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There shall be order

The legacy of Linnaeus in the age of molecular biology

he Swedish botanist, physician and zoologist Carl Linnaeus (1707-1778) used to describe his contribution to science as: God created, but Linnaeus organized (Blunt, 2004). This year marks the threehundredth anniversary of his birth, which was celebrated all around the world on 23 Mayparticularly in his native Sweden-to honour him as one of the most important contributors to modern biology. Linnaeus' gift to science was taxonomy: a classification system for the natural world to standardize the naming of species and order them according to their characteristics and relationships with one another. Linnaeus introduced a simple binomial system, based on the combination of two Latin names denoting genus and species: similar to the way that a name and surname identify humans. Although there have been several modern alterations to Linnaeus' original system, the basis of Linnaean taxonomy has allowed biologists to group related species into genealogical trees, which represent the evolutionary lineage of modern organisms from common ancestors.

Insights from molecular biology and our new understanding of the evolutionary relationships between and across species challenge Linnaeus' original system. Nevertheless, Linnaeus' work is still both valid and important, as noted by Charles Godfray, Hope Chair of Zoology at Oxford University in the UK. "Taxonomy is critically important in helping [to] understand and conserve biodiversity. I like to think Linnaeus faced the first bioinformatics crisis: the problem of organising information about the increasing number of species that were being discovered in the eighteenth century, and he developed solutions using the best technologies available at the time," Godfray said.

Before Linnaeus, many scientists and philosophers had tried to bring order to the plethora of life forms on Earth. The Greek philosopher Aristotle (384–322 BC) was among the first and borrowed from popular terminology. However, he never followed a precise scheme—his notes were based on an inconsistent range of anatomy, physiology and ethnology, and when he ran into something unknown, he simply classified it as an 'anonymous cluster'. Yet some of his classifications remained unchanged for centuries. For example, his distinction between 'blooded' or 'bloodless' animals actually mirrored the modern distinction between vertebrates and invertebrates, and he correctly grouped the Cetacea—sea mammals such as whales, dolphins and porpoises—with other mammals.

Theophrastus (373-288 BC), who coined the term 'botanic', was a close collaborator of Aristotle and tried to describe and order the variety of plants, with similar lapses and without any hierarchy. Theophrastus divided plants on the basis of their origin, such as spontaneous generation, birth from seeds, roots, branches and trunks. During the Roman Empire, the historian Pliny the Elder (23-79 BC) also dedicated himself to the classification of the natural world, but again without any real methodology. His colossal work, Naturalis Historia, mixed serious descriptions of flora and fauna with esoteric and astrological digressions. Nevertheless, Pliny's work had a huge influence on many scientific communities throughout the medieval period.

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During the Renaissance, European scientists vastly expanded their knowledge of the living world. Expeditions to other continents and to remote islands provided an endless supply of new animals and plants to be studied. It was an exciting period for natural history and reawakened an interest in a sensible classification system, which, until then, had often been based on personal criteria and caused more confusion than it gave insight. gainst this background, Linnaeus' arrival on the scientific scene was in the form of two publications, *Systema Naturae* (1735) and *Species Plantarum* (1753), marking the beginning of a true revolution. His systematic approach standardized the nomenclature and did away with subjective and ambiguous elements. At a time when a common flower had previously been described with 60 words, he established a definitive distinction between concepts of diversity, species, genera, orders and classes—which was, in part, anticipated by the Swiss naturalist Conrad Gessner (1516–1565).

As Latin was the *lingua franca* of the scientific world, it was logical for Linnaeus to give organisms Latin names to ensure stability and avoid linguistic fluctuation. In addition to his introduction of binomial names, the Linnaean system replaced a heavy string of names for various animals. For example, the honeybee, which had previously been called *Apis pubescens, thorace subgriseo, abdomine fusco, pedibus posticus glabis, untrinque margine ciliatus,* became *Apis mellifera*—a simple combination of genus and species.

Linnaeus' first version of the Systema Naturae presented the animal kingdom on one double-page spread and organized it into six main classes: Quadrupedia (quadrupeds), Aves (birds), Amphibia (reptiles and amphibians), Pisces (fish), Insecta (insects) and Vermes (worms and molluscs). Each class was then sub-divided into genera-some with recognizable names such as Leo, Ursus, Hippopotamus and Homo—and each genus into species. By its tenth edition, in 1758, the Systema had become far more elaborate and complex. Linnaeus judged that the presence of mammary glands was an important distinction in some animals and, as such, quadrupeds were redefined as mammals. He further divided mammals into primates, including apes and humans, and introduced the term Homo sapiens.

In his later publication, *Species Plantarum*, Linnaeus introduced a classification scheme for plants. He defined 24 classes of plant based on their reproductive organs because he thought that—as a father of five children—

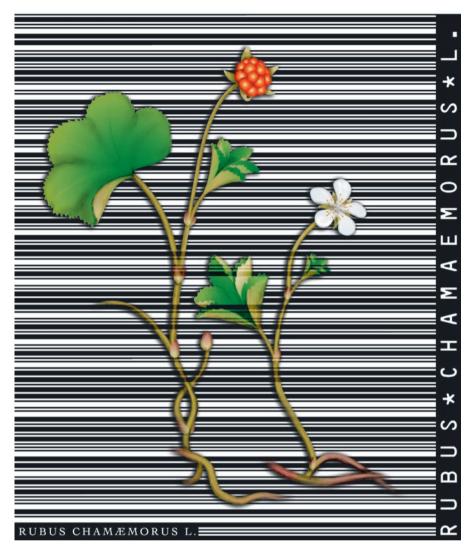
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reproduction was the most important function of an organism. Instead of looking at the whole of every plant, Linnaeus focused on one particular characteristic-the reproductive organs-and classified all plants according to their sexual morphology. His so-called sexual system organized plants based on the number, size and method of insertion of their stamens, and also on the female parts, the pistils. Despite some controversy and disapproval-Linnaeus was accused of being a botanical pornographer-the sexual system soon caught on because it was so straightforward. It also brought a democratisation of science because now anyone-not just a specialist-could look at a flower and characterize it by counting the number of male and female parts.

t the time of Linnaeus' scientific endeavours, Sweden was facing depression and hardship—having lost the Northern Wars against Russia, Denmark-Norway, Saxony and Prussia (1655-1661). His research afforded Linnaeus a way to regain wealth and prestige for his motherland. He was the first scientist to embark on an expedition to Lapland and travelled throughout Europe to build his career. Although his own excursions were limited to Sweden, his collaborators-whom he rather arrogantly dubbed 'apostles'-were encouraged to make trips around the world to collect new species. With their help, Linnaeus collected a huge variety of plant and animal species-5,900 plants and 4,378 animals (Muller-Wille, 2006)-most of which are now maintained at the Linnaean Society in London, UK. Linnaeus was also renowned as a witty conversationalist and a brilliant lecturer and attracted big audiences to his talks. As a master of public relations, and by maintaining a large network of collaborators and contributors, Linnaeus succeeded in making contact with naturalists all over the world.

Eventually, Linnaeus' work gained the fame that he sought, and his classification system received unanimous approval. However, as with any great historical and scientific transformation, there were numerous opponents and he became the target of many attacks. Immediately after the publication of *Species Plantarum*, it was the scientific rather than the religious community that was sceptical of his sexual system. One of Linnaeus' most bitter enemies was the French naturalist, Georges-Louis Leclerc, Comte de Buffon (1707–1788) who derided taxonomists. Buffon, perhaps rightly, considered the Linnaean system to be



artificial because it was based on only one element of comparison.

Although the concept of evolution was alien to Linnaeus, some elements of his Systema already pointed to it. For example, Linnaeus' description of the similarities between man and ape was clearly a starting point for a discussion of evolutionary principles, although he himself did not do so. Yet he did go so far as to abandon his earlier belief in the stability of species, and noticed that hybridization could produce new plant and, in some cases, animal species depending on geographical diversity. Overall, however, Linnaeus tried to describe all the things that had been 'put on Earth by God', and therefore approached taxonomy with the tacit assumption that this task was finite. Whatever new species might have arisen from the original inhabitants of the Garden of Eden, he reasoned, they were still a part of God's design

for creation, because they had always potentially been present. Although Linnaeus annotated the struggle for survival, he considered competition necessary to maintain the balance of nature, rather than to drive evolution. His writings inspired generations of naturalists, including Charles Darwin, who moved on from the simple description and classification of organisms to the study of their evolutionary relationships.

ore than two centuries later, biologists are still using Linnaeus' binomial system for the classification of life on Earth, even though taxonomy has undergone profound transformations. Electron microscopes have allowed scientists to observe organisms at a much higher level of detail, and the sequencing of the whole genomes of many species has allowed them to make finer distinctions between closely

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related organisms. The technological and scientific developments during the past 50 years have also shifted the focus of biologists. During Linnaeus' time, the crucial question was what 'God's plan' for his creations was; today, scientists want to understand the nature of life and the process of evolution.

These changes have triggered a lively debate between anatomists and palaeontologists on the one hand and molecular biologists on the other-between classically- and DNA-based taxonomy. Some would declare classical taxonomy to be an obsolete discipline, whereas others still place it at the centre of a system to explain biodiversity (Hajibabaei et al, 2007; Godfray & Knapp, 2004). "This is a magic moment for the science of life," commented Carlo Alberto Redi, Professor of Zoology at the University of Pavia in Italy. "We must be open to a monumental rearranging of the field, where classic taxonomy has to give the pace to DNA taxonomy." Redi, for example, has cited mammals as a class that might need to be redefined: "[I]f we instead rely on current DNA-based results, we will witness the creation of other groups, consisting of animals with completely different anatomical characters," he said. According to DNA analysis, mammals might include only four groups: Afrotheria, including elephants and the elephant shrew; Xenarthra; Laurasiatheria; and Euarchontoglires, which includes primates and rodents (Redi et al, 2007). "We cannot ignore DNA; rather, this has become our starting point of analysis," Redi said.

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However, other researchers consider classifications based on comparative DNA analysis to be preliminary or controversial, as they often cut across previous relationships based on morphological considerations. Indeed, despite all the challenges, classical taxonomy still finds wide support. "Nowadays, bacterial classification is based only on DNA, which is very sensible for these creatures," said Godfray. But this does not necessarily make sense for higher organisms. "We could start from scratch and construct a purely DNA-based taxonomy for all animals and plants, but I think this would be a disaster: we would lose all the information collected over 250 years associated with Linnaean names. Molecular methods will become increasingly important and taxonomy needs to change to mesh the old with the new as smoothly and efficiently as possible," he said.

To do so, taxonomists will have to change the way they are distributing and accessing information. "The taxonomy of a group of plants and animals consists of scientific papers and books published over many years and scattered throughout the literature: it is in a 'distributed state'. I believe modern taxonomy should be mounted on the web, at a single site for a particular group of organisms. We should move from a distributed to a unitary model of taxonomy," Godfray noted. "One of the problems of funding taxonomy is that it is perceived as an inefficient science that produces outputs [that are] difficult for other biologists and the broader community to use. A web-based approach to taxonomy would remove these problems."

ndeed. Linnaeus vastly underestimated the variety of plants and animals on Earth, whose number could be between four and ten million species-putting taxonomists under pressure to deal with the growing data on new organisms. One approach to speed up the task of classifying new species is DNA barcoding, developed by Paul Hebert, who leads the Canadian Barcode of Life Network-one crucial element in the Consortium for the Barcode of Life (CBOL), established in 2003 at the National Museum of Natural History in Washington, DC, USA (www.barcoding.se.edu). Hebert's contribution has been to standardize the technique that is used to tell species apart by DNAtagging, which uses short and specific DNA tags, or 'barcodes', to distinguish one species from another. Animals, for example, are distinguished by a small part of the mitochondrial genome—650 bases of the cytochrome coxidase I (COI) gene. In most eukaryotes, the variation in COI is far lower among individuals within a species than between different species. However, the aim is not necessarily to replace the Linnaean classification system. "I do not advocate DNA taxonomy and I do not forget Linnaeus' job," Hebert said. "I believe in reinforcing Linnaean taxonomy with DNA. In fact, when an unknown specimen does not return a close match to existing records in the barcode library, the barcode sequence does not qualify the unknown specimen for designation as a new species.

Instead, such specimens go back under the aegis of taxonomic analysis."

CBOL now involves more than 150 member organizations from 45 countries, including natural history museums, zoos, herbaria and botanical gardens, as well as university departments of biology and molecular biology, conservation organizations and governmental and intergovernmental organizations. It aims to develop DNA barcoding as a global standard for the identification of biological species. Moreover, supporters foresee many applications, from fundamental research on biodiversity to the enforcement of food laws, protection of wildlife and even biodefence.

In light of the potential synergy between classical and DNA taxonomy, and the issue of the ever-increasing amount of data, it might be that natural history and natural history museums will play a more central role in terms of collecting samples. "We still need a Linnaean state of mind and for modern taxonomy it is imperative, now more than ever, that physical samples are collected, together with a photographic image and a source of DNA, because ultimately this is still the only way to map the distribution and spread of organisms," commented Sandra Knapp, a botanist at the Natural History Museum in London, UK.

Regardless of the methodologies used, the classification of all living organisms on Earth remains a Herculean task. Yet Linnaeus' work was instrumental in bringing order to a world of chaos and distilling reason from the 'plan' of creation. In any case, the Linnaean *Systema* of giving structure to the living world is as important and relevant today as it was 250 years ago, and the achievements of 'God's organizer' remain as valuable and worthy of celebration as ever.

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