

# Chapter 5. The Good Species

## Abstract

Much of the species problem lies in trying to find necessary and sufficient theoretical criteria for both their explanation and delimitation. I argue in this chapter that species are instead “operative concepts”, built up by the collective experience and context of subdisciplines of systematics as the field develops, relying on assays and criteria that make a putative taxon a “good species”. I reiterate my view that species are phenomena that stand in need of explanation, and that the category itself is so polysemic, because of the haphazard way the concept develops in the various specialties’ history, that it is merely an epistemic notion.

## 1. Introduction

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. (Darwin 1859, p. 37)

In recent years, there have been attacks on the notion of there being an objective rank (or category, as Mayr called it) that all species, and only species, occupy in the living world. It is sometimes called a “level of organization” or a “natural kind”<sup>2</sup>. As we know from extensive work by historians and scientists themselves, while the ranks of species and genus were formally instituted in taxonomy by Linnaeus in the 10th edition of the *Systema Naturae*, they were in use in various similar ways since at least the publication of Caspar Bauhin’s *PINAΞ [PINAX] theatri botanici* in 1651 (Cain 1994). Moreover, although *species* was simply defined

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I am most grateful to Igor Pavlinov, Frank Zachos and Thomas Reydon for their critical responses to the drafts of this paper, that have made it much better than it was. Yuichi Amitani wrote the initial inspiration for this chapter and set up the historical and methodological issue (2015). I also acknowledge help from Staffan Müller-Wille. Of course, none of my many colleagues are responsible for anything silly I say here.

<sup>2</sup> Biologists sometimes refer to species as an objective level of organisation in the biological world. Philosophers often refer to species as “natural kinds”, following Mill’s *System of Logic* (1843). A natural kind in Mill’s sense is something that has shared unique sets of properties. A taxonomic rank like species, or sometimes genus, is a natural kind if and only if it is specified by a shared set of properties, usually called an “essence” (Wilkins 2013). There are still advocates for this, or related, views (Devitt 2018, LaPorte 2018).

by Ray in 1686 as “signs or indications of their specific distinction ... distinct propagation from seed”, it was not defined further nor were there universally accepted criteria for identifying and diagnosing species, Linnaeus notwithstanding.<sup>3</sup>

The question of what a species is has been answered in various ways, but one way is to deny that species are anything singular, but instead that a pluralism of species “concepts”<sup>4</sup> is required, leading to issues regarding the choice of metrics, the uses of these conceptions in conservation biology, horticulture and agriculture, and so forth. Brent Mishler, for instance, has long championed the idea that there is no species concept, and that if we were being true to evolution and the consequent phylogenetic approach to taxa, we should replace it with a “smallest clade” idea.<sup>5</sup> Others have argued this would cause massive taxonomic inflation. In this paper I am going to suggest a (practice-based) solution, or rather a description of how biologists come by the notions they employ. Famously, C. Tate Regan quipped that a species is whatever a suitably qualified biologist chooses to call a species, which has been called the “cynical species concept”.<sup>6</sup> I will argue that it is not cynical at all. I shall rely upon several claims:

1. That a taxonomist is a “prepared mind” when describing and delimiting a species;
2. That taxonomists have a prototypical notion of a “good species” for the group<sup>7</sup> of organisms they study;
3. That this “good species” notion is subject to revision by empirical experience, as well as being professional conventions; and
4. That a good species is defined by the scale of species criteria in that group.

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<sup>3</sup> Ray 1686; trans. Lazenby 1995. Ray does expressly reject the number of flowers and the size of plants as specific *discriminata*.

<sup>4</sup> I stand firm: there is only one species *concept*, but many species *conceptions* (or definitions, or specifications, etc.). Biology has many specific applications of the term *species* (see Wilkins 2011), but the term and concept is what is being applied, defined or modified. This is analogous to Mayr’s category–taxon distinction. Each conception of species, such as the General Lineage Concept or the Mate Recognition Concept, is an application of the concept *species*.

<sup>5</sup> In which I concur (Mishler and Wilkins 2018).

<sup>6</sup> The details are to be found in my 2018, p. 261. Philip Kitcher coined the term “cynical species concept” (Kitcher 1984).

<sup>7</sup> In this paper, when I refer to a group, I mean the close relatives of the specimens being observed, such as the group Psittaciformes (parrots) when dealing with a specific possible species (such as a newly observed lorikeet). Groups may be named in the Linnaean schema or they may be a clade or both.

Scale is something most often applied to ecological systems in biology, as well as to microbial and microscopic processes and entities. It is not usually applied to species. Instead, taxonomists, and biologists in general, usually speak of the “level” of species, or of species themselves being instances of a “level of organization”. This smacks of the Great Chain of Being, wherein taxa are assigned to a ladder of increasing virtue (complexity, intelligence, and so on), but rank has fallen into great disrepair in the last few generations as concepts like *family*, *phylum*, and *genus* are seen to be arbitrary and non-natural. The one level that holds out is *species*. The stubbornness of this calls for an explanation, and it may in fact teach us about how biology classifies the world it encounters.

## 2. Prototypes and “good species”

I swallowed [my master’s] incidental teachings and gradually got to know the “good” and “bad” species of my homeland through a kind of tradition, but I frankly admit that even then I could not be quite clear how to accept a given case without tradition and recognize whether one was dealing with a “good” or a “bad” species. (Kerner 1866, p. 5)

Despite a long history of naturalists and later biologists calling this or that species a “good species”, the importance of this conception was not picked up in the philosophical literature, so far as I can tell, until Yuichi Amitani proposed his prototypical notion of good species (2015). What did naturalists mean by it? As Amitani presents it, naturalists take some unproblematic species as a prototype of what a species was meant to be [implicitly: in that group], and they apply it until it breaks down in ambiguity or impracticality. For instance, in Notebook B, Darwin in 1837 or 1838, wrote:

A. B. C. D. (A) crossing with (B), and (B) being crossed with (C) prevents offspring of A becoming a **good species** well adapted to locality, but it is instead a stunted & diseased form of plant, adapted to A. B. C. D. Destroy plants B. C. D. & A will soon form **good species!**<sup>8</sup>

In the *Origin* itself, he said:

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

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<sup>8</sup> Page 211, emphasis added. From Darwin Online, at <http://darwin-online.org.uk/content/frameset?itemID=CUL-DAR121.-&pageseq=38&viewtype=side> accessed 22 December 2020.

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. [1859, page 425f, emphases added]

The phrase “good species” in English seems to have been adopted widely in botany in the first decade of the 19th century<sup>9</sup>, and it is no coincidence that Darwin uses it in a botanical context. It seems to have been required as systematists adopted the Linnaean “natural system”.<sup>10</sup> That such a concept was needed so soon after adopting a ranked system (by 1840) indicates the fact that naturalists were aware of the variation within species and genera quite early on, and the consequent vagueness of many species. As Amitani notes:

the concept of *good species*, a prototype of *species*, mediates the non-definitional, or perhaps implicit mode of understanding of species. A good species is a taxon judged to be a species according to more than one species criterion—such as reproductive isolation and phylogenetic properties—or a taxon judged generally to be a species by competent biologists, whether the phrase merely expresses one’s epistemic confidence in the taxonomic judgment or has even an ontological implication that the species category is divided into good and not-so-good species.

Amitani notes that for some a good species can be whatever all systematists would accept is a species, irrespective of the definitions used. There are undoubtedly some of these, but it would not be the rule, I think. Many systematists have historically treated good species as morphological cluster (e.g., Rensch 1954: 24–28, introducing his notion of *Rassenkreise*), or a monophyletic group (see Mishler and Wilkins 2018) and these are not universally accepted conceptions even within a subdiscipline (e.g., lichenology, see Kendig, *this volume*) or within a single group. However, Amitani’s point about a good species being one that is judged by

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<sup>9</sup> The term “*gute Arten*” in German seems to have come via the English phrase rather than vice versa. See the Müller-Wille and Hall 2016 translation of Mendel’s *Versuche* (1866), commentary page 39. This has now been published (Mendel 2020). Austrian botanist Anton Kerner von Marilaun, who they cite, published a series of 10 articles under the title “*Gute und schlechte Arten*”, later published as a booklet (Kerner 1866). The term was used in the 1820s in Germany botany. I could not find the term in French before the English, except simply to denote a species which is good to graft or eat or otherwise use in horticulture. Many thanks to Staffan Müller-Wille for his assistance with tracking this down.

<sup>10</sup> William Kirby, in his *Monographia Apum Angliae* of 1802, several times refers to “good genera” as well. Whewell later described a genus as being based around a “type” species, which is an exemplary species within the genus (Whewell 1840, p. vol 2, 517-519) see Wilkins 2013 p. 225.

more than one species *criterion* is a good point to make. Species do not have a singular criterion for being assigned *specieshood* (as Amitani – and Pavlinov, *this volume* – calls it), despite the mistaken assumption that single key diagnoses were required by the Linnaean scheme.<sup>11</sup> Instead they always have been, and increasingly are more so, delimited by a large number of criteria, including (but not restricted to) molecular, structural, adaptive, developmental, and behavioral characters<sup>12</sup>.

Any use of single key attributes (for example, DNA Barcoding) is either a methodological necessity made an epistemic virtue due to a lack of available data, or it must follow on from the identification of prototypical good species in that group (Whewell’s “type species” for a genus). For, without a type species or good species prototype, how can we know what the single key is identifying? If one finds that by a singular metric one has  $n$  OTUs,<sup>13</sup> can one say that one has  $n$  species? First, we’d need to know that the singular metric identifies good species before we could be confident in using it for as yet unknown species. Once we acquire that confidence, then it may be useful to use that criterion, such as a COI sequence in mitochondria or a *rbcl* gene from chloroplasts, or an sRNA sequence in fungi and single celled organisms. This then implies that we know ahead of time what a good species is for each group and subgroup, and so on.<sup>14</sup>

So, the question at issue is how we know what the prototypical form of specieshood is in any given group, in order to test whether a particular identifier technique or data type

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<sup>11</sup> The Linnaean scheme had single key “essential characters” but only to differentiate the type specimens from other related species. They were identification keys, not delimitation characters.

<sup>12</sup> Thomas Reydon notes in review that this is connected to the relatively recent shift towards “integrative taxonomy”, which makes use of more than a few types of evidence (Padial *et al.* 2010, Will *et al.* 2005; Will & Rubinoff 2004). However, Fujita and Leaché 2010, 2 note “Many good species will not exhibit fixed morphological differences or fixed DNA differences across multiple loci. An integrative taxonomy should not force systematists to search for diagnostic attributes that may have no relation to the data or process used for species delimitation.”

<sup>13</sup> Operational taxonomic units, see Sneath and Sokal 1973.

<sup>14</sup> An excellent example of this occurs frequently when barcoding insects – for example, ichneumon or braconid wasps (Sharkey *et al.* 2021) or pygmy grasshoppers (Lehmann *et al.* 2017). The number of possible species for the former groups are massive, and so in order to avoid what they call the “taxonomic impediment”, they do barcoding for “accelerated taxonomy”. However, in order to calibrate the sensitivity of COI differences used for species delimitation and subsequent description, they had to test it out first on known “valid species”. Lehman *et al.* specifically note that alpha taxonomy is still required and Krell (2004) call the resulting taxa “parataxonomic units” (PUs), not yet species. They are effectively OTUs or *phenons* (Sokal and Rohlf 1962). My thanks to Igor Pavlinov for pointing these references out to me and suggesting this may be a new case of good species criteria. I think that barcoding does not *supplant* good species, and in the absence of knowing what counts as ichneumon or braconid species, barcoding would be largely uninformative and probably uninterpretable.

reliably identifies species. And in turn, this raises the question of how biologists construct their prototypes of specieshood.

### 3. The making of a good species

The limits of the majority of species are so undefinable that few naturalists are agreed upon them; to a great extent they are matters of opinion, even amongst those persons who believe that species are original and immutable creations; and as our knowledge of the forms and allies of each increases, so do these differences of opinion; the progress of systematic science being, in short, obviously unfavourable to the view that most species are limitable by descriptions or characters, unless large allowances are made for variation. (Hooker 1859, p. iii)

Biologists in the field encounter not species but organisms. Sometimes organisms are difficult enough to delimit on their own, as in clonal stands, biofilms, obligate endosymbionts, superorganisms like eusocial hives, and so on<sup>15</sup>. Most of the time, however, a biologist knows more or less what an organism of the group they study is. The term “organism”, which supplanted the older “organized beings” in the early nineteenth century, connotes a system that maintains itself in its environment (Cheung 2006) and is the benchmark unit in most fields (not so much in clonal or colonial species). Most organisms have something like a developmental system, what used to be called a “life cycle”, and the development can be often observed more or less empirically without much in the way of ancillary theoretical assumptions, as the existence of agriculture and horticulture demonstrates. So how do biologists get from organisms to species?

The first and most obvious way is that biologists get their ideas from their training and education. That is, *species* are cultural transmits. But this merely pushes the problem a bit further back, leading to a chain of transmission that is indefinite. Moreover, while it is now agreed that science is a social process, that is not, nor could it be, the only thing it is. Social construction of taxa is not the whole story. So, let us consider a simplified sequence of species construction, beginning in the premodern period. All human cultures identify types of living organisms. Some are quite exact and commensurate with modern scientific types, while others are vague and generalized. I have previously suggested that precision in taxonomizing the living world depends a lot upon how economically important that knowledge is for the taxonomizers (Wilkins 2018a, p. 352f). For systematists, that importance is obvious (their living consists in being precise), while for hunter-forager societies success in classification is literally their meal ticket. People inveterately wrong in their classifications have a tendency not to flourish. So initially, taxonomy begins with folk

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<sup>15</sup> See, for instance, Queller and Strassmann 2016.

taxonomies, and these are not infallible, merely good enough. For instance, the cassowary was classified as a human for totemic reasons among the Karam people in Papua New Guinea.<sup>16</sup> But they would certainly have known a lot about their prey species and food plants.

In my historical review of the species concept, I noted that the idea of a concept for living things evolved initially out of folk botany, in the form of herbals, and folk zoology in the form of bestiaries, but that is not the whole story. There are horticultural reasons for finding natural units among potentially commercially significant plants such as ginger, pepper and so on<sup>17</sup>, and there are of course breeding reasons for commercially significant animals such as horses, cattle and sheep. Some noted that sheep and goats, horses and donkeys, and so on could interbreed with varying degrees of success and fertility of the progeny, but in the main, breeders knew to interbreed within species. As late as the nineteenth century Darwin himself was still relying upon breeders of pigeons, horses, and other livestock for information on species.

As naturalism developed into a scientific endeavor, folk taxonomies gave way to expert taxonomies. As Joachim Jung (1587–1657) said, botanists prefer finding novel stocks to making dry formal systems (paraphrasing his *De Plantis Doxoscopiae* 1.1.5)<sup>18</sup>, and he was one of the first to make a close study of the plants themselves rather than only using prior works to assemble his classifications.<sup>19</sup> He was, of course, followed by Ray and then Linnaeus, and all the taxonomists who had thereafter taken up the mantle of botanist. Each of them studied large numbers of specimens (the taxonomic equivalent of an organism), described them in the context of the group they were part of, and named them, leading to Linnaeus' genus–species epithet nomenclature and the broader system of the *Systema Naturae*. By the nineteenth century, botanists began to specialize either by flora (such as

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<sup>16</sup> Bulmer 1967. See also Berlin 1973, Atran 1998 and Media and Atran 1999 for further context, and Kendig 2020 for a neat case study among the Samí and other boreal cultures.

<sup>17</sup> “Spice” in English, and cognate terms in French (*espice*), Portuguese and Spanish (*la especia*), Italian (*spezia*), etc., are in fact derived from the Latin *species* (kinds) beginning in the 14th century. See the etymology for the entry “Spice” in the *Oxford English Dictionary*, which has also an obsolete usage (sense 3) in which “spice” still meant “kind” until the 17th century.

<sup>18</sup> Jung 1747, p. 69. Igor Pavlinov introduced me to this passage, and classicist Tim Parkin helped me interpret Jung's Latin.

<sup>19</sup> Jung was preceded by the work of Conrad Gesner (1516–1565), who unfortunately died before finishing his *Historia Plantae*, and so his work remained unpublished. Gesner's lovely watercolors can be seen in the library at the University of Erlangen–Nuremberg. I am indebted to Thony Christie for showing me these *objets d'art*.

Hooker's *Florae*), or by group (order, class or family).<sup>20</sup> The professionalization of botany and zoology that began in the late nineteenth century brought with it the formation of subdisciplines like the study of diatoms, flowering plants, fungi, onychophora, or bacteria, and so on. Each subdiscipline had its own ways of identifying, describing and diagnosing species, dependent upon the properties of the group members themselves.

#### 4. The criteria for identifying good species

So, the development of a notion for each field of study that diagnosed species was in part dependent upon folk taxonomies, then a tightening of methodologies, specialization and novel techniques. For instance, the taxonomy of fungi (mycology) depended a lot on the morphology of the fruiting bodies and the ecological niche in which they were found until molecular techniques came along. Fields like lichenology had to deal with two or more commensal organisms from distinct domains of the tree of life, and hence the notion of a lichen "species" is fraught when using criteria that were developed to deal with organisms that reproduce sexually and have a single zygote (Kendig *this volume*).

Each specialty in biology – zoology, botany, mycology, bacteriology and virology – and indeed each evolutionary group within those specialties has its own shared set of criteria for identifying a good species. These do not always apply, however, and when they do not, then specialists refer to "cryptic species", "species complexes", "micro species", "ring species", "quasispecies", and when all else fails, "subspecies", "varieties", and so on. But there would be an exemplary form of species in that group. Of course, many groups do not match the exemplar even in a minority of cases. In many animals parthenogenic species can form within a sexual clade, secondarily losing sexuality, or some aspects of it, via cross-species hybridization and/or polyploidy. One case – the whiptail lizard *Cnemidophora* (now *Aspidoscelis*) *lemniscatus* – "may actually represent a complex of independently formed hybrids, further complicating the situation in this 'species.' " (Gregory and Mable 2005). Other examples include snakes, other lizards, stick insects, wasps, cockroaches, salamanders, snails, fishes, nematodes, and rotifers, to mention a few. No naturally occurring parthenogenic bird or mammal species appear to be known, although parthenogenic eggs have been laid by turkeys in farms.

So, in the case of the whiptail lizard for instance, how do herpetologists identify an asexual group as a species, when lizards are usually identified as "biological species" *sensu* Mayr? It obviously cannot be reproductive isolation, since every individual in the asexual "species" ("agamospecies" or "paraspecies") is reproductively isolated and nobody would take them all to be individually distinct species. Also, they are typically clones of each other, so they

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<sup>20</sup> Kleinman 2018.

form a “clonal species”<sup>21</sup>. The answer must lie in the assay criteria used to group them. In the main, these differentiating or identifying criteria will be morphological, ontogenetic, and molecular. Each forms a slightly different grouping (since even clones individuate during development and behavior), and so something like a clustering notion must be used. The thresholds used will vary according to what is “usual” or “reasonable” in the case of the other species in the clade. The competency in Amitani’s quote does indeed lie with the systematists. For example, in single-celled organisms like lobose amoebae (Smirnov 2009), until the development of molecular methods, only morphology was available, which led to the loss of identification criteria as initial taxonomy was highly individualized. Smirnov notes

Naked lobose amoebae are among the most difficult protists to differentiate. Because they are believed to be agamous (clonal) organisms, the biological species concept, which involves defining species based on their reproductive isolation, is not applicable. The general consensus is that for such taxa the morphospecies concept is the only one practically available. However, analysis of the morphological differences between amoeboid protists is rather difficult, and conclusions are often unreliable, especially for closely related species. This is partly because the shape of an amoeba is dynamic; in stained preparations after fixation and dehydration specimens are often no longer representative. So, there is no way to preserve a type specimen of an amoeba – a holotype, so important in traditional biological systematics. Many amoebae species are culturable, and therefore type strains can be deposited in culture collections. However, this practice became widely used only after the 1960s and there are still many examples where strains deposited with the culture collections were lost. So, until the advent of microphotography, the only tools to document amoebae species were line drawings and text descriptions, both of which tended to be rather author-specific. For example, despite careful descriptions provided by E. Penard in his fundamental monograph published in 1902, and a large number of stained preparations left by him, many of his ‘species’ are now unrecognizable.

This case represents all the issues of identifying species over time. The assay techniques – microphotography, molecular analysis, and electron micrography – permitted finer (more precise and accurate) and more repeatable taxonomic discrimination. One might almost say that the species are made by way of these techniques, if not for the obvious fact that identifying something is epiphenomenal to the real things so identified. In recent years, for example, the use of “barcoding” techniques has teetered perilously on the edge of making

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<sup>21</sup> Like the “genets” of other species such as the North American Quaking Aspen (*Populus tremuloides*). See Mitton and Grant 1996, p. 27, and Kendig *this volume*.

the species whatever it is that has a unique COI gene (or whatever else is used in plants, etc.), rather than the species being putatively identified by the unique marker. In short, the sign is not the thing signified, as any logician knows.<sup>22</sup> Identifying a species based on a single criterion relies on a prior correlation between the criterion and known species.

That said, it is important to note that there are several scales involved in identifying species from early modern times to now. Morphology, of microscopic organisms in particular, involves being able to observe and record the forms of things at a *mesoscale*. That is, within the region of size where light waves are able to identify structure (even under a microscope). There is also a *macroscale*: the broader environment and distribution of the organisms. There is also, of course, the *microscale*: the size at which structures are no longer visible using ordinary light and must be assayed using electron micrography (EM) or DNA–DNA hybridization and so on<sup>23</sup>. This scale is obviously one of size. The criteria used to identify species have become increasingly smaller.

But scale applies to more than size. It also applies to functionality. Reproductive isolation is obviously one such. It occurs at the organism level and both above and below it. Reproductive isolation requires functional behavior at the genetic (very small), cytological (small), anatomical (medium) and organism (the benchmark level for that species) levels. Species delimitation also involves ecological, social, and geographical and meteorological scale criteria (*X*s can live in arctic or tropical conditions, for example). Molecular techniques rely upon the persistence, spread and functional role (or lack, in the case of pseudogenes) of the assayed sequences and structures. The morphology of molecules is only significant for diagnosing species if it happens to be aligned with species identity. Subspecific haplotype groupings for example, are not significant for species identification, although they are for population and subspecific structural identification. So, for a molecule (a “speciation gene” as well as a “barcode”) to act as a *discriminatum* for a particular species, it must have some “inutility metric” that underpins the inference (as characters used in taxonomy are very often nonfunctional or nonadaptive, to avoid convergences).

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<sup>22</sup> Something not always recognized by taxonomists, who sometimes tend to be wedded to the classifications of tradition and treat novel taxonomic techniques and results as *doing* something to their organisms (not generally, but I have seen it). Occasionally, it is overlooked by philosophers too.

<sup>23</sup> EM is used for very small organisms that are below the resolution of light microscopy. DNA–DNA hybridization was used, for example, by Sibley and Ahlquist to measure genetic similarity, which at the time was not otherwise observable (1983).

Finally, scale applies also to time: the duration of a species, either at geological scales (*macro*), population scales (*meso*)<sup>24</sup> or short-term lineages (*micro*) is relevant. As Darwin noted, varieties are more temporary, species are more permanent. Here again reproductive isolation is a good case. Reproductive isolation requires microscale proximity and activity (I cannot reproduce with Anne of Cleves, for example, for very different reasons than Henry VIII). Whether or not a species is reproductively distinct over geological time is merely speculative, but there are cases of persistent reproductive reach between species isolated for millions of years such as the snapping shrimp and sea urchins isolated by the isthmus of Panama for around three million years<sup>25</sup>. Moreover, many species will hybridize with other species, allowing the introgression of genes, as displayed in the Neanderthal and Denisovan genes in non-African migratory populations of humans (Stringer 2012).

Each of these scalars effectively defines an abstract phase space which will vary in its particular components for each species grouping. In keeping with the points made above, what these spaces encompass depends on the learned experience not only of the singular taxonomist but of all those who work on the groups being taxonomized. In short, the subdiscipline will always have an idea of “good species” for that group, which may be revised to be more or less inclusive as new data and re-analyses come in (“lumping and splitting”), or simply because a group has few specialists and the personal preferences of one or a few systematists skewed the approach taken.

This is what one might call an “operative concept” in that the driving forces are the use of operative data (unlike, say, the “biological” species concept, which would require large scale breeding experiments to employ it, as Ehrlich noted in 1961), only it is not a concept but a practice.<sup>26</sup>

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<sup>24</sup> Igor Pavlinov has drawn my attention to *mesospecies* in Dillon 1966, which he defines as “The second stage [of a species’ life cycle], or mesospecies, has stable range boundaries, a relatively great abundance, and extensive subspeciation”. I do not mean the same thing here.

<sup>25</sup> Genetic incompatibility does rise as separation persists, but there is still a shared developmental system inherited from the original populations. See Knowlton *et al.* 1993, Lessios and Cunningham 1990, Ma *et al.* 1978, Marko 2002, Ma *et al.* 1978, Schultz *et al.* 2000.

<sup>26</sup> This is what Kendig has called *kinding*, the process of making kinds via the practices of science (Kendig 2016). Brigandt (2003: 1309) called species “investigative kinds”: “An investigative kind is a group of things that are presumed to belong together due to some underlying mechanism or a structural property.”

## 5. Phenomena and explanations

Theoretical concepts of kinds and other generalizations in science are seen by many to be metaphysical universals that cover the domain of phenomena needing explanations. In short, if something is a species then it has a certain number of ideal properties as specified by the theory. This is sometimes known as the *Ramseyfication of theories* after Frank Ramsey's formalization method for theories (Melia and Saatsi 2006, Wilkins 2018b). In short, the idea is that a theory is reduced to logical sentences with variables that are quantifiable. The variables then denote the kinds or classes of objects in the theory (Quine sloganized this as “to be is to be the value of a bound variable”, 1948). I am arguing that instead, some general terms in science form out of practical considerations and specialist experience, with a strong admixture of sociopolitical interests (see my forthcoming chapter). As it happens the initial motivation for there even *being* a natural concept of species was intimately connected with a more literal interpretation of the Noah's Ark story in the Bible (*Genesis [Bereshit]* chapters 6 to 9, see my 2018a, 56–62). In order to fit all living kinds that breathed within the specifications of the Ark (*Gen.* 6:15-16), it was necessary to give “kind” (*min*, מין) a more precise definition (many later-named species were therefore considered local variants of the created kind). When John Ray gave his famous “definition”, he was also doing so to meet the needs of exploration and colonization, and so on.

But if species are not quantified variables in a Ramsey Sentence of biological theory, does this mean they are not something that can be treated as scientific? Surely 21st century biologists are unaffected by 15th century theologians? Of course they (in the main) are — biologists name species because their forebears named species, using operational criteria their forebears developed, not because of Athanasius Kircher's writings on the Ark. But the *need* for a rank or theoretical and metaphysical conception is not based entirely upon scientific tradition or experience. Instead, it really is a holdover of older religious and philosophical goals and intentions (see Wilkins forthcoming), which has been bequeathed to us via Mill and Venn as “natural kinds”.

As I have argued previously,<sup>27</sup> species are best thought of not as concepts that explain (*explanantia*) the phenomena, but as phenomena that stand in need of explanation themselves (*explicanda*).<sup>28</sup> The question then arises — what makes a phenomenon? This

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<sup>27</sup> Wilkins 2018a chapter 14, 2018b.

<sup>28</sup> Ingo Brigandt (2003) was first to argue that species are phenomenal objects in need of explanation, but Kim Sterelny (1999) had earlier mentioned what he called “phenomenological species”, which he defined as “recognizable, reidentifiable clusters of organisms” [p. 119]. Sterelny does not think these are sufficient for the acceptance of groups as species, as he instead argues for an evolutionary conception, a lineage

takes us back, apparently, to the problem of the criteria of specieshood.<sup>29</sup> In order to know whether the differentiating criteria used are sufficient to identify good species, we need to know what good species are, and in order to know what good species are, we need reliable differentiating criteria. However, in order to know a phenomenon, does it also follow that we need to know what makes something a phenomenon in the first instance? Consider Newton's list of phenomena at the end of the second edition (1713) of the *Principia*:

*Phenomenon 1*: The circumjovial planets, by radii drawn to the centre of Jupiter, describe areas proportional to the times, and their periodic times – the fixed stars being at rest – are as the  $3/2$  powers of their distances from that centre.

*Phenomenon 2*: The circumsaturnian planets, by radii drawn to the centre of Saturn, describe areas proportional to the times, and their periodic times – the fixed stars being at rest – are as the  $3/2$  powers of their distances from that centre.

*Phenomenon 3*: The orbits of the five primary planets – Mercury, Venus, Mars, Jupiter, and Saturn – encircle the sun.

*Phenomenon 4*: The periodic times of the five primary planets and of either the sun about the earth or the earth about the sun – the fixed stars being at rest – are as the  $3/2$  powers of their mean distances from the sun.

*Phenomenon 5*: The primary planets, by radii drawn to the earth, describe areas in no way proportional to the times but, by radii drawn to the sun, traverse areas proportional to the times.

*Phenomenon 6*: The moon, by a radius drawn to the centre of the earth, describes areas proportional to the times.<sup>30</sup>

These are not the phenomena of Bogen and Woodward (1988, see Bogen 2011) who specify that phenomena are “patterns in data”. There *are* patterns implicit in Newton's list (the  $3/2$  powers identified by Kepler, for example), but there are many patterns out there to be had, and so the selection rests with the state of the debate and the questions of how to explain

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undergoing changes in ecological conditions. He says that “it has to be shown, not assumed, that phenomenological species constitute a biological kind. Minimalists about species do not expect theoretical biology to vindicate the species category: they think it is merely a phenomenological kind. We can clump organisms into species, but the biology explaining the clumping pattern is so diverse that *species* does not name a biological kind”. I agree with this, but do not feel the need for a universal conception of *species* as Sterelny does.

<sup>29</sup> This is a form of *diallelus*, in which the problem of choosing a criterion for identifying something itself needs a criterion, ad infinitum; see Chisholm 1982.

<sup>30</sup> I am indebted to Kirsten Walsh for this list.

some patterns and not others (for instance with Newton, Ptolemaic patterns).<sup>31</sup> A phenomenon is a pattern that is *of interest*, or in the view of the scientific field of experts, needs explanation. Species are exactly that. This is an epistemic notion of *species*, but not one divorced from the biological world.<sup>32</sup>

The acquisition of these criteria for matters of interest is a matter of professional and epistemic development: science students are given conceptual tools along with the empirical tools and protocols during their initial education, becoming more detailed as they progress from laity to expert. This means that the majority of specialists in the natural sciences will acquire scattershot instruction, mostly via mimesis, and thus will have at best partial understanding of the major conceptions utilized in their discipline outside the fields or topics which they specialize in. In short, they cannot say all they know (for much of it is mimetic) and they cannot know all of their field. The construction of phenomena will therefore be a process of proposal and criticism or rejection by peers and instructors, as Kerner in the epigram above described.

The role that good species play, as opposed to bad species, lies in the adequacy of the phenomenon to require explanation. Prototypical species will not need much explanation beyond their individual properties; but bad species will require much more investigation and explanation than good species, until they either have been reconciled with the prototypical notions, or they refine the criteria used by the field (or a new prototype is chosen).

This approach to species has a number of virtues in my opinion: for a start it makes sense of species pluralism – each species is the result of historical contingency in the mechanisms that isolate it from other species (as understood by those working in that field or group); there may be underlying genes or developmental systems for speciation in that group, but there is no reason to think there will be universally shared such mechanisms across all groups, even when restricted to, say animals or plants. Each species gets an explanation based on whether or not it meets shared criteria or processes for that group (Wilkins 2003).

Moreover, species as phenomena explains why so many biologists are committed to the reality of the groups they study — they really do exist as phenomena. Whether or not they are more than conventional recognition of patterns depends on the group itself. It also resolves (or dissolves) the natural kinds issue. Species are natural groups which may or may not share properties or mechanisms that cause them to group the way they do. Some will - they have some sort of “essence”. Some will not — but they may share a homeostatic

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<sup>31</sup> There is also observational data listed in the full appendix.

<sup>32</sup> See Barker, *this volume*, for a critique of this approach.

property mechanism. Some will be multiply-realized (as in respeciation events, Turner 2002). And so forth.

I am not aware of any reason to think, however, that species are a level of biological organization or a fixed rank in biology. A species may be real, but *species* is not (Mishler and Wilkins 2018). In the end, what counts as “real” or “biologically meaningful” in biology depends upon the choice of criteria for naturalness, and the scale of the organisms and their differentia. I plump for monophyly, myself, but that is not surprising (Vanderlaan *et al.* 2013).<sup>33</sup> Monophyly is regarded as the “real” structure of living things based on actual patterns in the data by most biologists trained since the 1980s. However, species can be but often are not monophyletic, and restricting species to monophyletic lineages means having some prior notion of where to stop subdividing. So, a diagnosable group of organisms is a real group in the sense that the data is not merely subjectively interpretable, but a species is not, in the cladistic sense, “natural” unless it is also monophyletic.

A comment about “bad species”, or “not-good species”: these are basically species that do not fit the consensus criteria for that group. As there are an indefinitely large number of possible ways to be not-good, I’m unsure what to say about them (how many ways are there to not fit a set of criteria?). Dillon’s stages are supposed to be ontic, while “good species” are at least epistemic representations of specieshood in a group. A heterogenous meta-population might be difficult to diagnose as a species using the usual criteria. That doesn’t make it a bad species. A bad species is one that has been misdiagnosed. This places the entire weight of the concept on the criteria being used, and since that varies by the experience of the discipline, as well as the preferences of different specialists, the term is clearly based on disparate and often incommensurable epistemic criteria.<sup>34</sup>

From this we can make the general comment, following Cracraft (1989), about concepts like *species*: they have an *ontic* aspect and an *epistemic* aspect, and generally one aspect dominates their use. For species, we have previously considered, during the 20th century, that the category had a theoretical ontic aspect predominating. I would argue that by now we have to admit that *species* is primarily an epistemic notion.

## 6. The evolution of the concept

*Species* is what I call an “operative concept”, which is to say a concept formed from experience within the theoretical framework and methodological practices of a scientific

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<sup>33</sup> Monophyly is regarded as a single cut of a branch of an evolutionary tree. However, there is a debate over whether it includes the common ancestral taxon or not, which those who adopt the latter definition using *holophyly* for the former. This usage is not the consensus view, however. See the discussion in the citation.

<sup>34</sup> I do not mean Kuhnian incommensurability here, but merely that different uses of *species* use different metrics of identification, and that the metrics may not be interconvertible.

discipline, but which is not formulated in terms of either the theories that predominate or which underpin that discipline (Weber’s “ideal-type concepts”<sup>35</sup>), or the assay techniques used to identify them (including such techniques as the statistical clustering of data points). It is not a simple inductive empirical class, if such things exist, but neither is it a theory-derived natural kind (figure 1).<sup>36</sup>

Figure 1. A simplified diagram of the development of operative concepts out of folk usage.

Insert figure 1 here

Amitani’s prototype notion of “good species” leaves out the reasons why certain prototypical species are chosen to be, as it were, the exemplary type of species of the group. I have tried to fill this out in terms of education, experience and cultural context. Experienced observers of species have at their disposal a range of tools: practical training by prior experts; knowledge of related species (and thus expectations about what will be seen, so that novel features are highlighted); whatever theoretical prior information there may be about the group in question; and cognitive ancillary tools, such as what counts as a good explanation in that field.

Operative concepts<sup>37</sup> as I conceive of them are a kind of work-in-progress category that sciences and disciplines must construct as they develop the overall theory and protocols of their field. As such they often begin in ordinary language. This is what happened to *species* — it began life in early modern Europe as a vernacular term for “kind” in the academic language of the day, Latin, with biblical and logical connotations. Even when Ray first defined botanical and zoological kinds, it was a special case of the broader notion. Such operative concepts are very often revised (e.g., fishes), or abandoned (reptiles) as more precise and natural notions develop (clades).

For historical and professional reasons, *species* has not undergone this revision or abandonment due to it being fixed in protocols of naming and classification, and more recently ecological and conservational practice (figure 2). But it should be, at least as a category. We name kinds in our everyday lives, but nobody thinks that kinds of car such as

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<sup>35</sup> Drysdale 1996 gives a good treatment of this.

<sup>36</sup> An extremely useful historical review of the distinction between lawlike (“nomothetic”) and particularistic or token-based (“idiographic”) concepts in science can be found in Rieppel 2006. So far as I can tell, at least within philosophy of science, operative concepts have not otherwise been given a proper treatment. A nice general treatment of tradition and social construction of categories is given by (Stewart 2014).

<sup>37</sup> Not to be confused with *operationalization* as proposed by Percy Bridgman (1927), in which the meaning of a scientific term is defined solely by the operations of measurement and instrumental analysis of the science.

*cabriolet* need to have an underlying theoretical definition or usage. In biology we can name and describe, and maybe even define, species as kinds without needing to think they have anything more than an operative — empirical and conventional — nature.

Figure 2. A simplified sequence of the formation of species concepts.

Insert figure 2 here

Operative concepts are picked up by individuals from those who teach them (see the epigram above by Anton Kerner), through instruction, imitation, and the affordances of the discipline, such as instruments, techniques and locales. They can be acquired either consciously or unconsciously. When an individual reaches a certain social standing, their (usually retrospective) definitions of the operative concept becomes both explicit and constraining on how the term is used, leading often to conflicts with equally authoritative individuals in the race for funding and resources. But they are not theoretical terms, although the objects in the world that they pick out are susceptible to theoretical accounts. Basically, they are social, professional and practical terms of art, that developed from ordinary language and psychology.

## 7. Conclusion

That *species* as a category is not natural is hardly controversial these days, even if many still think that it is natural to identify them individually (see also Dupré *this volume*). That individual taxa called species are (sometimes) real objects (groups of organisms) is likewise hardly a surprise. However, the *category* of species is neither a biologically meaningful nor “real” rank, level of organization, or even a type of lineage. It is a purely *epistemic* notion, based upon the traditions of the disciplines in which species are named, to deal with the prototypical sorts of actual kinds each specialty has to accommodate. There is a tradeoff between generality in the group being studied, and precision in the individual cases, and this is what each specialty has to contend with in biology.

In sum, as Kerner said:

Abandoning at last the perspective of species constancy, would [cause us to] give up the childish argument about good and bad species... [page 8]

Once we characterize good species as epistemic objects, the attachment we have to the category of species must recede. As Brent Mishler and I have suggested, if we are looking for natural structure in the relations between living beings, monophyly is sufficient, and that means that there is of necessity no “rank” or “level” that makes something a species, and that species may be clades, or include many subclades, or be, in fact polyphyletic.

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