terms of grade of organisation. If it is, though, such grades must not trim away the genealogical relationships. Darwin was not a cladist[70], but he was pretty close to it. However, he recognises the practical necessity of representing overall differences in a classification scheme. It's just not the same as saying these differences are part of a **natural** classification; this point shall become significant in the argument presented in the final chapters. But even if Darwin were an "eclectic" in his approach to classification as Mayr suggests, this would be due to the fact that he had not yet completely worked out the implications of his view of species related by common descent.

Darwin then summarises the difference between the process by which things have evolved and the patterns that diagnose them – his argument is remarkably similar to Hennig's on "reciprocal illumination", which we shall examine later:

> With species in a state of nature, every naturalist has in fact brought descent into his classification; for he includes in his lowest grade, that of species, the two sexes; and how enormously these sometimes differ in the most important characters, is known to every naturalist: scarcely a single fact can be predicated in common of the adult males and hermaphrodites of certain cirripedes, and yet no one dreams of separating them. ... The naturalist includes as one species the various larval stages of the same individual, however much they may differ from each other and from the adult, as well as the so-called alternate generations of Steenstrup, which can only in a technical sense be considered as the same individual. He includes monsters and varieties, not from their partial resemblance to the parent-form, but because they are descended from it.
>
> As descent has universally been used in classing together the individuals of the same species, though the males and females and larvæ are sometimes extremely different; and as it has been used in classing varieties which have undergone a certain, and sometimes a considerable, amount of modification, may not this same element of descent have been unconsciously used in grouping species under genera, and genera under higher groups, all under the so-called natural system? I believe it has been unconsciously used; and thus only can I understand the several rules and guides which have been followed by our best systematists. As we have no written pedigrees, we are forced to trace community of descent by resemblances of any kind. Therefore we choose those characters which are the least likely to have been modified, in relation to the conditions of life to which each species has been recently exposed. Rudimentary structures on this view are as good as, or even sometimes better than, other parts of the

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[70] It would be anachronistic to apply to him terms that are only meaningful to describe a later school of thought. This is regarded as a historian's sin.

> organisation. We care not how trifling a character may be – let it be the mere inflection of the angle of the jaw, the manner in which an insect's wing is folded, whether the skin be covered by hair or feathers – if it prevail throughout many and different species, especially those having very different habits of life, it assumes high value; for we can account for its presence in so many forms with such different habits, only by inheritance from a common parent. We may err in this respect in regard to single points of structure, but when several characters, let them be ever so trifling, concur throughout a large group of beings having different habits, we may feel almost sure, on the theory of descent, that these characters have been inherited from a common ancestor; and we know that such aggregated characters have especial value in classification.
>
> We can understand why a species or a group of species may depart from its allies, in several of its most important characteristics, and yet be safely classed with them. This may be safely done, and is often done, as along as a sufficient number of characters, let them be ever so unimportant, betray the hidden bond of community of descent. Let two forms have not a single character in common, yet, if these extreme forms are connected together by a chain of intermediate groups, we may at once infer their community of descent, and we put them all into the same class. As we find organs of high physiological importance – those which serve to preserve life under the most diverse conditions of existence – are generally the most constant, we attach especial value to them; but if these same organs, in another group or section of a group, are found to differ much, we at once value them less in our classification. We shall presently see why embryological characters are of such high classificatory importance. Geographical distribution may sometimes be brought usefully into play in classing large genera, because all the species of the same genus, inhabiting any distinct and isolated region, are in all probability descended from the same parents. [p325f]

In the final chapter, the "Recapitulation and Conclusion", Darwin makes the now-famous comment about the reality of species which led so many to conclude he was a mere nominalist:

> When the views advanced by me in this volume, and by Mr. Wallace, or when analogous views on the origin of species are generally admitted, we can dimly foresee that there will be a considerable revolution in natural history. Systematists will be able to pursue their labours as at present; but they will not be incessantly haunted by the shadowy doubt whether this or that form be a true species. This, I feel sure and I speak after experience, will be no slight relief. The endless disputes whether or not some fifty species of British brambles are good species will cease. 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. This latter point will become a far more essential consideration than it is at present; 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.
>
> Hereafter we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations whereas species were formerly thus connected. Hence, without rejecting the consideration of the present existence of intermediate gradations between any two forms, we shall be led to weigh more carefully and to value higher the actual amount of difference between them. It is quite possible that forms now generally acknowledged to be merely varieties may hereafter be thought worthy of specific names; and in this case scientific

> and common language will come into accordance. 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. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species. [p371]

It will be worthwhile to look at this in detail, given the excerpts above as crossbearings on the subtlety of Darwin's views on species, and ask, has Darwin said that species are "merely artificial combinations made for convenience"? The answer is, no. He has said rather that naturalists shall be forced to treat them that way. We have seen repeatedly that Darwin did not insist *species* were unreal, merely that the *rank* was arbitrarily assigned and that we could not see if they were real on the basis of characters. The reason why the term *species* has no discoverable essence (does that imply it has a Real Essence?) is that each case is different in the biological particulars. But they are separated, he says, in that the "intergradations" between them are extinct. **That** is real enough. Darwin's definition of species is simply that they do not interbreed, or, in the case of "unisexual" organisms, that Natural Selection keeps them isolated in the "proper type" suited to the conditions of life in which they live. In this I am concurring with Kottler's and Ghiselin's conclusions; where Darwin seems to be a nominalist, he is in fact describing the problems of current taxonomic criteria, founded on creationist views of species, and so describing what species are **not** (Kottler 1978 p293f; Ghiselin 1984).

Unfortunately, the glossary to the later editions of the *Origin* does not give us a definition for species, and so we lack from Darwin the sort of epigrammatic slogan for species that so many other writers have given us.

3.3.5. After the *Origin*

After the *Origin,* Darwin is able to make some published generalisations about species. He does so in chapter 2 of the *Descent of Man* (2nd edition, 1871):

> If we consider all the races of man as forming a single species, his range is enormous; but some separate races, as the Americans and Polynesians, have very wide ranges. It is a well-known law that widely-ranging species are much more variable than species with restricted ranges; and the variability of man may with more truth be compared with that of widely-ranging species, than with that of domesticated animals.

The "well-known law" is in part of Darwin's own construction, as we have seen.

In the *Variation of Plants and Animals under Domestication* (Darwin 1998), published in 1868 and revised in 1875, Darwin discusses how species arise in nature, and proposes intersterility as a criterion of species-status.

> ... how, it may be asked, have species arisen in a state of nature? The differences between natural varieties are slight; whereas the differences are considerable between the species of the same genus, and great between the species of distinct genera. How do these lesser differences become augmented into the greater difference? How do varieties, or as I have called them, incipient species, become converted into true and well-defined species? [Vol I, p45]

Using domestic varieties as a guide to variation in nature, as he had in the *Origin*, he notes

> ...that the sterility of distinct species when crossed, and of their hybrid progeny, depends exclusively on the nature of their sexual elements, and not on any differences in their structure or general constitution. ... That excellent observer, Gärtner, likewise concluded that species when crossed are sterile owing to differences confined to their reproductive systems. [vol. II, p168f]

and in answer to the question how it is that extremely different domesticated varieties are "perfectly fertile" while closely allied species are not, he responds:

> [p]assing over the fact that the amount of external difference between two species is no sure guide to the degree of their mutual sterility, so that similar differences in the case of varieties [of domestic animals and plants – *JSW*] would be no sure guide, we know that with species the cause lies exclusively in differences in their sexual constitution. [vol. II, p172]

In a short letter to *Nature* (July 24, 1873), while discussing whether variations in brain structure could enable the evolution of instincts, Darwin noted in his own defence:

> [t]he writer of the article in referring to my words "the preservation of useful variations of pre-existing instincts" adds "the question is, whence these variations?" Nothing is more to be desired in natural history than that some one would be able to answer such a query. But as far as our present subject is concerned, the writer probably will admit that a multitude of variations have arisen, for instance in colour and in the character of the hair, feathers, horns, &c., which are quite independent of habit and of use in previous generations. It seems far from wonderful, considering the complex conditions to which the whole organisation is exposed during the successive stages of its development from the germ, that every part should be liable to occasional modifications: the wonder indeed is that any two individuals of the same species are at all closely alike.

In the end, Darwin proposed a "snowflake" theory of species – all members are alike in some ways, but they are also unique individuals. Variation occurs naturally, and it is weeded out according to how well-suited it is to the conditions of life. Species are held distinct incidentally to their being adapted to those conditions; they are real at the time, although no rank seems to be absolute, and there is no particular amount or kind of difference between them that marks out, or correlates with being, distinct species. For sexual organisms all that can be said is that they do not, in nature, interbreed (no matter whether they can be made to in captivity). He is not a nominalist, as he notes in his response to Agassiz's criticism,

> [I]f species do not exist at all, as the supporters of the transmutation theory maintain, how can they vary? And if individuals alone exist, how can differences which may be observed among them prove the variability of species?
>
> (in Lurie 1960 p297)

Darwin's reply, to Asa Gray, was

> I am surprised that Agassiz did not succeed in writing something better. How absurd that logical quibble "if species do not exist how can they vary"? As if anyone doubted their temporary existence?
>
> (Quoted in Gayon 1996 p229. Cf. also Ghiselin quoted above).

We need to note with Darwin, as with others, that there is a difference between denying that the **rank** of species has a definition, and denying that the **term** *species* has one. Darwin denies the former, but not the latter. He is not a nominalist, but a pluralist, with regards to what makes species distinct. Nevertheless, all these causes resolve down to an aversion to interbreeding in sexual organisms and differences in their sexual structures and constitutions, and selection maintaining the appropriate forms and organs for living in the conditions in which they find themselves, for asexuals. Of course, he also allowed that conditions of life can directly affect both the sexual organs and the structures of the organisms (e.g., Darwin 1998 Vol. II, p413). Nevertheless, I think we can dispose of Futuyma's and others' mischaracterisation. Darwin knew very well how to define species, given the fact of evolution.

3.3.6. Moritz Wagner and geography

Wagner (1813–1887) was a celebrated explorer and geographer, and his writings were influential. He had proposed, in opposition to Darwin's notion that species are formed from racial types through selection, that species must be isolated geographically (Wagner 1889). Mayr (1982 p562–566) discusses the reaction of Darwin and his contemporaries to Wagner's isolation model. Dismissed by Weismann and Wallace, as we shall see, the geographical isolation thesis was nevertheless adopted by the Rev. Gulick, whose work on Hawaiian landsnails (gen. *Achatinella*) led him also to claim that much evolutionary variation was due to chance (Amundson 1996; Mayr 1982 p555). Thereafter, there seemed to be two camps; those who thought that isolation was the *sine qua non* of speciation and that chance was the cause of variation between populations, and those who thought that speciation occurred equally if not entirely through the action of natural and perhaps sexual selection. After the later work of Sewall Wright had been accepted and promoted in the work of Dobzhansky during the mid-twentieth century, and following Poulton's and Mayr's coinages, this view came to be known as the *allopatric* theory of speciation, and Darwin's published view as the *sympatric* theory (Depew et al. 1995 p275-278).

3.4. After Darwin

3.4.1. Wallace's and Weismann's adaptationist definition

Alfred Russel Wallace, co-discoverer of natural selection as an agent of evolution with Darwin, never really admitted the action of anything else in evolution. It followed, therefore, that he would insist that natural selection was the agent of speciation, and hence that species are to be identified with their special adaptations.

Before he had gone public with his own evolutionism, Wallace asked if there was only an indefinable amount of difference which separated permanent varieties from species:

> If there is no other character, that fact is one of the strongest arguments against the independent creation of species, for why should a special act of creation be required to call into existence an organism differing only in degree from another which has been produced by existing laws? If an amount of permanent difference, represented by any number up to 10, may be produced by the ordinary course of nature, it is surely most illogical to suppose, and very hard to believe, that an amount of difference represented by 11 required a special act to call it into existence.
>
> (Wallace 1858; quoted in Kottler 1978 p294)

Kottler describes how Wallace's idea of species in this period involved lack of interbreeding, like Darwin's: "contact without intermixture being a good test of specific difference" (Kottler 1978 p295). In his *Darwinism* (Wallace 1889) he defined species as

> An assemblage of individuals which have become somewhat modified in structure, form, and constitution, so as to adapt them to slightly different conditions of life; which can be differentiated from allied assemblages; which reproduce their like; which usually breed together; and, perhaps, when crossed with their near allies, always produce offspring which are more or less sterile *inter se*.
>
> p167, (quoted in Romanes 1895, vol 2, p236)

He had earlier, in his *Contributions to the Theory of Natural Selection* (Wallace 1870), while discussing the numbers of species in the Malayan Archipelago of Papilionidae (a group of butterflies) discussed the principle by which he should give them the specific rank. He noted,

> One of the best and most orthodox definitions is that of Pritchard, the great ethnologist, who says, that "separate origin and distinctness of race, evinced by a constant transmission of some characteristic peculiarity of organization" constitutes a species. Now leaving out the question of "origin" which we cannot determine, and taking only the proof of separate origin, "the constant transmission of some characteristic peculiarity of organization," we have a definition which will compel us to neglect altogether the amount of difference between any two forms, and to consider only whether the differences that present themselves are permanent. The rule, therefore, I have endeavoured to adopt is, that when the difference between two forms

> inhabiting separate areas seems quite constant, when it can be defined in words, and when it is not confined to a single peculiarity only, I have considered such forms to be species. [p142]

He then discusses variation, polymorphisms, local varieties, co-existing varieties, and sub-species, and says,

> Species are merely those strongly marked races or local forms which when in contact do not intermix, and when inhabiting distinct areas are generally believed to have had a separate origin, and to be incapable of producing a fertile hybrid offspring. … it will be evident that we have no means whatever of distinguishing so-called "true species" from the several modes of variation here pointed out, and into which they so often pass by an insensible gradation. [p161]

Wallace is taking Darwin's approach to its natural conclusion, as it were. If varieties are incipient species, and species merely well-marked and more or less permanent varieties, then there is nothing *sui generis* about species as a categorical rank. In this he was followed also by August Weismann (1904), who treated species entirely as complexes of adaptations. Discussing a number of examples of series of forms that can only be arbitrarily delimited, he notes,

> All the individual members of these series are connected by intermediate forms in such a manner that a long period of constancy of forms seems to be succeeded by a shorter period of transformation, from which again a relatively constant form arises.
>
> We see, therefore, that the idea of species is fully justified in a certain sense; we find indeed at certain times a breaking up of the fixed specific type, the species becomes variable, but soon the medley of forms clears up again, and a new constant form arises — *a new species*, which remains the same for a long series of generations, until ultimately it too begins to waver, and is transformed once more But if we were to place side by side the cross-sections of this genealogical tree at different levels, we should only see several well-defined species between which no intermediate forms could be recognized; these would only be found in the intermediate strata. [Vol. II, p305]
>
> … the species is essentially a complex of adaptations, of modern adaptations which have been recently acquired, and of inherited adaptations handed down from long ago — a complex which might well have been other than it is, and indeed must have been different if it had originated under the influence of other conditions of life. [p307]

In contradiction to Nägeli, who thinks of species as "a vital crystallization" (in Weismann's words, p307), Weismann denies that there is an evolutionary force that impels species to evolve, and defends natural selection as the entirety of evolutionary mechanism. Since the major features of evolutionary groups are adaptive in their origin,

> … if the step from one species to the next succeeding one does not depend on adaptation, then the greater steps to genera, families, and orders cannot be referred to it either, since these can only be thought of as depending upon a long-continued splitting up of species. [p306]

Weismann appears to think that entire species transmutate and are changed into new species after a period of fragmentation of forms. However, he realises that species are variable:

> But of course species are not exclusively complicated systems of adaptations, for they are at the same time 'variation complexes,' the individual components of which are not all adaptive, since they do not all reach the limits of the useful or the injurious. [p307]

He recognises that selection applies to sub-organismic "vital units" (p308), and that there are "indifferent characters", or non-adaptive characters, which result as by-products, as it were, of selection for "a harmonious whole". Selection in the "germ plasm" may

> "… give rise to correlative variations in determinants next to them or related to them in any way, and that these may possess the same stability as the primary variation. This seems to me sufficient reason why biologically unimportant characters may become constant characters of the species. [*loc.cit.*]

An example of this is the vestigial hindlimbs in the Greenland whale (p313). So Weismann was not exactly the panadaptationist he is sometimes made out to be (e.g., Gould 2002 p198ff), and he allowed for the existence of neutral characters. However, he rejected outright the views of those who thought that isolation was a precondition to new species and that the characters that formed them were in any way neutral. In discussing variation, he notes (p286) that

> … there are very variable species and very constant species, and it is obvious that colonies which are founded by a very variable species can hardly ever remain exactly identical with the ancestral species; and that several of them will turn out differently, even granting that the conditions of life be exactly the same, for no colony will contain all the variants of the species in the same proportion, but at most only a few of them, and the result of mingling these must ultimately result in the development of a somewhat different form in each colonial area.

This is an early forerunner of the "founder effect" conception of the origin of new species proposed by Mayr (1954) and developed further by Hampton Carson (Carson et al. 1970; Carson 1971; 1975; Coyne 1994). What is most striking about this is that Weismann is effectively ascribing speciation in this case to stochastic sampling. This is something that, as the strict selectionist Romanes held him to be (see below), he should not have adopted. Weismann opposed, though, an exclusivist position such as that of Wagner's that **all** species had to be formed in this way.

3.4.2. Other Darwinians – Lankester, Romanes, Huxley, Poulton, Jordan

At least one of Darwin's most prominent followers, E. Ray Lankester, exceeded Darwin's published suggestion that the term "species" was arbitrary. He said that he was

> … inclined to think that we should discard the word species not merely momentarily but altogether.
>
> (Poulton 1903 p62)

Ernst Haeckel also thought this, stating in his *The Evolution of Man* (1874, third edition cited) that

> Endless disputes arose among the "pure systematizers" on the empty question, whether the form called a species was "a good or bad species, a species or a variety, a sub-species or a group", without the question being even put as to what these terms really contained and comprised. If they had earnestly endeavoured to gain a clear conception of the terms, they would long ago have perceived that they have no absolute meaning, but are merely stages in the classification, or systematic categories, and of relative importance only.
>
> (Haeckel 1883 vol 1, p115)

T. H. Huxley, who had disagreed in correspondence with Darwin over saltative evolution, likewise wrote of species (Huxley 1906 p226f) that

> Animals and plants are divided into groups, which become gradually smaller, beginning with a KINGDOM, which is divided into SUB-KINGDOMS; then come the smaller divisions called PROVINCES; and so on from a PROVINCE to a CLASS, from a CLASS to an ORDER, from ORDERS to FAMILIES, and from these to GENERA, until at length we come to the smallest groups of animals which can be defined one from the other by constant characters, which are not sexual; and these are what naturalists call SPECIES in practice, whatever they may do in theory.
>
> If in a state of nature you find any two groups of living beings, which are separated one from the other by some constantly-recurring characteristic, I don't care how slight or trivial, so long as it is defined and constant, and does not depend on sexual peculiarities, then all naturalists agree in calling them two species; that is what is meant by the word species – that is to say, it is, for the practical naturalist, a mere question of structural differences.[1]
>
> …
>
> [1] I lay stress here on the *practical* signification of "Species." Whether a physiological test between species exist or not, it is hardly ever applicable by the practical naturalist.

Huxley treats species here[71] as merely conventional definitional entities; that is, as a nominal essence. The note implies that he expects there may be some real essence in the form of physiological (i.e., reproductive?) differences, but that they are not useable by practising taxonomists. So long as there is a constant unvarying character, and a smallest diagnosable group, there is a species.

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[71] This series of lectures was collected in 1864 (my edition is Huxley 1894), but the essay was first delivered in 1863.

George Romanes, who coined the term "neo-Darwinism" to sneer at the extreme selectionist views of Wallace and Weismann[72], in his *Darwin and after Darwin* gave five definitions of species (1895 vol 2, pp229-231):

1. *"A group of individuals descended by way of natural generation from an original and specially created type"*. He calls this "virtually obsolete".
2. *"A group of individuals which, while fully fertile* inter se, *are sterile with all other individuals—or, at any rate, do not generate fully fertile hybrids*". Romanes calls this the "physiological definition" and claims that it is not entertained by any naturalist at that time, as it is incomplete.
3. *"A group of individuals which, however many characters they share with other individuals, agree in presenting one or more characters of a peculiar kind, with some certain degree of distinctness."* Romanes claims this is practically followed by all naturalists. But it is insufficient to enable a uniform standard of specific distinction, and so he adduces two more definitions, "which will yield to evolutionists the steady and uniform criterion required."
4. *"A group of individuals which, however many characters they share with other individuals, agree in presenting one or more characters of a peculiar and hereditary kind, with some certain degree of distinctness."* This merely adds hereditary characters to the previous definition.

And finally he adds one for the "ultra-Darwinians" who insist that species are formed through natural selection.

5. *"A group of individuals which, however many characters they share with other individuals, agree in presenting one or more characters of a peculiar, hereditary, and adaptive kind, with some certain degree of distinctness".*

These are the "logically possible" definitions of species, meaning by this that they include all the differentiae of the thing defined. Romanes presents something rather similar to some versions of the modern phylogenetic species concepts, but the "degree of distinctness" is still relatively vague, and relies on the judgement of the specialists. He rejects absolutely the idea that the characters which mark species from each other

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[72] Although Gould (2002 p198) ascribes this to Spencer in 1893, Romanes claims the honour in his 1895 as an earlier coinage of his own (see below).

must or even can be adaptive, and a discussion he instigated in the Biological Section of the British Association ended in

> … as complete a destruction as was possible of the doctrine that all the distinctive characters of every species must necessarily be useful, vestigial or correlated. For it became unquestionable that the same generalization admitted of being made, with the same degree of effect, touching all the distinctive characters of every "snark". [p235]

Lewis Carroll must have been pleased. Romanes then takes Wallace to task for his definition, and Weismann for his rejection of the inheritance of acquired characters (p241), which Romanes as a "proper" Darwinian had followed Darwin in defending; in fact this topic was the occasion for the "more Darwinian than Darwin" comment when he coined the terms "neo-Darwinian" and "ultra-Darwinism". He distinguished between species formed through non-hereditary influence of the environment as *somatogenetic species*, and those in which the environment makes changes to hereditable material – the germ plasm in Weismann's terms – as *blastogenetic species*. Neither term survived the rejection of neo-Lamarckism with the rise of Mendelian genetics in 1900 (Bowler 1989b).

E. B. Poulton wrote an extensive and influential essay on species (Poulton 1903) in which he coined the term *syngamy*. He noted that the fixity of species was not required by Augustine or Aquinas (itself arguable), and cites Aubrey Moore who fingers Milton as the guilty party for this doctrine, although he thinks it was due to the spirit of the age (which, as we have seen, is pretty right; the received view of the middle ages was non-historical[73]). He also cites Sir William Thistleton-Dyer as claiming that fixity was

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[73] Indications that species were not commonly thought to be fixed in that period can be found in the work of one of the translators of the *King James Bible* (1611), the Calvinist George Abbot (1562–1633), Archbishop of Canterbury. In his *A briefe Description of the whole world*, (1605), he wrote

> There be other Countries in *Africke*, as *Agtsimba* [?], *Libia interior*, *Nubia*, and others, of whom nothing is famous: but this may be said of *Africke* in generall, that it bringeth forth store of all sorts of wild Beasts, as Elephants, Lyons, Panthers, Tygers, and the like: yea, according to the Proverbe, *Africa semper aliquid apportat novi*; Often times new and strange shapes of Beasts are brought foorth there: the reason whereof is, that the Countrie being hott and full of Wildernesses, which haue in them little water, the Beastes of all sortes are enforced to meete at those few watering places that be, where often times contrary kinds haue conjunction the one with the other: so that there ariseth new kinds of species, which taketh part of both.
>
> (Nicolson 2003 p160)

I am indebted to Tom Scharle for the reference and the full quote. Andrew Criddle noted that "Agtsimba" is most likely "Agasimba" or "Agasymba", a region vaguely south of Libya (on the Usenet group talk.origins, 10 August 2003). It is noteworthy though that novel species are formed from hybridisation of extant, and presumably created, species.

Milton's culpability is hard to determine. In the *Paradise Lost*, book VII, the creation story of *Genesis* is repeated with little change, and the term used there is "kind", as it is in the Bible. Nowhere in his poetical works can I find a hint of the constancy or otherwise of species.

traceable to Bauhin (1550–1624) and Jung (1587–1657), and discusses Darwin's own views in some detail. He coined several terms to set up the discussion about species, some of which have entered into common usage (pp60–62). First, he defines groups formed by Linnaean diagnosis of forms as *Syndiagnostic*. Then, he names groups that freely interbreed as *Syngamic*, and in a privative fashion terms those that do not as *Asyngamic* (with the substantive noun forms *Syngamy and Asyngamy*). Next, he coins the term *Epigony* to mean breeding from a common parent. Finally, he provides a term for the organic forms that live in the same region *Sympatric*. Again, he uses a privative term – *Asympatric* – for those that do not. *Allopatry* had to wait for Mayr.[74]

With the technical apparatus in hand, Poulton moves from diagnosis to the underlying reality of species. He says

> Diagnosis … is founded upon the conception that there is an unbroken transition in characters of the component individuals of a species. Underlying this idea are the more fundamental conceptions of species as groups of individuals related by Syngamy and Epigony.

He argues, contrary to Darwin's views, that sterility is an effect of *Asyngamy*, not vice versa; reiterating Max Muller's and Moritz Wagner's views on *speciation*, as the topic came to be known later. Thistleton-Dyer had said that older writers employed

> … the word species as a designation for the totality of all individuals differing from all others by marks or characters which experience showed to be reasonably constant or trustworthy, as is the practice of modern naturalists. [p66]

He cites Darwin a week after the publication of the *Origin*:

> … I met Phillips, the palaeontologist, and he asked me, "How do you define a species?" I answered, "I cannot." Whereupon he said, "At last I have found out the only true definition,—any form which has ever had a species name!" [Poulton cites (Darwin 1972), vol. I, p127][75]

Similar views were later held by Tate Regan (Regan 1926), and were named by Blackwelder (1967), the "taxonomic species concept", and by Kitcher (1984) the "cynical species concept".

According to Poulton, though, species are interbreeding communities, syngamic communities. This came later to be termed, briefly (Lotsy 1931), a *Syngameon* as a neutral term for such communities, irrespective of their rank, although as Dobzhansky noted (Dobzhansky 1941 p311), Lotsy seemed to equate the syngameon with "species"

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[74] He defined it (Mayr 1942 p149) thus: "Two forms (or species) are *allopatric*, if they do not occur together, that is if they exclude each other geographically."

[75] As we see above, this anecdote occurs in Darwin's correspondence to Gray in 1857.

anyway. It underlay the gradual variation in forms from one end of a range of organisms to another, which he referred to as a transition. But while when clear this made diagnosis possible, there were cases in which it would fail: polymorphisms, seasonal dimorphisms, individual developmental adaptation (he calls it *individual modification*, and cites Baldwin), geographical races and sub-species, and artificial selection. Moreover, says Poulton, interspecific sterility is not an infallible test of specificity, because, as Darwin knew, related forms often can interbreed. Instead, sterility of hybrids is "an incidental consequence of asyngamy" (p80), of separation for a long period. Moreover, asyngamy itself is usually the byproduct of asympatry (p84), although he allowed that Karl Jordan was correct when he said that it could be due to *mechanical incompatibility* (Jordan 1905b; Jordan 1905a).[76] He also accepts Henry Bates' 1862 claim of preferential mating. All this notwithstanding, sterility is not, in his opinion, due to the action of selection. This seminal paper, republished in 1905, was greatly influential in setting up the terms, both literally and metaphorically, of the twentieth century debate over species and speciation.

Karl Jordan's paper (Jordan 1905b) seems to have had some impact on the way people discussed variation within species, and it contains the core of the biospecies concept later propounded by Mayr, who mentions Jordan as a forerunner (Mayr 1982 p272), and quotes Jordan's statement

> Individuals connected by blood relationship form a single faunistic unit in an area … the units, of which the fauna of an area is composed, are separated from each other by gaps which at this point are not bridged by anything.[77]

Jordan gave the criteria that he believed defined two organisms as being in the same or different species (p159) in the context of a discussion of the variation of physical traits in organisms that we use to establish the "blood relationships of individuals and thus the physical gaps between species". He said that individuals of two species announce themselves by having physiological differences that they always reproduce in their progeny, and by being able to live in the same region without blending into each other. He listed three criteria:

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[76] Poulton also cites an earlier paper of Jordan's, in *Novitates Zoologicae*, iii, Dec. 1896, pp518-522, to which I do not have access.

[77] Jordan (1905b p157): "Solche blutsverwandte Individuen bilden eine faunistische Eniheit in einem Gebeit …" which Jordan follows with the elided comment "zu welcher Einheit wir erfährungsgemäß alle andern Individuen des Gebeits rechnen müssen, welche ihnen gleichen", meaning roughly that we assign all individuals to these units as we empirically classify them as identical. Again, there is an epistemological element here that is overlooked. The subsequent statement Mayr quotes comes after a number of examples of this classification.

> The criteria of the *species* [he uses the Latin word "species" here – *JSW*] (= *Art*) concept are thus threefold, and each individual point is an applicable test: a species requires known traits, it does not beget descendents equally well with individuals of other species, and it does not coalesce into other species.[78]

Jordan's view seems to require not only geographical isolation, but also constancy of characters, which Mayr's later definition does not. He goes on to say that the non-coalescence (non-hybridisation) of species explains the "enormous number" of extant species, and that this is due to the internal organisation of the species (by which I take him to mean of the typical genetic structure of the species). He makes the comment that species act as if there were "*no* relationship between them, but as if they were doing business for themselves".[79]

3.4.3. Non-Darwinian ideas after Darwin

However, Darwinian ideas were not universally adopted. During the so-called "eclipse of Darwinism" period (Bowler 1983), in which neo-Lamarckian ideas overtook Darwin's mechanism of natural selection, species were often thought to be types again. Such American neo-Lamarckians as Cope and Hyatt adopted an "orthogenetic Lamarckism" in which species underwent a series of developmental changes in a kind of embryological analogy between individuals and species (Bowler 1983 p 121ff). In the period from Edward Drinker Cope's 1868 essay "On the origin of genera" through to the period immediately before the first world war, species were thought by this school to be the result of internal forces rather than selection or geographical isolation. Cope called this growth force "bathmism" while others, such as Alpheus Hyatt and Alpheus Packard, and Henry Fairfield Osborne, had other mechanisms. Osborne, in particular, adopted the Baldwin Effect as a (he thought) non-Darwinian mechanism (Bowler 1983 p131) which enabled organisms to direct their own evolution through individual adaptation, which tarred the Baldwin Effect as anti-Darwinian, or Lamarckian, for a long time to come (Turney et al. 1996). Osborne, under attack from Baldwin for saying that variation is non-random, then made the claim that there were linear variational trends that Darwinism could not account for (pp132f).

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[78] "Das Kriterium des Begriffs Species (=Art) ist daher ein dreifaches, und jeder einzelne Punkt ist der Prüfung zugänglich: Eine Art bat gewisse Körpermerkmale, erzeugt keine den Individuen andrer Arten gleich Nachkommen und verschmilzt nicht mit andern Arten." Thanks to Ian Musgrave for help with the translation.

[79] Page 160: "... als ob *nie* ein Zusammenhang zwischen ihnen gewesen, als ob jede Art für sich geschaffen ware." Italics represent emphatic spacing.

William Bateson (1894) produced a large book describing the sorts of variations that occurred from the type, in which he treated species as morphological classes, with no continuity of form between species, and hence no reason to think they varied sufficiently for Darwinian evolution to occur. Species are groups of organisms united by a common form, but there is no definite difference that divides them. He writes of what he calls "the Problem of Species":

> No definition of a Specific Difference has been found, perhaps because these Differences are indefinite and hence not capable of definition. But the forms of living things, taken at a moment, do nevertheless most certainly form a discontinuous series and not a continuous series. ...
>
> The existence, then, of Specific Differences is one of the characteristics of the forms of living things. This is no merely subjective conception, but an objective, tangible fact. This is the first part of the problem.
>
> In the next place, not only do Specific forms exist in Nature, but they exist in such a way as to fit the place in Nature in which they are placed; that is to say, the Specific form which an organism has, is *adapted* to the position which it fills. This again is a relative truth, for the adaptation is not absolute.
>
> (p2f)

For Bateson, though, form is more than a way of describing or diagnosing species, it *is* what species are – they are classes of forms. Adaptation is not relevant to the origin of these discontinuous forms, but variation is. Bateson stops short of saying that form is a causal factor in evolution, but he does say that symmetry of form and the repetition of forms (*merism* is his term for this) are causes of speciation (pp19 *et seq.*). Indeed, variation from the type (the Specific Differences) is due to a "pathological accident" (as he approvingly quotes Virchow on p75). Later, as one of the Mendelian geneticists, Bateson opposed the idea that there was genetic variation of the kind Darwinian selection required to form species.

Another Mendelian, Hugo de Vries, shortly after proposed a concept of "elementary species" as pure genetic lines in his 1904 lectures "Species and Varieties" (De Vries 1912) and in the earlier *Die Mutationstheorie* (1901). According to the Mendelian view that de Vries adopted, species in the Linnaean sense were actually comprised of a number of smaller lines of pure genetic stock:

> Species is a word, which has always had a double meaning. One is the systematic species, which is the unit of our system. But these units are by no means indivisible. … These minor entities are call varieties in systematic works. … Some of these varieties are in reality just as good as species, and have been "elevated," as it is called, by some writers, to this rank. This conception of the elementary species would be quite justifiable, and would get rid of all difficulties, were it not for one practical obstacle. The number of species in all genera would be doubled and tripled, and as these numbers are already cumbersome in many cases, the

> distinction of the native species of any given country would lose most of its charm and interest.
>
> In order to meet this difficulty we must recognize two sorts of species. The systematic species are the practical units of the systematists and florists, and all friends of wild nature should do their utmost to preserve them as Linnaeus has proposed them. These units, however, are not really existing entities; they have as little claim to be regarded as such as genera and families. The real units are the elementary species; their limits often apparently overlap and can only in rare cases be determined on the sole ground of field-observations. Pedigree-culture is the method required and any form which remains constant and distinct from its allies in the garden is to be considered as an elementary species. [p11]

De Vries came to his views through the observation of what we now know to be alloploid forms in *Oenothera lamarckiana*, the evening primrose, which de Vries had cultivated and maintained pedigrees (p17, lecture IX). He was of the view that these were straight mutations forming a single new elementary species at once. In a way, given the way alloploids occur, he was right, but his idea led fairly directly to the later views of Goldschmidt, who, like de Vries, felt that species **always**, or almost always, arose in sudden saltative leaps (see next chapter).

In the lecture discussing the evening primrose, de Vries further defines the marks of an elementary species:

> Elementary species differ from their nearest allies by progressive changes, that is by the acquisition of some new character. The derivative species has one unit more than the parent. [p253]

This meant that if the new elementary species were crossed with its parental elementary species, the progeny would be incomplete for that character (he clearly means Mendelian factor) and would therefore be unnatural (p254). Hence backcrossing would not occur in the wild or under cultivation (cf. p527). Elementary species thus do not exhibit subvarieties for they are the “real type” (p127). De Vries’ concept was fundamentally anti-Darwinian, in the sense that he rejected the idea of there being continuous variation within species on which selection could act in such a way as to form new species. In fact, he argued for his theory on the grounds that the length of time required for evolution would be noticeably shorter on his account. At that time, Lord Kelvin’s arguments against Darwinian evolution – that reasoning from the rate of cooling of the earth, evolution would need to have happened in tens not hundreds or thousands of millions of years – were still current. Rayleigh’s discovery of radioactivity as a source of planetary heat was not announced until about this time (1906), and it did not immediately filter through to the wider scientific community (see Bowler 1989a p207).

3.5. Twentieth Century

There were still Darwinians. In 1934, J. Arthur Thompson defined species extensively in the classical terms but with an emphasis on the role played by selection (Thompson 1934 vol 2, pp1333f). Thompson defines it in the context of the human species and races of man, and gives four criteria: non-trivial difference, true breeding and constancy of characters, interfertility and production of fertile offspring, and the constancy of specific characters in different environments. He says,

> To sum up: *A species is a group of similar individuals differing from other groups in a number of more or less true-breeding characters, greater than those which often occur within the limits of a family, and not the direct result of environmental or other nurtural influences. The members of a species are fertile with one another, but not readily with other species.* [p1334, italics original]

Races share some of these features, i.e., they breed true, but they are less marked than specific characters, and they may be maintained by natural and sexual selection. However, Darwinian notions of species were the exception rather than the rule for some time into the new century.

3.5.1. Lotsy and the evolution of species by hybridisation

In a work published in English (Lotsy 1916), J. P. Lotsy proposed both a definition of species and a conception of evolution. He begins by noting that the concept of species is vague:

> All theories of evolution have, until quite recently, been guided by a *vague* knowledge of what a species is, and consequently have been vague themselves. [p14]

Lotsy therefore proposes a definition based on "identity of constitution", and, citing Ray, discusses Jordan's discovery of variety within all Linnaean species. He says (p21)

> Jordan *consequently discarded morphological comparison as a criterium for specific purity* and, falling back to Ray (whom he may or may not have known) *substituted for it: nulla certior …. quam distincta propagatio ex semine.* [italics original]

From this, he says, Jordan drew the "well founded conclusion": "*The Linnaean species is no species*" (p22). Lotsy therefore proposed a term, the *Linneon*, for the product of Linnaean classification defined as "*the total of individuals which resemble one another more than they do any other individuals*" (italics original). The types contained *within* a Linneon Jordan called species, and Lotsy calls *Jordanons*, since "*[b]reeding true to type is … by itself no reliable test for specific purity*" (p23). He then gives his own, proper, definition of a species:

> *A species consists of the total of individuals of identical constitution unable to form more than one kind of gametes.* (p23)

Moreover, Lotsy proposes a genetic test:

> *Specific purity is indicated by the uniformity and identity of the F_1 generations obtained by crossing the individuals to be tested,* RECIPROCALLY. (p24)

Thus, a species is for Lotsy an operationally applicable concept. The result is three definitions of terms (p27):

> LINNEON: *to replace the term species in the Linnaean sense, and to designate a group of individuals which resemble one another more than they do any other individuals.*
>
> To establish a Linneon consequently requires careful morphological comparison only.
>
> JORDANON: *to replace the term species in the Jordanian sense, viz: mikrospecies* [sic]*, elementary species etc. and to designate a group of externally alike individuals which all propagate their kind faithfully, under conditions excluding contamination by crossing with individuals belonging to other groups, as far as these external characters are concerned, with the only exception of noninheritable modifications of these characters, caused by the influences of the surroundings in the widest sense, to which these individuals or those composing the progeny may be exposed.*
>
> To establish a Jordanon, morphological comparison alone consequently does not suffice; the transmittability of the characters by which the form was distinguished, must be experimental breeders.
>
> SPECIES: *to designate a group of individuals of identical constitution, unable to form more than one kind of gametes; all monogametic individuals of identical constitution consequently belonging to one species.*

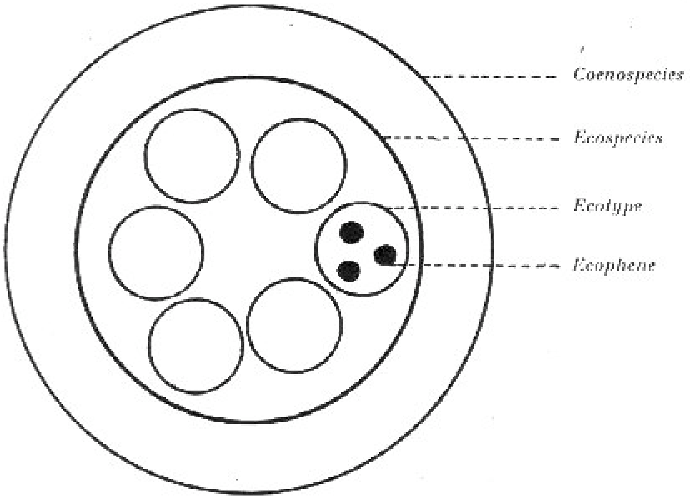
Lotsy rejects the idea of intraspecific variation in Darwin's sense, and is of the view that every homozygotic form is itself a species. It follows that every mixing of these "pure forms" is the origination of a new species if that novelty persists. Moreover, he thinks that species can be polyphyletic – they can arise more than once, because a species is formed in virtue of its "constitution", not in terms of its history (p45). Moreover, "nature primarily can make nothing but individuals" (p46), and it can secondarily group those individuals in various ways. Linneons are not natural, though – they are groupings formed by the human mind. He gives an example using human races (p47–49) supposing that even if there were four "pure races" arranged in army battalions we could divide them up in various ways, according to tattoo marks given from parent to child so that each child has two marks. If there has been no intercrossing, then although the individuals have changed, he says, the constitution would remain the same and we could arrange the progeny into those groups, but if crossings occurred, we could not assign them to the right armies.

In the forefront of his definitions, Lotsy has the Mendelian genetics then being first investigated in detail. He thinks that classification by the genetic constitution forms a kind of Lockean "real essence", which is the point of the race example. If our groupings match nature's real essence (i.e., genetic constitution), then they are natural groups. Otherwise they are not, and given the typological nature of his definition, ordinary species (i.e., what came to be called "biological species") were not natural entities. The remainder of his argument relies on Mendelian assortment forming novel varieties, as we would call them, or "allogamous forms" as he calls them (p159), from mutations.

3.5.2. Turesson – ecospecies and agamospecies

The Swedish botanist Göte Turesson undertook a series of experiments in the 1920s and early 1930s (Turesson 1922a; 1925; 1927; 1930), in which he transplanted the "ground stock" of widely distributed Swedish plants into various different habitats – dunes, seacliffs, woodlands, high altitudes and so on (Turrill 1940), p 52), and discovered that differing forms arose as a response to climate. He made a number of influential distinctions on taxa which later formed the basis for ecological species concepts (Turesson 1922b; 1929). He proposed *ecospecies* "to cover the Linnean species or genotype compounds as they are realized in nature" and related *coenospecies* (the Linnaean taxon) to ecospecies in a diagram (Figure 8, from Turesson 1922a p344).

Figure 8 – Turesson's view of coenospecies and ecospecies



Coenospecies are "the total sum of possible combinations in a genotype compound", and include one or more ecospecies, which include one or more *ecotypes*, the forms that develop in different *ecosystems* or habitat types. These are comprised of all the "reaction-types" of ecotypes that are elicited by extreme habitats, called *ecophenes*. In a similar inclusive hierarchy, he listed a genetical array of concepts – *genospecies* (the genetical construction of ecospecies), *genotypes* (Johannsen's 1909 term) and the "reaction-types" of genotypes, *genophenes*. This dual hierarchy between the ecological and genealogical was repeated later by Eldredge and Salthe (see Salthe 1985; Eldredge

1989). Turesson's "reaction-types" are in modern terms the reaction norms of genes, although the idea of a reaction norm for an ecotype appears to have been abandoned.

In one paper (Turesson 1929 p332-333), he gave succinct definitions of the major terms:

> a) *Ecospecies*: An amphimict-population the constituents of which in nature produce vital and fertile descendents with each other giving rise to less vital or more or less sterile descendants in nature, however, when crossed with constituents of any other population. …
>
> b) *Agamospecies*: An apomict-population the constituents of which, for morphological, cytological or other reasons, are to be considered as having a common origin. …
>
> c) *Coenospecies*: A population-complex the constituents of which group themselves in nature in species units of lower magnitude on account of vitality and sterility limits having all, however, a common origin so far as morphological, cytological or experimental facts indicate such and origin. …

Turesson criticises the Linnaean conception of species for not helping us to determine the *natural* limitations of species. He says that the Linnaean notion covers several senses, defined above, and that the

> … existence in nature of units of these different orders also makes it a logical impossibility to reach one standard definition of the "species". [p332]

This is, incidentally, the first use of the term "agamospecies" I have encountered, so he may very well have coined it. As far as I can tell, Turesson does not require that agamospecies cannot also be ecospecies or coenospecies.

Mayr (Mayr 1982 p277) accuses Turesson of being typological, and claims that he gives the impression of plant species being comprised of "a mosaic of ecotypes rather than as an aggregate of variable populations", but this is not how contributors to the 1940 *New Systematics* volume read him. Turrill (1940 p52) notes "He [Turesson] has clearly shown not only that the species, as usually accepted by the taxonomist, is a complex assemblage of biotypes, but also that the species population varies in its biotype composition with habitat conditions." Another contributor (Salisbury 1940 p332) also regards Turesson's approach as a populational one. In any event, it is clear that Turesson's conception of species taxa included **both** a "biological" (i.e., a genetic) and an ecological aspect. It may be that Turesson's scheme is itself typological, but its implementation and later influence is not, in itself, necessarily so.

3.5.3. Fisher and species

Ronald Fisher is famous as the founder of the modern synthesis between Mendelian genetics and Darwinian natural selection. *The Genetical Theory of Natural Selection*

(Fisher 1930) is a seminal work that introduced mathematical models to genetics and selection, and while often cited is rarely quoted. But Fisher addressed a number of questions in that book, including a rarely mentioned discussion about eugenics (Fisher was in favour of a form of eugenics, and chapters 8 through 12 are an argument for it), and one of these, almost as a parenthetical comment, is about species in the context of sexual and asexual reproduction.

The tradition in British evolutionary biology since Fisher has, on the whole, tended to treat species as names of convenience for communication, in the style of Darwin of the *Origin*, and of Locke. It is therefore somewhat surprising to note that Fisher had a realist approach to species, and one that predated the Dobzhansky 1935 article that is widely seen as kicking off the species debate of the modern era (see below). Fisher says of species that

> [t]he genetical identity in the majority of loci, which underlies the genetic variability presented by most species, seems to supply the systematist with the true basis of his concepts of specific identity or diversity. [p138]

Sexual species are, in fact, the "wild type" (p137) – the sum of all the genes in any species the great majority of which are uniform:

> … we have some reason to suppose that they [allelomorphic loci, or alleles in modern parlance – *JSW*] form a very small minority of all the loci, and that the great majority exhibit, within the species, substantially that complete uniformity, which has been shown to be necessary, if full advantage is to be taken of the chances of favourable mutations.

Fisher is here dealing with the existence of **asexual** species, as they present a problem for him, or rather, they would have if he had been (at that time) certain that any organisms existed without any sexual reproduction (the claim was not revised in the 1958 edition). In this case, he says, on p 135:

> In such an asexual group, systematic classification would not be impossible, for groups of related forms would exist which had arisen by divergence from a common ancestor. Species, properly speaking, we could scarcely be expected to find, for each individual genotype would have an equal right to be regarded as specifically distinct. And no natural groups would exist bound together by constant interchange of their germ-plasm.

Clearly, this exchange of genes in germ-plasm is the *sine qua non* of a species for Fisher. But, he goes on to say, there **would** be an analogue of species in asexuals:

> The groups most nearly corresponding to species would be those adapted to fill so similar a place in nature that any one individual could replace another, or more explicitly that an evolutionary improvement in any one individual threatens the existence of all the others.

So while Fisher is a realist about asexual groups, they are ecological groups adapted to the environment in which they find themselves, and kept distinct in virtue of selection against less-fit variants. This resolves also the problem of favourable mutations – if a novelty of value arises in an asexual lineage then it will not spread throughout the population, but instead it will replace the population. In sexual organisms that have proper species, selection maintains the identity of populations rather than of lineages, and favourable mutations can be spread by recombination of genes. But Fisher does not think that there will be many of these groups, and that if they did exist they would be those groups

> of so simple a character that their genetic constitution consisted of a single gene." [p137]

Of sexual species proper, Fisher presents the view that apart from geographical isolation, in which

> the two separated moieties thereafter evolv[e] as separate species, in almost complete independence, in somewhat different habitats, until such time as the morphological differences between them entitle them to 'specific rank'" [p139]

species are also caused to fission by what we now call sympatric speciation, because in

> many cases it may safely be asserted that no geographic isolation at all can be postulated.

A species subject to different conditions at the extremes of its range will adapt at those extremes, and hybrid forms will be disadvantageous if the migration rate is less than the rate of increase of the favourable forms in the environment to which they are adapted. Fisher champions as a mode of speciation the selectionist account of Darwin and Wallace, and yet still allows for the Wagner-style mode of allopatric isolation.

At this point we have reached the Modern Synthesis, and hence, the modern era. We are now equipped to put the modern debate into context, especially claims of conceptual novelty. To that we now turn, beginning with Theodosius Dobzhansky's discussion shortly after Fisher's book, which defined the modern species debate.

3.6. Summary and conclusions

The major break with the classical notions of species from the tradition of "universal taxonomy", as I have called it, has been allied with the Baconian insistence that instead of beginning classification with the universals, species of living things are found by a process of ascending abstraction and generalisation. Species have been understood to be propagative forms, which I have here termed the *generative conception*,[80] and in

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[80] Hull (1967 p312) did quote Aristotle (*De Anima* 415a26) on the generation of like forms. He notes that Aristotle and Theophrastus his student did deal with cases where breeding true did not result in like forms, though. This was not emphasised in Hull's later work.

various degrees and emphasis, this remained the basic conception until the modern era. For this reason, the focus has been on seed, the fructative apparatus, and the reproductive behaviours, according to then-current views on generation (Gasking 1967). The reason for a focus on species as units of biology derived from the medieval tradition and the neo-Platonic revival of the 17th century, but this was richer than the Received History supposes.

Many conceptions of species depended on, or were confounded by, the Great Chain. In one respect, a species was whatever was lowest in generality, but in another, species were conventions, or artificial divisions due to the fact that not all variant forms are to be found in a locality. Plenitudinous views expected that intermediate forms would be found, and, right into the 19th century with Macleay and Swainson, some held that while species might be discrete, there would be a continuity of form itself. There was disagreement about the level of organisation, too. Buffon thought that local forms were variants of the true species, the *premiere souche*, while Linnaeans tended to name any persistent variant form as a species. Bonnet and the early Buffon thought that specific forms were mere abstractions, a nominalist view that gradation imposed also on Lamarck and the later Charles Darwin. Even so, all these writers made use of a generative conception. Species may not exist, but if they did they were the result of heredity in reproduction of forms.

Species realists in the later biological tradition tended to be fixists, such as Cuvier and Agassiz, but of course, such a contrast was not possible until the possibility of transmutation over time was mooted. The process by which species came to be in the first instance, however, was irrelevant to how they were maintained, and a generative notion was used by realists as well, especially those who stressed form as an identifying or diagnostic factor. Most of them differed from the transmutationists as to whether the formal diagnosis was a mark of the real essence; fixists thought that the generative process **was** the reason for the form, transmutationists that the generative process (Lamarck's *feu éthéré*, for example) was the reason only for the form in a given time or place or conditions. In short, for fixists, the form gave the essence, while for transmutationists, the essence meant that the form would not remain constant. Some like Buffon and A.-P. de Candolle bridged the two camps, and declared that the real essence of species was modified to a certain degree by local conditions and hybridisation.

In the period before the *Origin*, in Britain and presumably elsewhere, species were declared to be the "property", as it were, of competent and recognised taxonomists, particularly in museums, as McOuat has discussed. A number of experts doubted the permanence of species, so that by the mid-century, several writers had made the suggestion in reputable forums that species did change.

Darwin's own views changed – at first he was quite comfortable with the standard generative notion, and made notes on the idea that it was either the physical impossibility of interbreeding, or the "repugnance" of species to interbreed in the wild. Diagnostic issues followed from the facts of the matter (the nominal essence did not give the real essence, in other words). But early on he started to toy with the notion that species were meaningless and conventional, and at the time of the *Origin* and shortly after, he seems to have taken this as his position – species are the outcomes of the evolutionary process acting on varieties, and are not real entities themselves. It doesn't seem to have made much impact on his own systematic practice, as it was not to do for anyone else either, for some time to come. The **rank** of species is arbitrary by the *Origin*. However, species could "do" things – they could even compete with each other.

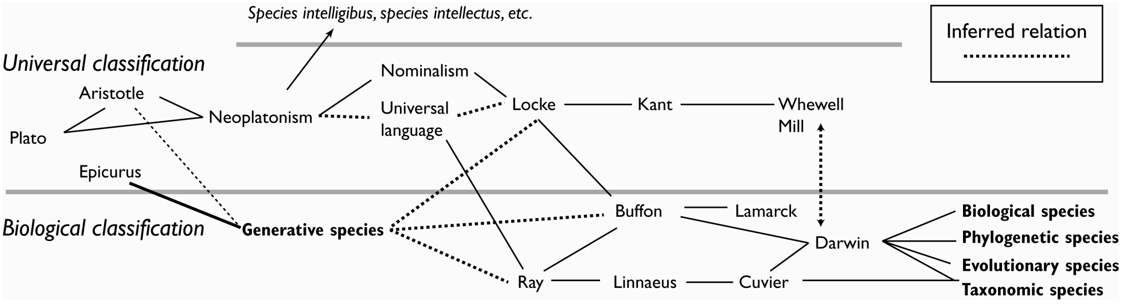
Darwin first thought that geographical isolation formed species most of the time but by the *Origin* had shifted to the view that selection against intermediates and hybrids was the major force. The geographic view of speciation, though, was to become the majority position in opposition to Darwin except for a few of his most devoted followers. However, while he may have been a conventionalist in his view of identification, he was not a nominalist, unlike several of his followers. He was a pluralist as to the degree of difference between, and causes of, species. It is significant that he thought that sexual constitutions were what caused the isolation of species, not form nor adaptive traits. Darwin's evolving views are significant, as his is the first and perhaps the most complete attempt to deal with the implications of the transmutation of species.

The adaptationists such as Wallace, Romanes and several others, however, were monists. Species were formed solely by selection. Weismann is an interesting exception here – he appears to have allowed for stochastic causes as well as deterministic selectionist causes of species. Poulton's essay, discussing these turn-of-the-20th-century arguments, effectively set the stage for the modern debates by introducing the notion of a genetic population as the boundary of species. Several contemporary writers such as Lotsy, Karl Jordan, and Turesson elaborated on that theme under the recent introduction of Mendelian genetics, with Turesson reintroducing the older notion of ecological habitat affecting form (albeit in a much more limited way). Several authors treated asexuals as a different kind of entity to species; Fisher even thinks asexuality is not a real phenomenon. This will become significant later in the century (see below).

One thing that is obvious, even at this early stage in the debates over the "species problem" is that there is a distinction to be made between "universalist" species concepts, which are intended to apply to all organisms, especially in regards to speciation mechanisms after Darwin, and those proposing more limited notions, which apply only to some sorts of organisms. In the twentieth century, most conceptions of species are universal conceptions; and the properties that mark them out are those derived from the proponent's preferred mechanisms of speciation. Biospecies are formed through the acquisition of reproductive isolating mechanisms in allopatry or sympatry according to the preference of the author. Saltationists claim that all species are formed through macromutations. Punctuated equilibrium theory later treats speciation as a rapid process followed by a period of stasis, and so species are universally delimited by this "sudden" event, thus finding the individualism thesis and the evolutionary conception of species congenial, and so on. Only a few people proposed limited conceptions, such as ecological conceptions of agamospecies, which had no general application.

We can summarise and abbreviate the history of species concepts in a diagram (figure 9):

Figure 9 – An abbreviated history of species concepts



The complexity of this history, highly simplified here, shows the limitations of the Received View.

Chapter 4. General species concepts

Let us now review the broad species concepts now in play. These are classes of concepts, which I divide into *Reproductive Isolation Concepts*, *Evolutionary Concepts*, *Phylogenetic Concepts*, *Ecological Concepts*, and a trashcan categorical of *Other Concepts*.

4.1. Reproductive isolation species

> They opened Buffon again and went into ecstasies at the peculiar tastes of certain animals.
>
> …
>
> They wanted to try some abnormal mating.
>
> …
>
> They made fresh attempts with hens and a duck, a mastiff and a sow, in the hope that monsters would result, but quite failing to understand anything about the question of species.
>
> This is the word that designates a group of individuals whose descendants reproduce, but animals classified as different species may reproduce, and others, included in the same species, have lost the ability to do so. (Flaubert 1976 p87)[81]

The notion that species are kinds of organisms delineated not by the decisions of the classifiers but by the reproductive behaviours and results of the organisms themselves is an old one. As we have seen, it was suggested as part of John Ray's definition in 1688, and also by Buffon in 1748. To a greater or lesser degree it has been a component of nearly all species concepts since Linnaeus (his sexual system implicitly required reproductive isolation), and even now, it is a key component (Cracraft 2000) of phylogenetic species concepts and most other operational definitions.

The generative conception of species has been applied to living beings effectively back to Epicurus and the neo-Platonists. That is to say, there has **always** been a requirement not only of constancy of form, but of the reproduction of form, in definitions of living species. This is surprising, since the implication or tacit assumption of many discussions, such as Mayr's (1982) or Hull's (1965; 1988c), has been that species had been for much of the history of the concept arid definitional constructs based on "essences". There can be no doubt that essence **has** played a role in species concepts. However, at least since Locke there has always been a tacit distinction between the **real** essence of a species (that is, what causes a species to **be** a species, its "real constitution") and the **nominal** essence (that is, how we know the species, describe it,

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[81] Thanks to Neil Thomason for bringing this passage to my attention.

and apply a name to it).[82] It is not clear that "essence" in these cases plays a definitional role – the Real Essence is not, by definition, definable.

The most well known reproductive isolation concept, the class of which we shall call for brevity "isolation concepts", is of course Ernst Mayr's biological species concept, or *biospecies*, and we shall look at this. However, Dobzhansky introduced the idea into the Synthetic debate; so let us now examine his views.

4.1.1. Dobzhansky's definition

Theodosius Dobzhansky was perhaps the most significant of all the synthesists through the middle of the 20th century. He introduced Sewall Wright's ideas on drift into the synthetic orthodoxy (often to considerable opposition), and his work on the laboratory and field genetics of *Drosophila* spp. revolutionised the field (cf. Depew et al. 1995 p291–297, 300–302).

Dobzhansky published a paper (1935), later substantially included in the chapter on species in his *Genetics and the Origin of Species* (Dobzhansky 1941), which discussed Lotsy's (1931) revision of Poulton's (1903) notion of syngamy as the foundation for a genetic population: "an habitually interbreeding community of individuals" (Dobzhansky 1941 p311). Dobzhansky says of the syngameon approach to species that it applies only to panmictic populations of organisms, and which, although attractive in its simplicity, is therefore inapplicable in the case of many species that are divided into reproductively separated populations. He proposes instead to base specific rank on the existence of reproductive isolating mechanisms, and provides a revision to Lotsy's definition:

> … a species is a group of individuals fully fertile inter se, but barred from interbreeding with other similar groups by its physiological properties (producing either incompatibility of parents, or sterility of the hybrids, or both).
>
> (Dobzhansky 1935 p353; cf. also Dobzhansky 1941 p312)

The **rank** *species* is something that arises in evolution when continuity of reproduction becomes discontinuous:

---

[82] Hull has noted (in correspondence) that it is ahistorical and whiggist in turn for historians such as myself to apply current standards to the Received Historians of the 1960s; he, Mayr and Cain had what scholarly resources were then available. In large part due to their work, later research has identified the "missing links", and I am certain later work will overturn some of the claims made in this and other modern work too. It should not be thought that I am criticising him or Mayr, etc., for failing to take into account later scholarship.

> Considered dynamically, the species represents that stage of evolutionary divergence, at which the once actually or potentially interbreeding array of forms becomes segregated into two or more separate arrays which are physiologically incapable of interbreeding.
>
> (Dobzhansky 1935 p354)

By "array of forms", Dobzhansky can be interpreted as meaning either diagnostic morphs, as Mayr does (below), or as the types within a population that affect reproductive isolation. His discussion makes it clear that he does not intend "form" in an essentialistic sense, I believe, but in a causal sense. In the 1935 paper, he treats reproductive isolation in terms of physiological differences – this is the sense I interpret him to mean by "form", although he may have equivocated on the distinction between diagnostic and causal structures, as many did before and after him.

He had noted in the *Genetics and the Origin of Species* the taxonomic definition (of an "affable taxonomist" – Regan? – that species are what competent systematists consider to be a species, p310), and puts this failure to deliver a universal definition

> … that would make it possible to decide in any given case whether two given complexes of forms are already separate species or are still only races of a single species

down to the general method of species formation,

> … through a slow process of accumulation of genetic changes of the type of gene mutations and chromosomal reconstructions. This premise being granted, it follows that instances must be found in nature when two or more races have become so distinct as to approach, but not to attain completely, the species rank. The decision of a systematist in such instances can not but be an arbitrary one. [p310f]

In short, evolution makes it impossible to determine if species rank has been reached. Nevertheless, the rank itself is real enough – it is the attainment of complete separation. He also notes (Dobzhansky 1941 p320f), that

> [w]e find aggregations of numerous more or less clearly distinct biotypes, each of which is constant and reproduces its like if allowed to breed. These constant biotypes are sometimes called elementary species, but they are not united into integrated groups that are known as species in the cross-fertilizing [i.e., sexual – *JSW*] forms. The term "elementary species" is therefore misleading and should be discarded.

It seems Dobzhansky was influential in this regard, because de Vries' term did largely disappear from the debate after this. He notes that biotypes can be cross-specific, and even cross-generic, and that

> [w]hich one of these ranks is ascribed to a given cluster is, however, decided by considerations of convenience, and the decision is in this sense purely arbitrary. In other words, the species as a category which is more fixed, and therefore less arbitrary than the rest, is lacking in asexual and obligatorily self-fertilizing organisms. …

> The binomial system of nomenclature, which is applied universally to all living beings, has forced systematists to describe "species" in the sexual as well as in the asexual organisms. Two centuries have rooted this habit so firmly that any thorough reform will meet with determined opposition. Nevertheless, systematists have come to the conclusion that sexual species and "asexual species" must be distinguished ... . In the opinion of the writer, all that is saved by this method is the word "species". A realization of the fundamental difference between the two kinds of "species" can make the species concept methodologically more valuable than it has been.

In the 1951 edition (Dobzhansky 1951 p275), he replaces the final sentence with

> As pointed out by Babcock and Stebbins ... , "The species, in the case of a sexual group, is an actuality as well as a human concept; in an agamic complex it ceases to be an actuality."

He also begins in that edition to discuss issues of typological thinking, under the influence of Mayr, in the chapter on populations, races and subspecies, where he notes (p268f)

> [t]he classical race concept [of human races – *JSW*] was typological. …
>
> Typology is at the bottom of the vulgar notion that any so-called Negro in the United States … has a basic and unremediable Negroid nature, just as any Jew partakes of some Jewishness, etc. There are no Platonic types of Negroidness or Jewishness or of every race of squirrel or butterflies. Individuals are not mere reflections of their racial types; individual differences are the fundamental biological realities.

There is little hint of discussions of typology or essentialism in the earlier works. Dobzhansky deals extensively with variation within populations – it is the *raison d'être* of the book, and so it might be a case of the wood not needing to be specified when the trees are so well described. By 1970, though, he is well in line with Mayr's program.

4.1.2. After Dobzhansky – the beginnings of the modern debate

At the time of the modern synthesis, announced in Huxley's book by that title in 1942, there was little dispute amongst those involved that species were real enough, but there was a wide range of opinion about what that meant. Darlington, for example (1940), explicitly appealed to Ray's dictum (in Latin) that to sort living beings into species we need no more than "*distincta propagatio ex semine*" (p137) but that

> [t]here are many kinds of species and many kinds of discontinuities between species. [p158]

He noted that

> We feel we ought to have a 'species concept'. In fact there can be no species concept based on the species of descriptive convenience that will not ensnare its own author so soon as he steps outside the group from which he made the concept. The only valid principles are those that we can derive, not from fixed classes but from changing processes. To do this we must go beyond the species to find out what it is made of. We must proceed (by collaboration) to examine its chromosomal structure and system of reproduction in relation to its range of variation and

> ecological character. From them we can determine what is the genetic species of Ray, the unit of reproduction, a unit which cannot be used for summary diagnosis, but which can be used for discovering and relating the processes of variation and the principles of evolution. [p159]

In contrast, Julian Huxley in his introduction to *The New Systematics* (Huxley 1940 p16ff), argues that Dobzhansky's 1937 definition "goes far beyond the facts". Huxley notes the constancy of cross-fertilisation among plants in particular, and says that therefore "Dobzhansky's definition is untrue, or, if true, taxonomic practice must be so re-cast as to rob the term species of its previous meaning" (p17). Muller's contribution to that volume (Muller 1940) agrees – there is no fixed rank dividing species from varieties or races (p258), although

> … divergence goes on very differently, and much more freely, between those which can and do cross, and it is therefore justifiable and useful, even though difficult, to make the species distinction, if it is made in such a way as to correspond so far as possible with this stage of separation. At the same time it must be recognized that the species are in flux, and that an adequate understanding of their relationships can be arrived at only on the basis of an understanding of the relationships between the minor groups and even between the individuals, supplemented by the study of the differences found through observations on the systematics of the larger groups.

In the book announcing the synthesis, Huxley later criticised Dobzhansky for underplaying the difficulties that a simple intersterility criterion encountered, particularly in plants.

> The dynamic point of view is an improvement, as is the substitution of incapacity to exchange genes for the narrower criterion of infertility: but even so, this definition cannot hold, for it still employs the lack of interbreeding as its sole criterion. "Interbreeding without appreciable loss of fertility" would apply to the great majority of animals, but not to numerous plants. In plants there are many cases of very distinct forms hybridizing quite competently even in the field. To deny many of these forms specific rank just because they can interbreed is to force nature into a human definition, instead of adjusting your definition to the facts of nature. Such forms are often markedly distinct morphologically and do maintain themselves as discontinuous groups in nature. If they are not to be called species, then species in plants must be deemed to differ from species in animals in every characteristic save sterility...
>
> (Huxley 1942 p162f)

He gives his own criteria a few pages later, after determining that single-criterion definitions are useless: (p164f)

> In general, it is becoming clear that we must use a combination of several criteria in defining species. Some of these are of limiting nature. For instance, infertility between groups of obviously distinct mean type is a proof that they are distinct species, although once more the converse is not true.
>
> Thus in most cases a group can be distinguished as a species on the basis of the following points jointly: (i) a geographical area consonant with a single origin; (ii) a certain degree of constant morphological and presumably genetic difference from related groups; (iii) absence

> of intergradation with related groups. ... Our third criterion above, if translated from the terminology of the museum to that of the field, may thus be formulated as a certain degree of biological isolation from related groups.

After discussing freely hybridising groups, sympatric ecological forms, plants, polyploidy[83] and asexuality, he notes (p167):

> Thus we must not expect too much of the term species. In the first place, we must not expect a hard-and-fast definition, for since most evolution is a gradual process, borderline cases must occur. And in the second place, we must not expect a single or a simple basis for definition, since species arise in many different ways.

The new geneticists tended, then, towards an eliminativist view on species, in what they perceived was the tradition of Darwin – sure, the lineages split and this was real, but the rank of the splitting was manifold and had no universally common criteria that could be recognised. There was a division in the way the synthesis Darwinians approached species, which can be traced back to Darwin's own published ambiguity on the subject. Into this ambiguity of opinion came Ernst Mayr.

4.1.3. Ernst Mayr and the biospecies concept

Mayr was a German ornithologist who had left Germany well before the war, and came to America (Hull 1988c p66f) and to the American Museum of Natural History and then to Harvard, after spending a number of years in New Guinea and the Solomon Islands studying bird populations and distributions. He was motivated to address the "species problem" because of the publication of another book, opposed to Dobzhansky's approach, by Richard Goldschmidt (1940), who became Mayr's *bête noire* for many years to come. Goldschmidt proposed that species evolved in a single step, through macromutations involving chromosomal repatterning forming "hopeful monsters" (pp390–393; it should be clear now that the term "monster" here refers to a sport or sudden variation from the type) in what is often called "saltation" (i.e., the opposite of *natura non facit saltum* quoted by Darwin). Goldschmidt repeatedly referred to species being separated by "bridgeless gaps" (c.f. p143), a term he took from Turesson (1922b p100), ignoring the fact that Turesson then went on to give a Darwinian account of species formation. Goldschmidt rejected the Darwinian idea

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[83] *Polyploidy* is the state of having three or more complete sets of chromosomes, in contrast to the usual state of diplody in sexual organisms. *Alloploidy* occurs when hybrids are formed through the fertilisation of gametes (sex cells) across species. It is usually also polyploidy, in which case it is called allopolyploidy. In plants, fertile individuals often result when chromosomes are duplicated and then separate to form symmetrical diploid chromosome sets. If the hybrid is significantly different from the parental populations, it will not interbreed with them, or will interbreed incompletely, so that eventually the novel karyotype (chromosomal type) will breed true with itself but not with either parental type. Speciation can be achieved in one or only a few generations this way (Grant 1975 p431ff).

that subspecific races were incipient species entirely, which seems to have motivated Mayr's ire and to have informed his allopatric account of speciation later.

Mayr was invited to give a series of talks on speciation as part of the Jesup Lectures in 1941 at Columbia University's Zoology Department. He was later invited to publish sufficient material to fill an entire volume for Columbia University Press after the other lecturer, Edgar Anderson, fell ill (p xvii, of the new Introduction to the 1999 reissue of his 1942). The result was the single most widely referred to volume of the synthesis.

Basically this work is a discussion at length of the modes of speciation according to the best knowledge of the day, and much of what Mayr discussed remains valid. In the case of "ring-species" for example, his discussions remain the canonical ones (pp 180–185). He also introduced several terms, including *allopatry* (p149), and *sibling species* (p151) which have worn well. But for our purposes, the most important aspect of the book is that here Mayr popularised the definition of species he had already given in his (Mayr 1940):

> A species consists of a group of population which replace each other geographically or ecologically and of which the neighboring ones intergrade or interbreed wherever they are in contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers.
>
> Or shorter: Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups. [p120]

Mayr contrasted this with the "typological" conceptions of taxonomy at the time, especially the "morphological species concept" as Mayr called it (for the first time, so far as I can tell), as well as the "practical species concept" (a version of Regan's definition), the "genetic species concept" (homozygous populations, which he attributes to Lotsy), and one based on sterility. He called it the "biological species concept"; and so the proliferation of general "species definition" names began. Mayr included Dobzhansky's definition under this rubric, but says of it,

> [t]his is an excellent description of the process of speciation, but not a species definition. A species is not a stage of a process, but the result of a process. (p119).

Hence, he proposed the definition above as a practical compromise, allowing the systematist the judgement call, since (as is noted later by critics of the concept) one cannot use reproductive isolation as a test in many cases, not least in allochronic and allopatric populations. Further,

> [t]he application of a biological species definition is possible only in well-studied taxonomic groups, since it is based on a rather exact knowledge of geographical distribution and on the certainty of the absence of interbreeding with other similar species. (p121)

Moreover, while it works for "bisexual organisms" (sexual species), it fails, he notes for "aberrant cases" like protozoans and plants which are either unisexual (asexual) or freely hybridising (p122). The remainder of the book discusses speciation processes, and Mayr presents a Wagnerian view that geographical isolation is a precondition for the formation of new species (pp154–185). Sympatric species are reproductively isolated absolutely ("*otherwise they would not be good species*", p149, italics original), but the gaps that separate allopatric species are "*often gradual and relative, as they should be, on the basis of the principle of geographic speciation*" (*loc. cit.*). He considers sympatric speciation as a possibility, but concludes

> Darwin thought of individuals when he talked of competition, struggle for existence among variants, and survival of the fittest in a particular environment.[[84]] Such a struggle among individuals leads to a gradual change of populations, but not to the origin of new groups. It is now being realized that species originate in general through the evolution of entire populations. If one believes in speciation through individuals, one is by necessity an adherent of sympatric speciation, the two concepts being very closely connected. However, fewer and fewer situations are interpreted as evidence for sympatric speciation, as it is realized more and more clearly that reproductive isolation is required to make the gap between two incipient species permanent and that such reproductive isolation can develop only under exceptional circumstances between individuals of a single interbreeding population. [p190]

This has a whiff of circularity. Mayr defines species as reproductively isolated populations formed in allopatry and absolutely distinct in sympatry. He then claims that sympatric variations cannot form reproductively isolated species because species are formed in allopatry since sympatric "species" have to be absolutely isolated. Of course, there is a lot more to it than this, and Mayr brings in all sorts of impressive empirical evidence, so the charge of plain circularity, once made, must be dismissed. However, this means that the strength of the biological species concept rests **entirely** on the absence of plausible **empirical** reasons to believe that reproductive isolation does not occur in sympatric populations. All it would take to undercut this definition of species, of course, or at any rate Mayr's argument in its favour, is to find an unambiguous case of sympatric speciation. There is a case – cichlid fishes in various lakes in Africa, for instance, where Mayr wonders if these "species flocks" are evidence

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[84] In fact, Darwin **explicitly** talked of selection and the struggle for existence as occurring between species, as we have seen.

for "explosive" sympatric speciation (p215). He rejects the idea on the grounds that the closest relatives of each species are not sympatric.[85]

Finally, Mayr considers the factors that cause species, since species are the "effect" of a process. He divides them into internal factors, such as genetic mechanisms, mutation rates, and the like, and external factors. Then he lists a number of subcategories, isolating mechanisms: geographical barriers that restrict random dispersal, ecological barriers, ethological factors, mechanical factors, and "genetic" and physiological factors (p237f).

A case Mayr does not insist on allopatry for is what he calls "instantaneous sympatric speciation" (p190ff), such as via polyploidy (the duplication of chromosomes and possible subsequent reduction to a diploid form of differing composition to the parental species), self-fertilisation, parthenogenesis and so on, but says this is "apparently rare, even where it is hypothetically possible" (p192).[86]

In later publications, Mayr introduced the notion of species being "non-dimensional"[87]:

> Noninterbreeding between populations is manifested by a gap. It is this gap between populations that coexist (are sympatric) at a single location at a given time that delimits the species recognized by a naturalist. Whether one studies birds, mammals, butterflies, or snails near one's home two, one finds species clearly delimited and sharply separated from all other species. This demarcation is sometimes referred to as the species delimitation *in a non-dimensional system* (a system without the dimensions of space and time).
>
> (Mayr 1970 p14f, italics original)

He also adds the distinction between the "species category" and the "species taxon" – the former "designates a given rank in a hierarchic classification" (p13), while the taxon is

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[85] Recent work has (unfortunately for Mayr) shown otherwise (Albertson et al. 1999; Mazeroll et al. 1995; Salzburger et al. 2002; Stauffer et al. 2002). Schilthuizen (2000) gives an excellent summary of recent work.

[86] Again, recent work has found sufficient examples, mostly in plants and other gamete broadcasters, to establish this as a real process (Aldasoro et al. 1998; Chepurnov et al. 2002; Dowling et al. 1997; Lee, Mummenhoff et al. 2002; Ramsey et al. 1998).

[87] According to Chung (2003 p285), Mayr first began to discuss the dimensionality of species in an address in 1946 (Mayr 1946), where he described the Linnaean conception as having no dimensions. Otherwise his tone is, as Chung remarks, fairly neutral on the difference between the "morphological" species concept and the "biological", "polytypic" species concept at that time. Chung traces Mayr's emerging view of species concepts as differing in their typology and populational nature from 1953 (Mayr et al. 1953) through to 1959 (Mayr 1959) and concludes that he discovered the typological aspect of the prior conceptions at around this time (especially in his 1955).

> ... the concrete object of classification. Any such group of populations is called a *taxon* if it is considered sufficiently distinct to be worthy of being formally assigned to a definite category in the hierarchical classification. *A taxon is a taxonomic group of any rank that is sufficiently distinct to be worthy of being assigned to a definite category.* [p14, italics original]

By the 1963 version, the biological species as defined by Mayr has become a reproductive community, an ecological unit, and a genetic unit:

> … species are reproductive communities. The individuals of a species of animals recognize each other as potential mates and seek each other for the purpose of reproduction. A multitude of devices insure intraspecific reproduction in all organisms … . The species is also an ecological unit that, regardless of the individuals composing it, interacts as a unit with other species with which it shares the environment. The species, finally, is a genetic unit consisting of a large, intercommunicating gene pool, whereas the individual is merely a temporary vessel holding a small portion of the contents of the gene pool for a short time
>
> (Mayr 1963 p21)

and by 1970 the definition has changed to read:

> *Species are groups of interbreeding natural populations that are reproductively isolated from other such groups.*
>
> (Quoted in Mayr 1970 p12, italics in original)

Gone is the phrase "actually or potentially" from the 1942 edition; Mayr now thinks that it is only in sympatry ("with respect to sympatric and synchronous populations", p13) that we can tell for sure that two organisms are distinct species. The definition is "biological", he says,

> ... not because it deals with biological taxa, but because the definition is biological. It utilizes criteria that are meaningless as far as the inanimate world is concerned.
>
> When difficulties are encountered, it is important to focus on the basic biological meaning of the species: **A species is a protected gene pool. It is a Mendelian population that has its own devices (called isolating mechanisms) to protect it from harmful gene flow from other gene pools.** Genes of the same gene pool form harmonious combinations because they become coadapted by natural selection. Mixing the genes of two different species leads to a high frequency of disharmonious gene combinations; mechanisms that prevent this are therefore favored by selection.
>
> (Mayr 1970 p13, emphasis added)

The bolded text above is surprising. From being the "effect" of a process in 1942, Mayr now treats species as a **mechanism** of protecting gene pools. Moreover, selection now plays a role in "protecting" species; previously species were not formed through selection, and reproductive isolation was a side-effect of geographical isolation. Still, isolating mechanisms are still "potentially or actually" active in sympatry and have to be intrinsic mechanisms of the organisms, and not, for example, "geographic or any other purely extrinsic isolation" (p56).

Mayr's view of species seems not to have changed much since the 1970 volume.[88] He repeats it in several places (e.g., Mayr 1976; 1985; 1988; 1992; 1996). To summarise his present position, let us consider the latest paper (Mayr 1996), where he claims that species are concrete describable objects in nature, that they are reproductively isolated even when there is "leakage of genes" and that the biological species concept (now abbreviated as BSC) is based on the properties of populations. Although Mayr has always stressed the populational nature of species as a result of his insistence on genetic and morphological polytypy in species, over time there is an increasing emphasis on "populational thinking" in opposition to "essentialism" in his works. For instance, in the introduction to his history of biology (Mayr 1982 p45–47), he discussed this, citing Hull and Ghiselin (Hull 1976; Ghiselin 1974b), dividing western thinking into two phases. The first phase was essentialism deriving from Plato, and the second, population thinking beginning with Leibniz's theory of monads but really taking root with the British animal breeders and Darwin and his contemporary systematists in Britain. One can take issue with the claim for Leibniz (as a Great Chain thinker, the sort of variation he admitted was scalar rather than distributional), and wonder why de Quetelet has been overlooked as the source of populational thinking and instead been called an essentialist (see, for instance, Krüger et al. 1990). Most oddly, what is missing here and elsewhere, is Karl Popper. Popper had attacked what he called "methodological essentialism" as a malign heritage from Plato (Popper 1957b; 1960; 1957a), in particular in his *Poverty of Historicism*, §10, where he set up *nominalism* – the doctrine that universal terms are mere labels attached to sets of things – opposed to "realism", or "idealism", which he renames as *essentialism*. Popper ascribes to Aristotle the problem this introduces into science:

> The school of thinkers whom I propose to call *methodological essentialists* was founded by Aristotle, who taught that scientific research must penetrate to the essence of things in order to explain them. Methodological essentialists are inclined to formulate scientific questions in such terms as 'what is matter?' or 'what is force?' or 'what is justice?' and they believe that a penetrating answer to such questions, revealing the real or essential meaning of these terms and thereby the real or true nature of the essences denoted by them, is at least a necessary prerequisite of scientific research, if not its main task. *Methodological nominalists*, as opposed to this, would put their problems in such terms as 'how does this piece of matter behave?' or 'how does it move in the presence of other bodies?' For methodological nominalists hold that the task of science is only to describe how things behave, and suggest that this is to be done by freely introducing new terms wherever necessary, or by re-defining old terms wherever necessary while cheerfully neglecting their original meaning. For they regard *words* merely as *useful instruments of description*. (Popper 1960 p28f)

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[88] Apart from flying an "ecological niche" variant in the 1982 *Growth of Biological Thought*, addressed below.

Popper's sympathies are clearly with the nominalists. Through Hull's seminal essay on essentialism in taxonomy (Hull 1965), Popper's distinction came to be widely accepted amongst taxonomists, and Mayr may be influenced either directly or indirectly by Hull.[89] It is unclear whether he was directly influenced by Popper's *Poverty*, but that work was a *cause célèbre* in its day, and since Mayr and Popper were both leading German-speaking academics in the English-speaking world, it would be surprising if someone as erudite as Mayr had not at least heard of Popper and his ideas.[90] In the 1982 history, Mayr cites Popper only for issues of theory falsification. Why is this? I conjecture that it may be due to the prominence given to Popper by cladists such as Farris, Wiley, Patterson, Platnick and Nelson as a justification for cladistic senses of naturalness (cf. Hull 1988c p129, 171, 197, 237–239, 247, 251–253, 268, and references cited there).[91] In any event, this is beyond our scope here; the point being that Mayr is assuming a nominalistic approach to species; the term (as a category) is a useful way of organising real, concrete objects (the taxa). He particularly criticises another philosopher, Philip Kitcher (1989), for instance, for failing to appreciate the difference between biological populations and classes of non-living (inanimate) objects (Mayr 1996 p266f).

Of particular note here is Mayr's version of the history of species concepts. He gives it again in this paper, but he has given various forms of it in his other writings (Mayr 1957; 1970; 1982; 1991). According to his version (Mayr 1996 p266f),

> [t]he biological species concept developed in the second half of the 19th century. Up to that time, from Plato and Aristotle until Linnaeus and early 19th century authors, one simply recognized "species," eide (Plato), or kinds (Mill). Since neither the taxonomists nor the philosophers made a strict distinction between inanimate things and biological species, the species definitions they gave were rather variable and not very specific. The word 'species' conveyed *the idea of a class of objects, members of which shared certain defining properties.* Its definition distinguished a species from all others. Such a class is constant, it does not change in

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[89] Hull (pers. comm.) tells the story that, as a graduate student, he delivered the talk on which this paper was based in front of Popper, and handed it in at the end of semester. Popper took it on himself to send the talk to the *British Journal for the Philosophy of Science* without Hull's knowledge, and the author had to ask for it to be returned for revision. Many of his conclusions were not strictly in line with Popper's own ideas, but Popper apparently never read the published work, and so Hull never came under Popper's withering attack himself.

[90] Polly Winsor believes, after discussing the issue with various of Mayr's students and associates, that Mayr did **not** know Popper's work until his attention was drawn to it by Hull's 1965 paper. Mayr does cite Popper in his later work (Mayr 1997 p59f) where he explicitly mentions Popper's attitude to words and essentialism, but prior to that, his ideas on typology seem to be his own, as Winsor calls it, his "dragon". According to Winsor, Mayr first used the term "essentialism" as a synonym for "typology" in 1968 (Winsor in press).

[91] Nelson and Platnick's focus on Popper is due to the work of Walter Bock (1974, Nelson, pers. comm.) although Hull (pers.comm.) recalls suggesting Popper to one of them.

> time, all deviations from the definition of the class are merely "accidents," that is, imperfect manifestations of the essence (eidos). Mill in 1843 introduced the word 'kind' for species (and John Venn introduced 'natural kind' in 1866) and philosophers have since used the term natural kind occasionally for species... [italics original]

In many particulars, this account is incorrect, as the preceding chapters show. A distinction **was** made in practice between living and nonliving things by many authors before the nineteenth century, Locke introduced the term "kind" for species, and typological accounts permitted variation in the "essential" characters of type to quite a degree before members of the type became monsters. Mayr seems insistent on finding "forerunners" to his own preferred conception. On the next page, he writes, of "the morphological, or typological species concept":

> Even though this was virtually the universal concept of species, there were a number of prophetic spirits who, in their writings, foreshadowed a different species concept, later designated [by Mayr, as it happens – *JSW*] as the *biological species concept* (BSC). The first among these was perhaps Buffon (Sloan 1987), but a careful search through the natural history literature would probably yield quite a few similar statements.

This tendency to seek precursors for a favourite personal view is known among historians as the "Whig interpretation of history" (Butterfield 1931) or as "presentism", or "creeping precursoritis";[92] it is the importation of modern views into the past. At least since Collingwood (1946), such approaches to history as the progressive leading-up to the modern day or some ideal state have been viewed askance by historians:

> Bach was not trying to write like Beethoven and failing; Athens was not a relatively unsuccessful attempt to produce Rome; Plato was himself, not a half-developed Aristotle [p329]

and, we might add, the writers on species in the period in question were not precursors to Ernst Mayr.[93] There has **always** been a "biological" (reproductive) component to discussions of species as applied to the living world, which I have called the "generative" notion of species. Moreover, few of the writers adduced by Mayr as forerunners actually are presenting anything much like his view, as most of them include a clear morphological component in their conceptions. Nevertheless, Mayr's

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[92] I am indebted to Neil Thomason for this phrase.

[93] Although this may sound harsh, Mayr **has** referred to his "precursors" as "prophetic spirits" (Mayr 1996 p269), noting "how tantalizingly close to a biological species concept some of the earlier authors had come" (Mayr 1982 p271), and claimed that "Buffon understood the gist of it" and the early Darwin also (Mayr 1997 p130), thus claiming authoritative precursors. Hull (1988c p372–377) discusses the role precursors play in scientific histories. One function for precursors is to give legitimacy to the views of the modern scientist and deflect criticism to dead white males. Similar things happened with Galileo, and also with the "rediscoverers" of Mendel.

claim of E. B. Poulton and K. Jordan as "precursors" would seem to be fair, at least in terms of a similarity of views, and given the number of times he cites them, he may even have them as direct antecedents – that is, they might have directly influenced **him**. Stresemann, as his teacher, clearly did (Winsor in press; Chung 2003).

In his "point paper" on the biological species concept (Mayr 2000a) in the Wheeler and Meier volume (2000), Mayr repeats most of the previous paper. One thing he does add here is that

> [t]he word *interbreeding* indicates a propensity; a spatially or chronologically isolated population, of course, is not interbreeding with other populations but may have the propensity to do so when the extrinsic isolation [is] terminated. [p17]

The shift in Mayr's thinking from "actually or potentially interbreeding" in 1942, to "actually or potentially operating isolating mechanisms" in 1963 to "propensity to interbreed" in 2000 is interesting. As a test of species-status, potential anything is obviously useless unless it can be made actual (which is the basis for his insistence that only in sympatry are species fully determinable[94]). But clearly one wants to be able to say that I and the inhabitants of 15th century England are the same species, even if I cannot interbreed with them **actually**, and so Mayr **must** introduce something like a propensity interpretation. However, "propensities to behave" are themselves no easier on the metaphysical eye than potentialities. They remain, in the end, conditional statements: a lump of sugar is soluble, if, when immersed in water, it dissolves (cf. Sober 1984 p76-78). But if there were no possibility of immersing it in water, would it remain a soluble substance? We want to say so, but if we examine our intuitions, this is because we know of other lumps of sugar that they **have** dissolved, and by analogy with this lump, which has the same composition, and no reason to think otherwise, so it too will dissolve.

Mayr's conception of species is, in the end, one of dispositions to behave in various ways. Henry IV and I are of the same species because we are of the same "substance", and were we in the same population, our genes could freely spread through it. But this is what Mayr wants to object to – this smacks of essentialism; though, as I will argue later, it isn't. In the meantime, let us note that Mayr tries to avoid counterfactual claims of "**would** have interbred, if in the same (natural) population" with his insistence on sympatry for full species-hood. It is a problem he makes largely for

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[94] Mayr once told Hull in conversation that not potentially interbreeding was the equivalent of there being isolating mechanisms present (Hull, pers. comm.).

himself, based on his conflation, I believe, of the epistemic and ontological aspects of being a species. In this, he is not alone.

4.1.4. Recognition concepts

There have been numerous conceptions of species following Mayr that are fully, or partially, isolationist. The views of Hugh Paterson (1985; 1993) in particular have influenced Niles Eldredge (Eldredge 1989; 1993) and Elisabeth Vrba among others (Lambert et al. 1995). Paterson's version of the biospecies concept requires that organisms share a mating system, which he terms the "Specific-Mate Recognition System", or SMRS. He intends this to apply to plants, animals and other organisms, so the voluntarist implications of the term "recognition" should be taken as the term "selection" is, without voluntaristic or cognitive implications. Paterson defines a species thus:

> *We can, therefore, regard a species as that most inclusive population of individual biparental organisms which share a common fertilization system.*
>
> (Paterson 1985 p25, italics original)

He refers to this as the Recognition Concept. Mayrian and Dobzhanskyan concepts he calls Isolation Concepts. Since Paterson's version applies, as did previous isolation concepts, only to fully sexual and gendered (anisogamous) organisms (p24), it follows that like them, he does not regard non-sexual organisms as forming species. Paterson's criticisms of the Isolation Concept include its being teleological, since species are seen as "adaptive devices" (p28), but this is hardly fair. Biospecies are not, on Mayr's account, adaptive any more than higher taxa, and on his account they are formed through isolation and subsequent local adaptation, not in virtue of their adaptations. The main difference between the isolation conception of Mayr and that of Paterson is well noted by the following contributor to that volume (Scoble 1985), who notes,

> … the BSC can apply to only *actually*, not potentially, interbreeding groups of organisms. However, if the recognition concept of species … is accepted … then we may be able to directly compare at least some of the very characters involved in mate recognition in allopatric and allochronic populations. (p33)

However, this does not follow, since we cannot say whether the mate recognition sequences are compatible enough to form viable progeny, either occasionally or repeatedly enough to make them count as the "same" species, until we have actually managed to test it in the lab and the wild. Scoble also notes the problem of uniparental species, and suggests that a homeostatic view might pertain. Since the SMRS is only one kind of homeostatic mechanism, there is no reason to restrict species-hood to sexual organisms only.

4.1.5. Genetic concepts

We have several genetic concepts of species, ranging from Dobzhansky's comment that species are "the most inclusive Mendelian population", and Carson's comment that a species is a "field for gene recombination" (Carson 1957) through to fully worked out genetic conceptions like Templeton's and Wu's.

Templeton's view is that a species is

> The most inclusive group of organisms having the potential for genetic and/or demographic exchangeability.
>
> (Templeton 1989 p25; cited in Ghiselin 1997 p113)

As Ghiselin (1997) observes, Templeton's conception resembles Mayr's in that species form as the result of genetic revolutions that constrict exchangeability, but he also favours Paterson's views on mate recognition. "Casting the definition in terms of one gene to be exchanged for another makes it roughly the same as the biological species definition." The requirement for demographic exchangeability means that organisms as units can replace each other in genetic populations, even if they do not do so in actuality.

Wu's views are harder to pin down exactly (Wu 2001). He claims that reproductive isolation (RI) has involved the entire genome under the BSC, but that it instead involves genetic isolation of *adaptive genes and gene complexes*, in particular what he calls *speciation genes*. Even if there remains gene exchange for the non-adaptive genes, if there is RI for the adaptive genes, good species have evolved. His view relies on speciation itself, the process, resulting in some degree of genome isolation. Species are defined in terms of their genes having reached a particular level of RI, either Stage III – where populations have diverged sufficiently that they will not fuse in sympatry – or Stage IV – where populations are entirely isolated and will not mix at all genetically. Speciation genes have become a topic of interest to researchers with the rise of sympatric speciation models and examples (Butlin et al. 2001; Orr et al. 2000), but Wu's genic conception is within the traditional genetic and biospecies concepts (Vogler 2001; Van Alphen et al. 2001; Rieseberg et al. 2001; Bridle et al. 2001).

4.2. Evolutionary species

Evolutionary species concepts derive from attempts to deal with the time dimension, something that the biological species concepts of Mayr and Dobzhansky tend to avoid – for them species exist at a given time horizon, and over evolutionary time, of course, they can change and split. Palaeontologist George Gaylord Simpson proposed a definition:

> An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies.
>
> (Simpson 1961 p153)

Earlier, in a classic paper (Simpson 1951), he had expressed it slightly differently:

> … a phyletic lineage (ancestral-descendant sequence of interbreeding populations) evolving independently of others, with its own separate and unitary evolutionary role and tendencies, is a basic unit in evolution.
>
> (Quoted in Ghiselin 1997 p112f)[95]

According to Cain (1954 p111), Simpson characterised the intergrading forms of an evolutionary species as "transients". Species are thus a number of things: they are *populations* that form *phyletic lineages* through *interbreeding*, and which have *independent evolutionary roles* and *independent evolutionary tendencies*. These properties are reiterated in the later version of the evospecies concept by E. O. Wiley:

> A species is a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate.
>
> (Wiley 1978 p18)

By 2000, this has ceased to be a "definition" and is now a "characterization":

> An evolutionary species is an entity composed of organisms that maintains its identity from other such entities through time and over space and that has its own independent evolutionary fate and historical tendencies.
>
> (Wiley et al. 2000 p73)

The novel elements here include the "entification"[96] of evospecies in place of the population stipulation, to accommodate asexual organisms (p75), and the inclusion of time and space to indicate the processual nature of the concept. However, one thing that all the evolutionary concepts fail to do adequately is to specify what counts as "independence". If a parasitical species coevolves with its host, which is commonly the case, are they still independent? And of course there is a metaphorical problem with "fate", given the universal view that evolution is not predetermined, but we can assume that Wiley and his colleagues understand that; this merely specifies that the outcomes

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[95] Ghiselin (*loc. cit.*) suggests the shift from the biospecies emphasis of this definition to the less explicitly interbreeding concept a decade later is due to his falling "increasingly under the spell of the set-theoretical treatment of the Linnaean hierarchy by Gregg …, who, although mentioning in passing the possibility that species are something else, insisted they are classes." However, a set interpretation does not make it, ipso facto, a class interpretation.

[96] I owe this term to Henry Plotkin.

of evolution for any one species are unique to that species. In a sense, this is a matter of evolving a unique set of traits.

Evolutionary species concepts have been assumed by some critics to imply a gradual and constant rate of evolution (Ayala 1982; Eldredge et al. 1972; Gould 1982). This need not be the case, however, as Simpson's own classical work on evolutionary rates indicates (Simpson 1944; Gould 1994), but it is also sometimes held that species change over the entire course of their duration. Opposing this, the punctuated equilibrium theorists (Eldredge et al. 1972; Eldredge 1985; Eldredge et al. 1997; Gould et al. 1977; Gould 2002) have argued that species tend to remain stable once evolved. If correct, or rather **when** correct, for it is now accepted to be the case for many species if not all, the "fate" of the species involves the stasis of the unique set of traits once achieved.

Evolutionary species concepts, as with some phylogenetic species concepts, tend to adopt the metaphysical species-as-individuals thesis of Ghiselin and Hull (Ghiselin 1997; Hull 1976; Ghiselin 1974b; 1988; Hull 1978; 1981; 1992b). As Wiley and Mayden note,

> Evolutionary species are logical individuals with origins, existence, and ends. [p74]

However, if species are correctly thought of as **logical** individuals, they need not be **historical** individuals, a point discussed in the next chapter.

Evospecies, as we might call these entities, are something of a hybrid notion, to my mind. They are phyletic objects, but they are often presented as achieving grades of organisation, and often run with evolutionary systematics (itself a hybrid, conjoining phylogenetic and adaptive conceptions of classification). We shall discuss this issue in the sixth chapter.

4.3. Phylogenetic species

4.3.1. Introduction

Species concepts based upon the phylogeny of the groups of organisms are called "phylogenetic", but there are several *phylospecies* concepts, as I will call them, and there are several sub-versions of them in turn. All proponents of phylospecies concepts claim both Darwin and Hennig as their inspirations, but it is arguable how closely the modern views relate to those initial expressions of classification of taxa by descent.

In some ways, phylogenetic classification is an outgrowth of the ideas expressed by Haeckel and others during the late nineteenth century. Haeckel coined the term *monophyly*, which Hennig later appropriated and more strictly defined. This is a critical notion in the context of phylogenetic systematics, or, as it is popularly known, cladistics. In Hennig's definition, a monophyletic group is a stem species and all of its descendent taxa. Under more formally defined notions of phylogeny, sometimes called pattern cladism, a monophyletic group is a proper subset of some set of taxa, without necessarily implying an immediate history. On this account, a monophyletic group is definable in terms of it having unique characters that are not shared by other taxa. These are called *apomorphies* in Hennig's terminology, or "derived characters". This is a relative term: an apomorphy for one set of taxa is a *plesiomorphy* (an underived, or primitive, character) for a more inclusive set of taxa. If one or more taxa share an apomorphy, it is called a *synapomorphy*, and if only a single taxon carries an apomorphy, it is called an *autapomorphy*.

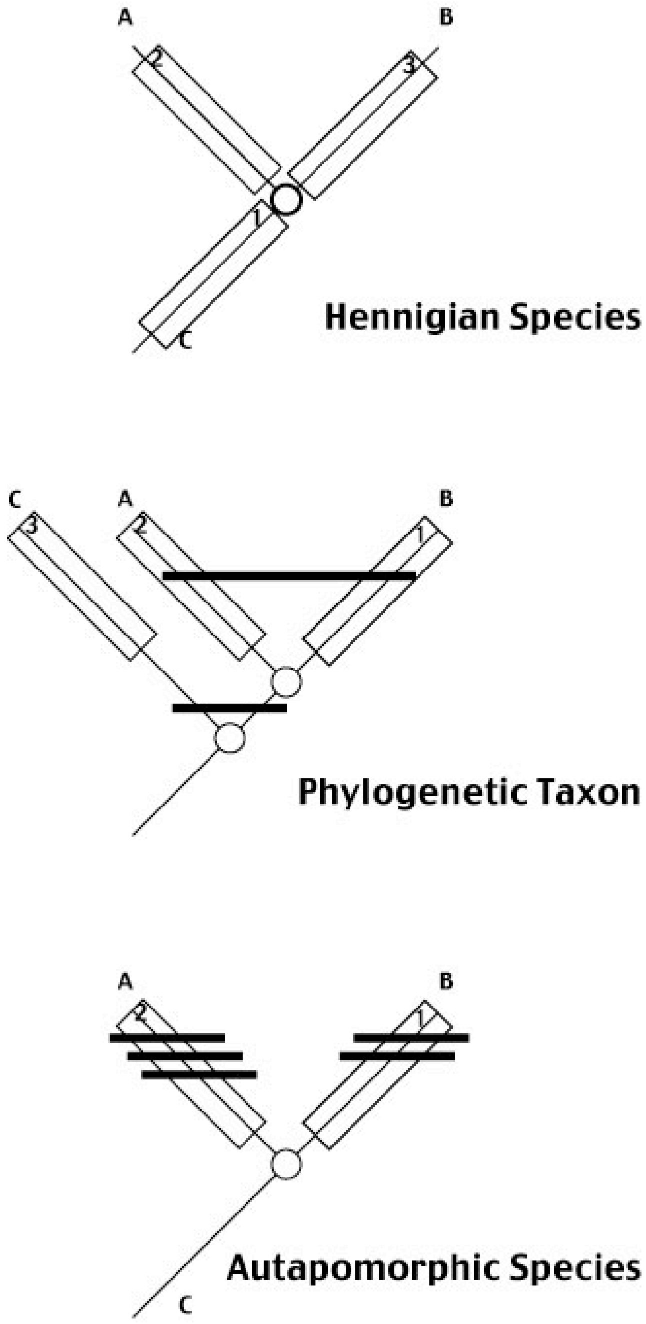

Figure 10 – Three phylospecies concepts.

A. Hennigian species *are formed at speciation, and extinguished at the next speciation event or extinction. The cladogram is a history as well as a classification.*

B. Phylogenetic Taxa species *are terminal nodes in a cladogram or evolutionary tree specified by synapomorphies. They are recognised by a lack of further discrete patterns of ancestry and descent (i.e., by having no further synapomorphies).*

C. Autapomorphic (diagnostic) species *are the smallest terminal nodes in a cladogram, marked by their autapomorphies. The cladogram is a synapomorphy scheme only, and needs to be converted to a history.*

There are fundamentally three phylospecies concepts. The first, defined initially by Hennig, is sometimes called the "Hennigian species concept" (Meier et al. 1997). It rests on a conventional decision Hennig made to be consistent with his broader philosophy of classification, and which we shall call the *Hennigian convention*. On this account, if a new species arises by splitting from a parental species, then we shall say that the parental species, no longer being monophyletic (that is, now being paraphyletic), has become extinct, and there are now two novel species.

The second phylospecies concept we might call the "Phylogenetic Taxon Concept" (PTC). It relies upon the notion that any monophyletic taxon is all the descendent lineages of a single stem lineage, and a species is an otherwise monophyeltic taxon with no desendent lineages, but there are some ambiguities here. It is sometimes unclear whether a species is defined recursively as any taxon that has only a single ancestral species and no sister taxa that share that species, or whether a species is held to be any taxonomic lineage that has no taxonomic sub-lineages; in any event the phylogenetic unit concept is a hierarchical notion based upon history and biology.

The third phylospecies concept, which I shall call the "Autapomorphic Species Concept" (ASC)[97], is derived from the work of Donn Rosen (Rosen 1979). In various versions, it tends to rely upon the diagnosability of taxa (Cronquist 1978), or, as we may otherwise say, it is a largely epistemological notion of species. All the Autapomorphic concepts rely upon a species being the "terminal taxon" in a cladogram. Some proponents apply an evolutionary exegesis to this, while others restrict it to a diagnostic relationship, a distinction often referred to as the ontology-epistemology aspects of species (cf. Wheeler and Meier 2000).

The division of the phylospecies into two main kinds, ignoring Hennigian species for the moment, is a reflection of the larger taxonomic debates. These raise the questions: (i) should classification proceed in terms of descent alone or on the basis of similarity (cladism versus gradism)? and (ii) if classification rests on clades, are homologies (apomorphies) indicators of history, or are patterns that are evidence in favour of a historical reconstruction but not themselves a model of evolution? Briefly, this is the distinction between ontological and epistemological notions of classification again.

Thos who take the epistemological classification position (grouping in terms of monophyly where that means homological relationships only) are generally those who fall under the rubric of pattern cladists. Those who take the diagnosis of monophyly to give an immediate hypothesis of evolutionary history are the so-called orthodox, or "traditional" cladists, called "process cladists".[98] Pattern cladism tends to treat taxa as relationships between organisms, while process cladism tends to see taxa as composite entities of which organisms are members. In this regard, the traditional orthodoxy is

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[97] Meier and Willman (1997 p36-37) call the Autapomorphic Species Concept the Phylogenetic Species Concept *simpliciter*, and Davis (1997) calls the process or Phylogenetic Unit Concept the Autapomorphic Species Concept, in direct contradiction to my usage. I shall use the terms as I here define them, but it should be noted that there are other senses in the literature.

[98] The term "process cladism" was introduced in Ereshefsky (2000).

more closely allied to some aspects of the evolutionary species concepts of recent times.[99]

Phylogenetic approaches to species are founded on one of three criteria – synapomorphy, autapomorphy or prior phenetic identity as OTUs. Roughly, synapomorphy acts as the classical notion of genera, autapomorphy acts as the classical notion of differentia, and in the case of phenetic OTUs as inputs into a cladistic analysis, species here are types that are known prior to the formal division. Therefore, it is something of a misconstrual to think that there are only two "phylospecies" concepts besides the Hennigian account. In fact, there are several, and I think that this binary division is a privative one; into diagnostic (Autapomorphic) species concepts, and all the other phylogenetic (cladistic) accounts.[100]

4.3.2. Hennigian, or Internodal, species

In the work that began the cladistic revolution, and which remains the source for much of the thinking, so clearly and consistently was it expressed, Hennig treated species in an unusual manner (Hennig 1966 p28–32). He begins by defining "semaphoronts", or "character bearers" as the elements of systematics. These are effectively stages or moments in the lifecycle of organisms of the taxon. Individuals themselves, or more exactly the ontogenetic lifecycles of individuals, are related through reproductive relationships he called "tokogenetic" relationships. When tokogenetic relationships begin to diverge, they form species, which arise

> … when gaps develop in the fabric of the tokogenetic relationships. The genetic relationships that interconnect species we call phylogenetic relationships. The structural picture of the phylogenetic relationships differs as much from that of the individual tokogenetic relationships as the latter does from the structural picture of the ontogenetic relationships. In spite of these differences in their structural pictures, the phylogenetic, tokogenetic, and ontogenetic relationships are only portions of a continuous fabric of relationships that interconnect all semaphoronts and groups of semaphoronts. With Zimmermann we will call the totality of these the "hologenetic relationships." [p30]

Hennig illustrated this with a now-famous diagram, his figure 6 on page 31 (figure 11):

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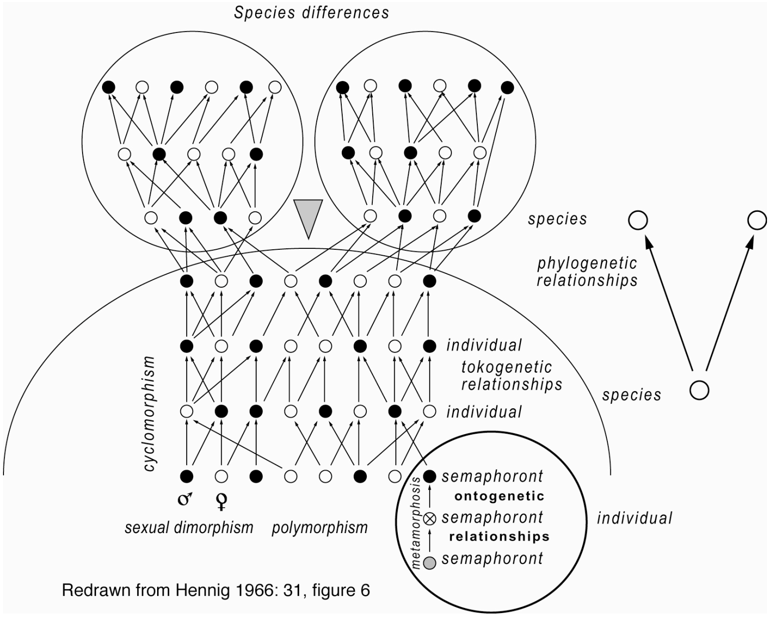
[99] It is not, in my opinion, true that pattern cladism commits its adherents to an antievolutionary view of taxa. Neither is it true that it is an essentialistic view of taxonomy, as some, notably Mayr, have claimed. It is, however, typological in a way that I will discuss further.

[100] Brent Mishler pointed out to me that what I had been calling a single class of species concepts, under the term "Monophyletic Species Concepts" (the Phylogenetic Taxon Concept) was actually pretty diverse, and that some (e.g., Cracraft) did not think species had to be monophyletic (see below).



Redrawn from Hennig 1966: 31, figure 6

Figure 11 – Hennig's view of systematic relationships

The larger circles are the hologenetic relationships that represent species.

Hennig is by implication asserting that species cease to exist when they are divided; that is, when the hologenetic relationships cease to be a single set (the species sets are represented in the diagram by the large ellipses). Although Hennig assumes that species are reproductive communities of harmoniously cooperating genes, as Dobzhansky had said, and that species are reproductive groups, as Mayr had said, he nevertheless assumes that species are phylogenetic lineages. In fact he says that species are defined over spatial dimensions as well, as

> … a complex of spatially distributed reproductive communities, or if we call this relationship in space "vicariance," as a complex of vicarying communities of reproduction. [p47]

The sort of vicariance he has in mind includes trophic replaceability (p49–50), but also other ecological dimensions, including temperature races.

But the most significant aspect of Hennig's definition of species lies in the temporal dimension (p58–60), where he notes that species are to be delimited by events of speciation:

> The limits of the species in the longitudinal section through time would consequently be determined by two processes of speciation: the one through which it arose as an independent reproductive community, and the other through which the descendants of this initial population ceased to exist as a homogenous reproductive community. [p58]

Transformations of the species morphology and genetic composition within these two events do not affect the identity of the species, because the species is defined here as a homogenous reproductive community. In effect, Hennig is taking the biospecies isolationist concept to its limits. Species are extinguished at the next speciation event. In his earlier work in German (Hennig 1950 p102), he was even more concise:

> When some of the tokogenetic relationships among the individuals of one species cease to exist, it disintegrates into two species and ceases to exist. It is the common stem species of the two daughter species.
>
> Translated by Meier and Willman (1997 p30)

This has become known as the *Hennig Convention*. It has been strongly criticised from all sides, by biospecies proponents, evospecies proponents and other phyogeneticists (see the citations in Meier et al. 1997 p31), not least because it seems to be an arbitrary way to delimit species taxa. Mayr, for example, takes Hennig to be making a substantive claim on the ways species are formed at speciation, and criticises it on the basis that the "parent" species can remain unchanged even though it is no longer monophyletic. But it seems to me that the critics have overlooked the most charitable interpretation of the Hennig Convention – it is a convention about *naming*. In short, the *name* of a species is extinguished at speciation. This follows from Hennig's views about the task of systematics. Using (and citing) Woodger and Gregg (see the excellent discussion in Wheeler and Platnick 2000) and the views of Woodger (1937) in particular about sets in classification, Hennig strives to ensure that there is no ambiguity of reference in the sets named in systematics. Since as soon as a set is divided there is ambiguity which of the two resultant sets is being referred to by a prior name, Hennig proposes to extinguish the now-ambiguous name and create two new ones. However, he seems to equivocate over whether or not they are new *entities* or not.

The Hennigian concept of species has been recently expanded and defended by several people. Meier and Willmann (Meier et al. 1997; cf. Willmann 1985b; 1985a; 1997) have proposed a modified Hennig Species Concept (p31):

> Species are reproductively isolated natural populations or groups of natural populations. They originate via the dissolution of the stem species in a speciation event and cease to exist either through extinction or speciation.
>
> (Quoted from Willmann 1985a p80, 176)

Like Hennig, and the proponents of the biospecies and other isolationist conceptions, they reject the use of a single taxonomic category such as *species* to apply to asexual ("uniparental") organisms. Instead, they call them "agamotaxa".

A set-theoretic model of Hennig's concept has been provided by Kornet (1993a; 1993b) under the title of "internodal species concept", who formalises the notion of inter-nodality (INT) in a cladograms in terms of the tokogenetic relations being permanently divided, so that any individual in the hologenetic group has a "gross dynastic relationship" (GDYN) with any other individual in that group. Type specimens thus fall out as an appropriate individual to start the GDYN analysis to establish the INT relation. Kornet thus makes the relation of type specimens to the rest of the species scrutable (see below) in set theoretic terms.

4.3.3. Phylogenetic Taxon species

The Phylogenetic Taxon Concept (PTC) is largely due to the advocacy of Brent Mishler, although earlier Joel Cracraft (1983 p170) had defined the species taxon as

> … the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent.

Mishler and Brandon (1987) summarise their Monophyletic version (Mishler et al. 1982):

> A species is the least inclusive taxon recognized in a classification, into which organisms are grouped because of evidence of monophyly (usually, but not restricted to, the presence of synapomorphies), that is ranked as a species because it is the smallest 'important' lineage deemed worthy of formal recognition, where 'important' refers to the action of those processes that are dominant in producing and maintaining lineages in a particular case.
>
> (Mishler et al. 1987; p310 in Hull et al. 1998)

They redefine "monophyly" in such a way as to be able to include species:

> A monophyletic taxon is a group that contains all and only descendants of a common ancestor, originating in a single event.
>
> (p313 in Hull et al. 1998)

De Queiroz and Donoghue, on the other hand, treat species as systems that may not be monophyletic, and indeed may be paraphyletic if a species has split from it, in a parallel with cohesive and functional individuals who lose cells and reproduce (de Queiroz et al. 1988; 1990). They therefore exclude asexuals and indistinct populations that are not assignable from being members of species. Mishler and Theriot (2000), extending the monophyletic conception, include asexuals (p52f) largely on the grounds that asexual taxa do not markedly differ in overall phylogenetic nature from sexuals – the number of autapomorphies, for example, are similar in both cases (one does wonder, though, if this is due more to the application of phylogenetic classification than anything else).

The PTC is based on the historical, actual, lines of ancestry and descent that are represented in a cladogram. As a phylogenetic taxon, a species is grouped by the synaporphies shared by organisms that indicates monophyly (Mishler et al. 2000 p47). It is a phylogenetic or cladistic replacement for the evolutionary species concept of Simpson. Mishler and Theriot (2000 p46-47) give the following broad definition:

> A species is the least inclusive taxon recognized in a formal phylogenetic classification. As with all hierarchical levels of taxa in such a classification, organisms are grouped into species because of evidence of monophyly. Taxa are ranked as species because they are the smallest monophyletic groups deemed worthy of formal recognition, because of the amount of support for their monophyly and/or because of their importance in biological processes operating on the lineage in question.

The dual nature of the epistemic and the ontological aspects of species are clear expressed, and the rank of *species* is restricted to "biologically important" lineages. Their version of the PTC allows for reticulation as a general problem in classification not merely restricted to species taxa.

De Queiroz and Donoghue (1988; 1990), however, do not think that species have to be monophyletic, because monophyly of populations does not offer a way to specify what the base rank is, and because species evolve from ancestral populations this will leave the species from which the ancestral population derived as paraphyletic. Of course, the monophyly spoken of here is somewhat different from the monophyly of the Mishler, *et al.* Version; this one is based on populations as the base entities; theirs is based on phylogenetic lineages. And both conceptions converge on a similar solution – species are regarded as singular phylogenetic *lineages*, which is de Queiroz's later conception of a cohesive object or group over phylogeny (de Queiroz 1998; 1999, see final chapter). The actual answer of the earlier paper, however, is that there is no single definition of species that will "answer to the needs of all biologists and will be applicable to all organisms" (quoting Kitcher 1984 p309), although they reject the sort of pluralism I propose in chapter 6.

4.3.4. Diagnostic (Autapomorphic) species

Diagnosis of species has always been involved in the debate, but few if any have until recently suggested that diagnosis is sufficient, apart from (and possibly not even there) the Taxonomic Species Concept. Cronquist (1978 p3) provided one of the first such conceptions:

> Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means.

Some (e.g., Ghiselin 1997 p106f) accuse Cronquist of presenting a "subjective" concept, but it all hinges on what "ordinary means" means. At one time, the use of a microscope was reviled (e.g., by Linnaeus); now assays for specificity ranging from molecular data to morphometric and acoustic traits are considered ordinary practice.

More common diagnostic concepts, though, arise from the recognition that what makes taxa distinct are their apomorphies. Species have diagnostic autapomorphies –

that is to say, they have unique constellations of characters – while higher taxa (clades) have <u>syn</u>apomorphies – shared constellations of characters, which group them together. One instance of this approach is found in the work of Donn Rosen:

> … a geographically constrained group of individuals with some unique apomorphous characters, is the unit of evolutionary significance.
>
> (Rosen 1978 p176; quoted in Wheeler and Platnick 2000 p55)

In Rosen's paper on Guatemalan fishes, he defined species in terms of individuals and populations:

> ... a species is merely a population or group of populations defined by one or more apomorphous features; it is also the smallest natural aggregation of individuals with a specifiable genographic integrity that cannot be defined by any set of analytic techniques.
>
> (Rosen 1979 p277; quoted in Mayr 2000b p99)

He then noted that this means that subspecies are, "by definition, unobservable and undefineable", since they have no such apomorphies. Subsequently, Nelson and Platnick proposed in passing that in their book on systematics and biogeography that they would treat species as

> … simply the smallest detected samples of self-perpetuating organisms that have unique sets of characters.
>
> (Nelson et al. 1981 p12; quoted in Wheeler and Platnick 2000 p56)

They, too, noted that this meant that diagnosable "subspecies" were thus species. This was not intended to be a complete definition but rather a description of the current practice (Nelson, pers. comm.). Even so, it was very influential on subsequent discussion. Independently, Eldredge and Cracraft (1980 p92; quoted in Wheeler and Platnick 2000 p55–56) defined a species as

> … a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind.

Cracraft subsequently tightened his definition by removing mention of reproductive cohesion ("like kind") to read

> … the smallest diagnosable cluster of individuals within which there is a pattern of ancestry and descent.
>
> (Cracraft 1983 p170; quoted in Wheeler and Platnick 2000 p56, and see discussion there.)

Quentin (not Ward) Wheeler and Platnick base their definition on this tradition as well (Wheeler 1999; Wheeler and Platnick 2000). They define species thus (p58):

> We define species as the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character traits. This concept represents a unit concept.

This concept is prior to a cladistic analysis (p59), and so unlike Nelson's earlier note that species are taxa like any other level of a phylogenetic tree (Nelson 1989), they do not worry about characters, apomorphies and homologies when recognising species. Species are found wherever characters are fixed and constant across all samples, while traits may be variable (see their figure 5.1 on p58). Their willingness to handle and include asexual taxa within their species concept marks them out from most other conceptions, and they bite the bullet on recognising clones of asexual lineages as species (*loc. cit.*):

> If the goal of distinguishing species is thereby to recognize the end-products of evolution, should we seek to suppress naming large numbers of species where large numbers of differentiated end-products exist?

Mishler considers a number of the diagnostic accounts to be phenetically based, including Cracraft's, Platnick's and Nixon and Wheeler's (pers. comm.). Whether this is so (that is, whether they make use of the Cartesian clustering of species in a state space of traits typical of phenetic practice), it is clear that they assume that species are phylogenetically speaking the terminal taxa on a tree. Diagnosis assumes that the traits are specified before the tree is constructed.

4.4. Other species concepts

4.4.1. Ecological species concepts

Turesson's species concept did not get taken up widely, but ecological concepts have been proposed from time to time. Mayr himself ventured one in his 1982 history:

> *A species is a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature.*
>
> (Mayr 1982 p273)

He did this with neither preamble nor followup, and the requirement for the "niche" here seems to have been allowed to quietly drift away, as he does not insist on it elsewhere. A prior instance of another partial ecological concept occurs in Ghiselin (1974b), who referred to species as

> The most extensive units in the natural economy such that reproductive competition occurs among its parts. [p38]

The competition here is for genetic resources, and comes in the context of a strong selectionist account of evolution at various levels (Ghiselin 1974a). It is called by

Ghiselin the "hypermodern species concept". He says that species are economic entities analogous to firms.

Van Valen in a paper that discussed the "odd" reproductive dynamics and evolution of American oaks (gen. *Quercus*), proposed that in these plants at any rate a species was an ecological type. He offered a definition as "a vehicle for conceptual revision, … not a standing monolith":

> A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range.
>
> (Van Valen 1976 p233)

This is self-consciously a mixture of the Mayr and Simpson definitions, and Van Valen justifies it in terms of evolution acting on phenotypes, controlled by "ecology and the constraints of individual development". It is therefore a definition founded on a particular view of evolution. He reprises Simpson's notion of a lineage, and defines a population in genetic terms. The novel element here is the idea of the "adaptive zone", which he describes as

> Some part of the resource space together with whatever predation and parasitism occurs on the group considered. [p234)

Quercus species are often sympatric, and freely hybridise, and yet they maintain their identity. He refers to these groups as "multispecies", as they exchange genes, but he does not require that they actually form viable hybrids that breed true thereafter. This concept is defined as

> A set of broadly sympatric species that exchange genes in nature... [p235]

and refers to the syngameon concept of Verne Grant, which, we have seen, is due to Poulton. Multispecies can occur without having component species as such, citing *Rubus*, *Crataegus*, and dandelions. The latter leads to the implication that asexuals are not to be considered species.

Elsewhere Littlejohn (1981) has comprehensively reviewed reproductive isolation, and makes some interesting comparisons between sexual reproduction and asexual isolation. He notes that asexuals (uniparental species; unlike many of his predecessors, Littlejohn does not exclude them from specieshood) must be seen as a "cluster or cloud of individuals representing an adaptive node or adaptive peak", and cites Dobzhansky and G. E. Hutchinson (1968). Hutchinson employs a "taxonomic space" model, and treats species as clusters in that space, formed through adaptation. This is somewhat different to the phenetic concept of an OTU. For a start, he requires independence of the axes of the space, and that they be adaptive characters. Asexuals, such as bdelloid rotifers, are just as good species as their close sexual relatives, the *Nebalia* class of crustaceans.[101] Similar points about the role of adaptation in delimiting species were previously made by R. S. Bigelow (1965 p458), who noted that

> Reproductive isolation [in Mayr's 1963 definition – *JSW*] should be considered in terms of gene flow, and not in terms of interbreeding, since selection will inhibit gene flow between well-integrated gene pools despite interbreeding.

Recently, the philosopher Kim Sterelny defended an "ecological mosaic" conception of species (Sterelny 1999), based on a reworking of Dobzhansky's (1937a p9–10) metaphor of species as occupying "adaptive peaks" in a Wrightean fitness landscape. Noting that species are typically *ecologically fractured* (p124), Sterelny concludes that most species are geological and ecological mosaics, and are not ecologically cohesive entities. He takes this to explain stasis in the duration of species, as interbreeding between populations within the species' range acts as an inhibitor, he calls it *Mayr's Brake*, on adaptive change over all the entire species. He thinks that this reinforces an evolutionary concept of species.

Ecological species concepts are partial rather than all-encompassing, and tend to act as adjuncts to more universal conceptions. It is clear that all ecological concepts rely heavily on the pre-eminent role of natural selection to maintain isolation between groups. Selection also plays a critical role in the definition and delimitation of asexual species, to which, among others, we now turn.

4.4.2. "Aberrant" concepts

"Aberrant concept" here merely signifies that the concept is either not attended to much by zoologists, or that it is not thought by some to be a "true" species concept.

4.4.2.1. Agamospecies

Agamospecies are asexual taxa. The term was defined by Cain (1954 p98-106) as the end result of parthenogenesis in animals and apomixis in plants (which is secondary asexuality), but it is now well-understood that most unisexual organisms are in fact neither (i.e., are primarily asexual – Kondrashov 1994; Schloegel 1999; Taylor et al. 1999). Cain defined agamospecies as

> … those forms to which [the biological species concept] cannot apply because they have no true sexual reproduction … (p103)

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[101] I am indebted to Dr Littlejohn for providing me with these references.

This is clearly unsatisfactory. For a start, it is a privative definition – agamospecies are what are **not** something else (in this case taxa comprised of sexual organisms). As we saw above with Fisher, asexuals are considered by Cain to be off the mainstream of evolution, something of a marginal occasional misfiring of the evolutionary process, since sexual recombination permits the more rapid acquisition and spread of favourable mutations, and asexual reproduction is subject to genetic load (the continuation of deleterious mutations). This is no longer the consensus.

So it has been questioned whether agamospecies are anything more than the morphological species concept applied to asexual organisms (noted by Sonneborn 1957 p283 of; Dobzhansky 1937b; 1941. See above on Dobzhansky). However, there is a notion that applies to asexuals that is, I believe, a more coherent way to understand asexuals, and which avoids privative definition. Originally defined for viruses (which are mostly, but not always,[102] asexual), the concept of Manfred von Eigen (Eigen 1993a; Stadler et al. 1994; Eigen 1993b) is called *quasispecies* (from the Latin for "as if", *qua si*), and it applies equally to uniparental lineages in artificial life simulations as in biology (Wilke et al. 2001). He notes that

> …A viral species … is actually a complex, self-perpetuating population of diverse, related entities that act as a whole (Eigen 1993b p32)

and defines the quasispecies as a

> … region in sequence space [which] can be visualized as a cloud with a center of gravity at the sequence from which all mutations arose. It is a self-sustaining population of sequences that reproduce themselves imperfectly but well enough to retain a collective identity over time. (p35)

The conception is based on the observation that in a cluster of genotypes of viruses, there will be a mean genotype (the wild type) maintained by selection for optimality for that particular environmental niche (figure 12). Eigen noted that it may eventuate that there is actually no single virus with that "wild type" genotype. Clearly, this makes the agamospecies conception a kind of ecotypical notion, maintained by natural selection; in fact, one might say that it is the purely ecological aspect of the ecospecies conception. Similar observations were made by Hutchinson (1968 p184), but no technical name was applied by him at that time. I therefore propose that "agamospecies" and "quasispecies" be treated as synonyms, and that the inferences made about quasispecies by Eigen be applied to agamospecies hereafter.

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[102] Viruses can crossover genetic material in a superinfected host (Szathmáry 1992; Boerlijst et al. 1996)

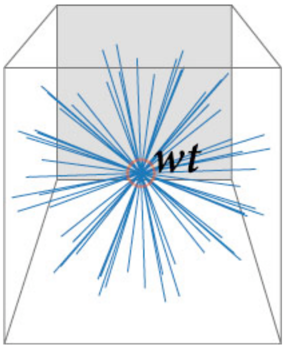

Figure 12 – Eigen's conception of a quasispecies.

Developed first to cover molecular and then viral species, Eigen's notion assumes that there is an "optimal wild-type" genome, which is here represented as a circle in an abstract "sequence space", divergences from which form a cloud of sequences constrained by selection. This applies to asexual organisms not otherwise constrained (e.g., by developmental constraints).

4.4.2.2. Nothospecies

The almost exact conceptual opposite of the agamospecies/quasispecies conception is pteridophytologist W. H. Wagner's (1983) conception of a *nothospecies*. Effectively, this is a species formed from the hybridisation of two sexual species (species formed by the usual method of cladogenesis of sexual species he refers to as *orthospecies*, pers. comm.). As Hull notes (Hull 1988c p103 citing Verne Grant), "According to recent estimates, 47 percent of angiosperms and 95 percent of pteridophytes (ferns) are allopolyploids" and ferns and their allies continue to cause problems for isolation conceptions of species (Barrington et al. 1989; Paris et al. 1989; Ramsey et al. 1998; Yatskievych et al. 1989; Haufler 1996; Vogel et al. 1996; Wagner et al. 1999). The notion is so generally applicable in botany that the concept of nothospecies has been written into the botanical rules for nomenclature.

4.4.2.3. Compilospecies

Harlan and de Wet (Harlan et al. 1963) proposed a concept of a species that "plunders" (Latin *compilo*) the genetic resources of another species through introgressive hybridisation (where the hybrids preferentially interbreed with only one of the parental species, causing a gene-flow from one to the other, one-way). It is therefore an asymmetric version of the nothospecies concept. It applies to some plant species (Aguilar et al. 1999).

4.4.2.4. OTUs and phenetics (phenospecies)

Phenetics developed from the work of Sokal and Sneath (1963; Sneath et al. 1973) who trace their attempt to produce a "natural" taxonomy back to Adanson, who used a multivariate classification scheme in *Familles des Plantes* (1763) (Panchen 1992 p132ff). The phenetic view, also called "numerical taxonomy" in virtue of the use of computers for the first time in systematics, basically involves a cluster analysis of continuously varying characters in a Cartesian space of *n*-dimensions (one dimension for each character) in the belief that species will fall out as clusters that agglomerate in different ways. While Sokal and Sneath (1963 p30f) generally give priority to the biological species concept (but see Sokal et al. 1970), they note

> In the absence of data on breeding and in apomictic groups ...., the species are based on the phenetic similarity between the individuals and on phenotypic gaps. These are assumed to be good indices of the genetic position, although they need not be. ... In this book it [the term "species"] will be used in the sense of phenetic rank ... .

Species are not unique in the phenetic approach; they are operational taxonomic units (OTUs) just as above-species and within-species ranks are (pp121f). The phenetic view, though, is that species are not monotypic, and Sokal and Sneath define a term, based on Beckner's discussion (1959), *monothetic*, and its antonym *polythetic* (pp13–15) to describe groups based on a single uniform set of characters versus those which vary or have alternative characters; Wittgenstein's family resemblance predicate is explicitly adduced (p14, see below).

4.4.3. Species deniers: pure "nominalism", or eliminativism

It is unfortunate that the alternative to the reality of species has been called "nominalism" by Mayr and others, because nominalism is a philosophical doctrine that asserts that *universals* are not real, and species are not held by many to be universal terms (see below, on natural kind terms). Strictly speaking, the individuals that "species nominalism" considers real in opposition to species are individual organisms. However, in logic, a universal is not comprised of individuals, so much as they instantiate the class. Species *are* comprised of individuals under evolutionary accounts, and so they are real to the extent that their components are (except under ideal morphological views). It would be wrong to call these nominalistic views simply because they are founded upon acts of naming. A species nominalism must be directed to the *category* or *rank* of species, and must claim that there is no sense in which that categorical term has any application. I would therefore rather refer to *species deniers* than to nominalists.

Species deniers include Vrana and (Ward) Wheeler (1992), Pleijel (1999; 2000) and Hey (2001a; 2001b). I have argued above that Darwin was not a species denier, and that Buffon was only inconsistently one. There are two varieties: conventionalism, and "replacementism", the latter involving replacing that term ("species") with another (e.g., "deme", Winsor 2000), as Pleijel does. Given the history of the term, there is no reason to do this, except to make it clear that only a particular sort or kind is being referred to, and history shows also that such attempts are always assimilated and subverted. *Species* keeps winning out.

4.4.3.1. Conventionalism: The taxonomic species concept

"I object to the term "species concept", which I think is misleading. … A species in my opinion is a name given to a group of organisms for convenience, and indeed of necessity." [J. B. S. Haldane (1956: 95)]

One major stream of thought, particularly in Britain, with regards to species is what we might call the *conventional* account, although it is sometimes called the "nominalistic" or "cynical" concept (Kitcher 1984). On this widely-held account, species are "whatever a competent taxonomist chooses to call a species". The complete quotation from Charles Tate Regan (Regan 1926 p75), given by Julian Huxley (1942 p157; see also Ghiselin 1997 p118; Trewavas 1973) is

> ... a species is a community, or a number of communities, whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name.

Huxley goes on to note that the "difficulty with this definition lies in the term *competent*, which is what we have recently learnt to call the "operative" word. And experience teaches us that even competent systematists do not always agree as to the delimitation of species." Ghiselin notes that there are no rules for deciding whether a reproductive community is a species or a subspecies, and that one should wonder whose view to accept when the experts disagree; and such disagreement is common.

In fact, this view is not new, and precedes Darwinian evolutionary theory, at least in Britain, for some time. Darwin himself was a member of the drafting panel that proposed just this standard for the new *Rules of Zoological Nomenclature* in 1842; the so-called Strickland Code. In so defining the basic taxon this way, the British Association for the Advancement of Science legislators "consciously and conspicuously distanced themselves from disputes over definitions of species" (McOuat 2001 p3), and, according to McOuat, established the naming rights of a species to be a delineation of what a competent naturalist was – basically, someone who was accepted by the naturalist community. Darwin himself in several places made this sort of definition, particularly in his *Natural Selection*: "In the following pages I mean by species, those collections of individuals, which have been so designated by naturalists" (Darwin 1975 p98; cited by McOuat 2001 p4n10).

It is interesting to note, in connection with Regan's view, that he refers to "communities". This word typically has been used to apply to ecological communities, i.e., ecosystems (Taylor 1992), but in this case and at this time it is more likely to refer to what we now call a "deme" (Winsor 2000), or a "Mendelian population". If this is so, then Regan is conflating two ideas well-known in our history here: that of a reproductive element and a diagnostic one. In short, Regan might very well have been putting forward an "operative" notion of the generative species conception we have so often encountered. A less biological version of this view, which he calls the "cynical species concept" is presented by Philip Kitcher:

> Species are those groups of organisms which are recognized as species by competent taxonomists.
>
> (Kitcher 1984 p308)

Here the operationalist aspect of the concept is primary. Species are made by acts of recognition by experts. Whether or not it includes a strong element of the biological (that is, reproductively isolated) nature of species, conventionalism takes seriously Locke's claim that species are made for communication, and objections to the recent Phylocode proposal (many by strict cladists no less) are in part founded on the idea that higher taxa, at least, should be convenient, since they are artificial taxa anyway.[103]

4.4.3.2. LITUs (Least Inclusive Taxonomic Units)

Frederick Pleijel, a leading specialist on polychaete worms (bristleworms), has proposed doing away with the notion of species altogether (Pleijel 1999; Pleijel et al. 2000). Instead, he proposes to replace it with the neutral term *Least inclusive taxonomic unit*, or LITU (in homage to the OTU of phenetics). Pleijel's and Rouse's (2000 p629) "definition" of the LITU runs

> … named monophyletic groups which are identified by unique shared similarities (apomorphies) … which are at present not further subdivided. … Identification of taxa as LITUs are statements about the current state of knowledge (or lack thereof) without implying that they have no internal nested structure; we simply do not know if a given LITU consists of several monophyletic groups or not.

The conclusions I draw are not so different from his, in that I also abandon the notion of a fixed rank. However, as the historical reviews above make abundantly clear, the notion of a least inclusive taxonomic unit historically **is** a species in both logic and biology. What Pleijel has done here is rediscover the past way of looking at things. Primarily, as we shall see in the final chapter, Pleijel and I disagree merely on what to

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[103] The Phylocode proposes to replace all Linnaean ranks with strictly monophyletic taxa based on the best cladograms (Cantino et al. 2000). It has been supported by eliminativists like Ereshefsky (2000) and Pleijel (2003), but some pattern cladists, such as Norman Platnick and Gareth Nelson (pers. comm.) oppose it due to its disruption of scientific communication and meaninglessness, as in their view cladograms are only hypotheses and are subject to revision. Others (Benton 2000; Berry 2002; Bryant et al. 2002; Carpenter 2003; Forey 2002; Gao et al. 2003; Keller et al. 2003; Kojima 2003; Nixon 2003) attack the proposal for a range of reasons, ranging from a personal distaste to a rejection of cladism. Most think that monophyletic taxa are not going to be stable as new results come in.

call these LITUs, although, as a systematist he is focussing entirely upon the epistemological aspects and leaving causal issues to one side.

4.4.4. Species concepts in paleontology (paleospecies)

The problem of applying any concept of species in paleontology has been long understood, and has spurred a number of discussions (Simpson 1943; Sylvester-Bradley 1956; Schopf 1972; Smith 1994). The difficulty lies in the way the data are presented. In neontology (the study of living organisms), the behaviours of organisms, both sexual and ecological, can be observed in some detail and repeated if the initial observations are inadequate. Under some circumstances, the organisms can be experimentally mated. Molecular evidence, in particular that of DNA, can be harvested and assayed, meaning that where a traditional taxonomist might have used at most around 40 characters, the molecular systematist has more like 40,000.[104] Also, polytypy can be investigated in extant species, enabling the investigator to delineate the populations and subspecific variants and to tell whether, on the concept used, these still are included in the specific group.

Not so the paleontologist. The information in that case is usually restricted to several individual specimens (except when the bulk of the population leaves fossils, as in the case of silaceous forams, whose shells are fossilised in sediments on the seafloor, and which when they are found provide information about distribution, variety in populations, and changes over time). The famous *Tyrannosaurus Rex*, for example, is known from around 20 specimens, not all complete.[105] Many hominid species are known from a single individual. In cases where the ancestors of a lineage lived in conditions unconducive to fossilisation – the study of which is known as taphonomy[106] – will have entire series of species unknown to science. For example, few ape fossils have been found for those species that lived in forest and jungle environments, where decomposition in the acidic soils, scavengers and plants will dispose of the carcase relatively quickly.

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[104] A point made at the Melbourne Systematics Forum during 2002. I did not catch the name of the person making the point, but it is important. In the end, unless we know the ways in which DNA is expressed developmentally in all the species being analysed, DNA is just a richer source of "morphological" data.

[105] Chris Brochu (pers. comm.)

[106] A taphonomist of my acquaintance once noted that taphonomists are people who walk along a deserted beach, and upon finding a dead fish or jellyfish will murmur, "Mmmm, data…".

So paleontologists rely almost exclusively on morphological data. This means that there is pressure on them to lump stratigraphic specimens together (since fossil taxa are often used as stratigraphic markers by geologists) if there is some subjectively acceptable similarity between specimens.[107] In the rare cases when many specimens are found, problems due to variation can cause taxonomic problems. If many locales are involved, that is if the specimens are allopatric, it is unclear whether they form a single species or allopatrically isolated but closely related sister species. The problem is critical in the case of *Homo erectus*, which has a range from southern Africa to east and southeastern Asia. If all that remains is skeletal information, can we really be sure if these are the same biospecies, for example? The now-amalgamated species *Canis lupus* includes morphs like the timber wolf, the Pekinese pug and the Great Dane, all interfertile or fertile along a series of intermediate forms. Any paleontologist would split them into distinct taxa on morphological grounds alone. In the case of many birds, on the other hand, skeletal changes between good species are minimal, and only behavioural and ecological differences will tell them apart.

4.4.4.1. Chronospecies (successional species)

A problem that used to be common in discussions of paleontology and species concepts was that of chronospecies, where speciation occurs over time such that at the starting and end points of a time series, the morphs are different species. This was discussed by Simpson, for example, in his book on evolutionary tempo and mode (1943). However, the notion of chronospeciation is no longer thought by many to be an urgent one – for a start, a number of specialists think that for animal species, such changes do not occur without lineage differentiation – in short, anagenesis is accompanied by cladogenesis – and that in most cases species remain largely unchanged after their initial period of adaptation until they go extinct (Eldredge et al. 1972; Eldredge 1985; Eldredge et al. 1997; Gould 2002).

Chronospecies are formed, according to those who proposed the notion (George 1956 p129), when a lineage changes sufficiently to be given a new name. In this respect, they are a temporal version of the taxonomic species concept, or even an interpretation of the paleospecies concept (Cain 1954 p106f; Simpson 1961 p166-168). A chronospecies is effectively an arbitrary division of a gradually evolving lineage (Eldredge 1989 p98), and seems to have been come to prominence as the “species concept” of “phyletic gradualism”, the target of criticism of the theory of punctuated equilibrium (Eldredge

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[107] An excellent discussion and a proposed resolution to this problem is Polly (1997). See also (George 1956; Simpson 1943; Smith 1994; Sylvester-Bradley 1956).

et al. 1972; Gould et al. 1977), although it is not often used in the interim, so far as I can tell.[108]

Let us now resume philosophical consideration of recent ideas about species.

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[108] Texts such as Mayr's and Simpson's (Mayr 1963; Simpson 1961) refer instead to "chronoclines" as the directional change of characters in the paleontological record, akin to geographical clines.

Chapter 5. Philosophical considerations

5.1. Names and nomenclature

Nomenclature is a major facet of the species problem, but this is a problem of operational convenience. Although Linnaeus thought that once identified binomials would be stable, it turns out that neither genus nor species names are in fact stable at all. In one group I examined – pinnipeds: seals, walruses and sea lions (Wilson et al. 1993; Riedman 1991) – as many as 75% of species names have been lost or amalgamated into other species, and varietal or subspecific names are equally unstable. In the Phocidae (earless or "true" seals) there are eight cases of genera being reassigned or created from existing genera out of the ten current genera (most of which are formed from *Phoca*, a genus assigned by Linnaeus himself). Therefore, there is both a problem of metaphysics in terms of how the species category changes under evolutionary assumptions, and one of conventional and operational considerations forced by the nomenclatural instability due to splitting and lumping.

I would like to distinguish diagnosis from causation; the epistemological from the etiological aspects of species and other taxa. In short, the appropriate way to approach the problem is to look at species as the results of history rather than of investigation – the "history, not characters" approach. If species are the results of a physical – that is to say, biological and causal – historical sequence, and it turns out that no empirically-based discipline can fully and reliably recognise them or talk about them, so much the worse for the science. That would be a fact about biologists and their capacities rather than biological organisms. But there is no need to be an epistemic nihilist. So far the science does very well, and the prospect of imminent catastrophic failure is remote. The point is, however, that the species problem cannot be resolved by convention, fiat, or practical decisions, for it is a problem about the organic world more than it is about the scientific community, even though there is an element of social construction in any discussion of a scientific concept (because, in order *to* discuss it, we must enter into the scientific community to some degree). How we resolve this depends a lot on what we individually conceive the relationship to be between scientists and their study objects. But we need not be scientific realists in order to think that a scientific term should have its meaning fixed by features of the objects to which it refers. All that is required is a strong empiricism, and experimentalism – the fitting of models to data, and not data to models. More abstract questions concerning the status of such concepts as "cause", "truth", "reference" and "meaning" can be bracketed off from any discussion of the causal role and referential status of a term like "species" and deferred to a more competent forum, since whatever is the case with "species", "gene", or any other disputed or accepted general scientific term, is true of all scientific terms or concepts. If "species" is theory-dependent, then so is "organism". If either are empirically-dependent, then so may be all scientific terms. If one can refer or fail to refer, then all of them can; if none can, none do.

However, terms do not exist in Plato's heaven – at least, not those derived from science. They exist in the practices of scientists in the scientific community, in scientific communication. Moreover, they do not remain constant. They can have different meanings at one time or at another. Agassiz "refuted" Darwinism by effectively arguing out of a dictionary: species are by definition static entities, and hence they could not evolve; Darwin could not therefore account for species.[109] To which Darwin reacted with a redefinition, species are temporary things. *Argumentum ad lexicon* can be countered by a different translation manual. Are Darwin's temporary species "the same" as Agassiz's permanent ones, or is Darwin just changing the subject? This could be an example of taxonomic incommensurability (Sankey 1998), though I prefer to think of theoretical terms evolving like biological lineages, at different rates to be sure, sometimes abruptly, sometimes smoothly. Since the terms are occasioned by the things they refer to, empirically or realistically, they are "the same" in some relevant sense.[110] As a child, I believed that journalists wrote journals. Recovering from the shock of what finding out, as a teenager, what they really wrote (such as our friend at the beginning of this essay) I nevertheless continued to use a term that still referred to the same entities as when I was a child. The properties I ascribed to them had changed because I had learned more. Learning more meant I could ascribe more accurately the properties journalists actually exemplify, and would no longer think of the local newspaper hack as if he or she were an essayist on a par with Voltaire or Stephen Jay Gould, but the term denoted "the same" people as it had before. It isn't important that these properties were collected under the term by my language community. A whole community could still be mistaken about the properties of that profession (as the misguided trust in journalistic integrity and objectivity in some sub-communities evidences). Likewise, scientific terms can mistakenly carry connotations, such as static existence or timeless denotation, even if we subsequently learn that the things referred to carry none of the critical properties connoted.

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[109] See above, under Darwin's conception. I owe the translation manual point to Paul Griffiths.

[110] I am therefore rejecting the Kuhn-Feyerabend notion of incommensurability, at least for some categorical terms, including *species*, in favour of a "baptismal" notion of reference. (Cf. Hull 1988c p500–502).

The study of the history and theoretical senses of a key term depends upon reconstructing the way a discipline has learned about the referents of the term. It may be that the term never had a denotation (e.g., “phlogiston”), and it may be that the consensus of the present meaning of the term is ambiguous, incomplete or inconsistent within its uses or with the data. In these cases, the philosopher of science tries, with the methods of philosophical analysis, to clarify or prune the term, or recommend its abandonment. This latter recommendation is, for example, made by Ereshevsky (1991; 1992; 1999; 2000) and others for “species”, on the grounds that it has no unambiguous referents and that other terms cover what is needed, while the implicit absolute ranking of the term is positively misleading if not outright false.

But what is this method of philosophical analysis that critics bring to bear? Is it something that only philosophers can exercise? Is it something distinct from the critical methods available to scientists and other theoretical specialists? I think not. There is nothing magical or *sui generis* to philosophical analysis, beyond it being the evolved practice of a tradition and community that has addressed abstract topics over many years. Consequently, to properly address the use of a scientific concept or term (for the purposes of this essay, I treat the two as roughly synonymous), knowledge of the science is a prerequisite, and the validity of the philosophical take on species stands or falls on that knowledge. This being said, there are philosophical concepts, arguments and considerations that are *not* available to the critical scientist, *qua* scientist (although they may be available to a philosophically-educated scientist, *qua* philosopher). Of particular relevance are the resources of metaphysics and formal logic (classes, sets, individuals, universals and particulars), and of linguistic philosophy and epistemology (natural kinds, sortals, theory-dependent objects). Hence, Michael Ghiselin in his role as analytic philospher (although he is a biologist) and David Hull (a philosopher, although he has studied a lot of biology and history of biology) have brought those resources to bear on species from a metaphysical and analytic perspective. Elliot Sober (1988) has likewise invoked epistemology to deal with issues of phylogenetic systematics.

This philosophical influence on biology is nothing new. Apart from the ubiquitous Popper, mathematical philosophers have strongly influenced the development of systematics. Russell and Whitehead’s *Principia Mathematica* inspired J. H. Woodger (1937; 1952) to recast biology in set-theoretic terms. This in turn influenced Hennig’s phylogenetic systematics (1950; 1966), and the resulting terms of grouping and order of branching that are now common property to biologists of all philosophies.

When Mill revived the discussion on logical classification, he revived the scholastic conception of the relation between *differentiae* and *relata*. Unlike the medieval philosophers, however, Mill was concerned with causal, not formal or logical, differentiae and relata. It is this tension, between wanting to carve nature at its joints and yet returning to carving language at *its* joints, that continually recurs throughout western philosophy. To pre-empt this recurrence, I have tried to consider how species differentiate *themselves*, rather than how we might do that, in the hope that systematics can retrieve the natural self-classification of the organisms themselves, but not in the expectation that systematics always will.

5.2. Speciation through reproductive isolation

5.2.1. Introduction

The modern debate over species is framed in term of several alternatives: realism/antirealism, monism/pluralism (Hull 1999; Dupré 1999), sets/individuals (Kitcher 1984), natural kinds/essentialism (Griffiths 1999) and integration/lineages (de Queiroz 1998; 1999, see chapter 6). In the case of sexually reproducing species, most of these contrasts depend upon the modes and processes that achieve reproductive isolation, and yet, the process of speciation itself is rarely discussed in detail in the philosophical literature on species, although it is debated extensively in discussions of cladism and other systematics techniques[111]. It seems obvious that if we are discussing species as entities, we would want to consider the boundaries in time and space of these entities, and so the process of speciation must be taken into account. I shall outline the most complete taxonomy of reproductive isolation, given by Littlejohn, and then propose several philosophical positions that might be given as accounts of how species as entities arise. This is, I believe, best understood as seeking to delineate when a population or lineage of populations has attained *specific-rank*; that is, when it has satisfied the criteria for being scored as a taxon at the level of species.

This will lead us to consider question of the relative rates of lineages: punctuational, gradual and saltative. We might think that if species arise in rapid and identifiable stepwise fashion, that the boundaries of specific ranking are more or less forced upon us, and so species are naturally identifiable as discrete entities, and so are real, unitary,

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[111] Nelson and Platnick (1981). Another notable exception is Kornet (1993a), whose *nodal species concept* is founded on considerations of population lineages diverging to specific isolation, and Abe and Papvero (1991) have also attempted to extend set theory to cover these cases, unfortunately for Anglophones, only in Spanish. Gary Nelson drew my attention to this work.

individual, have essences and are cohesive, or not depending on interpretation. I will argue that except in rare cases, such discontinuities are not able to do more than help taxonomists and paleontologists make less arbitrary discriminations.

5.2.2. Isolation concepts and speciation

Under the *isolation concepts* of species a speciation event is complete when reproductive isolation of the organisms in the novel lineage from the parental lineage has occurred. At that point, the isolated population has achieved specific rank. The *individuality thesis* of Ghiselin and Hull treats a lineage that is isolated in this way as a metaphysical individual, with a beginning and end in time. Proponents of *Punctuated Equilibrium Theory* have adduced this as support for their view that species (generally) arise rapidly, for if they do it then becomes easier to mark out the boundaries of new species, and so to recognise them as individuals that result from a branching event rather than as gradually changing lineages that attain species-rank through reaching a novel "grade", as in the more traditional "phyletic gradualism" approach.[112] The aim of this section is to consider whether isolation-concept species are properly resolved through rapid evolution, and what is the philosophical status of the species-rank.

Evolutionary theory generally (but not exclusively) predicts that speciation in sexually reproducing organisms occurs gradually (relative to generation time) as the founding population accrues novelties in the form of combinations of genes and traits[113], and mutations, that do not occur in the ancestral populations. Speciation through a single individual, such as happens in polyploidy and alloploidy particularly in plants, is merely the limit case. But the majority of studied cases show gradual changes, with each generation the limit of resolution.

5.2.3. Reproductive Isolating Mechanisms

There arises, therefore, a problem with isolation and individuality concepts of species. When is species-rank attained? This problem has two aspects – the first is one of actual physical processes and mechanisms; the second is a philosophical one about definitions. Let us take the physical aspect first. It involves empirical studies of enough cases to formulate an idea of how it happens in fact that populations become

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[112] E.g., Eldredge and Cracraft (1980), chapter 6.

[113] I add the rider regarding traits, since I think that the "standard" definition of evolution as shifts in the frequency of alleles is limited and in some cases misleading. Not all evolution is genetic, and not all features of organisms are determined by, or even biased by, genes. *Alleles* are alternative genes for a locus, or place in the genome, in a population. A population may have many alleles for a given locus, or none at all.

reproductively isolated and evolutionarily distinct. Reproductive Isolating Mechanisms (RIMs) have been categorised most fully by Littlejohn (1969 p461):

Table 2: A classification of Reproductive Isolating Mechanisms (RIMs)

1. Reduction of contact
(a) temporal
(b) ecological

2. Reduction of mating frequency
(c) ethological
(d) morphological

PREMATING

POSTMATING

3. Reduction of zygote formation
(e) gametic and reproductive tract incompatibility

PREZYGOTIC

POSTZYGOTIC

4. Reduction of hybrid survival
(f) hybrid inviability

5. Reduction of gene flow through hybrids
(g) hybrid ethological isolation
(h) hybrid sterility
(i) hybrid breakdown

Littlejohn also outlines the causal relationships between the reasons for isolation and selection:

Incidental action, which he ascribes to Darwin and Müller. RIMs are byproducts of selection in allopatric populations for adaptation to their local conditions.

Direct action, ascribed to Wallace, Fisher, and Dobzhansky. RIMs result from sympatric selection on premating mechanisms, such as niche occupancy.

Differential reproductive environments. Each (later isolated) population is located in different sympatric interactive circumstances (such as feeding on a particular fruit tree by tephritid (gen. *Rhagoletis*) fruit flies in California which fruits at different times even though the initial population is in the same region[114]). This causes premating isolation when the populations encounter each other.

General genomic interaction. Populations that sympatrically interact will be selected for genetic compatibility within, and incompatibility between, the populations. Littlejohn excludes this from being a case of selection for postmating isolation.

Littlejohn does not discuss random genetic drift,[115] since the focus of his paper is the role of selection in speciation. Reproductive isolation can occur through stochastic sampling of alleles, and it should therefore be included under incidental action.

5.2.4. The boundaries of species in time

At what point, given these modes and mechanisms of speciation, is speciation complete? In hindsight, we can identify a geographically isolated peripheral population as the founding point of a novel species, but nobody believes that the new species exists until at least one of the RIMs is in place. Some authorities reject the sufficiency of ecological or temporal isolation, others deny the sufficiency of ethological or morpological isolation. In other cases, the non-existence of certain RIMs is insufficient to *prevent* assignment to different species: lions and tigers are genetically and reproductively compatible in captivity, although in the wild they differ ecologically (savannah versus forest) and ethologically (lone or pair hunters versus social hunters, with mating behavioral differences).[116] They are considered "good" species because they have these premating RIMs. Other species incorporate a great degree of various RIMs *within* their metapopulations[117] such that if they were to lose intermediates they would be identified as distinct species: they include a high degree of regional variation or varietal races, and are sometimes called *racemes* or *Rassenkreise* because the varieties exhibit incipient premating RIMs but are insufficiently separated between

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[114] This case, which has long been a standard example for sympatric speciation, has now been well-studied by Berlocher and colleagues, to the point where it is widely accepted as such a case (Berlocher 1999; 2000; Filchak et al. 2000; McPheron et al. 1997; Smith et al. 1997; Katsoyannos et al. 2000).

[115] *Genetic drift* is a concept in population genetics due to Sewall Wright. It rests on the size of the populations. In large populations, it may be that the probability of genetic alleles being mixed is roughly equal for each allele, and so the frequencies of alleles will be due to selection of each allele. In smaller populations, random sampling effects may lead to the *fixation* (100% frequency) or elimination (0% frequency) of an allele with no selection of it at all either way (see Sober 1984).

[116] Lions now have a much restricted range, isolating them geographically from tiger species as well, but in the not-too-distant past this was not the case. Humans appear to have been the reason why lions and tigers are now in separate ranges.

[117] A *metapopulation* is the totality of all populations of a taxon, usually a species, but also of subspecific and supraspecific taxa.

adjacent forms to be actually isolated. As noted above, Mayr originally (1942) included the phrase "actually or potentially isolated" in his original formulation of the biological species concept in order to exclude geographical isolates that might, when sympatric, reproduce together, and the same point might be extended to cover other premating RIMs.

Postzygotic, and therefore postmating, RIMs have also been challenged as sufficient conditions for specific assignment, which as Littlejohn makes obvious by his use of the relational term "reduction"[118] in hybridisation, is not an absolute isolation but a matter of the probability of producing viable progeny that persist into the F_2 generation and beyond. In fact, we cannot say that cross-fertilisation, in the sense of the transfer and mixing of genes, is ever absolute. Even between a human and a mosquito, the probability of genetic exchange, mediated via retroviral transfer, is not zero. It may not be enough to count as reproduction, but the difference is a matter of degree. If there are, as is currently thought, around 40,000 functional genes in the human genome, then the degree of the successful insertion into a gametic cell of a single gene this way is 0.0000025, compared to the "normal" reproductive fusion in human reproduction of 0.5. A very great difference in terms of orders of magnitude, but not a qualitative or absolute difference. In fact, somewhere between 5% and 40% of the average mammalian genome is endogenously introduced in this way, although most of it, if not all of it, in the cases studied is non-functional (Hohenadl et al. 1996; Leib-Mosch et al. 1995; Liao et al. 1998; Patience et al. 1997; Sinkovics 2001; van der Kuyl 1997).

5.2.5. How much difference?

This leads to a philosophical aspect of the species problem: how much difference and what kinds of isolation are sufficient to mark out a new species from its ancestral taxon? This has three distinct subordinate aspects:

Causal: How much reproductive isolation is sufficient to **make** it a different species?

Metaphysical: When is an incipient species a distinct entity? This is a question of boundaries and structure.

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[118] Reduction of what? The "norm" of cross-reproduction? What is the norm? If he means the usual frequency, then this is a bit circular, since we can only observe that *post hoc* and it cannot be used to define "good" species, but if he means the propensity for cross-reproduction, then we are going to find that most fertilisation "attempts" are unsuccessful even in "good" species, since most gametes fail to result in a viable progeny, and most zygotes die *in utero* in many species. Griffiths and Gray (1994) make this point about norms with respect to the "purpose" of acorns from American oaks, most of which rot or feed chipmunks.

Epistemological: How much isolation or difference is necessary for us to **know** and **identify** that a population is a distinct species?

These are the questions that evolutionary and ecological accounts of species force upon us, and scientific and some philosophical discussions of speciation have tended to shift between these three different questions. For taxonomists and practical biologists, who must work with the data and techniques at hand and make inferences from them, this is entirely justifiable, but the philosophical issues are not resolvable in this way.

It appears that there are no necessary and sufficient conditions for either assigning specific-rank, or for being a species. Any population that exhibits several RIMs may be accounted a species even if it fails to exhibit all of them, and sometimes even if it fails to satisfy some core set of premating or postmating conditions, which we shall discuss later under the heading of "family resemblance predicates". However, typically the RIMs are required to be endogenous biological processes or properties (Ayala 1982) – for example, geographical isolation doesn't count, for two reasons. First, it is not a property of the organisms or the populations they are members of, and second, we often cannot know whether the two isolates are interfertile until they are brought back into sympatry.[119] Hence, geography is excluded as neither causally nor epistemologically sufficient. Similar considerations apply to morphological RIMs, unless it is the morphology of sexual organs (as it is in many plants), in which case it becomes an example of RIM case 3. In effect all of the RIMs can be, even if they are not usually, insufficient to mark species-rank, and all of them *can* be sufficient if they are marked enough.

Even geographical isolation **could** be considered to be enough in conjunction with other RIMs that on their own would be insufficient. Under Developmental Systems Theory (DST, see Oyama et al. 2000), organisms inherit all their developmental resources, including the ecological conditions in which their "normal", or wild-type, phenotypes develop. So far from being an exogenous non-biological property, DST treats some or all of the relevant ecological and biogeographical resources of a deme as necessary to produce the standard lifecycles and properties of its organisms.

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[119] This is not strictly accurate – we can rule **out** interfertility if the karyotypic or genetic compatibility can be ascertained to be low **enough**, e.g., through DNA hybridisation. But there will be enough cases where we cannot predict this. Chromosome number and other genetic measures are not entirely reliable indicators of the likelihood of interfertility, and we are often surprised, particularly in plants, but also in cases like horses and their close relatives, where chromosomal counts vary wildly, but the species may still hybridise.

Biogeography may very well involve an environmental range or niche, some of which may be constructed by the organisms themselves, that determines enough difference to mark out distinct species, even if reproductive isolation is incomplete (see Sterelny 1999 for a review of the ecological aspects of species). Mayr's original formulation of potential isolation tried to exclude such cases, but a DST theorist could dispense with that requirement, so long as differences in ecology had some appreciable effect upon phenotypic expression, including mating behaviours. Developmental norms of reaction have been treated as properties of entire species, so that a plant that grows as a bush in one climate or location but develops in a spindly and sparse way in another (or even has entirely different morphological and ecological properties, such as certain cactus-like plants in Hawai'i) is treated as one species with different morphs and lifecycles.

It therefore seems that isolation concepts of "species", and that includes the recognition concept of Paterson, are cluster concepts of definitions and prerequisite conditions.

5.2.6. Criteria of Individuality

If the causal mechanisms that result in species-rank are manifold, with neither necessary order of attainment nor essential combination, we might wonder about history-dependent notions of species such as the individuality thesis of Ghiselin (1974b; 1987; 1988; 1997) and Hull (1976; 1978; 1988c; 1992b). In this account, species are metaphysical individuals, and may also be causal individuals. How does such a lack of core criteria for the process of complete speciation affect this view?

We may consider four possible mutually consistent accounts of the development of species as entities, two of which have to do with the scoring or ranking of a nascent population or lineage as a species, and two of which are accounts of the *property* of being of species-rank.

Emergence. Specificity is an emergent property, a qualitative phase transition in rank that occurs when sufficient RIMs are in place (Mahner et al. 1997).

Supervenience. Specificity is a multiply-realisable supervenient property of populations that accrue RIMs.

Fuzziness. "Species" is a fuzzy rank that is increasingly attained as RIMs are developed.

Arbitrariness. Specificity is attained when some arbitrarily chosen boundary of sufficient difference is crossed (Dawkins 1986).

We are able to tell when a lineage is ended in the case of extinction. But when a species is being born, or in the case of anagenetic[120] change when one species or part of a species evolves into something else continuously, the boundaries are not clear. We might say that at some point the speciation is "good" and a species is distinct from the ancestral species, and that in the period of being *in statu nascendi* rank is indeterminate. In this case, the boundary would not be instantaneous, but would be of the form $t - dt$; that is, the boundary would have depth.[121] This would be analogous in time to a geographical gradient such as a ring species – at the end-points of the ring, there is reproductive isolation, but the intermediate populations are reproductively transitional. Such vague boundaries call for explanation, and we must seek to characterise the sorts of entities species are.

The first option is popular in artificial life and artificial intelligence writings – emergence. In that context it means roughly that some property or behaviour of a system arises out of less complex subsystems and their inter-relationships. The notion that specificity is an emergent state implies that some "critical mass" is reached that is enough to cause differences that slightly less difference does not (Mahner et al. 1997). It rests on the claim that the effects of differences at the genetic and other levels of biological organisation accrue in a non-linear way. For example, a peripheral isolate population may be on the tail of the distribution of some trait variances (including genetic variances), but still be insufficiently distinct from the rest of the species to count as a novel species in its own right. All that might be required to kick off a series of radical changes is allopatry, cessation of gene flow, or a novel ecological niche. None of these changes needs to be adaptive, although they all could be. Emergence is sometimes tied in with the untenable ideas of Goldschmidt's "hopeful monster" theory of radical genetic reorganisation (Goldschmidt 1940). However, recent work, particularly on regulatory (timing) genes such as *Hox* or *Pax*, implies that we cannot reject out of hand that qualitative phase shifts do occur.[122] If the variables that differ between populations (frequencies of alleles, pleiotropy, and ecotypical norms of

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[120] *Anagenetic* evolution is gradual evolution, not in the sense of a steady rate but in the sense of attainment of a new grade such as a morphology or ecological niche by a lineage. It contrasts with *cladogenetic* evolution, or branching evolution, which occurs through a splitting of a new lineage from the parental lineage. A third pattern of evolution is *stasigenesis*, which is the persistence over long evolutionary time frames of a species' morphology or type (Rensch 1947; 1960).

[121] Cain (1954 p102) calls this boundary the *time-quantum* of biospecies, which, if two populations share it, is enough to mark them as different biospecies.

[122] The literature is enormous and growing. Here I list only a few references (Abzhanov et al. 1999; Gibert 2002; Knoll et al. 1999; Kirschner et al. 1998; Zakany et al. 1999; Panganiban et al. 1997; Meagher et al. 1999; Shubin et al. 1997).

reaction) do not sum additively but nonlinearly, then the **removal** of contact or some other constraining condition might result in cascades of population-level changes that result in a distinct taxon.[123] So far, attempts to show that this is a common mode of speciation have not borne fruit, but it may occur in cases of polyploidy and karyotypic reorganisation, or in cases of microsatellite tandem repeats (the multiplication of a gene) as well as regulatory gene shifts. Insect pupation, for example, appears to have evolved through heterochronic shifts in endocrine expression.

The supervenience thesis is that "being a species" is a condition that can be multiply realised – there is nothing essential to the causes of species-rank so long as there is, in the end, reproductive isolation. Hence, the beginning of a species occurs when the **outcome** of isolation is attained, however that is specified. Since **this** sense of isolation is dependent upon the phenomenal behaviour of populations, we may choose to locate the birth of a species at geographical isolation rather than at the achievement of any post-mating RIM if it is observed that in later sympatry the two lineages remain distinct for whatever subsequent reason. This is, of course, an arbitrary choice we make. Equally arbitrarily, we may instead require sympatric reproductive isolation, with the now-common objection that this means we cannot really tell if two species are distinct if they are allopatric. Or we may choose to require karyotypic or developmental incompatibility (postmating) incompatibility, which would necessitate the taxonomist using breeding experiments or *in vitro* fertilisation techniques to discriminate taxa.

Supervenience and emergence are both drawn from the discipline of the philosophy of mind and its experimental cousins. Neither should be confused with another philosophy of mind doctrine – epiphenomenalism. In the context of the species problem, this view would have species-rank as an illusory effect of other things, such as the evolution of genes or traits (Eldredge 1989) and actual processes that occur at the level of organisms and demes. Both the supervenience and emergence hypotheses assume that species are real entities and seek to account for that reality. Epiphenomenalist accounts deny the reality of species. They are, in effect, conventionalist accounts.

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[123] Mayr seems to have had some similar notion (Mayr 1963) when he proposed that cessation of gene flow would be enough to kick-start speciation through a "genetic revolution", but more recent work suggests that this does not happen. Other candidates for emergence include Waddington's notion of "catastrophic" evolution through genetic assimilation (1968, in Waddington 1975), in the days before chaos theory became popular, but he consistently presented such state-space transition accounts since the 1940s.

Fuzziness of specific-rank is like the continuous function of a fuzzy logic control circuit of a modern refrigerator – there is no single point at which the thermostat that is operated by a fuzzy logic circuit is switched to "cold", but it gets progressively, and non-linearly, colder in response to internal temperatures. Being of specific-rank may be such a continuous function without there being any discrete boundary to be crossed. In fact, it may be the outcome of many such functions, which would bolster the supervenience hypothesis.

This leads us to the fourth option: that species-rank is arbitrary. By this, I do not mean that specific-rank is subjective, conventional, or capricious – the "a species is whatever a competent taxonomist chooses to call a species" definition. The characters, both genotypic and phenotypic, that form the basis for diagnosis are real and objective enough, and the choice of suitable and relevant characters for diagnosis – the choice of data sets – is not simply a matter of personal preference. At worst that choice is a matter of commensual agreement by a community of experts, and at best it is a choice forced by the discreteness and observable roles of the phenomena. What is meant is that the attainment of **enough** isolation or difference is a function that might be considered satisfied in different ways for the same data.

Suppose we specify that the reduction of crossbreeding success to 1 in 100,000 attempted matings, or better that 1 in 100,000 cross-fertilisations will result in viable and fertile progeny, is sufficient to mark out specific-rank difference between populations or types. Why that value and not some other?[124] We cannot require an absolute probability of 0 for two reasons. We know never that the frequency of hybridisation really **is** 0 for the duration of coexistence except in some rare and generally artificial conditions. Also, given the mechanisms of horizontal genetic transfer that are not dependent upon the reproductive organs of organisms, there is always some probability that cross-fertilisation can occur. So, if we can choose one value as significant, why not others? In this sense, isolation is arbitrary, although this only becomes a real problem when choices of arbitrary limits give greatly conflicting results. If there is little actual cross-fertilisation, then the difference in an order of magnitude of hybridisation may not cause us to revise our taxonomic boundaries much (while in other cases, no choice of threshold will give the same taxa as any other, in which case we have real problems).

We therefore have to ask in what way species are individuated. Evolutionary lineages are not clearly defined, and the "clade" notion of species is an abstraction formed by

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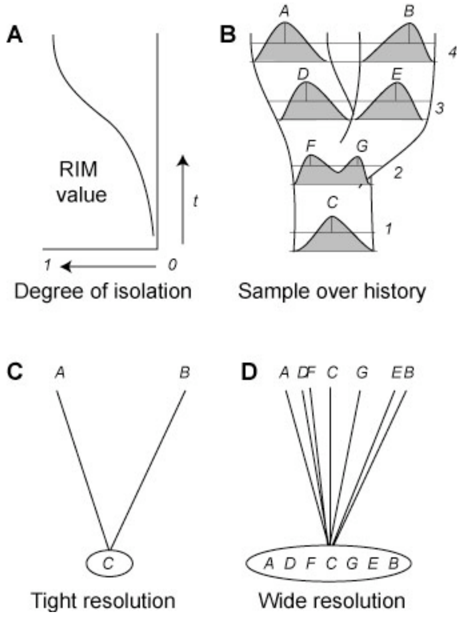
[124] We saw Darwin and Wallace raise this very question above (chapter 3).

sampling the character states of a population (or metapopulation) and comparing that sample with a similar instantaneous sample from another. These states are either very similar or they are not.[125] If they are not, then we draw a straight line between the ancestral state and the derived state and mark out species in that way, but the history from ancestral to descendent state may involve continuous and irregular transformation. The individuality of a taxon in this case would therefore be an artifact of the "depth of field" in which the sample set was collected (Figure 13). As the temporal depth of sampling is broadened, the sharpness of focus is lost. Instead of distinct and discrete character states, we approach a widening set of more or less continuous character state distributions.

Figure 13 – Resolution of isolation



This illustrates both the fuzziness of individuation (the RIM approaching 1 in (i)) and the arbitrariness of delineation relative to sample depth.[126] A cladogram formed in this way is hence termed "unresolved". This is an epistemological problem, not an ontological or causal problem. But there are corresponding causal questions and resultant metaphysical issues. Let us take the causal first.

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[125] Cladistic states are usually discrete values. Since actual states generally vary more or less continuously in natural populations, the hope is that the sample set is close to the mean or the mode of the actual distribution of the population. This introduces one necessary simplification that permits "similarity" to mean "within the same interval on a bar graph". See (Rae 1998).

[126] If the time index of each sample is unknown, or is a hypothesis to be tested, then the cladogram must represent each sample in its sibling relationships to the other samples. Only if the cladogram can be time-oriented by sample can it become a phylogeny. (See Nelson et al. 1981; Smith 1994).

There is considerable debate over the causes of speciation. Most speciation is allopatric, and the emergence of RIMs is consequent upon that, but there are now many credible models of sympatric speciation events, the most famous being the cichlid fishes of Lake Victoria. Here there are no geographical boundaries, since any mechanisms such as temperature gradients or feeding ethology or ecological niche must precede speciation, and are therefore premating RIMs. Heterozygote fitness in such cases is generally lowered, and so disruptive selection stabilises the phenotypes, including endogenous RIMs. Other speciation mechanisms include *ploidy*,[127] and *karyotypic* speciation.[128]

And yet, for every causal mechanism that has been proposed, there are cases that are counterexamples to the sufficiency of this sort of mechanism. Nevo has studied the Israeli Naked Mole Rat[129] which has several karyotypic races, several of which are mutually infertile, and which has existed as a reproductive metapopulation for over three million years without speciation, well beyond the threshold for speciation by karyotypic RIMs. A single bulldozer might very well make two species where one now exists, without any changes to the surviving populations (figure 14). Viable polyploids can breed back into the parental populations in some plant examples. Sympatry usually leads to a distinct **lack** of speciation, although it can lead to geographical races that are better adapted to local conditions (which can be **very** local indeed. Geographical races in snails can live no more than a few hundred meters apart). And allopatry, even of long duration, is no guarantee that reproductive isolation will be attained.

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[127] The multiplication of genomes (polyploidy), or the hybridisation of genomes across taxa (alloploidy), to form, almost instantaneously, a novel and isolated lineage. Selection follows this form of isolation, as it does in the case of allopatric speciation, to stabilise the novel phenotype and genotype.

[128] Chromosomal rearrangement, which creates isolated races that are less interfertile (postmating RIMs), as in the case of the central Australian morabine grasshoppers studied by MJD White (1978).

[129] *Spalax ehrenberghi* (See Nevo 1969; Nevo et al. 1972; Nevo, Bodmer et al. 1976; Nevo and Heth 1976; Nevo, Filippucci, Redi et al. 1994; Nevo, Filippucci, and Beiles 1994; Nevo et al. 1999) distinct from the famous Ethiopian Naked Mole Rat that is the only known eusocial, colonial, caste mammal known (Dawkins 1989 p313).

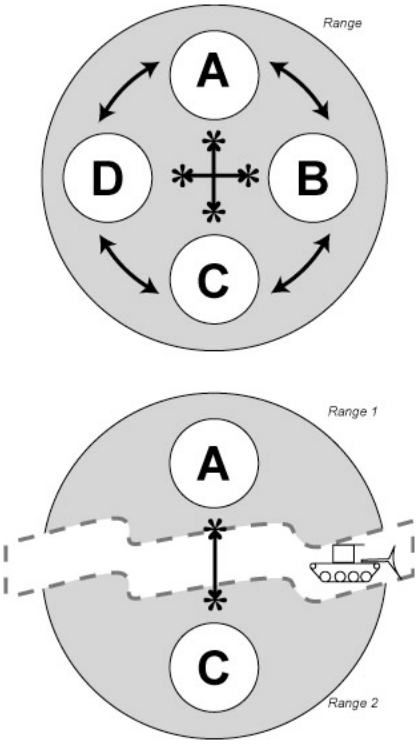

Figure 14 – Mole rat races

A stylised version of Nevo's naked mole rats. Each chromosomal race (A–D) can interbreed with the immediately adjacent race, but not with those opposite. If the races were isolated geographically as well as chromosomally, a single bulldozer could disrupt the range, destroy the intervening races, and create two new biospecies in a single instant.

So, it seems that speciation is not a monotonic process. These causal variations lend support to the supervenience thesis – speciation is a multiply-realised effect (that is, it can be achieved in many different physical ways). Supervenient properties are properties that may have many different underlying causes, but which will be realised identically in physically identical circumstances. According to Sober, fitness is a supervenient property (Sober 1984), and in the philosophy of mind, so is consciousness. Being of species-rank is a supervenient property in this sense. If two populations are physically identical, then we should expect that they will speciate identically from the parental metapopulation.[130] The problem with the supervenience thesis, both here and in the domains of selection and mind, is the complexity of the systems, and the nonlinearity and sensitivity to initial and boundary conditions. Very minor differences will cause qualitatively large differences in outcome, and conversely, many systems are buffered to change, so that large differences lead to little or no difference of outcome. It is virtually impossible before the event to ascertain that the organisms' developmental and populational structures and processes, and the

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[130] Neil Thomason offers genetic drift as a counterexample here, which is a stochastic process. Of course it is true that drift involves sampling errors in populations, but the fact remains that any two **identical** populations (i.e., with the same samples of the parental genepool) can be expected in identical circumstances to evolve in the same manner. However, this depends on what we mean by *identical.* Very small differences can magnify under reproduction and the accrual of contingently different events into large differences. How small is small enough to not make a difference is a matter of empirical investigation.

environments in which they exist, are identical in all relevant senses.[131] Due to these complications, the supervenience thesis is merely notional, and is impractical to test.

The emergence thesis is perhaps easier to test, because the causes of a given speciation event can be observed and analysed to see whether the differences are chaotic in the relevant sense, but it requires the good fortune to sample a population before, during and after speciation. However, all that is required to establish that *some* speciation is emergent is a single observed case. What would *count* as an emergent speciation, though, and indeed what counts as the threshold of a novel taxon is not so clear. Consideration of the concept of emergence itself demonstrates this.

An emergent property, as proposed by J. Smuts, C. Lloyd Morgan, R. Alexander, A. N. Whitehead and others all the way back to J. S. Mill and W. Whewell,[132] is one that cannot be predicted from knowledge of the properties of the components of the entity that has it. The classical illustration is the wetness and fluidity of water. These properties are unpredictable from the knowledge of the properties of hydrogen and oxygen molecules, Mill said. But this unpredictability is surely due more to the computational load on a limited but well-informed physicist. With the laws of molecular attraction, thermodynamics, and some general equations governing the behaviour of an ensemble of points in a dynamic system, it is in principle possible to describe and predict how water molecules will behave *en masse* from just such a knowledge of the elemental atoms (which will have to include isotopes and so forth if the prediction is to be complete). From just this general and basic knowledge, such predictions about the microscopic structure of water in biological systems are being made even now.

Any impossibility of prediction in fully-determined systems is a *practical* impossibility, akin to predicting the behaviour of a non-linear ("chaotic") deterministic system. It represents, therefore, an epistemological barrier.[133] For this reason, with complex phenomena it is a better bet to first observe and try to retrofit equations that model or

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[131] An exception is the case in which the "same" species recurs through repeated instances of alloploidy. Also see below, under "Classes, sets and individuals" for the *respeciation problem*.

[132] The history of emergence is well told by Blitz (1992; See also Grantham 1995; Michod 1999; Morgan 1923; Peters 1995; Quastler 1964; Sabates 1999; Stidd et al. 1995; Wimsatt 1996; 1997).

[133] See Dupré (1993) and Rosenberg (1994) for a discussion of this sort of impossibility. If physical systems are nondeterministic, of course, then the impossibility may be formal as well, but in the case of biological systems, it seems to me that this is the least of our worries in biology, and that in macroscopic systems, stochastically distributed propensities to behave in given ways is sufficient to make prediction formally possible, within certain error limits.

approximate what is observed. It requires less cognitive investment and provides a higher return rate.

Consequently, many decisions as to what count as "emergent" phenomena are sensitive to, in part, the amount of cognitive computational capacity available to the observers. At one time, Newtonian orbits for more than two bodies were intractable. Today, they are a matter of automated number crunching. It may therefore be that the achievement of taxonomic difference represents the passing of a computational threshold, rather than a mechanism-based one. If this is so, then emergence collapses into arbitrariness in the absence of a theoretical account of phase shifts in that respect. As complex problems of isolation and probabilities of successful mating or ecological persistence of populations are attacked, the threshold of emergent differences might recede under novel techniques and better experimental and field observations.

Supervenience suffers the reverse difficulties. Any assertion of supervenience requires that the supervenient property would have been attained if the lower-level componential properties had been the same, as well as in other, perhaps specifiable, perhaps not, ways. However, counterfactual knowledge involves knowledge of unrealised states ("possible worlds"), and the extreme sensitivity mentioned before to initial or boundary conditions makes that knowledge devilishly hard to come by. In "butterfly effects", almost unmeasurable differences and contingencies can cause longer-term differences such that we could not truly be sure if the property – species-rank via reproductive isolation – would have occurred in an "identical" situation, and so any probability assignments will be subjective.

In conclusion, then, the boundaries of individual lineages are both fuzzy and arbitrary, although the criteria used apply to objective and measurable phenomena. Claims of emergence are subjective, relative to the "surprisal" value (Dretske 1981) of the qualitative change observed. Supervenient speciation is impracticable to test, and isolation concepts are therefore also arbitrary. This extends to claims of division on the basis of rates of change. Even in the extreme case of allo- and polyploidy, speciation is only abrupt relative to observers –that is, not every case of ploidy difference results in a novel species and stabilising selection and backcrossing means that several generations are required in order to assess whether isolation, and therefore speciation, is complete.

5.2.7. Species-rank as an evaluative property

It has been observed that being a species is like being the Thirty Years War.[134] Any newspaper that declared in its headlines in 1618 “Thirty Years War Begins” would have been stating a nonsense. Not until the war ended could it have made sense to call it that. Speciation is like the Thirty Years War. The event is not recognisable until much later, when isolation is sufficiently completed. Being a “founder population” or, in the relevant cases, the “first” member of a novel species, is a retrospectively evaluative state. Membership of the group at t depends crucially on what happens at $t + n$.

Yet, whether or not the lineage ends up being a permanent species or just a temporary isolate or subspecific variety, the physical processes are identical in kind. It follows that species-rank is not a physical property. It is instead an evaluative property based upon and relative to the criteria chosen for “significant difference” by the classifier. It depends upon the position in time of the observer and the evidence available. Incipient species are neither – at t – new species nor yet full members of the parental species. The answer to the question, “are they species in their own right?” before isolation is “complete”, is neither yes nor no but “unresolved”. Of course, the lack of resolution is not an even 50% necessarily. We may assign them a higher or lower (Bayesian) probability of attaining species-rank according to how long the isolating processes have been in play and how many RIMs have been accrued and how fully. Assignment of species-rank for *in statu nascendi* populations may range from mere possibility to high probability.

The observer’s **objective** situation relative to **objective** states of affairs and phenomena makes it unreasonable to claim that species are mere constructs. Similarly, the fact that species-rank can be assigned only in retrospect, no matter how well-founded we may have been in prediction before the event or well-informed during it, makes it impossible at the time to locate exact boundaries to specific individual lineages. Until complete, the boundaries are unrecognisable, because they are not, in fact, boundaries then. We know this, because experience has taught us that small differences can sometimes count and large differences can sometimes not count in defining specific boundaries. The need for these boundaries is sometimes asserted for conceiving species as individuals, because as individuals, species have a temporal beginning and end, and in phylogenetic conceptions of species the speciation event itself is sometimes

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[134] Neil Thomason suggested this example. In a different context, Hull has a similar illustration of a newspaper declaring that World War I had just broken out (Hull 1988c p127).

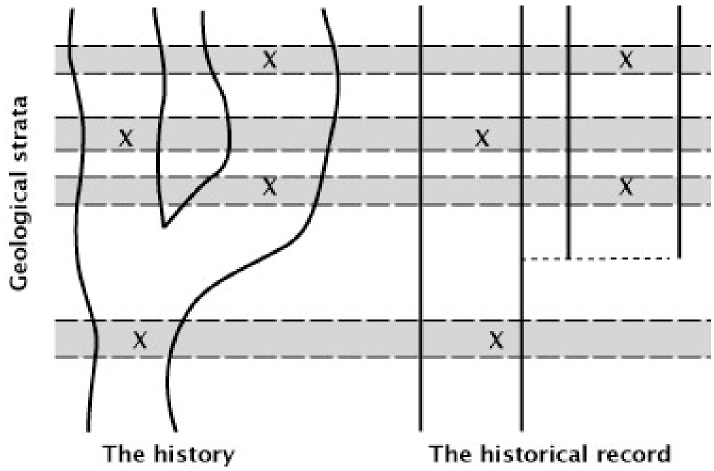
held to extinguish the parental species. If boundaries are vague, fuzzy or retrospective, it may seem that species cannot be individuals.

But canonical individuals, that is, human beings and things like them, also have a fuzzy boundary on various measures of different properties (i.e., maturation, biological separateness, viability, cognitive and motive abilities, ethical responsibility, etc), although they are not all located at the same stages in development. Should this be a difficulty for the individuality thesis? It would seem not, although it must be understood that while the individuality thesis is consistent with the way species come into being, it remains a metaphysical stance rather than an empirical and operational notion.

Others wish to establish fixed and essential criteria for mereological inclusion in a species; a specimen is part of a novel species insofar as it satisfies criteria that are definitive of some other species than the parental one. Sharp boundaries would help to establish these criteria, because we could observe when differences caused isolation and identify what those differences are. Fuzzy and arbitrary criteria make this impossible in some cases. No such fixed criteria are available that are not dependent on observer-dependent surprisal values. Qualitative difference is either an arbitrary threshold of the biological model chosen (gene-flow, mate recognition, ecological niche, etc) when non-linear rates of change are unexpected from a linear, additive, perspective, or it is the result of sampling intervals.

For example, consider punctuated equilibrium theory. On this account, most, if not all, speciation occurs rapidly, followed by predominant stasis for the remainder of the duration of the lineage. Since paleontological deposits are rare, the fossil record shows a number of sudden shifts in morphology. Each deposit therefore records an instant in the lineage's history. Any gradual variation in the morphological profile of a population is most likely to occur between fossil depositions (figure 15).

Figure 15 – History versus records of character evolution



Consequently, the discontinuity between the parental and the daughter lineages is, to some degree of error in the metrical observations, absolute. Similarly, in the absence of finer resolution in datasets on Recent species, distinctness may appear where there is continuity in the underlying biological mechanisms. With the finer resolution of molecular data, what appears to be distinct at the macrolevel is "the same" at the microlevel. Minor genetic differences, as we have noted, can separate "good" species as well. For example, on morphological, ecological and ethological grounds, the highland and the lowland gorilla populations have been considered a single species. In the light of recent molecular analyses, the splitters appear to have won out, and each is now considered a distinct species.[135] In the end, we are still left wanting a "scorecard" criterion of species-rank.

5.3. Class versus set versus individual

> … the analogy between a "species" and an "individual" is a very incomplete one. The word "individual" denotes a concrete whole with a real, separate, and distinct existence. The word "species," on the other hand, denotes a peculiar congeries of characters, innate powers, and qualities, and a certain nature realized indeed in individuals, but having no separate existence, except ideally as a thought in some mind. (Mivart 1871 p13f)

Considerable ink has been employed to argue whether species are classes or individuals. The debate continues even today. Hull (1980) argued that species cannot be sets, because sets cannot be historical; that is, they cannot change over time, and species do. Kitcher (1984) on the other hand, argued that they can, and do. This is a complex issue that we should discuss briefly, given the confusions that result from it.

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[135] Most consider them distinct species, *Gorilla gorilla* and *Gorilla beringei*, (Groves 2000; Jensen-Seaman et al. 2001; Taylor et al. 2003) but see Stanford (2001) for a dissenting (lumping) opinion.

When people say, as Ruse does (Ruse 1987; 1998), that species are classes, they typically mean that species are natural kinds in an intensional sense. Species are things that share some set of criteria that function as the essence of the species. It might be a genome, a wild-type, or just some simple morphological criterion, but all members of the species have that set of properties. Hence, says Ruse, we can regenerate *Tyrannosaurus rex* because if we have the genome and a suitable egg, we have the essence of that terrible lizard. According to Hull, though, if we have recreated a dodo by breeding it from its ancestral pigeon stock, it is not the same species as *Dodo ineptus*, destroyed by animals introduced by sailors on the Indian Ocean islands where it once lived. Species, like people, can only be born once – everything else is a knock-off, like a Tiffany-style lamp is a knock-off of an actual Tiffany lamp (with a difference in the price tag to match, Hull 1988c p78).

A problem for Hull is that species have been observed, under certain conditions, to evolve more than once – in plants which can duplicate their chromosomes to "instantly" form new species, or in fishes which independently evolve deep water morphs in different lakes, and which will breed preferentially with similar morphs in other lakes – I call this the *Respeciation Problem* (Turner 2002). Moreover, the new individuals formed this way are interfertile with their predecessors, and fold their genetic complement into that of the established lineages. How can Hull deal with this?

One way might be to take the Hennigian approach (Meier et al. 1997) and say that the two new species are extinguished when they merge and form a new one. Like the application of the Hennig Convention in cladogenesis discussed above, this is a purely nomenclatural solution to an ontological problem. Yes, the new species has a somewhat different character (unless the modifications are infinitesimally distinct from each other), but if, in order to save the individuality thesis one has to say that every time a change occurs you have a new individual, the thesis borders on banality. Anyway, it is not Hull's (1988c) solution; he wants to be able to restrict species in time, but not to reject their mutability. In a discussion using the Hobbesian Ship of Theseus example, which being rebuilt ends up entirely replaced, and then duplicated from the older parts, Hull proposes that there is no fact of the matter which is the "same" ship, but that this does not mean Theseus's ship is a universal.[136]

So perhaps here Hull might wish to treat species as having vague boundaries in time – there is a point x at which there is no species A, and a point y where there is, and in

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[136] See Ghiselin's (1997) argument, Lee's and Wolsan's view (2002) and Thomas Reydon's forthcoming paper in *Biology and Philosophy* on this subject.

between we have a vague border where it is ambiguous whether or not *A* exists, or whether the two still-distinct prior lineages *M* and *N* are *A* or not. After all, this is the case when we discuss nascent species anyway. But this seems counterintuitive as well – if ontology is what we are discussing, then each lineage, say *M*, is identical physically to *A*, and all that is missing is a date indexical. This seems odd.

For this reason, Ruse wants to treat *A* as a class which can be instantiated in actual historical entities or processes as many times as needs be. It avoids the respeciation problem. The disagreement lies in different answers to the question, "what do we need to capture in our metaphysics for things that can arise more than once?" Consider a different problem – that of the identity of Individual[137] persons. We typically say of an Individual that he or she has some *terminus a quo* at a particular point – it might be conception, or nativity, or some point of development. In taxonomic terms we would say that this Individual is monophyletic, being the ancestral cell population and all descendent cell populations. But it is possible, in biology, for an Individual fetus to be a mixture of two genetically distinct fertilised cells or zygotes; these are called *chimerae* after the mythical monster. Are **these** Individuals in the ordinary sense? To make matters worse, what if one zygote had been commenced *in vitro* some years before the second and frozen in nitrogen before it was fused with the other? What **then** is the *terminus a quo*?

If we want to capture this in our definitions of what it is to be an Individual, then we have the same sorts of problems for identity of organisms that we have for *species*, and how we deal with them will depend largely on how we think meaning inheres in such terms. We might say that to be an Individual, say Socrates, to use the classic example, is to instantiate Socratic properties – that is, to treat Socrates as a class that can be instantiated in many different individuals courtesy of some science fiction replicating machine. That would be what Ruse would say about species. Or, we could say that there is only one Socrates, who was born, perhaps chimerically, at a relatively exact period, only in this case the chimeric Socrates was "born" or "begun" in an extended process unlike the monophyletic Individuals we usually see. Even if the unfused zygotes were viable and developing organisms, we might say that they ceased to be upon being fused; and so on for all the exotic cases we might imagine.

Chimeric species are not a counterexample to our intuitions of what species are, metaphysically speaking; they may extend our conception, or we might (arbitrarily) exclude them, but I see no reason to reject the individuality thesis because of these

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[137] Capitalising the word "Individual" to avoid confusion with the metaphysical notion being discussed.

cases and be forced to instead adopt a "natural kind" class conception of the species categorical term. What we choose as the boundary for the term may be arbitrary, within limits, or it may be forced by the biological realities, but species are still, in Caplan's (1980) phrase, déclassé.[138] Species **are** individuals. Let us now consider what that actually means.

5.4. Individual or concrete

There is a major equivocation on the term *individual* that causes some confusion in the literature. There are three kinds of individuals that one finds in the discussions, and they are not always disambiguated by the authors.

Metaphysical or logical individuals: these are entities that are not classes, i.e., which are particulars. A class is defined (in my preferred metaphysics) as the denotation of a non-restricted predicate. The metaphysical meaning of "individual" sensu Ghiselin-Hull is that a taxon (in particular a species) is a *concrete* object not an *abstract* one. Concrete objects are spatiotemporally restricted, or, to put it another way, have an indexical space-time coordinate or range of coordinates. Abstract objects do not have such an index (Zalta 1988).

Functional or cohesive individuals: these are objects that happen to have some common systematic set of interactions (either temporal or formal). This is the sense of "individual" that applies to a Mayrian biospecies – his notion of gene flow as a homeostatic mechanism that maintained the isolating mechanisms of related populations within a species suggests that he thought of species as functional units .

Phenomenal individuals: these are objects which can be observed in their entirety as entities. This is very often scale-dependent (a colony can look unified at one scale and appear as a multiplicity of objects at a finer scale).

Now, this gives us a field of eight options: a putative entity can be one of the following (where 0 is not-individuated and 1 is individuated, ordered on binary numbering):

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[138] Caplan, however, thinks species **are** classes.

Table 3: Varieties of senses of "individual"

Individual type	*Meta*	*Cohes*	*Phenom*
A. Pure abstraction	0	0	0
B. Phenomenal individual	0	0	1
C. Integrative individual	0	1	0
D. Phenomenal, Integrative individual	0	1	1
E. Historical individual	1	0	0
F. Historical, Phenomenal individual	1	0	1
G. Historical, Integrative individual	1	1	0
H. Full individual	1	1	1

The question is then what sort of entity/individual a species is (note: this can be different for different species). Let us leave out the metaphysically abstract species (A–D), which is what Ghiselin and Hull[139] do, for obvious reasons (as no individual organism would ever be a member of its species, only a "realisation" of it, if species are abstract objects and individuals are concrete). Now we are left with four options: a species is a historical entity without cohesion or phenomenality (E); a species is a historical individual with no cohesion but phenomenality (F); a species is a historical entity with cohesion but no phenomenality (G); or a species is all three (H). Individual E fits any spatiotemporally delimited group of organisms (including any lineage or clade); the second, F, represents any "taxonomic" species that lacks a single mechanism as such for keeping it distinct, and the third, G, and fourth, H, fit any Mayrian species (the third being cryptic species).

Consequently, I can't agree with the major premise sometimes expressed (e.g., Lee and Wolsan 2002) that to be an individual requires cohesion or functional integration.[140] Exemplary individuals (i.e., organisms) do have this cohesiveness, and are usually phenomenally distinct, but this is not an argument that all metaphysical individuals must be. A hive is functionally cohesive but sometimes not phenomenally distinct, for example (of course, as phenomenal distinctiveness is scale-relative, a hive might look

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[139] Ghiselin (1974b) is influenced, I think, by Strawson's *Individuals* (Strawson 1964 chapter 8; cf. 1997). Hull's metaphysical influences are less clear – he says (pers. comm.) that he settled (in Hull 1976) on "class" and "individual" as the key terms due to Ghiselin's earlier use of these terms (Hull 1981 p145), and earlier (Hull 1976) he merely notes that there is a traditional view of species as classes, and that Kripke and "logicians" have defined these terms. It must be noted, Hull points out, that Kripke's work postdates this initial debate over species in the philosophy of biology.

[140] Although as Lee and Wolsan argue, phenomenal individuality might require some integration in order to occur. This needs further argument, not relevant here.

very distinct in, say, time-lapse photography, as also other vague individuals like fungal mats, etc.). What is true for individuals is true for species, and vice versa. Species are no different to any other kind of individual, in this respect.

Moreover, the distinction between species as a time-slice (synchronic) entity and lineages as a time-extended (diachronic) entity also seems to me to fail as a sharp distinction. All species are lineages, as de Queiroz has it (1999; 1998), but not all lineages are species. A synchronic species is just a very foreshortened lineage in a slight time horizon. It is never entirely "nondimensional", and so I do not see the need for a complex and in my opinion unsupportable metaphysics of "potentials" or "propensities" (following Quine 1953). Calling on the potential to interact in a given manner is question-begging; this is only known *ex post facto*. In the end, a species must be seen logically as an individual lineage, extended over time and space. The rest is a matter of fact, not principle.[141] However, in order to be **known** as a species, there has to be some coherence, some integration, or else the group is either artifactual or arbitrary.

5.5. Naming and the *qua* problem

5.5.1. Wittgenstein and resemblance

Are species family-resemblance terms? In the famous and often-discussed sections 66 and 67 of the *Philosophical Investigations*, Wittgenstein discusses what is common to all games, and argues that if one does not assume that the term "game" has something common by definition but instead "looks and sees",

> "you will not see something that is common to all, but similarities, relationships, and a whole series of them at that. ... we see a complicated network of similarities overlapping and criss-crossing: sometimes overall similarities, sometimes similarities of detail. ... I can think of no better expression to characterize these similarities than "family resemblances"; for the various resemblances between members of a family: build, features, colour of eyes, gait, temperament, etc. etc. overlap, and criss-cross in the same way. – And I shall say, 'games' form a family."

This is an account of names, and it is curious that Wittgenstein applied an analogy between naming and resemblance based on inheritance. For species terms are names, and their extension is just such a criss-crossing of inheritance lines and related individuals. As I understand the family-resemblance predicate (FRP) notion, it suggests that the extension of such a predicate is a cluster of intersecting sets, but not proper subsets, of cases. Their "identity" lies in the general similarity of the individual

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[141] Similar conclusions are reached by Mayden (2002).

terms to each other in some metric. FRPs can be cases of (i) general similarity of sufficient but not necessary conditions (ii) identity by descent but not unity of defining character, or (iii) practical identity, i.e., it is useful to group terms together. What they are not are classes. All members of a class instantiate a necessary and sufficient set of characters. As Pitcher (1964 p 221n) observes, there are predicates like "brother" and "vixen" that are defined by essential conditions like being male or being female. How to characterise the distinction between FRPs and these other relational predicates is the subject of a large literature, but for our purposes here it is enough to note that an FRP is one that relies on similarity but a general lack of essence. "Species" can be a family-resemblance term in three ways:

A. As a taxon concept

The several competing species concepts are often classified into various "higher" categories, and there is nothing much common between them that is not true of any general notion. However, with fine irony, the categorisations themselves appear to be FRPs, as they also crisscross but are not reducible to each other. Mayr (1982) classifies species taxon concepts into essentialistic, nominalistic, arbitrary, and biological (which further bifurcates into non-dimensional and dimensional). Wiley (1981), on the other hand distinguishes between the biological, the evolutionary and the phylogenetic. Eldredge (1989) and Salthe (1985) distinguish between two hierarchies – the ecological/economic and the genealogical – and define species as classes at some level of either of these two hierarchies. Panchen (1992 p337f) recognises seven: platonic (archetypical), essentialist (Aristotle), isolationist (Mayr), recognitionist (Paterson), cohensional (or ecological) (Van Valen/Templeton), evolutionary (Simpson/Wiley), and the phylogenetic (Cracraft/Mishler and Brandon, and Hennig/Ridley). These may not be inconsistent, but they are clearly different ways of defining the biological category. Other classifications that are called species include the morphologically similar group, the karyotypic group (i.e., any group that has the same genetic structure and a restricted set of alleles for various loci), and the undivided lineage (Hull 1976).

B. As a classification of organisms

If a taxonomist has three species to classify in relation to each other, the defining characteristics of each species (i.e., those that are different across all three) are used in cladistic and morphological taxonomy to establish the similarity relations. The result is mostly just the sort of relationship one finds in Wittgenstein's games. Species *A* and *B* may share some characters that *C* lacks, and *A* and *C*, and *B* and *C*, may share characters exclusively as well. A complete list of characters may give numerous set inclusions and intersections that are not consistent across the whole list of characters.

[This is due to several evolutionary cases in the theoretical situations where an explanation is given in terms of phylogeny: convergence, reticulation, canalisation, and other cases covered by the cladistic term homoplasy (Wiley 1981).]

C. As a measure of conspecificity

The literal case of family resemblance can be extended to cover all members of inclusion within a species. Individual organisms cover a distribution curve for any given trait in a sizable census, but location in the curves is not uniform for all individuals – that is, an individual at the mean for one or most traits may be on either tail for any other trait. Use of an FRP to describe an individual in order to justify inclusion in a species classification is in effect the only alternative to an essentialist approach, with the treatment of variance as degradation that it involves.

The use of a term of morphological similarity due to ancestry – "family resemblance" – by Wittgenstein indicates that the sort of classification principles appropriate to the natural biological world (and by extension to the sociolinguistic world) are very different to those appropriate in the mathematical sciences that served as the source for so much of modern western thought. There are some deep issues involved: temporal lineages of information or structure appear to generate groupings that are complex, fractal, and stochastic. The "linear" treatment of natural kinds that may (or then again may not) be useful and effective in the physical sciences where history and individuality are not relevant to the state description of a system or process, are less useful and less effective in biology. The treatments of species as natural kinds of the physical/mathematical variety are severely Procrustean, and eventually artificial and therefore subjective (cf. Ridley 1986)). Wittgenstein's FRP is a non-biological attempt to generalise a class of "nonlinear" predicates, ones that are appropriate in biological work.

5.5.2. Do Family Resemblance Predicates work for biological species?

The taxonomic movement known as "numerical taxonomy" at the time, and later as "phenetics" attempted to use something like Wittgenstein's FRP. Indeed, the originators of phenetics, Sokal and Sneath (1963) drew for inspiration on the work of Morton Beckner (1959) who had explicitly used the Wittgesteinian FRP to discuss species (see Winsor 2003 for a discussion). However, phenetics ran up against a problem – their clustering through the use of computer analysis of characters in a morphological metric space led to instability and sensitivity of the results to the choice of characters chosen. Effectively, phenetics was an attempt to find the natural groupings of the populations themselves, in the hope that species would appear as clusters in a Cartesian metric isolated from other populations, and that this would be possible no matter which characters were used. This hope was misplaced, it transpired.

The problem appears to rely on two facts about actual species: first, as Darwin and Wallace argued, there is no absolute measure of difference in, say, morphological metrics or genetic distance that is either common to all separate species or absolutely enough to prevent interbreeding in sexual organisms. Second, species do not all vary commensurately in all characters. Some characters are evolutionarily conserved for various reasons; they may be strongly buffered against change due to developmental linkages (pleiotropy), or they may be held constant by stabilising selection because they are functionally important. So the choice of which characters to use is significant. Typically, taxonomists use "useless" characters, which can change more or less at a constant rate over evolutionary time. This is because homoplasies (convergently evolving characters) lose phylogenetic information the way that a pathway that joins another pathway is no longer as informative about the prior journey of a walker as a single pathway would be. The walker may have travelled along either of two pathways, and knowing the current location of the traveller is no help in determining which way he or she went (Sober 1988).[142]

So, the FRP, while true, is no real help in specifying which groups of organisms are distinct unless you already know which characters to use (Hull 1965). When I asked one specialist in cladistic methods how he selected the right characters to use, his reply to me was that he should hope that he knew his organisms well enough by now to choose correctly.[143] Here we see the reciprocal illumination of which Hennig spoke – knowing something about one's group of organisms enables one to choose the characters that will uncover the relationships that allow one to test which characters one should use. The circularity is not vicious – each step acts to further test the next, and iteratively to refine the overall picture. [144]

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[142] In a forthcoming review of Gould's *Structure* (Gould 2002), Hull notes that homologies are due to history, while homoplasies are not. In effect, this is because homoplasies are grades, defined abstractly.

[143] See Wheeler and Platnick (2000 p58–59) for a discussion on whether characters are prior to hypotheses of species or not. They think that if characters are invariable, then you have the species, and the rest is a matter of cladistic analysis. Ghiselin (1997, chapter 13) disagrees.

[144] The charge was made and discussed by Hennig (1966 p206, 222) that phylogenetic reconstructions are circular – it is not a worry in my (or his) opinion. Such things as observed ontogenetic sequences are introduced into the data set (it's called polarity) to make comparisons commensurate. Once you do this, you have a phylogenetic tree that is refined empirically, a process he called "reciprocal illumination". When clades are defined, obviously with some tentativeness, then you can start to compare such things as modes of reproduction within the clade. See also chapter 12 of (Ghiselin 1997).

Nevertheless, many of the algorithms used by pheneticists to analyze character sets have been incorporated into cladistic analysis; only now they are used to cluster basal taxa (species, as represented by a specimen, or by a "wild type" character which is known or suspected to be invariant across the species, and which is unique to it – an autapomorphy, in other words). One wonders how things would go if cluster analyses were used exclusively on taxonomically informative characters (homologies without homoplasy) over populations of organisms expected to be in the same taxon.

Cladistics is often accused of being typological for this reason. There is a sense in which this is harmlessly true, and a sense in which it is malign, but false. The type that is usually implicit in cladistic analyses is a *modal type*; it is the mode that most, if not all, of the members of the species bear at the same stage in their lifecycle (the semaphoronts, as Hennig calls them). It is, as Winsor calls it, an exemplar, rather than an essence. This is gained empirically, by fieldwork, large-scale sampling, and biogeographical methods. Such typology is universal in alpha taxonomy and studies of organisms. If we had perfect knowledge of a species, then we could draw the distribution curves for each trait, and specify the modal value for use in the data matrices used in taxonomic analysis. But the "essentialistic" sense that supposedly derives from Aristotelian logic as delivered by the Received History, that a species is to be **defined** by the presence or absence of some character/s is no more a part of cladism than it is of any other approach that is not strictly "Aristotelian" in that sense. Indeed, Aristotle's empirical work, where he recognises "the more and the less" in species essences, is not, in this popular understanding of the term, Aristotelian, either.

The discovery of modal distributions of homological characters that are not homoplastic in other ways is independent of phylogenetic analysis, and we might be able to do something akin to a "nearest neighbour" analysis of populations to see how they do cluster, in order to distinguish species, as phenetics attempted. However, there can be no prior absolute values even of the cluster distance that will settle the issue, for species can be polytypic, and the variation within them can be greater than the variation between them, a point made by Hull (1965) in his rejection of the FRP approach. The FRP is not an analytic tool, or operational concept, because as we saw Wallace note, there is no amount of difference that makes species but which if slightly less does not, but it is a good metaphysical conception of how species are comprised.

Thus, we have two senses in which FRPs are to be applied to *species*. One is that a species *taxon* itself is not defined by an essential set of characters. The other is that species conceptions form a family of notions, and that the **category** is an FRP. Neither is operative, though. They avoid the metaphysical implications of essentialism, but add little enough to our ability to resolve particular or generic definitions.

5.5.3. The Qua Problem

Species are thought by some to be named in a causal account similar to the Kripkean baptismal notion of general names. We first encounter a Tiger, and give it a name and a kind to match. When we meet other tigers, we learn what can vary and what is common to all. In this way, the first tiger acts as a kind of "type specimen" for subsequent uses of the name. Now this goes to a matter in the philosophy of language over meaning and (semantic) essentialism that to most if not all biologists is rather recondite, but, like essentialism and exemplars, it has direct biological relevance. One of these is the issue of essentialism as a way of defining kinds, of course, but another derives from an extension of a problem raised first by Willard Van Orman Quine in his *Word and Object* (1960 p29), known as the *Gavagai Problem*.

Quine, a behaviourist, is wondering how words in one language or idiolect can be translated into another and imagines a field anthropologist trying to work out what the locals mean by their words purely empirically in terms of the stimuli that elicit the verbal responses. A rabbit scurries by and the local says, "Gavagai!" What does "gavagai" mean? According to Quine it might mean "rabbit", "rabbit part", "extended rabbit" and so forth. Since the stimulus in each instance of the word so far encountered is to the anthropologist's eyes identical, how could we ever know?

The idea that species names are anchored in the biological world in terms of the type specimen, or the initial experience of naturalists and taxonomists is commonly held, at least implicitly. Why else do specialists apply the name to the holotype, and sometimes assign a replacement (lectotype) if the holotype is lost (Levine 2001)? The problem with this is that the causal account underdetermines the extension of the term. Devitt and Sterelny (1987) call this the *Qua Problem*. How, they ask, do we know what it is that we are referring to when we name a general kind term like Tiger? Is it the striped fur (if so, what about albinos?), or the teeth (then what about toothless old and circus tigers?) and so forth. What is it, that makes us refer to the species *Panthera tigris, qua* tiger?

The Qua Problem is known to taxonomists. There are numerous cases in which the extension of a named taxon, particularly species but also genera, turns out to be other than the biologist expected, sometimes requiring that the species name be subsumed to a prior designation, sometimes requiring that the taxon be divided into separate taxa. There are cases where taxon names have been given independently to male and female forms, and where the females of many species in a genus of butterflies are so similar that they were put into one taxon while the gaudy males, each individually distinguishable by humans, have been placed into different taxa, the mistake not realised until the two morphs were observed actually mating.

As a response to essentialism, the baptismal account has something to recommend it; under it, general kind terms do not have to have definienda, since the commonality is provided by the causal relations between the initial specimen and the other members of the kind. However, it does not manage to release us from the problems of *knowing* that other specimens are in the same kind.

In order to resolve the Qua Problem, we would have to range too far from the present subject, and so I shall merely note here that this problem occurs for any and all general terms; whether they are terms that cover only an extensional set, a causal lineage, or an abstract class. A more interesting problem in biology is how we know that the name applied to a holotype "refers" to all other members of the species. As always, there is the distinction to be made between what is, and what we can know about it. We can stipulate that the idea of species as interlocking lineages (the Hennigian notion of tokogenetic, or reticulating, lineages) answers to the reality of sexual species. The ontology of species is due to a set of causal processes (as yet unspecified) that maintain the species' identity. What we can know, unsurprisingly, depends on what methods we have of determining the differences and similarities between organisms, such as genetic sequence distance, or Nei distance, (cf. Berlocher 2000) or perhaps the degree of hybridisation of DNA; in short, what assays we have. Assuming that we happen to have or can develop an assay that touches on the actual causal mechanisms (whether we know that or not), then we can identify the **rest** of the species through a nearest-neighbour analysis until we reach some threshold, which may be abrupt or not.

The function of type specimens in naming a species goes back to Linnaeus, and it calls for an explanation; for as Mellor notes (1977), the type specimen is causally "downwind" of the type to which it is supposed to constrain reference. One explanation is that type specimens make species **scrutable** (Levine 2001; LaPorte 2003); how can they do this? LaPorte thinks that type specimens are only contingently part of their species, for example. The answer in the case of sexual species, is that the type specimen is embedded in a network of relationships not unlike the FRP, the *tokogenetic* relationships of Hennig. It will allow us to delineate the rest of the type by a "nearest neighbour" analysis, in which we gather all members on the basis of their inherited similarity to each other. Sexual reproduction – in a Mendelian, Weismannian sense – constrains the typical form of organisms by requiring that organisms are similar enough to each other in terns of developmental mechanisms, prezygotic and postzygotic features, and so forth, that reproduction is successful over several generations. In this way, a type specimen is an *entrée* into the lineal relationships that lead to all members of the species, even allowing that this does not entail a strict boundary. By picking up one node in the reproductive network, we can, in effect, find out the extent of the network itself. But what about asexual organisms? How are they kept stable? I have already discussed Eigen's notion of "quasispecies" – what makes them stay at the general region of genospace where the mean genotype lies, is selection; they will stay close to the current niche optimum genotype, even if no actual individual **instantiates** that genotype. So selection acts as a kind of brake on change here. This, however, has an interesting implication for species concepts as a whole.

What makes agamospecies (quasispecies) remain distinct lineages is selection, but what makes sexual species (biospecies) distinct are sexual isolating mechanisms. *Species* applied to both sorts of organisms generally requires features of the organisms which, in a given situation, allow them to remain at or about the same point in the state space in which they are mapped. It might be genospace, it might be morphospace, or it might be ecospace. In effect, then, sexuality is not privileged as an isolating process. This makes the point in a different way – why sex is important is that *it* is part of a general class of lineage-distinguishing processes, which also includes ecological isolation, developmental entrenchment, and the other processes that are, as a matter of fact, causally **upwind** of of making species distinct. This then explains why a type specimen gives us a scrutable introduction to the type – even if it is a juvenile form like *Arctocephalus pusillus* (the South African, or Cape, fur seal) mistaken for an adult form. The juvenile still retains sufficient "semaphores" (characters unique to that species) to act as the *entrée*. Since a type specimen for an agamospecies is equally causally downwind of the relevant isolating processes as one for a sexual organism (only different isolating mechanisms are involved), a type specimen for either will work as well (or as poorly) depending on the nature of the processes. This undercuts much of the importance claimed for biospecies. Moreover, the models of Dobzhansky, Mayr and Carson and others that sexual species are formed through geographical isolation, leading to the inadvertent evolution of isolating mechanisms is under severe challenge, at least as the sole mode of speciation.[145] So let us now see how we might extend this insight to propose a more general concept of species.

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[145] The literature is increasingly in favour of sympatric speciation via selection, whether assortative mating, hybrid infertility or local adaptation (Berlocher et al. 2002; Dieckmann et al. 1999; Dres et al.

2002; Gavrilets et al. 2002; Filchak et al. 2000; Kondrashov 1986; Kondrashov et al. 1998; Schilthuizen 2000; Turelli et al. 2001; Via 2001; Schilthuizen 2001). So far as I can tell, none of these workers oppose **any** kind of allopatric speciation happening, but they are becoming increasingly confident that a lot of speciation **is** due to selective pressures not directly connected to sexual isolation or reproductive isolating mechanisms in the first instance.

Chapter 6. Species modes

Warren Herb Wagner's Syncretic and Eclectic Species Definition

A convenient taxonomic category that defines a unit of organismic diversity with one or more ancestors in [a] given time frame and composed of individual organisms that resemble one another in all or most of their structural and functional characters, that reproduce true by any means, sexual or asexual, and constitute a distinct phylogenetic line that differs consistently and persistently from populations of other species in character state combinations including geographical, ecological, physiological, morphological, anatomical, cytological, chemical, and genetic, the character states of number and kind ordinarily used for species discrimination in the same and related genera and if partially or wholly sympatric and co-existent with related species in the same habitats, unable to cross or, if able to cross, able to maintain the species distinctness.

Circular sheet, dated 19 November 1998[146]

... we should be careful in seeking justification for a particular species concept if it cannot embrace the vagaries of real-world data with aplomb. No hemming. No hawing. It must work.

Joel Cracraft (2000 p14)

6.1. Introduction

The number of "live" species concepts in the modern literature ranges from 7 to 26 depending on the ways concepts are divided and grouped (Mayden 1997; Cain 1954).[147] Monists battle for the hegemony of a single species concept, while pluralists declare in weary resignation that there is no such single concept (e.g., Boyd 1999; de Queiroz 1999; Dupré 1999; Hull 1997; 1999; Mishler et al. 1982; Mishler 1999; Mishler et al. 1987; Wilson 1999). Each response brings its own problems. Monists must either claim that not all terminal taxa are species or attempt to trim other concepts in a Procrustean manner to be at worst consistent and at best consonant with their favoured alternative. Pluralists must accept that species are not commensurate entities, bringing a host of theoretical difficulties in comparing, for example, ecological biodiversity and evolutionary processes. No consensus has emerged, despite the species problem being a core issue in evolutionary biology and taxonomy for decades if not centuries, although there is a trend towards pluralism in recent work.

Some monists attempt to reconcile this embarrassment of richness under a more general concept. Pluralists, on the other hand, despair of ever finding a One True Species Concept, instead counselling a strategy of operational convenience – specialists should use whichever concept suits their theoretical and methodological purpose. Still others declare that no matter what species concepts are applied in particular cases, all

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[146] Pers. comm.

[147] The bulk of this chapter was published as Wilkins (2003).

useful species concepts must cohere with some broader metaphysical concept. All species must be individuals, for example, bounded by space and time and physically contiguous throughout their history (Ghiselin 1997; 1987; 1976; Hull 1978; de Queiroz 1999; de Queiroz, 1998 #3111, see Ereshefsky 2000 for discussion).

I take it that the basis for the debate over species concepts rests, explicitly or tacitly, on acceptance that the task of systematics is to differentiate **natural**, or **real**, groups of organisms (Nelson et al. 1981; Panchen 1992; but see Hey 2001a; Hey 2001b). We might group organisms on the basis of their mass or colour, but unless this reflects the biological processes that make them that mass or colour, and these are theoretically significant causal processes (that is, they are processes that we must expect to be important in differentiating the groups), the group is merely artificial. Separating organisms within a few kilograms of, say 40kg, from organisms more than 80kg separates me from my daughter – we would be different species.[148] This will not do, of course. Lineal descendency is a key causal process of biology, and species are related by descent. Any species concept that purports to capture natural groups must incorporate reproduction as a key variable – species consist of **related** organisms.

The problem with this is that descent is insufficient to distinguish species. In Linnaeus' time, but not long afterwards, descent was sufficient because all species were supposed to be the descendants of an original created pair of organisms. But if species evolve, then not all descendants of a given organism or pair of organisms, if any, are members of the original species. So, other causal processes are essential to defining the conditions by which being of the same species occurs. This leads to a further problem – there appears to be no single set of causal mechanisms that define all and only species.

David Hull sets up the philosophical context of the species concept debate quite nicely, if strongly:

> One reason why philosophers find the monism-pluralism debate so interesting is its apparent connection to the dispute over realism and antirealism. Of the four possible combinations of these philosophical positions, two seem quite natural: monism combined with realism, and pluralism combined with antirealism. …

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[148] Hull (1988c p150) reports that this is what forced E. O. Wiley to reject phenetics – the phenograms kept showing conspecific males and females as being different OTUs. Just this sort of error is frequently made through the use of phenetic criteria. In sharply polymorphic species, males and females can end up being classified more closely with members of other species than with the opposite gender of their own, especially if one sex (e.g., the female in songbirds) is typically more conservative than the other sex in that clade.

> The other two combinations … are somewhat strained. It would seem a bit strange to argue that one and only one way exists to divide up the world, but that groups of natural phenomena produced on this conceptualisation are not "real". They are as real as anything can get! … A combination of pluralism and realism seems equally peculiar … . The world can be divided up into kinds in numerous different ways, and the results are all equally real!
>
> (Hull 1999 p25)

The alternatives Hull mentions are not exclusive alternatives, as he notes himself. And it is important to understand that this field of combinations is applicable here to the question of the species category only. One can be a species antirealist without thereby denying the existence of other kinds, say, elements or electrons. One might be a species monist, but a pluralist on other matters. There is thus a 2 □ 2 matrix:

Species …	Pluralist	Monist
Realist	A	B
Antirealist	C	D

Now realist monists (B) are common, and so are pluralist antirealists (C) (Hull 1999). Monist antirealists (D) are around (arguably, Darwin was one, Buffon another). But the conundrum is pluralist realism. If we are to be realists about the species category, and there are many concepts in play[149], how do we tell whether we are properly applying the various categories in a particular case? What monists like Hull fear is the slippery slope that pluralism puts us on. Pluralism will lead to conceptual promiscuity, to epistemological anarchism. Once admit that the central concept of evolutionary theory is many-fold, and we will end up unable to restrict ourselves to any useful theoretical concepts. Species will become incommensurable categories. There will be no end to the problems that arise from a constant and idiosyncratic revision of the units of evolution. So he and others plump for a unitary monistic conception of species on which all others rely – in this case, the evolutionary species concept.

I do want to defend one of the "strained" combinations Hull mentioned. I want to be a species pluralist, and at the same time admit that species and other terminal taxa are

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[149] This is not a historical claim, so much as a viability claim, for all that it has a historical element. I am not (here, at any rate) trying to explain the behaviour of systematists over the past 150 years. My argument goes to this, but there are other considerations, such as the amount of empirical research done, and sociological biases – most evolutionary research has been confined to metazoans until relatively recently, and even plant specialists tended to do little evolutionary biology until Grant (1971; 1975) and others woke them up in the late 1960s and 1970s. But if the current practice and amount of work done by, e.g., bacteriologists, or mycologists is any guide, this is exactly what is happening. They are studying clades as trees are constructed and comparing them.

real (A), for the question of realism is germane to the scientific enterprise.[150] The things that are identified as real are the things we wish to learn about. Our classifications are there in order for us to learn about the natural world. A proper classification is one that tells us what to study, and what correlations to draw. However, if, in the process of uncovering the natural groups in the world we find that a category answers to many rather than one kind of natural thing, then that is an advance in knowledge. I will argue for a chaste pluralism, one that is led by the empirical data about the organisms themselves, without a ticket for runabout inferences.

My argument is this: In one class of species concepts – the reproductive isolation concepts of species – being a species depends upon a natural kind: sex. We tend to generalise from zoological, and particularly avian and mammalian, sexual modalities, but the biological reality is that sexuality is pluriform. Nothing that we can set up as necessary and sufficient criteria captures all and only sexual reproduction. On the cladistic account, the only natural group is a monophyletic group, known as a *clade* (a single taxon plus all and only its descendants). Sex is not a trait of only a single monophyletic group, and hence is polyphyletic (and indeed paraphyletic).

The most widely accepted and used species concept is the biological species concept (the BSC), an unfortunate name since it is not the only concept that is biological. Others include ecological species concepts, genetic species concepts and, of course evolutionary species concepts. The BSC is a reproductive isolation concept, sometimes called the *biospecies* concept. As we have seen, its popular formulation is due to Ernst Mayr:

> A species consists of a group of population which replace each other geographically or ecologically and of which the neighboring ones intergrade or interbreed wherever they are in contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers.
>
> Or shorter: Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.
>
> (Mayr 1942 p120)

However, the many different modalities of sexual reproduction are due to the many monophyletic origins of these modalities. It follows that biospecies are evolved modes, and that there are therefore many different modes of biospecies. Since biospecies have independent origins, on the cladistic convention different modes of sexual species

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[150] Kitcher (1984) also defends a pluralist realism, but his relies on species being natural kinds, which I will not rely upon.

must be seen as distinct groups within the tree of life, and the more general kind of species is the (more inclusive class) asexual species, or agamospecies. Hence, there is no natural group of biospecies. But the actual processes that isolate the many kinds of sexual species are empirically determinable, and so just in terms of this one concept we are limited pluralists, constrained by the evidence. By induction, other concepts that aim to capture biological realities will be likewise constrained. This I take to be a virtue.

6.2. Heterogeneity of biological species

In common with all other species concepts that are intended to capture biological realities – as opposed to those that are merely conventional or diagnostic – the biospecies concept relies upon the intrinsic processes and properties of the organisms and their lifecycles to distinguish one species from another. In this case it is the fact that organisms within the species interbreed, and organisms between species do not. The definition of a biospecies is therefore dependent upon the organisms reproducing sexually, and this forces us to ask the question – is the category "sexual reproduction" a natural group or class?

Varieties of sexual production are many. Some of the main processes of genetic exchange and recombination are, in order of increasing variance from the "standard" conception of sexual reproduction:

- Animal sexual reproduction
- Plant sexual reproduction
- Mating strains in fungi
- Nuclear fusion in yeast
- Vegetative fusion in algae
- Conjugation in amoeba and in bacteria
- Viral crossover
- Horizontal genetic transfer through plasmids and phage-mediated retroinsertion (*transduction* and *transformation*)

In addition to this, there are numerous cases of *hybridisation*, particularly in plants, across species (and even genus) boundaries. To complicate matters, even in many sexual groups such as in anapsids (reptiles and turtles), and in vegetative and flowering plants, there are *secondarily asexual taxa*. In animals, secondary asexuality is called *parthenogenesis* and in plants it is called *apomixis* (a form of which, apogamy, is common in ferns). Defining or diagnosing asexual species generally requires ecological, morphological or developmental differences.

Even when first proposing the biospecies concept, Mayr observed:

> A … difficulty which confronts us in our attempt at a species definition is that there is, in nature, a great diversity of different kinds of species. Even if we do not consider such aberrant phenomena as the apomictic species in plants and the strains of bacteria, there is, even among animals, a great variety of different taxonomic situations which are generally classified as species. The question as to whether the species of birds, of corals, or protozoa, and of intestinal worms are the same kind of evolutionary phenomena is entirely justified. … It may not be exaggeration if I say that there are probably as many species concepts as there are thinking systematists and students of speciation. (Mayr 1942 p114–115)

Mayr calls apomixis, protozoan mating types, self-fertilisation, and parthenogenesis "aberrant". Plant species are not really biospecies either:

> Polyploidy, apogamy, and sympatric hybrid swarms are phenomena which are common in plants and unknown, or at least decidedly rare and unimportant in animals. (Mayr 1942 p122)

In denying the universality of sex, Mayr states negatively the positive claim being made here – that species modes are clade-relative and are traits of evolutionary lineages. By declaring some kinds to be "aberrant", his metazoan and vertebrate focus shows up as a prejudice. If most kinds of organisms are "aberrant", something is wrong with the way we specify "normal".

Over the entire tree of life, biospecies are by definition restricted to those clades which have evolved sexual reproduction, and in the main, this is limited to the metazoan (animal), metaphyte (plant) and fungal clades of the eukaryotic domain, although Bacteria and Archaea are gene exchangers, ranging from partial exchanges of plasmids, for example, through to recombination of the entire genetic complement and subsequent reduction to the normal complement. But for the usual meaning of sexuality, we typically require sex cell haploidy, gamete sequestration from the somatic cell lineages, necessitating that sexuality involves multicellularity or at the minimum colonialism, and also that there is sexual dimorphism, either anisogamy (difference in gamete size) or genders. These conditions were probably realised in the pre-Cambrian era, and so biospecies evolved around 600–1000 million years ago. Before then, and for the bulk of the extant biological world even today, there are no biospecies.

The obvious implication of this observation is that the species mode "biospecies" is an evolved trait, analogous to the eukaryotic nuclear membrane, the vertebrate body plan, or hominid bipedality. Being a biospecies is a derived character of a clade, i.e., of a natural group of lineages of organisms. This simple observation (which I base on comments made by Hull 1988c p103) has some interesting ramifications. I would like to explore them in connection with two leading issues of the species problem –

whether species concepts are historical, and in what sense we might think species concepts are unified by organic evolution.

6.3. Natural taxa and monophyly

Given that we are concerned with "natural" species modes formed by the evolutionary process, some account of a natural group is required, and the generally accepted definition – although not universally accepted – is the cladistic account of *monophyly*.[151] A natural (monophyletic) group is any clade formed of a stem species or lineage and all of its descendants. If all animals or all vertebrates including their last common ancestor were sexually reproducing, then animal or vertebrate sexual reproduction would form a monophyletic – and hence natural – group.

Since what follows relies heavily upon cladistic categories and argument, a few words are due about why I take cladism so seriously. Some taxonomists do not. One has to start somewhere, though, and one primary virtue of cladistics is that it is clear in what it asserts. Given that Hennig (1950; 1966) founded it in part on the set-theoretic ideas of Woodger (Woodger 1937, with no less than Tarski's imprimatur in an appendix), this is understandable. But more to the point, cladistic taxa, including species, do not require that there is some prior theoretical model; they are formed by aggregating empirical types of organisms and restricting the resulting groups to proper sets and subsets. If one requires that species meet some kind of model of populations, gene flow, adaptation, ecological niche occupancy or whatever, then there is no point in further debate. "Species" has been defined by fiat. So, I prefer instead to adopt the cladistic approach for naturalness (Wiley 1981); at least it allows for an open mind as to what it is that forms particular taxonomic groups. It may turn out that the mechanisms that do this are the same ones proposed by the biospecies, or some other, definition; if so, then that model is supported by empirical data. But given that an indefinite number of (more or less viable) models can be proposed, we need to test them somehow; cladistics is a way to do this, and so I think that its notion of a natural group is conceptually prior to those of the models.

Two kinds of non-natural groups are recognised and rejected by cladistic convention. The first is *polyphyly*, or convergent evolution, whereby some character is independently evolved in more than one clade. Polyphyletic taxa are formed out of

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[151] Ashlock (1971) and Mayr and Ashlock (1991) have objected to the term "monophyly" as Hennig (1950; 1966) defined it, proposing instead "holophyly". So far as I can tell, the latter term does nothing that Hennig's definition doesn't do, and they reserve the former term for uses that are conventional but ill-defined. Hence, I shall adopt cladistic usage unqualifiedly.

grades, rather than clades. A clade is a branch or group of related branches on the phylogenetic tree – the taxonomic equivalent of a historical, or extensional, set. A grade is a "level of organisation" – the taxonomic equivalent of an intensional set.[152] Polyphyly is rejected as a criterion of naturalness because it is subjective; which is to say it is arbitrarily sensitive to the criteria selected for inclusion relations.

The second non-natural group in cladistics is *paraphyly* – which is a clade minus some parts of it. For example, it has been argued that humans ought to be considered a species of chimpanzee because we are all part of a monophyletic group. If we separate the genus *Homo* from that clade, then chimpanzees are no longer a natural phyletic group.[153] Like polyphyly, paraphyly is sensitive to the choice of inclusion relations, in this case based on subjective assessments of what counts as "too different to include" in the taxon.

Clades are marked by their sharing evolved, or "derived", characters which no other clade shares. These derived characters are called *apomorphies*, and shared apomorphies common to all members of a monophyletic clade are called *synapomorphies*. The original, or "primitive", character is called a *plesiomorphy.*

The advantage of cladistic monophyletic conceptions of naturalness over other conceptions such as the evolutionary grade, or natural kind, conception is that they are the most reliable way of grouping so that inductive generalisations are projectable (Griffiths 1994; 1999; Nelson 1989). Monophyly enables us to inductively predict that if a member of the clade has a property *X* – say a particular enzyme – most likely so does some other member. If, on the other hand, we classify gradistically, knowing for example that an organism is a member of the "predator grade" does not enable us to inductively predict the sharing of other properties not involved in the recognition of the grade.[154] This inductive projectability is enough in itself to justify the adoption of

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[152] The pattern cladist Colin Patterson called groups formed by grades "timeless abstractions" (Gareth Nelson, pers. comm.).

[153] Diamond (1991). However, John Harshman has convinced me that this depends on the topology of the cladograms for chimps. If the two chimps diverged *after* the Pan lineage split from the Homo lineage, then they and all their ancestors after the last common ancestor can be monophyletically grouped, while all subsequent Homo species can be independently grouped. If, on the other hand, one chimp species shared a more recent common ancestor with any Homo species than with the other chimp, chimps are not monophyletic.

[154] Mayr (1997) has called classification into clades "cladification", a way of mocking cladistics. Of course, this invites the converse response – the kind of intensional classification into grades he espouses should be called "gradification", not "evolutionary systematics" (cladistic classification is evolutionary, at least in Hennig's eyes and those of the process cladists).

non-grade classification. So far as I am aware, there is nothing besides the cladistic approach that offers it. However, I do not think that gradistic classification is illegitimate as such, merely that it is not something we can take for granted is a natural classification until we have been able to test it through natural methods.[155]

6.4. Reproductive modes

Treating the intrinsic physical processes by which lineages are kept distinct as evolutionary characters presents the biospecies concept with a problem. In most large clades, the mode of reproduction is not universal. Not all vertebrates, or animals or plants reproduce sexually. Secondary asexuality in an otherwise sexually reproducing group means that we cannot treat that group as a natural group with respect to the way its taxa are (bio)species, because the synapomorphy scheme is paraphyletic. The differences in the way sexuality independently evolved in animals and plants mean that the category "sexual reproduction" is polyphyletic. We are left with two alternatives. Either secondarily parthenogenetic and apomictic modes of reproduction are to be included in the category of sexual reproduction, or that category must be recognised as an artificial grade. Both alternatives are viable. Snakes, which have secondarily lost all limbs, are cladistically considered to be members of the Tetrapoda clade.[156] They exhibit four-leggedness in an unusual way (by not developing legs throughout their life, although they retain genes for limbs in inactivated sequences). And Reptilia is now dissolved into monophyletic clades such as the diapsids, which includes lizards, because birds (Aves) which derived from a common ancestor with reptiles, was not included in the group.

If we do take secondary asexuality as a derived kind of sexuality, then there must be a number of synapomorphic sexual reproduction modalities for each monophyletic group, rather than a single grade of sexual reproduction for all similar modalities. This means that for each such monophyletic group, there is a unique monophyletic biospecies category, the synapomorphic species mode for that clade. The same conclusion can be drawn for each of the independent modes of asexual reproduction in secondarily parthenogenetic and apomictic taxa. Each species mode or category is

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Gary Nelson has pointed out to me that a grade which coincides with a clade – that is, a monophyletic grade – is an inductively natural group. A paraphyletic or polyphyletic grade, however, is not. I think that the inductive projectibility depends on monophyly.

[155] In this regard, gradistic classification is not unlike a Just-So adaptation story; it is easy to generate but not worth acceptance unless tested. The basis for testing has, to avoid circularity, to be something other than grade based data.

[156] At least one python has vestigial leg bones. Likewise, all cetaceans are tetrapods in this respect.

defined by the actual intrinsic mechanisms that keep the taxa distinct. Since (or if) birds share unique reproductive and chromosomal mechanisms, there is an avian biospecies concept, but there is no diapsid or "piscine" species concept, as these groups do not share their genetic mechanisms for sexual reproduction. Birds have a chromosomal structure in which females have the sex-determining chromosome (are *heterogamous*), unlike mammals and other most vertebrates in which males do.[157] As a result, there are no known parthenogenetic bird species (and they are a well-studied group), and so the biospecies concept applies to them fairly well, ring species to one side. Reptiles, which share this chromosomal arrangement but which do have obligate parthenogenetic taxa[158], only **mostly** answer to the biospecies concept. If we want a monophyletic notion of "reptile" species, either we must define their asexual species in terms of their ancestral sexual mechanisms (that is, treat their asexuality as a derived form of their ancestral sexuality) or we must deny that they have a single species concept based on reproductive isolation. In this case, we would find ourselves with a biospecies concept for each family or genus with a common modality of sexual reproduction. If only one species in a genus was parthenogenic – a not unusual case – and the remainder of the genus was paraphyletic, we would need to have a distinct concept for each species or monophyletic subgroup. To avoid this we must treat secondary asexuality as a derived form of the ancestral sexuality.

We can extend this point to all species modes that are mechanism-based, excluding purely diagnostic and conventional concepts. If a mechanism evolved that makes

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[157] In some insects, such as grasshoppers, females have a full complement of chromosomes, while males lack one. In other insects and most animals, the heterogametic gender is the male, which has a different chromosome, the Y chromosome, that determines male sex. In birds, the heterogametic gender is the female, which has a ZW pair of sex-determining chromosomes, while males are homogametic with ZZ. Some fish also have this arrangement. Other forms of sex determination include that of liverworts (which may be the representatives of a group that first colonised the land), the organisms alternate between asexual (XY), and sexual (males are Y, females are X) stages. The ways in which sex is determined get more complex as specific organisms are investigated in detail. In *Drosophila*, the primary oocyte is XXY, which is reduced by "secondary nondisjunction", so that eggs end up XX (4%), Y (4%), X (46%), or XY (46%). Polyploid sexes are also possible. In the end, the following mechanisms for sex determination and therefore reproduction are possible: genetic sex, gonadal sex (chemical inductors acting on gonads), genital sex (hormones acting on genital development), somatic sex (hormones acting on somatic development) and in humans (and other primates?), sociopsychological sex, which is irrelevant here (Burns 1976 p 198ff).

[158] For example, the whiptail lizards of the southern United States and Mexico, gen. *Cnemidophorus* include both sexual and parthenogenic species: some of the asexuals being *Cnemidophorus uniparens* (the whiptail lizard), *C. neomexicanus* (the New Mexico whiptail) and *C. tessellatus* (the checkered whiptail lizard), along with *C. perplexus*. Sexual species include *C. inornatus* which is one of the parents of a number of parthenogens, *C. tigris*, the western whiptail familiar over much of the west, *C. sexlineatus*, the sixlined racerunner of the southeastern USA, and *C. gularis*, the spotted whiptail common over most of Texas. I am grateful to Scott Chase for the details. Asexuals in this clade may have been formed through polyploidy and hybridisation (Dowling et al. 1997).

terminal taxa distinct, then the species mode evolved, and this implies that if the original organisms were asexual reproducers, and hence formed agamospecies, then the varieties of sexual reproduction-based species modes found in plants and animals are modified forms of that asexuality. Sexually-reproducing organisms exhibit asexuality in unique and unusual ways.

It follows that *agamospecies* – a functional, morphological and phylogenetic concept – is also not a natural category. It is either defined privatively – as not-sexual taxa, or it is properly applicable to **all** species, sexual or not, since all sexual species are derived from an initial state of asexuality in eukaryotes, or it is different in the different clades that are synapormorphic for the reproductive mechanisms they share.

Similarly, isolating mechanisms themselves are an extremely heterogenous lot; one might almost call the class a trashcan categorical. Littlejohn (1969) presented the most complete list of reproductive isolating mechanisms (RIMs; see Table 2, above), and examples of each of these classes of RIMs can be quite physiologically, developmentally or otherwise different. For example, isolation is more rapidly attained in viviparous organisms than in oviparous ones, due to a range of mechanisms including fetal immunological incompatibility, regulatory gene mistimings, and so on. Zeh and Zeh (2000) document the 10-fold quicker attainment of isolation between mammal species than between frogs or birds (up to 8 million years versus as much as 60 million years; the lower limit is not bounded, of course). Viviparity is not the only synapomorphy that explains the mammalian speciation and isolation differences – we must avail ourselves of investigations into the evolution of gene signalling in development and of immunological mechanisms and markers, and so on.

6.5. Pluralism explained and restricted

I introduced this discussion in the context of pluralism in biological taxonomy. It may seem on reflection to exacerbate the problems of pluralism, because each sister species pair will tend to have unique mechanisms that make them distinct. Indeed, one of the two main phylogenetic conceptions is that a species is the smallest diagnosable group that is defined by its <u>aut</u>apomorphies, the constellation of features only it has. At one extreme, there are as many species modes as there are species pairs; a trivial conclusion. At the other extreme there is another truism – species are groups of organisms that differ. Neither is really informative or helpful, but the middle ground is not clear either. Taxonomists specialising in a particular class of organisms – say, insects, mammals, ferns or fungi – tend to generalise from the dominant species mode in their speciality. For example, the two initial modern leading proponents of biospecies as the core concept of taxonomy, Dobzhansky and Mayr, were respectively an entomologist and an ornithologist. Plant specialists tend to be less monistic (e.g., Grant 1975; 1977; Van Valen 1976; Wagner 1983), favouring a mixed strategy. The real issue over the pluralism and monism of species concepts is how **many** concepts should be in play, and in what circumstances. If we treat species modes as synapomorphies, this becomes an empirical question: there should be as many species concepts as there are ways, common to evolved clades, of **being** species.

This seems to support de Queiroz's recent view (1998; 1999) that what all species concepts have in common is that they represent lineage segments. Of course, any "natural" species concept involves lineal descendency and the derivation of populations from prior contiguous populations. An evolutionary understanding of species modes makes lineages fundamental and prior to species (and other taxa), although many operational concepts are not equivalent to any construal of a lineage (e.g., phenospecies or morphospecies). But an abstraction such as this does not resolve the plurality of species concepts at the operational level, and on the account given here, nor should it. Apart from anything else, distinct lineages occur **within** species. A pluralism of species concepts is to be preferred, therefore, not because (or rather, not merely because) we have diverse and irreconcilable theoretical interests and limitations, but because in the nature of evolution, no species mode is synapomorphic to **all** natural groups of organisms other than those classes that, like the class of all sexually reproducing organisms, are paraphyletic and conventional. Species are not, in short, the units of evolution so much as the results of it. Not only are species historical individuals, so also are species modes.

Adopting this approach overcomes some criticisms of the phylogenetic species conceptions. For example Vrba (1995 p11) criticises the former on the grounds that if a species is the "smallest diagnosable cluster" of lineally related organisms, then she and her family who share a unique rib phenotype are different species from their sexual partners. Of course, this is not a criticism of how the various phylospecies concepts are applied, but on the synapomorphic species conception I am proposing here, that criticism would have no purchase unless rib morphologies were the traits that **caused** the distinctness between lineages; in short, if she and her cophenotypes did not or could not interbreed with lesser-ribbed humans. The causal role of the phenotype may, or may not be, a RIM for biospecies. Hence it may, or may not be a phylogenetically significant character, as an autapomorphy.

6.6. Groups, kinds, clades and grades

This is an argument for species being natural groups, not natural kinds. Natural kinds fall out of the distinctions made in an explanatory model, not in a classification, although there is of course reciprocal illumination between them. But whether or not species are natural kinds, they **are** natural groups, as are all taxa monophyletically comprised of them. Natural kinds need not be monophyletic. Sexual reproduction is not a derived natural kind since it is a heterogenous collection of evolved characters that are not instantiated in a natural group. Of course, it may be a natural kind in more general ahistorical terms (although I think that the empirical evidence makes that a *very* hard claim to uphold – there just is too much difference once you get past the superficial, zoological, mammalian, prejudices). But if so, it is a kind in the sense that "predator" is a natural kind – it's defined in relation to a model (in this case, an ecological model of trophic relations), and so it is itself open to the charge of promiscuous pluralism – you have as many kinds as you have models to apply. Pick a model, and *voila*, a natural kind. Moreover, theoretical interest determines the application of these sorts of kinds or grades. As Paul Ewald noted, such natural kind terms such as "parasite", "predator" and "commensual" shade into each other, so that the real difference between a parasite and a predator, is the rate at which they exploit their "hosts". But viewing matters alternately from a parasite's perspective or the host's changes the expectations. Ewald says, "If a group of 2500 vampire bats attacked and killed a person by feeding on him, would we call the bats parasites or predators?" (Ewald 1994 p60). Our preferences for a certain class of theoretical models are insufficient grounds for claiming a natural kind.

So, sexual reproduction is not a defining property of a natural group. Is it therefore not a natural kind? On the essentialist account of natural kinds, kinds are essences; properties that are severally necessary and jointly sufficient not only to mark out something as an instance of the kind – a diagnostic criterion – but also which causally constitute that kind. Given the heterogeneity of sexual mechanisms, modes and frequencies, it appears that there are no such essential diagnostic *or* causal properties. Either the adduced properties are too general and capture things that we do not consider sexual reproduction, such as the occasional case of transduction or transformation, or they are too restricted and exclude things we do want to cover, as when mammalian paradigmatic modalities fail to cover plants. Deviations from the "normal" modalities, such as haplodiploid eusocial insects or obligate clonal organisms like bdelloid rotifers or darwinulian ostracods, which are "ancient asexuals" (Judson et al. 1996; Welch et al. 2001; Schön et al. 1998), should have a salutary effect on the tendency of researchers to treat a local reproductive mode of some clade in the tree of life as "normal", but they also show up the tensions in natural kind definitions inherent in biology.

If we want species concepts to delineate natural groups of organisms rather than merely reflect our cognitive, perceptual, or theoretical, abilities and propensities (see Hey 2001a; 2001b), we must adopt a criterion for grouping based on the endogenous properties of the organisms themselves. This is the *naturalness requirement*, and I have adopted monophyletic clades over such concepts as evolutionary grades and the concomitant adherence to the natural kinds that grades entail, since monophyly is empirically, rather than theoretically, determined (cf. Wiley 1981 p71-77 for a discussion and references).

Chapter 7. The synapomorphic species concept

… somehow a species definition must be inclusive of an ontology and an epistemology.

Joel Cracraft (2000 p13)

7.1. *Species* defined

The properties that make organisms group distinctly from others are themselves evolved, and many of them have evolved independently, making them homoplasies rather than homologies. Classes comprised of these homoplastic properties are not therefore natural. They are artificial classes, either because of paraphyly or polyphyly. "Sexual reproduction", and hence the biospecies concepts that depend on it, is one of these artificial classes, generated on the grounds of theoretical convenience and apparent similarity. It follows, if we adopt a monophyletic conception of what is a natural group in biology, that there are as many ways of being a species as there are synapomorphies that are causally responsible for making organisms distinct lineages. Species concepts are (more or less good) representations of synapomorphies. Any clade of organisms that is highly polytypic in its speciation mechanisms will have many applicable species concepts, and those that are monotypic will have few. Specialists working in the domain of that clade will therefore need recourse to as many concepts as adequately capture these synapomorphies, but no more than is empirically demanded. I therefore term this approach the Synapomorphic Species Concept. This concept can be defined briefly:

> *A species is a lineage separated from other lineages by causal differences reflected in synapomorphies.*

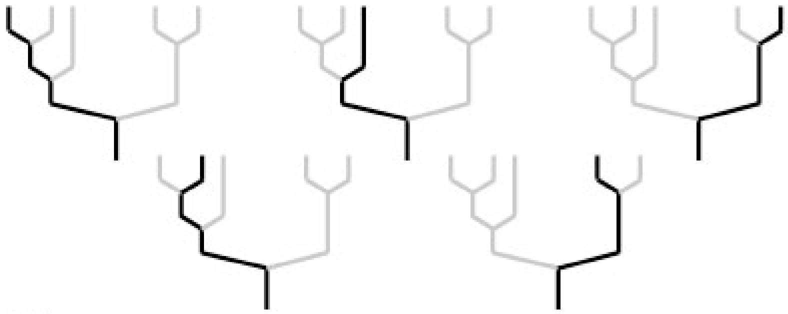
7.2. Lineages

The key term *lineage* is taken from Hull's metaphysics of evolution (Hull 1980; 1981; 1984d; 1988c; 1988a; 1989), based on Simpson's evolutionary species definition (1951; 1961), as revised by de Queiroz (1998; 1999, see figure 16). It represents the *generative* aspect of species that we saw from early in the history of the concept. It broadly means

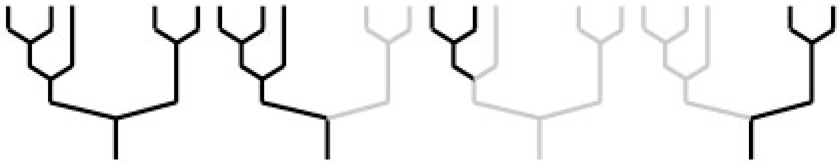
> … a series of entities forming a single line of ancestry and descent. …
>
> Lineages in the sense described above are unbranched; that is, they follow a single path or line anytime an entity in the series has more than one descendant. … Consequently, lineages are not to be confused with clades, clans, and clones – though the terms are often used interchangeably in the literature. (de Queiroz et al. 1990 p50)
>
> … a lineage (an ancestral-descendant sequence of populations) … (Simpson 1951)

The sense in which lineages are *separated* will vary according to the organisms. In sexual organisms, it will involve the variety of prezygotic and postzygotic isolating mechanisms. In ecospecies it will involve the occupancy of an ecological role in vicariant ecosystems (i.e., in similar roles in each system, interchangeable with each local instance). In quasispecies (agamospecies) it will involve approaching the mean "wildtype" genotype through selection against intermediates. In phylospecies, it will mean remaining diagnosably distinct (although I have added the requirement that diagnosis be founded on actual causal mechanisms in the ultimate case). The first aspect here is that there is a pattern of distinctness – on which we can refine our diagnoses to uncover the processes that cause them.

Figure 16 – De Queiroz's conception of lineages



(a) lineages



(b) clades, clans, or clones

Figure 3.1 from de Queiroz 1999: p51. Caption reads: "Lineages contrasted with clades, clans, and clones ... . All of the branching diagrams represent the same phylogeny with different lineages highlighted in (a) and different clades, clans, or clones highlighted in (b). Notice that the lineages are unbranched and partially overlapping, whereas the clades, clans or clones are branched and either nested or mutually exclusive. Additional (partial) lineages can be recognised for paths beginning at various internal nodes."

Note that the second and fourth examples in (b) are paraphyletic (excise a sub-branch of the tree), not monophyletic. It looks as if the stem of the tree should have been greyed out. I would not call these clades, nor, I think, would most cladists. The grey portions of those trees are, however, and may be what is intended.

Lineages are formed in various ways – in quasispecies by adaptive fitness and in sexual species by a heterogenous set of isolating mechanisms. They may comprise populations, kin groups/tokogenetic lineages, organismic relations between parent/s and progeny, genetic phylogenies, and the like. What the actual lineages are is also a matter of the evolutionary novelties of that group of organisms; tokogenetic lineages don't apply to asexuals, for example.

A lineage is therefore any biological series over time of causal reproduction, no matter what the level. We choose a certain level depending on the organisms as "the" lineage for those organisms. Obviously this is different for asexuals than for sexuals. Although in some cases it may involve genetic cohesion as Templeton expects, or specific mating recognition mechanisms as Paterson expects, or a heterogenous set of mechanisms as Littleton outlines, or even the occurrence of "speciation genes" as Wu discusses, there remains the fact that for each group, they are distinguished from each other.

Synapomorphies need not be considered as elements of lineages. Synapomorphies are characters of semaphoronts (organism life-cycles), and as such are abstractions – representations of features of organisms. However, there are many features of lineages even if you take a process cladist view – there are autapomorphies, plesiomorphies, tokogenetic lineages, and of course cladogenetic lineages. There are also reticulated lineages. Thus, I am picking out one aspect of phyletic lineages (shared, derived, characters representing traits of the actual organisms), and noting that some of these traits are causes for the lineages being distinct over some time horizon. Representations of these, and only of these, "define" (or rather, describe) the individual species pairs.

7.3. Unpacking the synapomorphies

Assuming you take the process cladist view, then you might unpack the brief definition above this way:

> *Species are lineages of organisms that have differences in shared traits that keep them distinct from other lineages.*

Or, if you prefer the evolutionary approach,

> *Species are lineages of populations with homologies that are differently expressed, and which prevent the populations from recombining.*

Each of these is thus an "object-level" species concept. There are unanalysed terms in each version, but which interpretation you select will depend on the organisms themselves. For example, if you are dealing with asexuals, what makes them stay "together" is clustering around the optimal wild type genome through selection for some ecological niche (Eigen's notion of "quasispecies"). In sexuals, sex often does that job. So one cannot use the evolutionary notion for asexuals unless one redefines "population" in an ecological way. In the case of sexual species, all you need are mating differences of one kind or another to maintain the identity of the populations. Unless, of course, you are dealing with one of the many species where facultative crossing with other species is rampant, as in flowering and fern ally plants, or corals, ... then you need to use a more general notion, such as the process cladist definition of species.

Not every variation on the clade theme that is unique to all members of a species is sufficient to cause that species; in fact, most are not. It follows, assuming that a putative species **is** different from another group of organisms, that we need some account of what differences to take into account in defining species. If species are terminal taxa in a tree of lineages separated from other lineages by traits in which differences are causally effective lineage isolators, the question naturally arises – which traits make species? In short, which synapomorphies form a synapomorphic species? Obviously, one cannot specify *a priori* which synapomorphies must be significant, because this is in effect to ask which lineage isolation mechanisms were in play when the species evolved, and this is different in many cases for different speciation events. So instead, we can only answer this problem by empirical, biological and paleontological, investigation.

A problem arises, though. If we do not know before the investigation what causes two species in a clade to be different, then how do we begin to investigate whether they *are* species at all? For example, if the diagnostic concept of species is used, then taxonomists may find many times the species as if a morphological concept is used as an operational stand-in for a biological species concept. So how to proceed? If we identify the autapomorphic groups without previously determining what apomorphies are **causally** significant, then we may look at synapomorphies for the clade that may have no role in the distinctness of any lineages. We cannot, of course, directly investigate the processes of lineage separation (speciation) in nearly all cases, so how do we first diagnose the lineages to investigate? On the other hand, if we adopt a prior biological species concept like the SMRS, or we take species to be vicariant avatars in an ecological context, then we no longer require the synapomorphic conception to help us organise our research.

This issue can be tackled through something akin to Hennig's "reciprocal illumination" for phylogenetic reconstruction in general. If a researcher takes as her starting point some operational conception in the literature, and attempts to refine this through the use of some mix of species concepts until she and other practitioners are satisfied that the conception is adequate to deal with the known causal mechanisms of the group (i.e., of the clade, although it need not be the clade at the level being considered for species' synapomorphies), then a starting point is both empirical and available. Specialists tend to have a lot of tacit and multivariate knowledge about their organisms, and we can expect them to be able to make a start somewhere (or else surrender to a Pyrrhic scepticism about the possibility of this kind of science). But there is a more basic point to make – science is a historical process. At no point in any investigation do we begin *tabula rasa*; there is always prior knowledge about or impinging upon the phenomena under study. If there weren't, then we would literally be unable to even identify the boundaries of the domain to be researched. We build upon the work and successes, and the errors and misconceptions, of those who came before. So the answer to, *which synapomorphies?* is, whichever ones seem promising based on what we know about these organisms, and see where that takes us.

How then do we test hypotheses about lineage isolation? On what grounds might we **reject** a hypothesis about what makes species *A* distinct from species *B*? I surmise that this is very like the question as to what in a phylogenetic classification is to be treated as a homology and what as a homoplasy or convergence (De Beer 1971; Fitch 2000; Donoghue 1992; Hall 1994; 1999; Mindell et al. 2001). In the absence of accurate information about the evolutionary history of the rest of the characters used in the analysis, we make some assumptions based on knowledge of ecology, the geological record, development of modern and related organisms, etc., and see if what results is a consistent and coherent picture. This is a matter of the relative weights one must assign to prior knowledge before the current analysis; in short, of Bayesian priors. Since these are relative to the specialist's or sub-discipline's state of knowledge underlying the problem itself, there may not always be a single or best answer (Mayo 1996). There are always problem cases and anomalies in science, and we must do the best we can.

7.4. Comparing the concepts

A species is thus whatever is kept a separate lineage by differences in shared traits. We can list the ways other species concepts relate to the SSC: A species is

- a biospecies, if sex keeps the lineages apart over a very short time horizon and in the same geographical range;
- a kind of evolutionary species, if "lineage" is taken as "evolutionary lineage";
- a phylospecies, both diagnostic since it relies on characters, and process (PTC), since it can be interpreted as historical;
- ecological for lineages kept distinct by adaptation to different niches, and hence it also applies to agamospecies, but not to morphospecies, nor paleospecies.

The SSC operationally restricts taxonomists to **causal** differences rather than pattern recognition on any old characters. It includes isolation mechanisms, where these are evolved traits, but allows for asexual species kept distinct by ecological adaptations.

Hybrid species have caused problems for phylogenetic concepts, since it can turn out that what distinguishes the hybrid from the parental species are plesiomorphies, and they appear in a cladogram as unresolved polytomies. If they are distinct lineages despite this, then the SSC will treat them as different species.

Ring species are not many species unless the various populations are kept distinct through the shared mechanism. E.g., if they interbreed, and sexual isolation is the mechanism, they are a single species, as they are in the biological species family of concepts.

The synapomorphic concept is not intended to provide a definition of the term "species" that is in any way the essential meaning of that word. That is, other than the fact (which we have seen derives from Aristotle via Porphyry out of Boëthius) that a "species" is whatever group that can be differentiated out of a larger group of a more general kind, and which, since Ray, has been the smallest or least general such group that reproduces its characters. Really, we have not come so far from Ray, but like his concept, and unlike Aristotle's and his philosophical descendents', the application of the synapomorphic concept is empirically determinable, at least in principle. If we have an assay that tells us what keeps two lineages distinct (the philosopher's stone of taxonomy[159]), then we can give an account of the **fact** of the matter, without relying upon *a priori* essences and categories or the arbitrary and subjective choices even of specialists. A species must be what a competent taxonomist is **forced** to call a species by empirical considerations. It must also be what that specialist is forced to identify in the same way as **any** competent taxonomist in possession of the same empirical data. Otherwise, there is little point to taxonomy at all, so long as specialists can communicate, and this can be done a lot more easily in these days of computer indexing and database searches without species, as Pleijel and the other species deniers propose.

7.5. Conclusion

The overall problem of species derives from its neo-Platonic history as a top-down conception of the logic of classification (Boodin 1943). Modern taxonomy works in the opposing direction; beginning with the organisms, the individuals in the medieval

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[159] Thanks to Gary Nelson for this phrase here.

system, and thence to lineages, populations, and then species. Species in biology are the result of inductively generalising from individuals, rather than dividing general conceptions into subaltern genera to reach the infimae species. We still desire to treat *species* as a natural kind term, and hence to find essential features that define all and only those taxa. Between-species synapomorphies are not like this; all they have in common is that they keep lineages distinct (either causally or cognitively, the ontological and the epistemic sides of this issue). They necessitate a bottom-up classification logic, or perhaps better, an *in media res* logic (cf. Ghiselin 1997 p182ff). The reason I have made such play with cladistic conceptions of classification in this work is that cladistic classification is – depending how you interpret the matter – either a prolegomenon to induction, or an act of induction in itself. Bottom-up classification involves projectible inductive inferences and predicates, and "being a species" is one of these predicates. We predicate of some group that it is a species, and mean by that, that it is held distinct from other groups; this is all that the biological taxon concept has in common with the medieval conception of classificatory categories. We need to resist the tendency to fall back into the older way of thinking about classification. There is no universal grammar or language of nature. John Ray was right, and John Wilkins (the **other** John Wilkins) was wrong.

The SSC is intended to capture what it is that makes something a species in general, not in particular. One might think of it as a genus of species concepts. My argument has been that species are the actually separate lineages of evolution, but not that there is either a single grouping criterion, nor a single commensurate rank, that species occupy in the tree of life. If species are a phenomenon of evolution rather than a unit of it, then a species should be understood not as a rank, nor as a category, but as the effect of the causes that make lineages diverge. Thus, the reality of species as these terminal nodes of phylogenies does not imply that they are all of equal inclusiveness. Species can be real without there being a natural rank (Horvath 1997). Since evolution following the establishment of a clade need not proceed in the same manner for all subsequent lineages of that clade, there can be more or fewer splits for any lineage leading to a species. If we mark out a rank in terms of some absolute number of cladogenetic events, then species cannot be specified in terms of a top-down rank. But bottom-up ranking merely means that we reach a point in the evolutionary tree where two (current or terminal) lineages are divided. So there are no ranks in evolution.

The SSC provides a way to reconcile the various universal conceptions, such as the phylogenetic concepts founded on monophyly and autapomorphy (both the process and pattern conceptions), and the evolutionary concept, into a single framework. Of course, some species are not monophyletic and some are not autapomorphic (on present knowledge[160]) and some evolutionary species comprise more than one of the phylogenetic species, and may be respeciated. All of these exceptions are handled by the SSC.

It also enables us to discover *a posteriori* whether the species studied are biospecies or quasispecies or ecospecies or genetic species, for none of these are universal species concepts, and at best have application to only **some** groups of organisms. If we seek to find the synapomorphies that **do** isolate lineages, we may find that differently evolved traits do it in individual clades, rather than needing to impose theoretical or practical limitations on the organisms.

In cases like ring species, chromosomal races, species clusters, super species, and so forth, in which there are problems applying the universal or limited criteria of a given "object level" species concept, the SSC allows us to learn from the organisms and choose the species concept that best represents the features of the lineages of organisms to represent that group. It may be that none does; if so we might choose to be lumpers and put what we thought were distinct species (albeit in heterogenous modes) into one, and likewise should we find that the most natural notion for a group involves splitting them into what may seem an outrageous number of species, so be it. That is what best represents the nature of the organisms, and we must also learn that from them. Procrustes must be prohibited here; systematics is not about his bed, but about the sleepers that lie in it.

We still do not have the Ideal Species Concept. This is the best I can propose.

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[160] One opportunity for confusion here is the level of the lineages that are being defined as having phyletic standing, that is, of being monophyletic, paraphyletic or polyphyletic. A species in which the **gene** lineages have crossed over **phylogenetic** (taxonomic) lineages is not **genetically** monophyletic, but it may still be **taxonomically** monophyletic. The Respeciation Problem indicates that some species might be **taxonomically** polyphyletic too. Part of the problem is that *phylogeny* is defined as the topology of the taxonomic tree, but, circularly, taxa are understood to be groups that form phylogenetic trees. In any case, calling a taxon monophyletic implies that it is phylogenetically so; that is, it is a clade, and so we assume some level at which this is true. It must at least be at or above the level of organisms (i.e., not genetic or at the level of phenotypic traits). Thanks to John Harshman for discussion on this point.

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