Heed the father of cladistics

The way Willi Hennig discovered evolutionary relationships should not be forgotten, say **Quentin Wheeler, Leandro Assis and Olivier Rieppel**.

In *On the Origin of Species*, Charles Darwin proclaimed that “our classifications will come to be, as far as they can be so made, genealogies”. That turned out to be easier said than done. Even as late as the 1970s, biologists were still grouping animals and plants largely on the basis of overall physical similarity and whether they possessed or lacked certain traits, such as a backbone or the ability to produce flowers.

The German entomologist and palaeontologist Willi Hennig transformed the classification of organisms into the rigorous science of cladistics^{1–5}. His book *Phylogenetic Systematics*⁶, published in 1966, laid out how to construct phylogenetic trees and how to use their branching patterns as the basis for classifications.

Paired with DNA sequencing, Hennig’s theories revolutionized our understanding of the relationships among the nearly two million species known today. In the history

of biological classification, the little-known Hennig arguably deserves a place alongside Aristotle, Carl Linnaeus and Darwin.

But two key messages from his book have been lost in the nearly half-century since it was published: the importance of detailed studies of the development and evolution of complex characters, such as the horn of a rhinoceros or the pincer of a fiddler crab; and the use of all relevant evidence — molecular, anatomical, fossil and developmental — in mapping evolutionary relationships. Too often these days, DNA information is favoured over everything else, and when conflicts arise between DNA-based analyses and those reliant on morphology, the former is frequently assumed to be correct, even though many uncertainties surround the molecular basis of evolution.

Hennig was born 100 years ago this week, on 20 April 1913. In celebration of his impact on phylogenetics and classification, we urge

biologists to heed his call to embrace all the relevant data.

BIOLOGICAL BEGINNINGS

Hennig, who died in 1976, was born in the village of Dürrhennersdorf in Germany⁷. He worked as a volunteer at the Dresden Museum, where he became fascinated by the extraordinary diversity of flies, and later as a researcher at the German Entomological Institute in Berlin until he was conscripted when the Second World War broke out in 1939. Badly injured on the Russian front, Hennig ended up serving in the German military medical services after his recovery.

Germany surrendered in May 1945 and Hennig, along with other German soldiers in Italy, came under Allied control. Recognizing his entomological expertise, the British assigned him to their malaria research unit, where he remained until his release in October of that year. While in this unit, Hennig produced a handwritten draft of his 1950 work, *Grundzüge*, the forerunner of his 1966 book, based in part on his observations of insect evolution.

From 1947, Hennig commuted for an hour-and-a-half each way from his home in West Berlin to the German Entomological Institute in East Berlin. The erection of the Berlin Wall in 1961 halted his commute, as well as plans to make him director of the institute. In 1963, he became head of a new department for phylogenetic research at the State Museum of Natural History in Stuttgart.

Hennig received numerous awards in his lifetime for succeeding where generations of natural historians had failed, including gold medals from the Linnean Society of London and the American Museum of Natural History. Yet the remarkable achievements of this quiet, unassuming man are mainly appreciated only within systematic biology. That cladistics is widely used today is thanks in part to Hennig’s American ‘bulldogs’, who promoted his ideas: Norman Platnick, a spider expert, Gareth Nelson, a fish expert, and James Farris, a theorist in phylogenetics¹.

Before the 1970s, many biologists viewed phylogenetic trees and classifications with suspicion, and for good reason. The construction of trees was often based more on a hunch than on testable hypotheses, and classifications did not strictly reflect branching patterns. The class Reptilia, for example, included crocodiles but excluded birds, even though the anatomical evidence strongly suggested that crocodiles and birds share a common ancestor. Meanwhile, all that held the ‘invertebrates’ together was their lack of a backbone. Like Darwin, Hennig believed that groupings of species could and should be strictly genealogical. He reasoned that such phylogenetic classifications could have the same organizing function in biology ▶

► that the periodic table of elements had been in chemistry.

This led him to define a 'monophyletic group' as one that included an ancestral species and all (and only) its descendant species. He also insisted that all the members of a monophyletic group share at least one evolutionary novelty that arose in the common ancestor, such as wings in insects. Until this point, monophyly loosely meant sharing a common ancestor, whether or not all the descendants were included. Using Hennig's approach, Reptilia could be considered a monophyletic group only if it included birds. At the time, his proposal was severely criticized by several prominent biologists, including Ernst Mayr, yet this use of monophyly is now standard practice.

A great challenge for systematic biologists is to work out where in a genealogy an evolutionary novelty first appears and at what level on the phylogenetic tree it is informative. The fact that an organism has six legs, for instance, indicates that it belongs to the group Hexapoda (insects and their near relatives), but says nothing about whether it is a fly (order: Diptera). Hennig emphasized that every evolutionary novelty that arose in a common ancestor, either in its original or modified form, is potentially informative at the appropriate phylogenetic level, and advocated the use of all available data — from biochemical pathways to skeletal structures and genetically controlled behaviours. In fact, he argued that living species provide a far richer source of historical information

than fossils, in which only a small fraction of features are preserved.

HARD TRUTH

Hennig never implied that fossil evidence should be ignored. But his take on fossils surprised many contemporary palaeontologists and evolutionary biologists. In the early twentieth century, and to a lesser extent, even while Hennig was writing his book, the fossil record was treated as if it revealed the truth of evolutionary history. We think that — as Nelson⁸ argued almost a decade ago — DNA has similarly come to be wrongly viewed as the key to phylogeny, rather than just one among several sources of evidence.

DNA sequencing has clear advantages: vast amounts of data can be collected quickly and cheaply, and sequences seem to offer a more objective measure than assessments of complex morphological features. But DNA analyses also involve subjective judgements. For instance, the assumptions used to produce models of molecular evolution, on which such analyses are based, may differ. And when conflicts arise between DNA analyses and those based on morphology, fossils or ontogeny, there is no theoretical justification for favouring one source of data over another.

Take the relationships among the

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some 9,000 scaly reptile species. Iguanas, chameleons and their close relatives had long been placed in the lower branches of the phylogenetic tree, but various DNA studies conducted over the past decade have suggested that they are actually higher up, near snakes and Gila monsters (a venomous lizard species). A recent analysis of more than 600 morphological characters now indicates that the traditional placement of iguanas in the tree is correct after all⁹. The original phylogeny certainly seems more plausible; for the DNA-based branching pattern to be correct, an extraordinarily large number of complex forms would have had to have independently evolved back into an ancestral state.

Furthermore, used in isolation, DNA-sequencing technologies cannot fully explain the characteristics, history and origins of complex characters, such as xylem vessels, seeds, flowers or feathers, that have arisen over millions of years. It is hard to see how biologists can understand the many ways in which organisms have adapted to their environments without analysing their physical adaptations.

The progress in exploring and classifying biodiversity that Hennig's work unleashed is just the beginning: biologists estimate that eight million to ten million plant and animal species remain unknown to science, and possibly even more microbes¹⁰. To understand the details of evolutionary history that help to explain this incredible diversity, biologists should remember Hennig's message: the clues are in evolutionary innovations at all levels, molecular, anatomical, developmental and behavioural. ■

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Willi Hennig stressed that every evolutionary novelty, from a spider's web-making ability or a giraffe's neck to a fiddler crab's pincer, is potentially informative in mapping evolutionary relationships.