

What are Species? Or, on Asking the Wrong Question

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ABSTRACT The question, ‘What are species?’, has had a long history in biological systematics with no success at achieving a scientifically viable consensus. This failure is due in large part to the obsession with this one taxon to the exclusion of asking the epistemically more relevant question, ‘What are taxa?’ The problem has been exacerbated by the fact that systematics rarely operates in accordance with the overarching goal of scientific inquiry. This essay offers solutions by defining ‘taxon’ and ‘species’ such that they are consistent with that goal. Some notable consequences are then discussed.

INTRODUCTION

Biologists have maintained an obsession with the biological status of species for several hundred years (Mayden, 1997; Stamos, 2003; Wilkins, 2009a, 2009b; Richards, 2010). The outcome thus far is that over 25 species concepts have been put forward. Ironically, from the voluminous literature on the subject, especially after the advent of Darwinian and neo-Darwinian thinking, consensus on the subject remains elusive. Biologists gravitate to one school of thought or another, often consistent with the organisms that are one’s specialty or one’s general perspective on the nature of biological systematics, or both.

The time is long overdue to cut through all the indecision, which means approaching that interminable question, ‘What are species?’, from an entirely different point of view; one that is not derived from within the limits of biological thinking. Rather, the search for a solution should begin outside biology. We must look to the generally acknowledged reason we engage in scientific inquiry as well as understand the basic principles of reasoning we apply in response to observations of organisms. When we consider the nature of the relations

that exist between an observer and the organisms they perceive, coupled with the goal of inquiry, we find that asking ‘What are species?’ is not the appropriate question. In this essay, I will show that the question we should have been asking all along is ‘What are taxa, and how do they serve the goal of scientific inquiry?’ It is only after answering that question that the subsidiary ‘What are species?’ can be answered. But answering that question will expose the notable deficiencies of the one term species for accurately representing the products of our interactions with organisms in the name of inquiry.

Pursuing the task outlined above first requires acknowledging the goal of scientific inquiry. Next we will need to take a short foray into the nature of reasoning to be able to link our reactions to the observations of organisms with the goal of inquiry. This provides the basis for stating the goal of biological systematics, which should be consistent with the goal of science, as well as showing that the term taxonomy is synonymous with systematics rather than being a sub-operation within or distinct from systematics. And since the field of science is systematics, as the act of systematization, our concern is not with classification since the latter

does not serve the intended purpose. We will then have a clearer conception of how to proceed from observations of organisms to the conclusions we call species, as well as all other taxa. And from there it is straightforward to give basic definitions of taxon and species that are consistent with scientific inquiry. The implications of those definitions for DNA ‘barcoding’ will be discussed, as well as pointing out that a single definition of species is both too biased and limited to effectively encompass all of the endeavors in systematics and biology.

THE GOAL OF SCIENTIFIC INQUIRY

To what end do people involve themselves in a field of science? Certainly if you ask a physicist working with the Large Hadron Collider you will receive an answer very different from a malacologist examining the radulae from a group of gastropods. But while answers from different fields of science might appear dissimilar, it is the overarching objective of all scientists that is distinctly uniform. Simply put, the goal of inquiry in the sciences is to pursue causal understanding (Hempel, 1965; Hanson, 1958; Salmon, 1984a; Mahner & Bunge, 1997; Thagard, 2004; de Regt *et al.*, 2009; Hoyningen-Huene, 2013). We want to know why things are as they are, as well as anticipate what we might encounter in the future. The philosopher of science, Carl G. Hempel, offered a good characterization of the goal of scientific inquiry:

“Broadly speaking, the vocabulary of science has two basic functions: first, to permit an adequate *description* of the things and events that are the objects of scientific investigation; second, to permit the establishment of general laws or theories by means of which particular events may be *explained*

and *predicted* and thus *scientifically understood*; for to understand a phenomenon scientifically is to show that it occurs in accordance with general laws or theoretical principles.” (Hempel, 1965: 139, emphasis original)

Note that while descriptions of the objects and events we encounter are of utmost importance, they are the impetus to pursue causally understanding what is observed. Such pursuit is in the form of explanations of the present by way of what occurred in the past. And the better that causal understanding, the more effectively we can anticipate what might occur into the future.

As we will see later, the interplay between the descriptive and causal understanding form the basis of systematics, and is critical to correctly referring to all taxa, including species. But first we must understand the relations between observations, descriptions, and the pursuit of understanding, which derive from the basic principles of reasoning.

THE NATURE OF REASONING, FROM PERCEPTIONS TO HYPOTHESES

In its simplest form, reasoning is the act of proceeding from evidence to conclusion(s). It is the act of making an inference (Salmon, 1984b). If presented as a set of statements, called an argument, the evidence comprises the premises that support a statement that is the conclusion. The ancient Greeks recognized that the content of and relations between premises and conclusion allows for a classification of reasoning. The ideal form of reasoning is deduction, and it is on the basis of the rules of valid deduction that all other forms of reasoning are compared. Of these rules for deduction, the most basic is that if the premises are true, then

the conclusion must be true. Consider this example,

- [1] All humans are mortal
 Kirk is a human

 Kirk is mortal.

The line separates the premises above from the conclusion below. Given that the premises are true, the conclusion must be true. In fact, the conclusion is already implied by the premises since I am a subset of the group 'humans.' Valid deductions are indicated by a single line, whereas non-deductive reasoning is denoted by a double line separating premises and conclusion. For instance, changing the relations of premises and conclusion in [1] will give a non-deductive argument,

- [2] All humans are mortal
 Kirk is mortal

 Kirk is a human.

While the premises are true, they cannot guarantee the truth of the conclusion. At best, the conclusion has some probability of being true, contingent on the content of the premises. The fact that I am mortal does not necessarily mean I am human, as mortality applies to all organisms. In standard logic, any argument that is not deductive is said to be inductive, as indicated by the double line. The conclusion contains or implies information not stated in the premises. In other words, the content of the conclusion goes beyond what is offered by the premises.

While the rules of deduction have the benefit of providing the foundation from which all reasoning is compared, deduction is of limited use for scientific inquiry. We saw earlier that a deductive conclusion only reiterates what

already is in the premises; it does not allow for introducing or considering new ideas. The act of explaining phenomena for the purpose of understanding requires that we go beyond mere descriptions; we have to consider unobserved and sometimes unobservable objects and events. Thus, growth of scientific knowledge is not by way of deduction. But to label all non-deductive reasoning as inductive is not an effective approach to characterize the actions in scientific inquiry. Subtleties have to be acknowledged.

At a minimum, inquiry in everyday life as well as the sciences proceeds from surprising or unexpected observations to inferences of hypotheses that offer explanatory accounts of those observations. This involves a form of non-deductive reasoning known as abduction or abductive reasoning (Thagard, 1988; Josephson & Josephson, 1994; Aliseda, 2006; see Fitzhugh 2006a, 2008, 2010, 2012, 2014 for considerations of abduction in relation to biological systematics and evolutionary biology). Abduction has the form,

- [3] Background knowledge
 Theory X : if cause x occurs, effect y will
 ensue
 Surprising effect e_y is observed

 Hypothesis h_x : cause x occurred.

Abductive reasoning is the source of both hypotheses and theories, and also represents the everyday cognitive process proceeding from our sense data to observation statements. An observation statement is a hypothesis accounting for sense data by way of the existence of some object. And as we will see in the next section, references to taxa, species, or phylogenetic hypotheses are all products of abduction, which will be the key to properly defining terms like taxa and species.

Though this essay will not pursue these issues, brief mention should be made of the relations of abduction to the broader context of scientific inquiry. Abduction is the productive component of inquiry; it is the stage in which new ideas are put forward. As with any non-deductive inference, hypotheses are probable, not certain. Empirically evaluating the credibility of a hypothesis then requires that it be tested, which involves two steps. First, if the hypothesis is true, then specific consequences should be anticipated, such that those consequences, as potential test evidence can offer support for the hypothesis. The prediction of potential test evidence is deductive,

- [4] Background knowledge
 Theory X : if cause x occurs, effect y will ensue
 Given hypothesis h_x : cause x occurred
 Proposed conditions to carry out test
-
- Effect e_y originally prompting h_x
Predicted test evidence, i.e. independent effects associated as narrowly as possible with causal conditions outlined in h_x should be observed.

Subsequent to the prediction of test evidence, the hypothesis is subjected to testing by determining if the test evidence does occur. Hypothesis testing is an instance of induction,

- [5] Background knowledge
 Theory(ies) relevant to original effects
 Test conditions a, b, c , etc., established
Predicted test evidence is observed/not observed pursuant to test conditions
-
- Hypothesis h_x is confirmed/disconfirmed.

Since hypothesis testing is non-deductive, finding evidence that confirms a hypothesis offers support for the hypothesis but the truth of

the hypothesis remains probabilistic. Future test evidence could reduce confidence in lieu of an alternative explanation.

THE GOAL OF BIOLOGICAL SYSTEMATICS AND HOW IT IS ATTAINED

Having presented an overview of the goal of scientific inquiry and the basic steps taken in the pursuit of that inquiry, we can identify the goal of systematics. Consistent with all the sciences, systematics pursues causal understanding of the differentially shared features of organisms. Unlike the nebulous view that systematics seeks to find the ‘tree of life’ or ‘reconstruct phylogeny,’ the more precise characterization is that systematics deals with hypotheses across a spectrum of causal contexts, ranging from the descriptions of organisms to ontogenetic, reproductive, intraspecific, specific, and phylogenetic hypotheses, among others (Hennig, 1966: fig. 6). The goal of systematics is therefore consistent with the intent of systematization (Hoyningen-Huene, 2013). This means use of the term taxonomy is unnecessary. While systematics and taxonomy are often considered synonymous, current usage tends to equate taxonomy with species ‘descriptions’ and systematics with phylogenetic hypotheses. Since species are not described, as shown in the next section, all actions within systematics serve the purpose of systematization, which makes it straightforward to show that all taxa are inferential products directed at our desire to acquire causal understanding of organisms. Similarly, classification cannot be equated with systematization. A process of grouping objects according to shared properties lacks the theoretical and causal depth desired in systematics.

FORMAL DEFINITIONS OF ‘TAXON’ AND ‘SPECIES’

Reiterating what has been developed in the previous two sections, we encounter surprising or unexpected objects and events every day and in most instances spontaneously infer by way of abduction at least tentative answers to implied or explicit questions. For instance,

“Why is traffic so slow on this street (as opposed to moving the speed limit)?”

– “Perhaps there’s a wreck down the street.”

Or,

“Why is broken glass on the sidewalk (as opposed to being clean)?”

– “Maybe someone dropped a bottle.”

Notice that both questions refer to what is observed in contrast to what is expected. It is that contrast that prompts inquiry in the form of proceeding from observations to abductive inferences to possible causes as answers to questions.

Let’s extend such considerations to systematics. The objects of concern in biology are organisms. We observe individuals at particular moments during their life history, what Hennig (1966) referred to as *semaphoronts*, and we perceive these individuals by way of their properties or characters. It is our differential observations of characters among semaphoronts that prompt causal questions, leading to abductive inferences of hypotheses that explain these differences. Those explanations address a host of different observations, thus the inferences to

explanations require different sets of theories depending on what are being explained. The discussion so far has centered on our reactions to conditions of observed objects; reactions in the form of abductive inferences to explanatory hypotheses. Those hypotheses are what are often called *taxa*, whether species, genera, families, classes, etc. Since taxa are explanatory hypotheses, the consequence is that we *do not* observe or describe taxa. As noted already, taxa are nothing more than inferential reactions, in the form of explanatory hypotheses, to observations among semaphoronts. This means formal definitions of *taxon*, *species (partim)*¹, and *supraspecific taxon* (= phylogenetic hypothesis) would be as follows (cf. Fitzhugh, 2005, 2009, 2013):

Taxon: Any of a number of classes of explanatory hypotheses in biological systematics that causally account for differentially shared characters among observed organisms.

Species (partim): An explanatory account of the occurrences of the same character(s) among gonochoristic or cross-fertilizing hermaphroditic individuals by way of character origin and subsequent fixation within reproductively isolated populations. This is but one of at least five possible classes of explanatory hypotheses commonly called species. The other definitions will be given later.

¹ As will be noted later, the term species entails at least five different classes of causal conditions, such that it is not possible to give a definition that is appropriate to all of them.

Supraspecific taxon: A class of explanatory hypotheses accounting for particular characters by way of character origin/fixation among members of an ancestral population, and subsequent population splitting events. Collectively known as phylogenetic hypotheses.

Per the structure of abduction in [3], formal representations of inferences to specific and supraspecific/phylogenetic hypotheses take the respective forms:

[6] **Species (*partim*) Theory**: If character *Y* originates among gonochoristic or cross-fertilizing hermaphroditic individuals of a reproductively isolated population with character *X*, and *Y* subsequently becomes fixed throughout the population, then individuals observed in the present will exhibit character *Y*.

Observations (effects): Individuals have a dorsal margin with antennae in contrast to a smooth dorsal margin as seen among individuals to which other specific hypotheses (*a-us*, *b-us*, etc.) refer.

Causal Conditions (specific hypothesis *y-us*²): The antennate dorsal margin condition originated within a reproductively isolated population with smooth dorsal margins and eventually became fixed throughout the population.

[7] **Phylogenetic Theory**: If character *X* exists among individuals of a reproductively isolated, gonochoristic or cross-fertilizing hermaphroditic population and character *Y* originates and becomes fixed within the population, followed by the population being divided into two or more reproductively isolated populations, then individuals to which descendant species hypotheses refer would exhibit *Y*.

Observations (effects): Individuals to which specific hypotheses *x-us* and *y-us* refer have ventrolateral margins with appendages in contrast to smooth as seen among individuals to which other species hypotheses (*a-us*, *b-us*, etc.) refer.

Causal Conditions (phylogenetic hypothesis *X-us*): Ventrolateral margin appendages originated within a reproductively isolated population with smooth ventrolateral margins, and the appendage condition became fixed in the population (= ancestral species hypothesis), followed by a population splitting event that resulted in two or more reproductively isolated populations.

Notice that while specific and phylogenetic hypotheses are inferred by way of abduction, the respective theories used differ in that the former considers character origin/fixation within reproductively isolated populations, and the latter refers to character origin/fixation followed by population splitting events. The representations in [6] and [7] are highly schematic in that neither actually stipulates details regarding the various causal mechanisms necessary to offer useful explanatory accounts. Yet, this lack of causal specifics is typical in references to specific and phylogenetic hypotheses, *e.g.* cladograms. The intentional

² The uninomial name used here and in [7] follows from Fitzhugh's (2008) argument that a species hypothesis is inferred separate from the phylogenetic hypothesis referred to by the rank of genus, and should be recognized as such. The binomen required by the International Codes of Nomenclature incurs the requirement that monotypic genera be recognized when in fact the genus name is empirically vacuous and cannot be defined.

limitation of the definition of species in [6] to intersexual organisms highlights the fact that the term species requires special consideration regarding several different classes of reproduction and genetic exchange, which will be discussed later (see **THE PROBLEM WITH SPECIES**).

Finally, let me reiterate that neither species nor any other taxa have the status of individuals; they are causal accounts intentionally inferred as part of the goal of inquiry. To speak of a ‘species description’ means describing the observed features of organisms, not the species. A formal species name refers to a hypothesis, e.g. specific hypothesis *y-us* in [6]. What is required is a definition of that formal name; that being an explanatory account of particular characters of organisms. The same conditions apply to supraspecific taxa, regardless of rank. And in the case of these latter taxa, all are phylogenetic hypotheses, e.g. [7].

THE PROBLEM WITH SPECIES

The definition of species in the previous section (see also [6]) is intentionally limited in scope for the fact that the one term cannot accurately entail the variety of causal events typical across all organisms, especially those that do not display the uniformity of sexual reproduction. Fitzhugh (2013) identified at least five classes of causal events to which the term species have been applied:

Species₁ (cf. [6]): if character *Y* originates among gonochoristic or cross-fertilizing hermaphroditic individuals of a reproductively isolated population with character *X*, and *Y* subsequently becomes fixed throughout the population, then individuals observed in the present will exhibit character *Y*. This is essentially

equivalent to the ‘biological species concept.’

Species₂: if character *Y* simultaneously originates and is fixed by hybridization, e.g. polyploidy, among gonochoristic or cross-fertilizing hermaphroditic individuals to which respective ‘species₁’ hypotheses refer, such that subsequent interbreeding events are limited to individuals with *Y*, then individuals observed in the present will exhibit *Y*. This is a common occurrence among plants that exhibit polyploidy, wherein polyploid individuals immediately result in reproductive isolation.

Species₃: if character *X* exists among individuals with obligate reproduction that is asexual, apomictic/parthenogenetic, or self-fertilizing, and character *Y* originates, then individuals observed in the present exhibiting *X* and *Y* are respective reproductive products of individuals with those characters. This characterization addresses the most distinct limitation of the ‘biological species concept.’ Among organisms that are obligate asexual, parthenogenetic, or self-fertilizing, the introduction of novel characters result in divergent lineages of individuals with those characters explained by the species₃ hypothesis. A complicating factor that will not be pursued here is that phylogenetic hypotheses (cf. [7]) are not applicable to these kinds of organisms since the only type of ‘lineage splitting’ that occurs is by way of reproductive events, not population splitting events.

*Species*₄: if character *Y* originates among individuals with *X* during one of the alternative phases of asexual or sexual reproductive events, and *Y* subsequently becomes fixed throughout the population during tokogeny, then individuals observed in the present will exhibit *Y*. This class of hypothesis considers organisms with metagenetic or ‘alternation of generation’ life histories, as observed for instance among some cnidarians [e.g. alternate polyp (asexual) and jellyfish (sexual) stages; sporocysts (asexual) and adult (sexual) digenetic trematodes].

*Species*₅: if character *X* exists among individuals and character *Y* subsequently occurs due to horizontal genetic exchange with other individuals, then individuals observed in the present exhibiting *X* and *Y* are respective reproductive products of individuals with those characters. Horizontal gene transfer is a widespread phenomenon, especially among bacteria. The standard species hypothesis, e.g. *species*₁, aimed at sexually reproducing organisms cannot accommodate hypotheses explaining characters obtained via horizontal genetic exchange.

What is most apparent is that the one term *species* is inadequate to represent the variety of non-phylogenetic hypotheses required to explain the presence of shared characters among organisms. The five classes of hypotheses outlined here are not immediate solutions to the problem, but rather illustrate that the problem exists and needs to be acknowledged.

As noted in the previous section that all taxa, including species, represent explanatory hypotheses. Taxa do not have the status of individuals or things, and when one points to an organism-as-semaphoront they are not referring to a species, genus, etc. Hypotheses are explanatory constructs. Their relations to organisms only stand as vehicles that provide causal understanding, per the goal of scientific inquiry.

DISPELLING THREE MYTHS: DNA BARCODING, ‘CRYPTIC’ SPECIES, AND THE PREEMINENCE OF SEQUENCE DATA

The fact that species are multiple classes of explanatory hypotheses, and phylogenetic hypotheses also have explanatory standing, has significant implications for the growing methodological fad known as DNA barcoding. The reliance on snippets of DNA to ‘identify’ species suffers from the erroneous premise that species can be regarded as spatio-temporally localized individuals. As species do not have this quality, sequence data cannot serve as a surrogate for the actuality that species hypotheses can and do refer to explanations of characters other than nucleotides. Barcoding fails on both epistemic and scientific grounds (Fitzhugh, in prep.).

There is a common tendency among systematists to think that sequence data offer clues to ‘cryptic’ species, where ‘traditional’ (i.e. ‘morphological’) characters fail to discriminate between species. This is a specious perspective that derives not only from the failure to recognize species as explanatory hypotheses, but also not understanding the abductive inferences that lead to those hypotheses. No one class of characters, sequence data in this case, can be held up as the basis for inferring species hypotheses. Instead, the decision-making

process of what observed effects to include in the minor premises of an abductive inference to species hypotheses, *cf.* [6], will depend upon the investigator's choices of what observations are to be conjoined with the major premise that is a particular theory, *cf.* species₁ through species₅ in the previous section. Excluding all observations except sequence data is irrational if it is the case that there are non-sequence data that have to be explained via the same theory. And, since species are neither class constructs nor ontological individuals, there can be no 'cryptic' species; only explanatory hypotheses that fulfill the inferential requirements necessary to attain rational conclusions.

Finally, the view that sequence data offer some sort of superior avenue to inferring species suffers from not understanding that causal understanding is our goal (Fitzhugh, 2006b, 2012, 2014, in prep.). The tools of such understanding include the theories of natural selection and genetic drift. But as it is the case that selection cannot operate at the level of individual nucleotides, but rather at the higher organizational levels of phenotypes, we would have to restrict explanations of sequence data to drift, which is not entirely realistic. Explaining particular phenotypes by way of selection will determine distributions of lower-level structures, including associated sequences by the phenomenon of downward causation (Campbell, 1974; Ellis, 2012; Martínez & Esposito, 2014). The consequence is that the naïve inclusion of sequence data in inferences of specific and phylogenetic hypotheses, coupled with the exclusion of other relevant characters that are in need of being explained, will result in hypotheses that have little if any explanatory merit. There must be discrimination between sequences to be explained by drift as opposed to higher-level selection for particular phenotypes. In other words, not all sequence data can serve the purposes of inferring taxa at the exclusion of

other characters also in need of being explained. Like barcoding, the popular bias toward sequence data is founded on significant misunderstandings of the goal of biological systematics as a scientific endeavor.

CONCLUSIONS

The title of this essay alludes to the view that asking 'What are species?' is not the right question. The relevant question is, 'What are taxa?' I have provided the answer to the latter question such that the former can be cogently answered. If you now feel confused about what is a species, then I have done my job. You should feel confused for the fact that the pursuit of causal understanding within biological systems is not always a clear-cut process and cannot be represented by simple classificatory procedures. Systematics is about systematization. There are no activities called taxonomy or classification *simpliciter* that usurp the intent of systematization. There are only our efforts to describe objects, *not* species, and pursue causal understanding of our observations through the inferences of various taxa-as-explanatory hypotheses. Recent tradition in systematics has focused too much effort on methodology at the expense of integrating the coherent philosophical foundations that pervade all sciences. And the victims of this neglect have been thoughtful treatments of the question, 'What are taxa?'

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Taxonomic Note - new species: *Typhinellus jacolombi* Houart, 2015

This new species from the Caribbean sea, apparently endemic to Portobelo Bay, Panama, is relatively large for the genus ranging in size from 19 to 28 mm in length, and is substantially broader in length/width ratio than other species in the genus, with a spiral sculpture of low, rounded, broad smooth primary and secondary cords and narrow tertiary cords, a long tapering broad ventrally sealed anal tube, a small and rounded protoconch, with color ranging from completely white to light brown. The holotype figured above measures 19.2 mm in length. (Houart, R. 2015. Description of a new species of *Typhinellus* (Gastropoda: Muricidae: Typhinae) from the Western Atlantic. *Zootaxa* 4007(3) 427-432.) Photo credit: Roland Houart, with permission.