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Excerpt
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Introduction: Carving Nature at Its Joints, or Why Birds Are Not Dinosaurs and Men Are Not Apes

> We have a tendency to look back on the feuds among writers and artists [and scientists] of the past with a fond chuckle – to find something cute in the sparring, or perhaps poignant in the testimony such quarreling proffers to the notion that at least the world of ideas *mattered* to those tempestuous souls of the days gone by.
>
> *(George Prochnik 2014,* The Impossible Exile*, p. 181)*

> Some persons see the value of these recent developments [cladistics] as revolutionary, liberating us from the burdens of the past, and particularly from the necessity to understand the work and thought of our predecessors. I see recent developments as embedded in, and shedding light on, an old tradition, dating from the days of Cuvier and his colleagues, if not from the time of Linnaeus, or for that matter from the time of Aristotle.
>
> *(Nelson 1989, p. 61)*

The phrase in the title above – 'carving nature at its joints' – comes from Plato's *Phaedrus* asking how and why people 'carve-up' and partition the organic world in the way they do. In short: "How do we classify the world?" There are, of course, many ways to classify, but the central question for biology is why are some groups of organisms, such as birds, recognised as real groups, when others, such as invertebrates, are rejected as such? This, of course, begs an additional question as to what 'real' might mean in terms of classification.

Children soon learn that animals with 'beaks' often have 'wings' and because they have wings, they usually fly: they learn that these animals are called birds. But some of the words used (beaks, wings) are open to interpretation: turtles also have 'beaks', beetles also have 'wings'. There are plenty of definitions of the word 'wing', but in biological terms it normally refers to the parts of an animal that allow it to become airborne, to fly. Beetles and birds both have wings, but the wing of a bird is formed from a set of bones, muscles, blood vessels and feathers, whereas the wings of beetles are membranous, having two sets, the forewings (elytra) are hardened and not used for flying. Animals with elytra are beetles; animals with feathers are birds.

These distinctions – what makes a bird a bird, a beetle a beetle – have occupied minds since Aristotle and are the basis for classifying scientifically. One might see in this simple example all that one needs to know of taxonomy: the union of evidence from the parts of organisms (elytra, feathers) with conclusions (beetles and birds).

One might still persist in thinking of classification as a harmless pursuit, an 'art-form' even, a question of taste, rather than a scientific topic. But there have been more contentious interactions on the topic of biological classification than almost any other area of biology.

For example, much ink has been spilt describing the famous 'battle' between the French anatomists Georges Cuvier (Jean Léopold Nicolas Frédéric Cuvier, 1769–1832) and Étienne Geoffroy Saint-Hilaire (1772–1844) in the 1830s, often (but mistakenly) portrayed as a tussle concerning evolution, with the 'creationist' Cuvier winning and the 'proto-evolutionist' Saint-Hilaire losing (a useful account can be found in Appel 1987 and Le Guyader 2004). As usual Thomas Henry Huxley (1825–1895), Charles Darwin's (1809–1882) bulldog, captured the poignancy of that fight and its significance:

> The Lecturer [Huxley] commenced by referring to a short essay by Goethe–the last which proceeded from his pen–containing a critical account of a discussion bearing upon the doctrine of the Unity of Organization of Animals, which had then (1830) just taken place in the French Academy. Goethe said that, for him, this controversy was of more importance than the Revolution of July which immediately followed it – a declaration which might almost be regarded as a prophecy; for while the *Charte* and those who established it have vanished as though they had never been, the Doctrine of Unity of Organization retains a profound interest and importance for those who study the science of life. (Huxley 1854, p. 72)

That was 1854. Huxley came to review and modify his views on the 'Unity of Organisation' after 1859 inspired by the publication of Darwin's *On the Origin of Species*:

> [. . .] that community of descent is the hidden bond which naturalists have been seeking, and not some unknown plan of creation, or the enunciation of general propositions, and the mere putting together and separating objects more or less alike. (Darwin 1859, p. 404)

And so 'community of descent' – 'descent with modification' – became the suggested organising principle for creating and naming groups of organisms, ushering in an apparent revolution in biology, if not the world at large.

It was the German biologist Ernst Haeckel (1834–1919) who took up one of Darwin's challenges by creating the first genealogical charts depicting the relationships between organisms, encouraging the view that birds, for example, 'evolved' from reptiles (Figures I.1a and b[1]). It was these harmless but frequently used phrases – 'birds evolved from reptiles', or its modern version, 'birds evolved from dinosaurs' – that inspired the next revolution in classification, one every bit as hard fought as the Cuvier–Hilaire battle of the 1830s.

The clash was between those who wished to recognise groups such as 'reptiles' and those who did not, the former persons eventually being called 'evolutionary taxonomists', the latter cladists. Broadly speaking, however, the issue was once again, "how do we classify?":

> Like the reds and the greens of Byzantium, or the Guelfs and Ghibellines in Dante's Italy, the cladists and their opponents have on occasion turned departments of paleontology into fields of passionate but obscure dispute. (Wade 1981, p. 35)

Nowadays the cladistic revolution has seemingly waned, disappeared altogether, the fruits of its labours absorbed silently into the everyday life of the comparative biologist, if such people still exist. Today molecular biologists, mathematicians and bio-informaticians conjure up massive genealogical trees, documenting the entire tree of life in one go – a recent effort utilised more than 30 000 genomes from all three currently recognised domains of life (Bacteria, Archaea, Eukarya) yielding a tree with 3000 organisms (Figure I1c, reproduced from Hug et al. 2016; see also Puigbò et al. 2009; McTavish et al. 2017), an impressive contribution towards the completion of Haeckel's original project, placing all organisms, fossil and Recent, from 'Monad to Man' (Ruse 1997), on a single gigantic tree (Lecointre & Le Guyader 2007). For cladists, those purveyors of 'passionate but obscure dispute', and with a phrase perhaps more relevant to the earlier battle between Cuvier and Hilaire but since adopted for the modern age (Nelson 2004, p. 127), their time was over: "Citoyens, la Revolution est fixée aux principes qui l'ont commencée. Elle est finie" (Napoleon Bonaparte 15 Dec 1799, in Nelson 2004, p. 127).

Or has it. . .

"la Revolution est fixée aux principes qui l'ont commence"?

[1] Haeckel's diagrams are not always easy to interpret, many having more than one tree on them. The images reproduced here as Figures I1a and b are taken from Haeckel (1866, Taf. VII). This diagram has two trees, one depicting the relationships of the organisms (reproduced here as Figure I1a), the other depicting an assumed 'genealogy' (reproduced here as Figure I1b) (see Richards 2008, for more details).

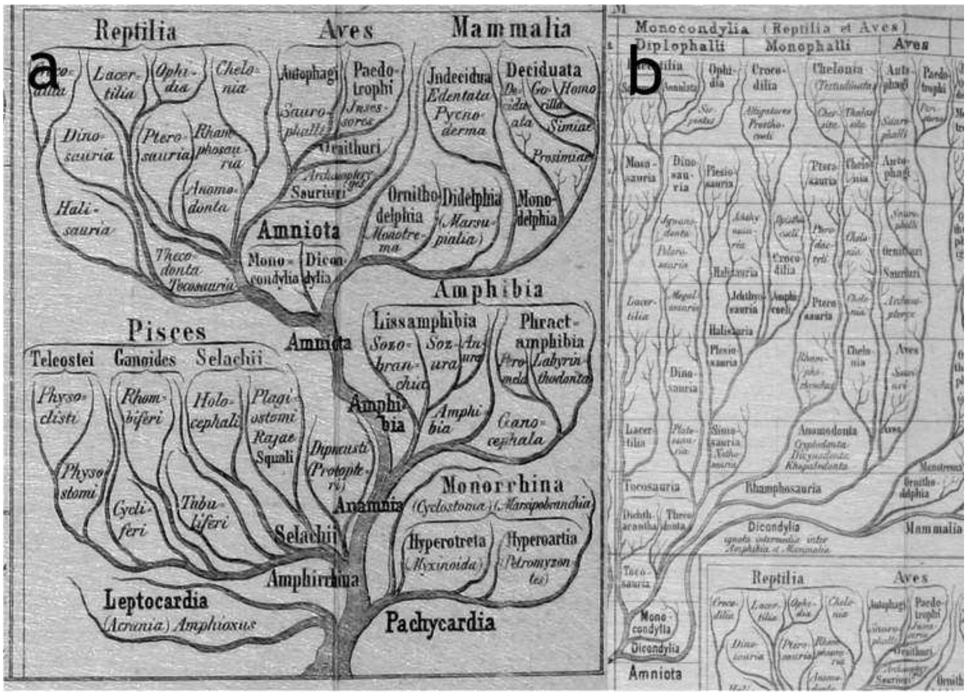

Figure I.1 This diagram of Haeckel's has two trees, one depicting the relationships of the organisms (a), the other depicting an assumed 'genealogy' (b). After Haeckel (1866, taf. VII). (c) "A current view of the tree of life, encompassing the total diversity represented by sequenced genomes", composed of "92 named bacterial phyla, 26 archaeal phyla and all five of the Eukaryotic supergroups". After Hug et al. (2016, fig. 1).

Received wisdom tells us that the cladistic revolution was born from the work of Willi Hennig (1913–1976), in particular the publication of his book *Phylogenetic Systematics* (Hennig 1966), an English translation of a revised version of the less well known and less easily obtained *Grundzüge einer Theorie der phylogenetischen Systematik* (Hennig 1950). The revolution's midwife (Wanntorp 1993), Lars Brundin (1907–1993), via his monograph *Transantarctic Relationships and their Significance, as Evidenced by Chironomid Midges* (Brundin 1966), was the conduit through which a group of comparative biologists – primarily ichthyologists and palaeichthyologists, Gareth Nelson, Colin Patterson, Niels Bonde, Philipe Janvier, Roger Miles, among others – were able to put Hennig's ideas to practical use (Greenwood et al. 1973).

Running parallel to these developments were the explorations of some more evolutionarily inclined zoologists who were attempting to utilise the many different aspects of the previous generation's numerical taxonomy and use them to

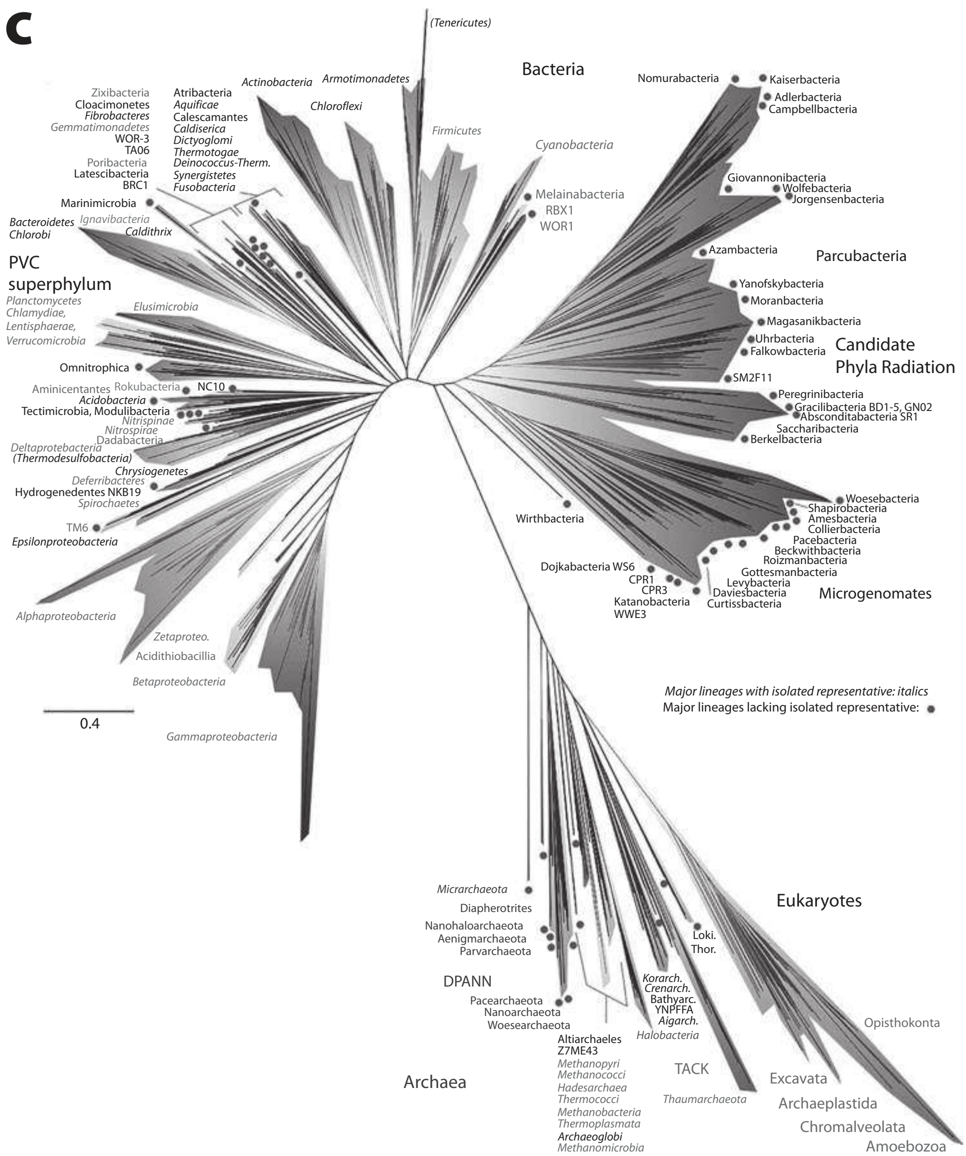

Figure I.1 (*Cont.*)

'reconstruct' phylogenies, which could then be used as the basis for classification. Of significance to these developments was something first called *Quantitative Phyletics*. The initial description of this approach was described so:

> Classical evolutionary taxonomy has been widely criticized for the lack of precision in its methods, while the far more precise numerical phenetic taxonomy has been even more widely censured for its failure to take into account the

> evolutionary basis of relationships among organisms. We believe it is worth while to develop still another taxonomic methodology, incorporating the precision of numerical techniques and the power of evolutionary inference. We refer to this hybrid methodology as *quantitative phyletic taxonomy* (Kluge & Farris 1969, p. 1)

Steve Farris went on to develop the Wagner parsimony program (Farris 1970), which searched for the shortest trees derived from a matrix of binary characters abstracted from the organisms under study (Farris 1988). Received wisdom tells us that over a few short decades Hennig's *Phylogenetic Systematics* became cladistics and cladistics became synonymous with Wagner parsimony:

> The 'grand alliance between the Wagner tradition and the Hennig tradition' (E. O. Wiley, pers. comm. 2001) formed the basis for the revolution in systematics during the last three decades of the 20th century (Schmitt 2003, p. 376)

With the profusion of numerous sophisticated statistically based methods to find – or reconstruct – phylogenetic trees, Wagner parsimony became (almost) redundant and hence cladistics too became (almost) redundant.

The trouble with this account is that while it contains elements of historical truth, it is, in its essence, false. True, Hennig's and Brundin's work did influence a generation of zoologists and palaeontologists; true, the method first called *quantitative phyletics* did evolve into Wagner parsimony; true, over time certain elements of the cladistic 'movement' did try to equate cladistics with Wagner parsimony (some parts of the first two editions of this book contributed to that movement); but significantly, the equation 'cladistics = Wagner parsimony' is patently false. To equate an entire world view with a single computer algorithm retrospectively justified with selected thoughts and ideas from Hennig's *Phylogenetic Systematics* is hopelessly narrow minded and would be the cause of its eventual demise, which does seem to be its destiny. Significant to the taxonomic enterprise, then, is the realisation that cladistics is a far more general field of endeavour than simply equating it with one particular approach to 'phylogeny reconstruction', or with one or another computer algorithm, or with one or another methodology – even with Hennig's 'phylogenetic systematics' itself (Wiley & Liebermann 2011).

Setting all that to one side for the moment, cladistics, in its most general form, has been enormously successful, if that success is judged not by methodology but by the parameters of a general approach to biological classification: monophyly based on evidence derived from homologues (homology), coupled with a precise understanding of relationship (more details of this in Chapter 3). Reflecting on an earlier era, historian Polly Winsor noted that

> [. . .] it may seem paradoxical that naturalists should use the word 'related' without agreeing on its meaning [. . .] (Winsor 2009, p. 1, we return to this in Chapter 2)

Paradoxical, too, that we now have a much better understanding of relationship but both monophyly and homology remain areas of contention and are still endlessly debated, even among those supposedly in the cladist camp (to sample these debates, see any issue of the journal *Cladistics* between the years 2011 and 2016). We attempt to tackle these topics afresh in later chapters of this book.

So cladistics might be seen differently. Not as revolution, but reform, specifically the reform of taxonomy, which we see as a modern version of comparative biology.

Revolution usually means the overthrow of something considered outdated, irrelevant even wrong in its basic tenets; reform means the improvement of something that might be considered to have become corrupted, or mutated in the wrong way, something that at its core is sound, save for faulty progress mistaken as profound. Although we are not certain, the idea of a 'Cladistic Revolution' was first given currency by Beverly Halstead (1933–1991), not known as a friend of cladistic taxonomy ('The cladistic revolution: Can it make the grade?', was the title of Beverly Halstead's first diatribe against cladistics, Halstead 1978). The phrase 'Cladistic Revolution' has since been used, and in many different contexts (e.g., Cartmill 2018). It is true that some have seen early developments in cladistics as the 'reform of palaeontology' (Nelson & Platnick 1981; Williams & Ebach 2004), but we have since come to understand cladistics as greater in reach than that: from the start it was, and remains, an attempt to reform taxonomy, an attempt to understand past efforts and eliminate contemporary confusion.

By way of a brief example, consider these words of William Whewell (1794–1866, which we return to later in Chapter 2):

> The basis of all Natural Systems of Classification is the Idea of Natural Affinity. The Principle which this Idea involves is this:–Natural arrangements, obtained from *different* sets of characters, must *coincide* with each other

If we interpret the words above such that 'Natural Systems of Classification' means roughly the same as 'taxonomy/systematics', and that 'Natural Affinity' refers to 'natural relationships', or more simply 'relationships', then the subject matter is identical to what became cladistics in the sense we wish to use it in the following chapters of this book:

> If cladistics is merely a restatement of the principles of natural classification, why has cladistics been the subject of argument? I suspect that the argument is largely misplaced, and that the misplacement stems, as [A.P.] de Candolle suggests, from confounding the goals of artificial and natural systems. (Nelson 1979, p. 20)

We will return to this subject – the 'goals of artificial and natural systems' of classification – in several chapters.

The generality of cladistics was recognised years, decades, even centuries ago (under different names, of course), and was most recently clearly articulated by a group of taxonomists, blessed or cursed, depending on your point of view, with the label 'Pattern Cladists'. What was not obvious, or at least not made abundantly clear at the time, was that the subject matter under discussion should have been *Taxonomy, the Scientific Study of Classification*, a subject we believe subsumes systematics, comparative biology, phylogeny reconstruction and so on. We are aware that each of these subject areas – systematics, comparative biology, phylogeny – are beset with varying definitions, but it is possible to see the commonality as expressed by the term 'relationship', discussed in more detail later.

Taxonomy has itself been the victim of much discussion and, in our view at least, harmed immensely by what can only be called historical inaccuracies. For example, discussions of the central role of essentialism and typology and their role in how taxonomists were supposed to have operated prior to any evolutionary considerations have been almost entirely debunked by some historians of science. These discussions have come largely from the work of Polly Winsor and, more recently, Joeri Witteveen; we lean heavily on their historical research when discussing matters relating to essentialism and typology.

Our task, then, is to describe cladistics as a manifestation of what was, and will probably always be, the effort to find a natural classification of organisms. With respect to the 'goals of artificial and natural systems', we hope to assist in disentangling the very many modern versions of artificial classifications from what we understand as *the* natural classification.

We are painfully aware of the many and varied critiques of 'Pattern Cladistics', most, in our view, mistaken in their understanding of the generalities as well as the particulars. We tackle some of these issues later, but there is no better way of capturing the tone of those critiques than words written some while ago by Richard Dawkins in his immensely popular and influential *The Blind Watchmaker:*

> My own interpretation is that they [pattern cladists] enjoy an exaggerated idea of the importance of taxonomy in biology [. . .] (Dawkins 1986, p. 286, 1996, p. 402)

With this book we hope, at the very least, to suggest why we believe taxonomy is not just exceedingly important, not just central to all biology, but has a vibrant research agenda of its own (rather than a subject that simply needs to embrace modern technology, e.g., compare Bik 2017 to Grimaldi & Engel 2007); we will attempt to document what taxonomy is, its basis, methods and problems via the lens of what became known as cladistics but in the broader interpretation we adopt here. This book is an attempt to articulate the approaches used, but left largely unexplained, in most of the contributions to contemporary taxonomic journals, a methodology we understand that extends in one form or another far back, its basis being found in the writings of Carl Linnaeus (1707–1778), Michel

Adanson (1727–1806), Antoine-Laurent de Jussieu (1748–1836), Augustin Pyramus de Candolle (1778–1841) and many others – perhaps extending even further back than that (Pavord 2005; Ogilvie 2006; Williams & Ebach 2017).

These topics will be the subjects of this book: taxonomy, systematics and natural affinity; in short, scientific classification, which we believe is synonymous with cladistics, providing answers as to why Birds are not Dinosaurs and Men are not Apes.

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