

The difference between “what should be considered a cow” and “what should be considered a Texas Longhorn.”

## Cycles in Evolutionary Biology

The first biologists to describe and delimit species tended to think typologically: species were viewed as fixed entities, and variation among individuals was seen as imperfection. Hence, biologists designated "type specimens," which were viewed as close to the "ideal" for the species.

The evolutionary revolution precipitated by Darwin's book, "On the Origin of Species," began to change that view, but slowly at first. Field biologists began to examine species in more detail, across varied geographical landscapes, and began to document extensive morphological variation within species. In the field of herpetology, for example, the careful studies of Alexander Ruthven on Garter Snakes (1908) set new standards for statistical analysis of geographic variation. His students, including Frank Blanchard and Helen Gaige, would extend and expand his work and publish many important monographs on major North American groups of reptiles and amphibians that became standards for systematic revisions of many groups of animals.

Although biologists were gaining an appreciation of geographic variation within species, they still had a limited understanding of genetics, and hence of the root cause of variation within species. But as genetics and evolutionary biology matured, there was an eventual and inevitable synthesis of the fields. In the 1910s to early 1930s, R. A. Fisher, J. B. S. Haldane, and Sewall Wright laid the foundations for population genetics. In 1937, Theodosius Dobzhansky wrote the influential "Genetics and the Origin of Species," which synthesized the mathematical papers of Fisher, Haldane, and Wright with field biology and natural history. He emphasized that species contained far more genetic variation than had been previously acknowledged, and that geographic variation within species was important for understanding both local adaptation and long-term evolution.

In 1942, Ernst Mayr followed this up with "Systematics and the Origin of Species," in which he emphasized the importance of understanding geographic variation within species. He noted that many wide-ranging species were polytypic, showing different local adaptations to different environments. He emphasized the importance of reproductive connections in understanding

species boundaries, as well as the role of reproductive isolating mechanisms in speciation.

Although theoretical population genetics and evolutionary biology were synthesized in the first half of the Twentieth Century, it would not be until the second half of the century that biologists developed the direct means to examine genetic variation at the level of genes and individual gene products. The first broad studies of population genetic variation were conducted using allozyme electrophoresis, which identified individual alleles of genes of specific enzymes. These studies revealed even more genetic variation in individuals and populations than had been imagined by people like Dobzhansky and Mayr. Many systematists quickly embraced these new empirical population genetics approaches for studies of geographic variation within species, reproductive interactions at contact zones, and relationships among closely related species. For most of the last four decades of the Twentieth Century, allozyme studies dominated genetic systematic investigations of variation within and among species.

The development of methods for DNA sequencing in the late 1970s would eventually shift the focus from examining gene products (proteins) to direct studies of gene variation at the level of DNA sequences. This shift happened slowly through the 1980s, but then sped-up with the development of the Polymerase Chain Reaction (PCR) in the late 1980s. By the 1990s, amplifying and sequencing regions of the mitochondrial genome using PCR became routine, and mitochondrial-based studies of genetic variation became commonplace.

Mitochondrial (mt) DNA is easy to examine, but it has some odd peculiarities. With rare exceptions, the entire mt-genome is inherited as a single haploid locus, generally from the female parent in animals. The general lack of recombination, and the inheritance of a single haplotype, makes analysis of individuals easy. Almost every individual has a single mt-haplotype. Mitochondrial variation still exists with species, but in many species with limited dispersal, local populations often become fixed for a single mt-haplotype as well.

The ease of examining mt-DNA, combined with a desire to develop automated methods for species identification, led to a return of sorts to typological thinking with regard to species delimitation. Mt-haplotype differences were

easy to assess, and often varied geographically in a consistent manner. The early decades of the Twenty-First Century saw a return to division of many wide-ranging species by mitochondrial haplotype, with little or no regard to broader indicators of long-term reproductive interactions (a trend that unfortunately continues to this day). This was basically a new-age return to the typological thinking of the early days of systematics, with mt-haplotypes replacing the "type thinking" of earlier biologists.

Within the last decade, we are beginning to see the pendulum swing back in the other direction once again, with yet another synthesis of fields. Biologists now recognize that reproductive boundaries between closely related species are often not as complete and absolute as visualized by Mayr and other biologists of his era. In addition, biologists now tend to view species as evolutionary lineages that exist through time, rather than as fixed entities at a single point in time. Species are the individual branches in the evolutionary tree of life, and we now understand that these branches contain considerable variation in space and time. The histories of individual genes (including mt-genes) are constrained by these lineages, but not absolutely. Mt-genomes often cross species boundaries, and for reasons that are still debated, species or local populations can often have their mt-genomes replaced by those of other species or populations.

Once biologists began to examine the biparentally inherited nuclear genomes (most of our genes), they found many mismatches between the histories of nuclear and mitochondrial genomes. Many proposed "species" that were based largely or entirely on mt-haplotypes are now being re-examined, and many are being re-interpreted as geographic variation within wide-ranging species. A major focus of systematic studies today is once again distinguishing geographic variation within species from the species boundaries that allow evolutionary lineages to remain distinct through evolutionary time. Many end-users of biological nomenclature express frustration that "biologists are always changing names back and forth." I share this frustration to some degree, as I've argued that we should change scientific names conservatively, and only when needed to reflect broad consensus across biologists and studies. There is indeed an unfortunate tendency among many biologists to draw attention to their studies by changing names, even when the old names are not misleading (as, for example, by dividing monophyletic genera into ever-smaller genera, or by naming geographic variants within species as species). On the other hand, some name changing simply reflects

changes in our biological understanding. Scientists SHOULD change their minds in the face of new data. In the case of scientific names, we should change the names that mislead end-users about what we currently know. But that does not mean that we should use limited and likely misleading data (such as a single uniparentally inherited gene locus) to change well-established taxon names that are based on decades or centuries of study.

I've linked an article below that discusses some of the issues that surround recent arguments about geographic variation versus species boundaries, with some additional papers linked in the comments. There are lots of papers coming out about this topic right now, and I predict that we will see many of the "mt-haplotype species" that were proposed over the past few decades appropriately re-evaluated and reconsidered as geographic variation within species.

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