What in the World is a Species?

By Michael J. Donoghue

any people are aware that species have formal names with two parts—a genus name combined with what's called a specific epithet. Homo sapiens is a well-known example; for botanists, Ginkgo biloba will do. In their fullest form, they also include the name (or abbreviation) of the person or people who originally described the species. Homo sapiens was described by Carl Linnaeus in 1758, and in 1771 he named Ginkgo biloba, so you may see his initials after these names: Homo sapiens L., Ginkgo biloba L. There are very detailed (and ever-evolving) rules for how the description of a new species must be done for the name to be considered validly published. In botany, we refer to the International Code of Nomenclature for Algae, Fungi, and Plants for the exact procedures. It turns out that anyone-yourself included-can describe a new species if they follow these rules. You don't have to be certified as an authority to do this. Once you've published your new species, it generally would have one of two fates. Your new species could stand the test of time, in the sense that knowledgeable botanists would adopt it when they conduct their studies. However, unless you really know what you are doing, in 2022, it's likely you have named something that has previously been described. In this case, your proposed species name would be regarded as a synonym of the earlier one, and would henceforth be ignored.

A key point is that you can validly publish a species name only to have it rejected by other botanists on the grounds that they don't consider it to be a "real" species. This implies that there are some criteria being applied by scientists to judge whether something is a real species or not. It seems reasonable to assume that long ago there would have been agreement on what a species is—on a species concept. This, however, is not the case. In fact, many different definitions of species have been published over the years, and to this day there are major

Scientists track biodiversity in plots at the Cedar Creek **Ecosystem Science** Reserve in Minnesota. Photo by Jacob Miller



camps of biologists who disagree (sometimes passionately) over which should be adopted as the universal standard.

The use of different species concepts by different scientists has a very important consequence: the various species that you are familiar with may not be equivalent to one another in ecological, evolutionary, or organismic terms. For the most part, however, we proceed as though they are. By "we," I mean not just the general public, but also the scientific community, who, despite knowing full well that multiple concepts are in use, still treat species as being somehow equal to one another. In reality, the only equivalence you can count on when you see species names is that they have been named according to some agreed-upon rules, and that they haven't been rejected by the scientific community. The potential non-comparability of species seems like a recipe for miscommunication. We proceed under the hope that species will somehow be "equal enough" for most purposes, and that the differences among species won't interfere too much with scientific progress or public understanding.

The best-known definition, provided by ornithologist Ernst Mayr in 1942 and widely taught in introductory biology classes since the 1950s, is short and snappy: *"species are groups of actually or potentially* interbreeding natural populations, which are reproductively isolated from other such groups." This is the so-called "biological species concept," which many biologists accept in theory, although information on which organisms can interbreed is almost always lacking in practice. So, one generally just assumes such gene flow based on similarities and differences in the visible characteristics of the organisms, hoping that actual interbreeding will be tested directly someday. It has long been pointed out, however, that interbreeding and reproductive isolation aren't relevant criteria for organisms that reproduce through asexual reproduction. Such is the case with many bacteria, for instance, and with some plants as well. And there's the associated question of whether any level of interbreeding could or should be tolerated. This has been a special concern for botanists, where hybridization is often possible between species that appear to be quite distantly related (consider all of the strange orchids that have been produced in this way).

Although the biological species concept is the most widely known, there are a variety of alternatives that feature different criteria. One such alternative focuses on species as occupying particular ecological niches that differ from related species. Another one focuses on shared common ancestry, delimiting species based on

A Cryptic Species in the Tangled Bank

n eastern North America, botanists have long recognized Viburnum nudum L. and Viburnum cassinoides L. as separate species, though the two can be difficult to distinguish. In studying these species in more detail, we recently discovered the existence of a "cryptic species," which, although most closely related to V. cassinoides, has long been lumped with V. nudum in the southeastern US (Spriggs et al., 2019b; see also Spriggs 2019). This species was validly named V. nitidum by Scottish botanist William Aiton in 1789. We hypothesize that V. nitidum is indeed a separately evolving species based on multiple lines of evidence, including genetic data, differences in several morphological characters and in their ecological niches, and the apparent absence of interbreeding between V. nitidum plants and members of the other species.



Beth Spriggs in 2016 with Viburnum nudum L. (left) and V. nitidum Aiton (right). Photograph by Michael Donoghue

evidence that certain organisms and populations share a common ancestor separate from related species.

One concept I find especially appealing is known as the "evolutionary species concept," proposed by the paleontologist George Gaylord Simpson in 1951. Working with fossils of long-dead mammals, he wanted to take the emphasis off of interbreeding (which he certainly couldn't test). Instead, he conceptualized species in terms of a full evolutionary life cycle, from inception to extinction. Simpson said a species is: "a phyletic lineage (ancestral-descendant sequence of interbreeding populations) evolving independently of others, with its own separate and unitary evolutionary role and tendencies." Under this view, the populations that we study today are time slices through an extended lineage evolving independently of other lineages. This concept provides a nice image of species, though for many people, "role and tendencies" have seemed a bit squishy and difficult criteria to apply in practice.

One very nice "solution" to the species problem was proposed by herpetologist Kevin de Queiroz in 1998, and reinforced in his subsequent work (e.g., de Queiroz, 2005). He noted that all of these concepts focus on populations or lineages extended through time and evolving independently of one another. In his view, reproductive isolation, ecological differentiation, and exclusive shared ancestry may arise in different temporal sequences as the process of speciation (the origin of independently-evolving lineages) proceeds. At any given point in the process, species might have some of these properties, and not others. For example, gene flow may be cut off early in the process, perhaps by the simple geographic separation of populations, as compared to, for example, ecological differentiation.

Under de Queiroz's so-called "general lineage concept" of species, phenomena formally viewed as necessary and sufficient defining criteria for species-hood, are instead understood to bear on whether, in fact, two lineages are evolving *separately*. If we find, for example, that the organisms in two populations are unable to breed successfully with one another, this provides pretty good evidence that the populations are evolving separately. Likewise, the finding that populations are occupying different ecological niches provides evidence of independence, as do consistent differences in morphological characteristics. These things don't *define* species, but instead help us to *discover* them.

The general lineage concept of species has been steadily gaining popularity among evolutionary biologists, but it is still far from universally accepted. Personally, I like it very much, but would stress a



Viburnum cassinoides 593-2008*C at the Arnold Arboretum. Photograph by Suzanne Mrozak



Viburnum nudum 'Winterthur' 431-2002*A at the Arnold Arboretum. Photograph by William (Ned) Friedman

Species are best viewed as hypotheses to be tested with evidence coming from as many different angles as possible.

few additional points. First, I think that the delimitation of a species is best viewed as putting forward a hypothesis to be tested with evidence of lineage independence coming from as many different angles as possible. By this I mean to include not only information on breeding, but on geography, morphology, DNA sequences, ecology, and a host of other criteria. Second, I would like to preserve Simpson's reference to the future and predicting the likely fate of a lineage. It seems reasonable to add into the decision-making process whether it seems likely that two lineages will continue to evolve independently into the future. Evidence bearing on fate may also come in different forms. For example, consider the two species of tulip tree: the familiar eastern North American Liriodendron tulipifera, and the eastern Asian Liriodendron chinense. These can readily be hybridized, and the offspring plants (L. tulipifera × chinense) are fertile. Living proof of this can be found at the Arnold Arboretum, on the lawn in front of the Hunnewell Building. But, it seems reasonable to suppose, based on their very widely separated geographic ranges, that individuals of these two species will not naturally be exchanging genes any time in the foreseeable future. Finally, I also really like the reference to "tendencies," as this highlights the idea that a separately evolving lineage will often show a propensity to generate certain variants again and again as compared to another species. Mind you, I don't at all mean to

suggest that such tendencies should define species; rather, in keeping with the general lineage concept, they can potentially serve as evidence of independent evolution.

Allow me to end with a few observations about my own favorite plant group, Viburnum. When I was a graduate student at Harvard, in the late 1970s, I lived on the grounds of the Arnold Arboretum, at what used to be 383 South Street. Of course, I wandered the grounds often, and it was there that I became well acquainted with around 40 of the roughly 165 Viburnum species, many of them from eastern Asia, where Viburnum is the most diverse. You can learn a lot about species differences in an arboretum, but not nearly enough to critically assess their evolutionary independence from one another. For one thing, you don't see the species that can't be grown in the arboretum (e.g., Viburnum species from tropical forests in Borneo, or from high elevations in the Andes), or the many species that could potentially be grown but have never been brought into cultivation. And, you really need to study organisms in their natural surroundings to understand the range of variation that they exhibit, their ecological niches, and which species might encounter one another in the wild.

I did, however, manage to observe something about *Viburnum* species that has turned out to be more important than I ever imagined. I went out on a regular basis to record the times when plants of different *Viburnum* species were flowering in the arboretum. I found that they were flowering each year in a consistent sequence, staggered through the spring and early summer. In fact, these observations were the basis of my very first publication, in 1980, which happened to be in *Arnoldia*, and was entitled "Flowering times in *Viburnum*."

As we have learned since that time, related species of Viburnum living in the same geographic area very often flower at different times, which means that they are reproductively isolated from one another in this temporal way. For example, as shown recently by my former graduate student Elizabeth Spriggs, the species of the Viburnum lentago complex in eastern North America (nannyberry and its relatives) bloom at different times, and this minimizes hybridization between them where their geographic ranges overlap (Spriggs et al., 2019a; Spriggs, 2019). We know that individuals of these different species can breed together successfully. In fact, Viburnum × jackii, a hybrid between V. lentago and V. prunifolium, was described from a plant first noticed in 1908 at the Arnold Arboretum. However, in the wild these species rarely do hybridize, simply because they are flowering a week or so apart. Importantly, given the discussion above, I am not supporting the biological species concept with this observation. Instead, I am adopting the general lineage concept and using this flowering offset as one line of evidence that these are timeextended lineages evolving on their own.

I hope that these few reflections will heighten your appreciation of species when you see your next specimen label in the Arnold Arboretum—perhaps even a *Viburnum lentago* L. plant in the superb *Viburnum* collection near the Centre Street Gate!

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