



What Is a Species?

KEY CONCEPTS

- Formal taxonomic systems first identified species based on visual traits such as fins or fur. Later, the species concept changed, specifying that two organisms should be capable of breeding.
- Today biological diversity can be ascertained by sampling DNA and tracking how a species descended from a common ancestor.
- The debate over species definition is far from over and is more than a mere academic spat. Proper classification is essential for designating the endangered list.

—The Editors

To this day, scientists struggle with that question. A better definition can influence which animals make the endangered list

By Carl Zimmer

If you visit Algonquin Provincial Park in Ontario, you may hear the high, lonesome howls of wolves. You may even be lucky enough to catch a glimpse of a distant pack racing through the forests. But when you show off your blurry pictures back home, what species should you boast that you saw? Depending on the scientist you ask, you may get a different answer. Some may even offer you a few different answers all at once.

In the 18th century European naturalists dubbed the wolves of Canada and the eastern U.S. *Canis lycaon*, because they seemed distinct from *Canis lupus*, the gray wolf of Europe and Asia. By the early 1900s North American naturalists had decided that they were actually gray wolves as well. But in the past few years Cana-

dian researchers who have analyzed wolf DNA have come full circle. They argue that gray wolves only live in western North America. The wolves of Algonquin Provincial Park belong to a separate species, which they want to call *C. lycaon* once more.

Other wolf experts do not think there is enough evidence to split *C. lupus* into two species. And both sides agree that the identity of the Algonquin wolves has become far more murky thanks to interbreeding. Coyotes (another species in the genus *Canis*) have expanded east and begun to interbreed with *C. lycaon*. Now a sizable fraction of these eastern coyotes carry wolf DNA, and vice versa. Meanwhile *C. lycaon* has been interbreeding with gray wolves at the western border of its range. So the Algonquin ani-



mals are not just mixing *C. lycaon* DNA with *C. lupus* DNA—they are passing on coyote DNA as well.

Even if *C. lycaon* was once a species, is it a species anymore? Many researchers find that the best way to think of a species is as a population whose members breed mostly among themselves, making the group genetically distinct from other species. When it comes to wolves and coyotes, it is hard to say quite where one species stops and another starts. “We like to call it *Canis* soup,” says Bradley White of Trent University in Ontario.

The debate is about much more than naming rights. Wolves in the southeastern U.S. are considered a separate species, the red wolf (*Canis rufus*). This wolf has been the subject of an enormous

project to save it from extinction, with a captive breeding effort and a program to reintroduce it to the wild. But the Canadian scientists argue that the red wolf is really just an isolated southern population of *C. lycaon*. If that is true, then the government has not in fact been saving a species from extinction. Thousands of animals belonging to the same species are still thriving in Canada.

As the case of the Algonquin wolves demonstrates, defining species can have a huge effect on whether an endangered group gets protected and whether a habitat is saved or lost. “In one sense, it’s a very esoteric subject, but in another, it’s a very practical issue,” says Alan Templeton of Washington University in St. Louis, “even a legal issue.”

▲ **WOLVES illustrate why species classification befuddles. *Canis lycaon* was a wolf species that roamed the woods of Ontario in the 18th century. Biologists reclassified the animals as *C. lupus* in the early 1900s before renaming them *C. lycaon* during the past few years. Some wolf experts now consider them a mix of several species, including coyotes (*C. latrans*) and gray wolves.**



FOLK WISDOM

Early folk classification systems still in use by the San and other indigenous peoples designate plants and animals based on observable features. Later methods, such as Linnaean taxonomy, often made similar categorizations.

At least 26 published concepts attempt to provide a definition of what a species is.

An Embarrassment of Definitions

It may come as a surprise to see scientists struggling to agree on something so basic as how to decide that a group of organisms form a species. Perhaps it is the Latin that gives species names the whiff of absolute certainty and that has misled the public into thinking the rules are simple. Perhaps it is the 1.8 million species that scientists have named in the past few centuries. Perhaps it is laws like the Endangered Species Act, which take for granted that we know what species are. But in fact, the very concept of species has fueled debates for decades. “There is no general agreement among biologists on what species are,” says Jonathon Marshall, a biologist at Southern Utah University. At last count, there were at least 26 published concepts in circulation.

What makes this disagreement all the more remarkable is that scientists now know vastly more about how life evolves into new forms than when the species debate first started. Not long ago taxonomists could only judge a new species based on what they could see—things like fins, fur and feathers. Today they can read DNA sequences, in which they are discovering a hidden wealth of biological diversity.

Templeton and other experts think that the debate may finally have reached a turning point. They believe it is now possible to combine many competing concepts into a single overarching one. The unification would apply to any kind of organism, from mockingbirds to microbes. And these researchers hope it will lead to powerful tools for recognizing new species.

Long before the dawn of science, humans were naming species. To be able to hunt animals and gather plants, people had to know what they were talking about. Taxonomy, the modern science of naming species, emerged in the 1600s and came into its own in the next century, thanks largely to the work of Swedish naturalist Carl Linnaeus. Linnaeus invented a system to sort living things into groups, inside which were smaller groups. Every member of a particular group shared certain key traits. Humans belonged to the mammal class, and within that class the primate order, and within that order the genus *Homo*, and within that genus the species *Homo sapiens*. Linnaeus declared that each species had existed since creation. “There are as many species as the Infinite Being produced diverse forms in the beginning,” he wrote.

Linnaeus’s new order made the work of taxonomists much easier, but trying to draw the

lines between species often proved frustrating. Two species of mice might interbreed where their ranges overlapped, raising the question of what name to give to the hybrids. Within a species there was confusion as well. The willow ptarmigan in Ireland, for example, has a slightly different plumage than the willow ptarmigan in Scotland, which differs in turn from the one in Finland. Naturalists could not agree about whether they belonged to different ptarmigan species or were just varieties—subsets, in other words—of a single species.

Charles Darwin, for one, was amused by these struggles. “It is really laughable to see what different ideas are prominent in various naturalists’ minds, when they speak of ‘species,’” he wrote in 1856. “It all comes, I believe, from trying to define the indefinable.” Species, Darwin argued, were not fixed since creation. They had evolved. Each group of organisms that we call a species starts out as a variety of an older species. Over time natural selection transforms them as they adapt to their environment. Meanwhile other varieties become extinct. An old variety ends up markedly different from all other organisms—what we see as a species in its own right. “I look at the term ‘species’ as one arbitrarily given, for the sake of convenience, to a set of individuals closely resembling each other,” Darwin declared.

Like the taxonomists before him, Darwin could study species only with the naked eye, observing the color of a bird’s feathers or counting the plates on a barnacle. It would not be until the early 20th century that scientists could start to examine the genetic differences among species. Their research led to a new way of thinking. What made a species a species were the barriers to reproducing with other species. Genes could flow among its members as they mated, but these individuals usually remained within the species, thanks to reproductive barriers. Species might spawn at different times of the year, they might find courtship songs of other species unattractive, or their DNA might simply be incompatible.

The best understood way for these barriers to evolve is through isolation. Some members of an existing species—a population—have to become unable to mate with the rest of their species. A glacier could thrust across their range, for example. The isolated population evolves new genes, and some of those new genes may make interbreeding difficult or impossible. Over hundreds of thousands of years so many barriers

ers evolve that the isolated population becomes a distinct species.

This understanding of how species evolve led to a new concept of what it meant to be a species. Ernst Mayr, a German ornithologist, boldly declared that species were not convenient labels but real entities, like mountains or people. In 1942 he defined a species as a gene pool, calling it a set of populations that can reproduce with one another and that are unable to mate successfully with other populations. The biological species concept, as it is now called, became the textbook standard.

Eventually many scientists grew dissatisfied with it, finding it too weak to help them make sense of the natural world. For one thing, Mayr's concept did not give any indication of how reproductively isolated a species had to be to qualify as a species. Biologists were left to puzzle over species that looked relatively distinct but interbred regularly. In Mexico, for example, scientists have recently discovered that two species of monkey that split off from a common ancestor three million years ago regularly interbreed. Do they have too much sex to qualify as two species?

Although some species seem to be having too much sex for the biological species concept, others seem to be not having enough. Sunflowers, for example, live in extremely isolated populations across North America. Genes flow rarely from one population to another. One could use Mayr's concept to treat them all as individual species.

Most difficult of all are species that have no sex whatsoever. Take a lineage of microscopic marine animals known as bdelloid rotifers. Most rotifers reproduce sexually, but bdelloid rotifers abandoned sex about 100 million years ago. All bdelloid rotifers are female, and they make embryos without any need for sperm. By the standards of the biological species concept, the rotifers went from being a species to being not a species, whatever that means.

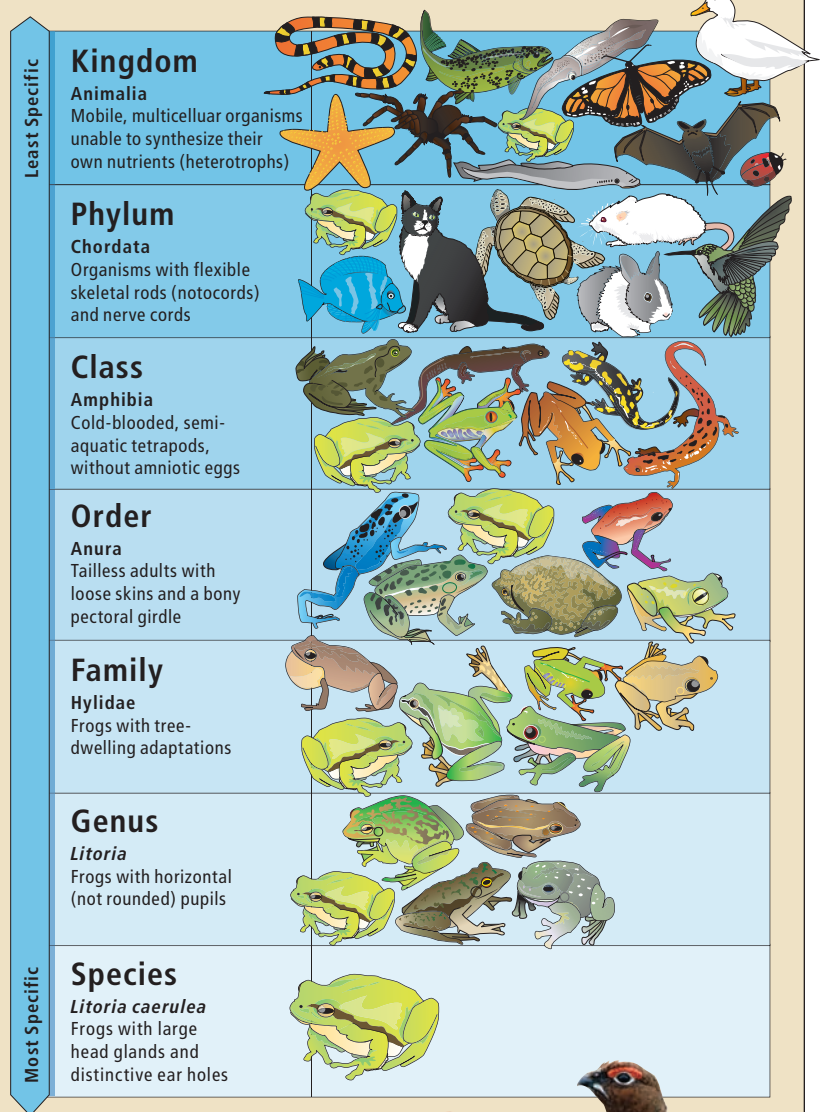
A Sexless Equation

This kind of dissatisfaction led some scientists to devise new species concepts. Each concept was crafted to capture the essence of what it means to be a species. One of the strongest rivals to the biological species concept, called the phylogenetic species concept, takes sex out of the equation and puts descent from a common ancestor in its place.

Related organisms share traits because they share the same ancestry. Humans, giraffes and

Linnaeus's Universe

Carl Linnaeus developed the basis for modern taxonomy in the 1700s, sorting all things biological into hierarchical groupings that range from the kingdom level (such as animals, plants, fungi) down to individual species, each having a unique collection of observable traits.



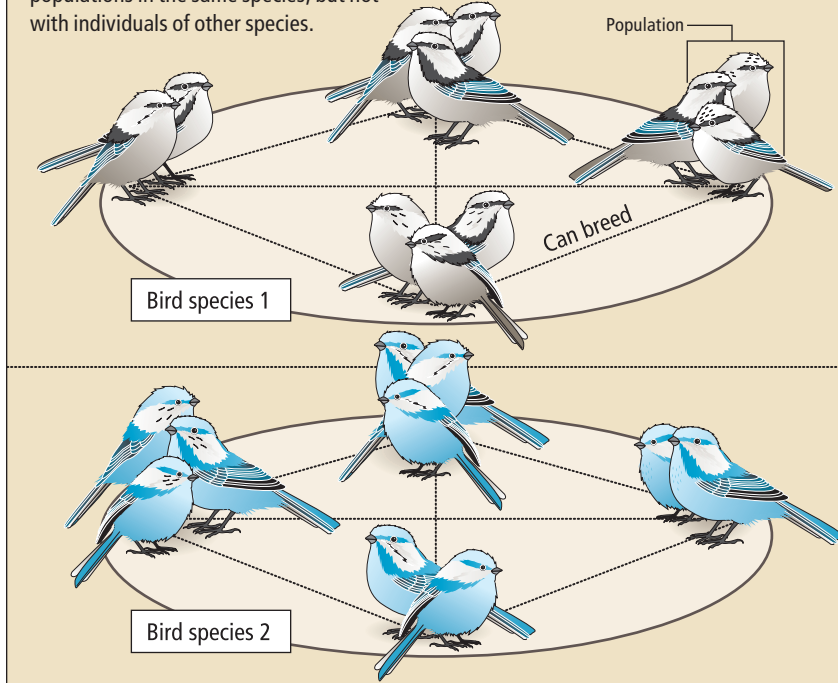
But ...

Naturalists often encounter difficulties distinguishing one species from another. The willow ptarmigan in Scotland has distinctive plumage from the one in Finland (*left*)—whether that difference justifies dividing the two creatures into separate species in the Linnaean system is unclear.



Biology Is Destiny

Textbooks often define a species—the lowest ranking on the Linnaean hierarchy—as consisting of organisms sharing a cohesive gene pool. The members of a population, according to the biological species concept, can mate successfully with one another and with other populations in the same species, but not with individuals of other species.



But ...

Some organisms—take the bdelloid rotifers—do not have sex. And two species of Mexican howler monkeys (*photographs*), which diverged from a common ancestor that lived three million years ago, can still mate with each other.



Alouatta palliata ▶

Alouatta pigra ▶

bats all descend from ancient mammals, and as a result they all have hair and milk. Within mammals, humans share a closer common ancestry with other primates. From the common primate ancestor, primates inherited other traits, such as forward-facing eyes. You can zoom in on smaller and smaller sets of organisms this way. Eventually, though, the zooming in comes to a stop. There are organisms that form groups that can no longer be split. These, according to the phylogenetic species concept, are species. In a sense, this concept takes Linnaeus's original system and updates it in light of evolution.

The phylogenetic species concept has been embraced by researchers who need to identify species rather than just contemplate them. Recognizing a species is a matter of finding a group of organisms that shares certain clear-cut traits. Scientists do not have to depend on slippery qualities like reproductive isolation. Recently, for example, the clouded leopards on the Indonesian island of Borneo were declared a species in their own right, distinct from the clouded leopards of southern Asia. All the Bornean clouded leopards shared certain traits not found in the cats on the mainland, including a distinctively dark coat.

Some critics think that there is far too much

[THE AUTHOR]

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species splitting going on these days. “The problem with it is that it doesn’t give you a natural level at which to stop,” says Georgina Mace of Imperial College London. A single mutation might, at least theoretically, be enough to earn a small group of animals a species name. “It’s a bit silly when you split them so far,” she comments. Mace also argues that a population should be considered ecologically distinct—as defined by geography, climate and predator-prey relations—before someone decides to split it off as a new species.

But other researchers think that they should go where the data lead them rather than worrying about oversplitting. “That’s the tail wagging the dog,” says John Wiens, a biologist at Stony Brook University. “The argument that there’s some sort of ceiling of how many species there should be doesn’t seem very scientific.”

Confusion over Substance

A few years ago the endless arguments of this kind convinced Kevin de Queiroz, a biologist at the Smithsonian Institution, that the species debate had gone too far. “It was just getting out of control,” he says, “and I think a lot of people were just getting sick of it.”

LUCY READING-IRKANDA (illustration); BEN STECHSHULTE (Zimmer); THOMAS AND PAT LEESON (Photo Researchers, Inc. (A. pigra)); D. TIFLING (Peter Arnold, Inc. (A. palliata))

De Queiroz stepped forward and declared that much of the debate did not deal with substance but rather with confusion. “The confusion is actually a pretty simple one,” he says. Most of the competing species concepts actually agree on some basic things. They are all grounded in the notion that a species is a distinct, evolving lineage, for instance. For de Queiroz, that is the fundamental definition of a species. Most of the disagreements about species are not actually about its concept but are about how to recognize a species. De Queiroz thinks that different methods work best in different cases. Strong reproductive isolation is good evidence that a population of birds is a species, for example. But it is not the only yardstick that can be used. For bdelloid rotifers that do not have sex, scientists just have to use other kinds of criteria.

Many (but far from all) other experts on species share de Queiroz’s optimism. Instead of trying to use just one gold standard, they are testing new species against several different lines of evidence. Jason Bond, a biologist at East Carolina University, and his student Amy Stockman took this approach in a survey of an enigmatic genus of spiders, *Promyrmekiaphila*, found in California. Taxonomists have long struggled to determine how many *Promyrmekiaphila* species there are. The spiders resist easy classification because they look almost identical. And yet scientists also have known that they probably form very isolated populations, thanks in large part to the fact that each spider is unlikely to move very far from home.

“Once a female digs a good burrow with a trapdoor and a silk lining, it’s unlikely she’s going to move,” Bond says. He has dug up *Promyrmekiaphila* burrows containing three generations of female spiders that have lived there for years. Males will leave their birthplace burrows, but they will not move far before mating with a female from a neighboring burrow.

To identify the species of the spiders, Bond and Stockman adopted methods developed by Templeton. They studied the *Promyrmekiaphila* evolutionary history, measured gene flow between populations and characterized the spiders’ ecological role. For the evolutionary history, Bond and Stockman sequenced parts of two genes from 222 spiders at 78 sites in California. They surveyed the DNA for genetic markers that showed how the spiders were related to one another. The evolutionary tree of the spiders turned out to be made up of a number of distinct lineages.

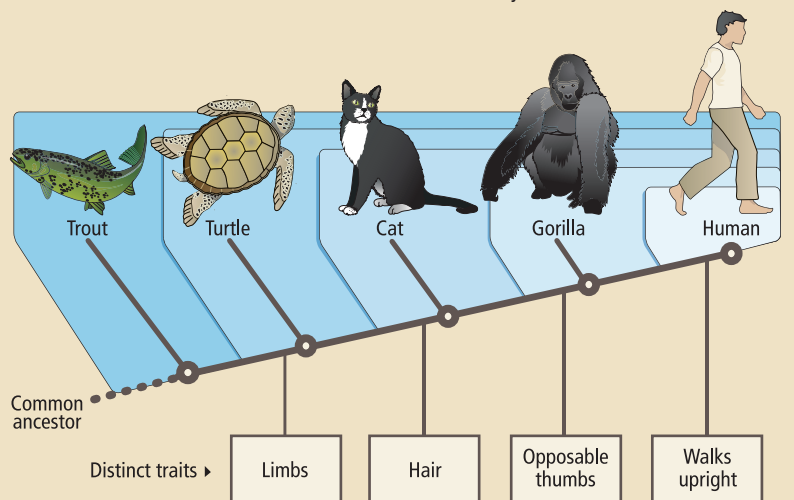
Bond and Stockman then looked for versions of genes in different populations to find evidence of gene flow. And finally, they recorded the climate conditions in which each group of spiders lived. In the end, they identified six species that met all three criteria. If accepted, these findings would double the number of *Promyrmekiaphila* species.

This kind of approach is allowing scientists to study organisms that once seemed not to fit

[PHYLOGENETIC SPECIES CONCEPT]

Linnaeus Updated

The phylogenetic species concept emerged from a new approach to classifying life, known as phylogenetic systematics. Unlike Linnaeus’s system, it takes evolutionary history into account. Ignoring the issue of whether two populations can mate, it classifies an individual species as an organism that shares a common ancestor with other species but is set off from others by having acquired newer, distinctive traits. A phylogenetic tree, also known as a tree of life, shows how different species branch off from a common ancestor as they acquire traits the ancestor did not have. The tree below lists some of the traits that land animals and fish accumulated as they evolved.



But ...

Some critics assert that the phylogenetic approach tends to overcategorize. For instance, the clouded leopard on the island of Borneo was recently classified as a species because of a distinctively dark coat and other traits, but some argue that those features may not by themselves warrant grouping it as a separate species from other clouded leopards of southern Asia.

LUCY READING-IRKANDA (Illustration); ALAIN COMPOST (leopard)

Two closely related species of bacteria might be more different than humans are from all other primates.

into species concepts. Because bdelloid rotifers do not have sex, they do not fit well under the biological species concept. Tim Barraclough of Imperial College London and his colleagues used other methods to determine whether the rotifers belong to specieslike groups. They sequenced the DNA and built an evolutionary tree. The tree had just a few long branches, each one topped by a tuft of short twigs. Then they examined the bodies of the rotifers on each tuft and found that they had similar shapes. The diversity of rotifers, in other words, is not just a blur. The animals form clusters, which are probably the result of separate lineages adapting to different ecological niches. If those clusters are not species, they are awfully close.

Where Microbes Fit In

Most of the work that has been done on the species concept in recent years has been directed at animals and plants. That bias is the result of history: animals and plants were the only things that Linnaeus and other early taxonomists could study. But today scientists know that the vast majority of genetic diversity lies in the invisible world of microbes. And microbes have long

posed the biggest puzzle of all when it comes to the nature of species.

When microbiologists began naming species in the 1800s, they could not inspect feathers or flowers like zoologists and botanists can. Microorganisms—especially bacteria and archaea—generally look a lot like one another. Some are rod-shaped, for example, and some are tiny spheres. To distinguish two rod-shaped bacteria from each other, microbiologists would run experiments on their metabolism. One kind of microbe might be able to feed on, say, lactose, whereas the other could not. From clues of this sort, microbiologists described such species as *Escherichia coli* or *Vibrio cholerae*. Underlying their work, however, was no clear concept of what it meant for microbes to belong to a species. And when Mayr came up with his biological species concept, it seemed to exclude many microbes. After all, bacteria are not made up of males and females that have to reproduce sexually like animals. They can just split in two.

The confusion got worse when scientists began to analyze the DNA of microbes. They tried to figure out how different the DNA of two microbial species was, selecting small fragments for comparison. To their surprise, the differences could be huge. Two species of bacteria placed in the same genus based on their metabolism might be more different than humans are from all other primates. And the bacteria within a species could make their living in radically different ways. Some strains of *E. coli* live harmlessly in our gut, for example, whereas others can cause fatal diseases. “The genetic variation within a species is so enormous that the term ‘species’ does not really have the same meaning for bacteria and archaea” as it does for multicellular plants or animals, says Jonathan Eisen of the University of California, Davis.

Microbes are not some minor exception to the rule that can be ignored. As investigators have surveyed the microbial world, they have discovered that the diversity of all animals is puny in comparison. “It’s always struck me as rather odd that if Mayr is right, then 90 percent of the tree of life doesn’t come in species,” says John Wilkins, a philosopher of science at the University of Queensland in Australia. “That’s got to give you some pause for thought.”

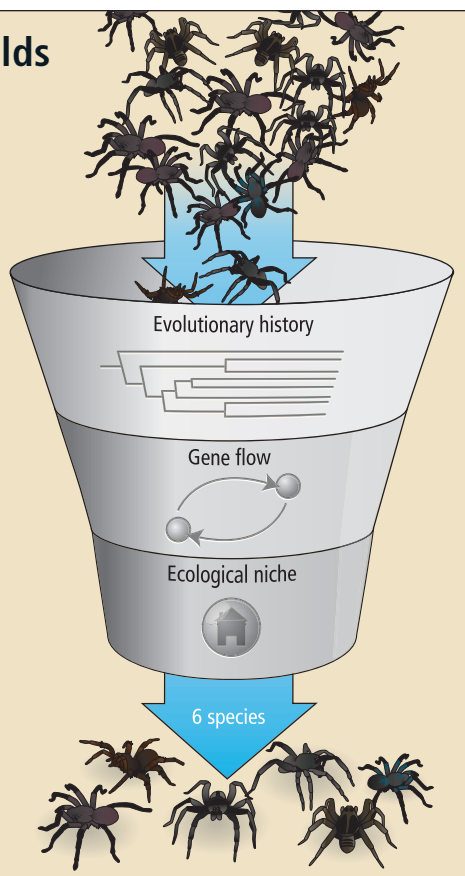
Some researchers have argued that perhaps microbes fit the biological species concept, but in their own peculiar way. Bacteria do not mate like animals do, but they do trade genes. Viruses may carry genes from one host to another, or



[A UNIFIED APPROACH]

The Best of All Worlds

Because of the turmoil, some researchers have begun to create phylogenetic classifications by looking beyond evolutionary history and combining it with molecular, ecological, behavioral and biological data. As an example, Jason Bond and one of his students at East Carolina University studied a genus of spider, *Promyrmekiaphila* (above), found in California. They studied the spider’s evolutionary history and ecological role and sequenced the genes of 222 spiders at 78 sites, using the full collection of information to group the animals into six species.



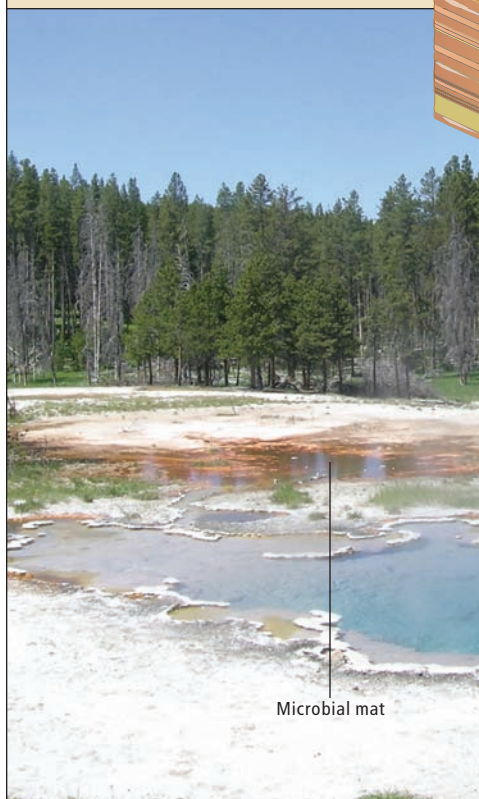
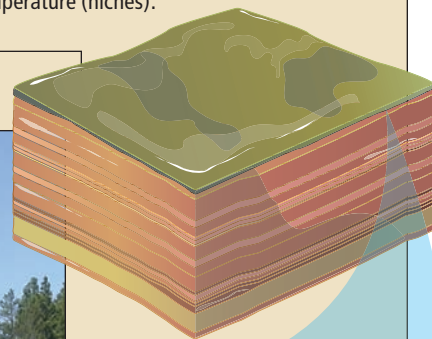
LUCY READING-IKANDA (illustration); JASON BOND/East Carolina University (spider)

[BUGS ARE SPECIAL]

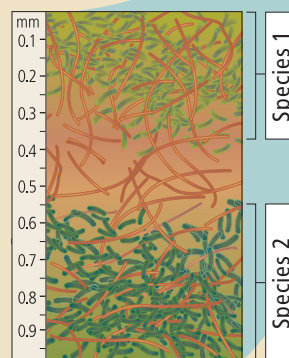
Do Microbes Belong to Different Species?

Biologists have always had difficulty grouping microbes into species. Bacteria do not engage in sex as we normally think of it. They just divide in two—and genetic differences between bacteria that purportedly belong to the same species based on similar outward appearance and behavior can be huge. Some researchers assert that bacteria can be classified as separate species by genetics and ecological niche. At a hot spring in Yellowstone National Park (*photograph*), different species of the cyanobacterium *Synechococcus* inhabit different depths or areas of varying temperature (niches).

Three-cubic-centimeter cross section of a mat made entirely of microbes in Yellowstone's Octopus Spring



Microbial mat



▲ Different species of sausage-shaped *Synechococcus* bacteria make their home at different depths (yellow-green at surface and dark green in lower layer) within the top millimeter of a microbial mat.

bacteria may simply slurp up naked DNA, which then slips into their genome. There is some evidence that closely related strains trade more genes than distantly related ones—a microbial version of the barriers between animal species.

But critics have pointed to some problems with the analogy. Although animals and plants can trade genes every time they reproduce, microbes may do so very rarely. And when they do trade genes, they do so with amazing promiscuity. Over millions of years they can acquire many genes, not just from their close relatives but from other microbes that belong to entirely different kingdoms. It would be as if our own genome had hundreds of genes from centipedes, birch trees and truffles. Critics assert that this flow of genes helps to undermine any concept of species in microbes. “I think species are kind of an illusion,” says W. Ford Doolittle of Dalhousie University in Nova Scotia.

Some researchers are taking microbial species more seriously. They contend that microbes, like rotifers, are not just a blur of variation but clusters adapted to particular ecological niches. Natural selection keeps their clusters from blurring by favoring new mutants that are even better adapted to their niche. “There’s just one slim lineage moving forward,” says Frederick Cohan of Wesleyan University. That slim lineage, he argues, is a species.

Cohan and his colleagues have found these microbial species in the hot springs of Yellowstone National Park. The microbes form genetic clusters and ecological clusters. Each genetically related group of microbes lives in a certain niche in the hot springs—enjoying a certain temperature, for example, or requiring a certain amount of sunlight. “It’s pretty cool,” Cohan says. For him, this evidence is enough to justify calling a group of microbes a species. He and his co-workers are now translating their experiments into a set of rules that they hope others will follow to name new species. “We’ve decided we have to go beyond nudging people,” Cohan asserts.

The rules will probably lead scientists to a division of a number of traditional microbial species into many new ones. To avoid confusion, Cohan does not want to come up with completely original names. Instead he wants to add an “ecovar” name at the end (“ecovar” stands for “ecological variant”). The bacterial strain that caused the first recorded outbreak of Legionnaires’ disease in Philadelphia, for example,

should be called *Legionella pneumophila* ecovar *Philadelphia*.

Understanding the nature of microbial species could help public health workers prepare for the emergence of other novel diseases in the future, Cohan says. Disease-causing bacteria often evolve from relatively harmless microbes that dwell quietly within their hosts. It may take decades of evolution before such organisms cause an epidemic large enough for public health workers to notice. Classifying these new species could let them anticipate outbreaks and give them time to prepare a response. Solving the mystery of species turns out not just to be important for understanding the history of life or preserving biodiversity—our own well-being may depend on it.

➔ MORE TO EXPLORE

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