SYSTEMATIC PALEONTOLOGY

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Contents

Summary

Systematics is the study of the diversity of organisms, and any relationships between them. This includes not only classification (taxonomy), but also their evolutionary history and relationships (phylogeny), and their geographic relationships (biogeography). As such, systematics is the foundation upon which all other comparative studies in biology and paleobiology are based. The systematist uses the *comparative approach to the diversity of life to understand all patterns and relationships that explain how life came to be the way it is*. Put this way, systematics is one of the most exciting and stimulating fields in all of biology and paleobiology.

The methods of systematics have undergone a revolution in the past 40 years, with the old, vaguely defined method of "evolutionary systematics" popularized in the 1950s by Ernst Mayr and George G. Simpson being replaced from the 1960s to the 1980s by the

more rigorous and testable methods of cladistics or phylogenetic systematics. Today, research in the methods of systematics is still an exciting area full of controversy, although not as wildly controversial as it was in the 1970s when the clash between old and new methods was in its early stages. Today, the traditional methods of systematic analysis using anatomical and embryological features of an organism are being supplemented by molecular systematics, where the genomes of organisms provide an entirely new method of comparative analysis. Many insoluble problems in the history of life (such as the phylogeny of the animal kingdom) have been resolved by molecular phylogenetic methods. Others are still controversial, since the fossil record or anatomical or embryological data give completely different answers than do the molecular data.

Like systematic biologists, paleontologists must be familiar with the rules of systematics and taxonomy, particularly the requirements of the codes of zoological and botanical nomenclature, when they are naming and describing new fossils. Most important among these are rules of priority (which have made many familiar names of fossils invalid) and rules about the criteria for naming type specimens, as well as incorporating biological and population species concepts when deciding the limits of fossil species.

Because more than 99% of the species that have ever lived are now extinct, paleontology provides important perspective on the reliability of phylogenetic and biogeographic analyses. Study after study has shown that if fossils are left out of the cladistic or biogeographic analysis, completely erroneous conclusions are reached.

1. Systematics and Biodiversity

What is a species? How are species grouped into larger categories? How are classification schemes set up, and what do they mean? The science of classifying is known as **taxonomy** (Greek, "laws of order"); any named grouping of organisms (a species, a **genus**, etc.) is called a taxon (plural, **taxa**); the rules of creating taxonomic names are called **taxonomic nomenclature**. Deciding how to name a new taxon may seem to be a highly specialized, legalistic dimension of biology and paleobiology, not nearly as glamorous as ecology or behavior or physiology. But taxonomy is not just naming taxa, because species and higher taxa reflect evolution. Taxonomists do much more than label dusty jars in a museum. They are interested in comparing different species and deciphering how they are related and ultimately in deciphering their evolutionary history. They look at the diversity of organisms in time and space and try to understand the large-scale patterns of nature. They look at the present and past geographic distributions of organisms and try to determine how they got there. In short, they look at the total pattern of natural diversity and try to understand how it came to be. Contrary to stereotypes, they are among the most eclectic of biologists and paleobiologists.

All these various enterprises go beyond conventional taxonomy and are usually given the broader label **systematics**. Systematics has been defined as "the science of the diversity of organisms" (Mayr, 1969, p. 2) or "the scientific study of the kinds and diversity of organisms and of any and all relationships among them" (Simpson, 1961, p.

7). Its core consists of taxonomy, but it also includes determining evolutionary relationships (phylogeny), the study of character evolution, and determining geographic relationships (biogeography). The systematist uses the *comparative approach to the diversity of life to understand all patterns and relationships that explain how life came to be the way it is*. Put this way, systematics is one of the most exciting and stimulating fields in all of biology and paleobiology.

Taxonomists and systematists may not be as numerous or well funded as molecular biologists or ecologists or physiologists or behaviorists, but their labors are essential. All other disciplines in biology and paleobiology depend upon taxonomists to give their experimental subjects a name and, more important, to give them a comparative context. If a physiologist wants to study the organism that is most like humans, it is the taxonomist who points to the chimpanzee, our closest evolutionary relative. If an ecologist wants to understand how a particular symbiotic relationship may have developed, or the ethologist wants to understand a peculiar type of animal behavior, they need to know the evolutionary relationships and phylogenetic history of each organism—these are the domains of the systematist. Systematics provides the framework of understanding and interconnections upon which all the rest of biology and paleobiology are based. Without it, each organism is a random particle in space, and what we learn about it has no relevance to anything else in the living world.

In our present age, taxonomists have become scarce as grant funding dries up and students go into more glamorous specialties that require big, expensive machines. Yet one of the most important issues on this planet today—**biodiversity**—is within the domain of systematists. Without someone to describe, name, and count all the species on this planet, how will we know whether we are wiping them out catastrophically, or whether they are holding their own, or even flourishing? Without the perspective of past diversity changes on this planet, how can we assess the severity of the human-induced mass extinction? Each time someone surveys a patch of rainforest, trying to determine how humans have impacted the life there, their first task is taxonomy. Ecologists complain that they cannot find anyone who has the right training to identify and describe all the new species of insects and birds and plants that are being destroyed even before we get to know them (Dubois, 2003). Without knowing that they are there, how can we decide how important they might be? One of these species might hold the cure to some deadly disease or the solution to the control of a nasty pest, but without systematic and taxonomic research, these species go extinct before we even encounter them.

In the context of paleontology, the situation is analogous. The public may think that collecting big dinosaur specimens in exotic places is exciting, but it is just a tiny part of paleontology. Collecting and preparing fossils is a specialized task, often performed by people with little advanced scientific training. Analyzing and understanding their taxonomy, geography, and phylogenetic relationships is the domain of the systematic paleontologist. Without a properly trained paleontologist to correctly identify, name, and analyze the fossils, they are mute stones. Hours in the laboratory and museum collections spent measuring and describing specimens may not seem as glamorous as visiting exotic places, but they are equally essential. From this naming and description comes the understanding of larger problems in paleobiology, such as: how is all life interrelated? What is the past history of life? How has diversity on this planet changed? Without the foundation of systematics, these questions cannot even be approached.

Compared to most biologists, paleobiologists are much more likely to practice taxonomy as part of their research, because nearly every study requires some kind of taxonomic or phylogenetic analysis at its foundation. In some cases, one can use the work of previous taxonomists, but in most research, there is more taxonomy to be done or updated, or the paleontologist needs to do his or her own taxonomy just to determine if past taxonomy can be trusted. A paleontologist without adequate training in systematics is severely handicapped.

2. Evolution and Classification

There are many ways to classify things. Children often classify objects by similarity in color, or shape, or texture. As adults, we may use more subtle means of telling things apart. For example, a child may label all objects with four wheels as “cars” but as adults, we recognize the difference between cars, trucks, and vans, or between cars with diesel or gasoline engines, or between Fords, Chevys, and Toyotas. Some classification schemes attempt to have a logical basis or structure to make them easier to use. For a long time, the Dewey Decimal system was the most widely used means of cataloging books, until it was replaced in many libraries by the Library of Congress system. Both try to cluster books by **natural groups** (such as a category for science books, subdivided into physics, chemistry, biology, geology, and so on) but the Library of Congress system is apparently more flexible at handling larger numbers of books. Both natural classification schemes attempt to organize the same array of objects, but one is apparently more successful than the other.

In the realm of life, a wide variety of classification schemes were developed since the 550 kinds of animals recognized by Aristotle. Some grouped organisms on properties that humans favored (“good to eat” vs. “eat only in emergency” vs. “inedible” vs. “poisonous”) or on properties of their ecology (for example, most animals in the ocean were called “fish,” including “starfish” and “shellfish” and whales). By the early 1700s, there were over 6000 recognized species of plants and 4000 of animals, organized into a great array of classification schemes proposed by natural historians. Most of these classifications were arbitrary and highly unnatural (for example, flying fish and birds were put together because they both fly, or turtles and armadillos because of their armor), and everybody had his/her own favorite scheme. The nomenclature method that eventually won out was proposed by the Swedish botanist Carl von Linné, known to us by his Latinized name, Carolus Linnaeus (1707-1778). As a botanist, Linnaeus recognized that the most fundamental and diagnostic properties of plants occur in their reproductive structures, particularly their flowers. His “sexual system” for classifying plants was published as *Species Plantarum* in 1752 and created a scandal. Eventually it won out over all the competing systems, since flowers are clearly more useful than any other structure. Linnaeus tried a similar approach in animals, using fundamental structures (such as hair and mammary glands in mammals) rather than superficial ones (such as flight or armor). His *Systema naturae, regnum animale* (“the system of nature, animal kingdom”) was first published in 1735, and its tenth edition (1758) is now regarded as the starting point of modern zoological nomenclature.

Linnaeus' original classification became outdated as thousands of new species were described since 1758, but his nomenclatural system still survives. Each species is given a **binomen** (two-part name), consisting of the **genus** (plural, **genera**) name (always italicized or underlined, and always capitalized) and the **trivial name** (or specific epithet) indicating the species (always italicized or underlined but never capitalized). For example, our genus is *Homo* ("human" in Latin) and our trivial name is sapiens ("thinking" in Latin), so our species name is *Homo sapiens* (abbreviated *H. sapiens*). The trivial name can never stand by itself (since trivial names are repeated over and over in taxonomy), but must always accompany its genus. To prevent confusion, the genus name can never be used for any other organism in the animal kingdom (few generic names are reused for different animals and plants and bacteria). Genera are then grouped into taxa of higher categories, such as families (whose names are always capitalized, but never underlined or italicized, and with the "-idae" ending in animals, the "-aceae" ending in plants), then orders, classes, phyla (singular, "phylum"), and kingdoms. For example, humans are members of the Kingdom Animalia (there are also kingdoms for plants, fungi, and single-celled organisms), the Phylum Chordata (including all other backboned animals), the Class Mammalia (mammals), the Order Primates (including lemurs, monkeys, apes, and ourselves), the Family Hominidae (including our own genus and the extinct genera *Australopithecus*, *Sahelanthropus*, *Orrorin*, *Ardipithecus*, and *Paranthropus*), the genus *Homo* (including other extinct species such as *Homo habilis* and *H. erectus*), and our species *H. sapiens*.

Notice that this classification scheme is hierarchical. Each taxon of a given rank is grouped into taxa of higher ranks, so that there may be several species in a genus, several genera in a family, and so on. However, some genera have only one species, some families have only one genus, some orders have only one family, and so on; these one-member groups are called **monotypic**. The great reason for the success of Linnaeus' scheme is this flexibility created by groups hierarchically clustered within larger groups, with room for expansion as new species are discovered. The Latinized binomen is also very flexible, and universally recognizable in science. Local vernacular names in a single language may vary greatly. The word "gopher" refers to both a tortoise and a burrowing rodent in English, and every other language uses completely different names for the same animals. But in all languages, the scientific name is always based on Latin or Greek (since these were the languages of scholars in Linnaeus' time, and do not change meaning since they are dead languages), or a Latinized version of other words. A scientist can pick up a publication in any language, such as Cyrillic or Hebrew or Chinese, and not recognize a word except the scientific names; these stand out and at least communicate some of the essential content of the paper.

Linnaeus and his contemporary natural historians viewed their task as a religious mission. They thought that deciphering the "Natural System" of life would reveal the workings of the mind of the Creator that set up this "Natural System." But the obvious clusters of organisms into groups within groups suggested something else to Darwin. This hierarchical, nested, branching structure of life only made sense if life had descended from common ancestry in a branching fashion. Although Linnaeus has not intended to provide evidence for evolution, a century later his classification scheme became one of Darwin's best arguments. In doing so, Darwin changed the goals of classification. It was no longer just a nice but arbitrary system of arranging things into pigeonholes. Taxonomy now had an evolutionary meaning as well, and taxonomists were trying to create natural groups that reflected evolutionary history. Although these goals are not contradictory, they do not always agree, either. Some taxonomists view organisms of similar descent and ecology, such as the fish, as a formal group, "Pisces." But in evolutionary terms, not all fish are created equal. Lungfish, for example, are more closely related to four-legged land vertebrates (tetrapods) than they are to a shark or a tuna. In other words, a lungfish and a cow are more closely related than a lungfish and a tuna. Here we see a clear tension between ecological and similarity groupings, such as "fish," and evolutionary groups, such as the lungfish-tetrapod group (known as the Sarcopterygii). Which is better? The different priorities and goals of taxonomists have led to much debate over the proper methods of classification.

3. Competing Systematic Philosophies

3.1. Introduction

What is the proper way to classify organisms? That question had been the center of a very intense scientific debate since the 1960s. As the historian of science David Hull (1988) pointed out, the debate reveals almost as much about the sociology of science as it does about the science itself. In the late 1950s, there was relatively little argument, since the majority of taxonomists practiced a vaguely formulated method later called "**evolutionary taxonomy**," exemplified by Simpson's (1961) book *Principles of Animal Taxonomy* or Mayr's (1966) book *Principles of Systematic Zoology*. This mainstream, orthodox school of taxonomy was challenged by two upstarts in the 1960s and 1970s. Both schools of thought followed very different basic assumptions and used new jargon to distinguish themselves from the amorphous orthodoxy. Sometimes they took very extreme positions so that they could be seen as different and not be absorbed into the mainstream as a minor variant. Those extremes may have been moderated by later systematists as the controversies died down, but they were important in the early phases of the movements. Hull pointed out that both these movements had great similarities to religious movements in trying to establish themselves, attract converts and grow, and make themselves distinct and recognizable. They both had "prophets," a "bible," a "high priest," a "Mecca," "acolytes," and a central philosophical dogma. The first movement, **numerical taxonomy** (later known as **phenetics**), was introduced by "prophets" Robert Sokal and Peter Sneath in several papers in the late 1950s, culminating with their 1963 "bible" *The Principles of Numerical Taxonomy*. Their "high priest" was bee taxonomist Charles Michener, and phenetics was promoted by important "acolytes," such as James Rohlf, Steve Farris, and Paul Ehrlich. The movement spread from the "Mecca" of the University of Kansas at Lawrence. Their central philosophical tenets revolved around statistics and objectivity and the idea that computers could do taxonomy better than humans.

By the mid-1970s, numerical taxonomy had been eclipsed by the second movement, cladistics, which began with its "bible" *Phylogenetic Systematics*, written by "prophet" Willi Hennig, a German entomologist. First published in German in 1950 as *Grundzüge einer Theorie der phylogenetischen Systematik*, it had little impact outside of entomology until it was translated into English by Rainer Zangerl under the title *Phylogenetic Systematics* in 1966. It was then promoted by its "high priest," the

American ichthyologist Gareth Nelson in the late 1960s and 1970s. Other important "acolytes" included ichthyologists Donn Rosen and Colin Patterson, and arachnologist Norm Platnick. The central tenets of cladistics were that phylogenetic hypotheses must be testable and that classification should reflect evolutionary history and nothing else. Nelson, Rosen, Platnick, and their colleagues at the "Mecca"— the American Museum of Natural History in New York were at first regarded as too radical and extreme, but by the mid-1980s cladistics itself had become mainstream and it is now used by most taxonomists.

3.2. Phenetics

Let us take a closer look at these two movements. Numerical taxonomy was precipitated by several factors: the availability of the first practical computers; an increase in interest in statistical methods; and a widespread dissatisfaction with conventional taxonomy as being an intuitive, arbitrary "art" that was only valid and reproducible in the mind of the same taxonomist. To get away from this element of subjectivity, the numerical taxonomists argued that classification should be a purely *objective*, statistical exercise that can be coded and deciphered by a computer. Numerical taxonomists concluded that since classifications cannot reflect both evolutionary history and degree of overall similarity, we should give up trying to make our classifications phylogenetic and instead base them on objective statistical similarities and differences, or overall **phenetic similarity**. To them, a "natural" classification is judged by how successfully it clusters groups with the most in common and how well it creates stable classification schemes that are maximally useful to scientists. Typically, this is accomplished by measuring and coding numerous anatomical features, or characters, in each specimen or taxon (called **OTUs,** or **operational taxonomic units**) to create a large **data matrix** of OTUs versus characters. Next, a computer program sorts the data and finds clusters of OTUs that have the most characters in common. When the computer analysis is finished, a branching diagram of similarity is produced.

The response to numerical taxonomy was predictable: most systematists did not like computers and statistics intruding into their arcane domain. According to Hull (1988, p. 120), "one systematist volunteered that he hoped they would never succeed in making taxonomic judgments sufficiently quantitative so that a computer could make them, because, if they did, it would take all the fun out of systematics." Remember, in the late 1950s and most of the 1960s, computers were still huge machines that filled entire rooms and required hours to analyze big stacks of punched FORTRAN cards just to run a simple program that your laptop computer can now run in seconds. Most people did not have access to one, and even those who could run them were severely limited by their clumsy operations. In response to this hostility and rejection, the more outspoken numerical taxonomists, such as Sokal and Ehrlich, did not hesitate to step on toes. When Ehrlich was asked indignantly, 'You mean to tell me that taxonomists can be replaced by computers?' Ehrlich responded, 'No, some of you can be replaced by an abacus.' Thereafter, Ehrlich did not consider the give-and-take after a paper truly successful unless he brought at least one taxonomist to the point of tears" (Hull, 1988, p. 121). At first, the establishment fought back by preventing numerical taxonomic papers from being published. The editor of the journal *Systematic Zoology* in 1961 was Libbie Hyman, who reportedly said, "One paper with numbers is enough." Shortly thereafter, she was replaced as editor and the journal moved to Lawrence, Kansas, where it became almost the unofficial house organ of numerical taxonomy. *Systematic Zoology* went from a staid, obscure journal to a "must-read," almost doubling its page count and circulation with the excitement of the debates.

A few years after numerical taxonomy gained this status, it went into decline. According to Hull (1988), several factors were responsible. The original concentration of pheneticists in Lawrence, Kansas, broke up as Sokal, Rohlf, and Farris all went to the State University of New York at Stony Brook in 1969. Another problem was that the numerical taxonomists tried to apply their methods so widely that their efforts in systematics were dissipated. More important, the majority of systematists never accepted the fundamental goals of phenetics. Most still wanted classification to reflect evolutionary relationships in some way, even if this was a difficult task. Many were alienated by the great emphasis on computers and statistics (this was when computers were difficult to use, and only a few scientists had access to one). Taxonomists preferred to study their favorite organisms and were less interested in math or statistics for its own sake.

The most serious blows came when a number of studies showed that the "objectivity" of phenetics was a myth. Coding and weighing the importance of the characters in the data matrix cannot be done objectively. When one systematist decides that a wing represents a single character state and another subdivides it into numerous character states, which is the correct approach? Once again, the "art" of systematic judgment comes into play. Taxonomists ultimately must decide what a character is, and that decision is filtered by their own prejudices. Even more serious were studies that showed that the same data matrix gave different results with different computer programs, and occasionally even with the same computer program! If the methods were not truly objective and reproducible, and gave up on the whole idea of evolutionary classification, then what was the advantage? If a purely phenetic classification placed unrelated animals such as whales and fish together, then what good was it?

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Biographical Sketch

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